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

4

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17

18 **Highlights**

- 19
- Freshwater springs sustain *Acacia*-palm woodlands near saline Lake Eyasi (N edge)
  - KN1A pollen record shows Kisima spring woodlands existed since >1200 yrs
  - KN1A pollen record infers today is wetter than LIA which was also wetter than MCA
  - Fresh groundwater remained easily accessible even during dry periods like MCA
  - KN spring likely responds to IOD events and regional precipitation changes
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23

24

25 **Abstract (334 words)**

26 Kisima Ngeda (KN), a spring on the northern margin of saline Lake Eyasi, Tanzania, sustains an  
27 *Acacia-Hyphaene* palm woodland and *Typha* swamps, while the surrounding vegetation is semi-desert.  
28 To study the vegetation changes associated with this spring, which represents a plausible modern analog

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

47

48 **Keywords:** Climate, Paleovegetation, Hydrosystem, Hominin, Olduvai, Ngorongoro

49

## 50 **1. Introduction**

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

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

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

91 (Behrensmeyer and Reed, 2013). Real-world data offering adequate temporal resolution are therefore  
92 needed.

93 Olduvai Gorge is a world-famous site located in the Crater Highlands at the southern edge of the  
94 Serengeti Plains (Leakey, 1971, 1966). The abundance of tufa mounds in paleosurfaces associated with  
95 anthropological and archaeological sites has been recognized at several Olduvai sites including FLK N  
96 (1.79 Ma) and FLK Zinj (1.89 Ma) (Ashley et al., 2010a, 2010b). Oxygen isotopic analyses of the tufas  
97 indicates groundwater was fresh (Ashley et al., 2010a), while paleolake Olduvai was saline/alkaline (Hay  
98 and Kyser, 2001). Phytolith and pollen data from FLK Zinj and FLK N paleosurfaces show that localized  
99 palm woodlands within an otherwise grass-dominated landscape were present near the springs (Arráiz et  
100 al., 2017; Ashley et al., 2010a; Barboni et al., 2010; Bonnefille, 1984). These paleo-springs have enabled  
101 the development of dense wooded vegetation despite the semi-arid paleoclimate (paleoprecipitations of  
102 250 to 700 mm/yr, Magill et al., 2013) and saline/alkaline waters of paleolake. The presence of paleo-  
103 springs is also suspected in the nearby paleontological sites of Laetoli and Peninj (Barboni, 2014), and  
104 many springs are still active today in this region of northern Tanzania, such as at Esere near Laetoli  
105 (Barboni et al., 2019), and at the northern edges of Lake Manyara (Greenway and Vesey-Fitzgerald, 1969)  
106 and Lake Eyasi (Albert et al., 2015). Springs are therefore persistent hydrogeological features in the  
107 Crater Highlands region of north Tanzania, which modern representative may serve as analogs.

108 We focused our research on the spring of Kisima Ngeda locality at the northern edge of Lake  
109 Eyasi because this spring is associated to a palm woodland and is located at the edge of a saline/alkaline  
110 lake. Kisima Ngeda spring offers the opportunity to study the dynamics of an hydrosystem analog to the  
111 fossil springs of Olduvai Plio-Pleistocene hominins sites. Kisima Ngeda spring recharge occurs in the  
112 Ngorongoro Volcanic Highlands (Deocampo, 2002), like for Olduvai paleo-springs located about 50 km  
113 north of Lake Eyasi (Ashley et al., 2009). Rainwater infiltrates and is transported to the dry lowlands by  
114 moving groundwater. Groundwater flows down-slope in the sub-surface within pyroclastic beds (tuffs)  
115 between relatively impermeable basaltic beds (Norton, 2019). Under pressure, groundwater discharges  
116 within alluvium at the surface or near the surface in the lowlands at the foothills of Ngorongoro Volcanic  
117 Highlands (Norton, 2019; Shilling, 2013), but it is not clear yet if groundwater discharges through faults,  
118 fractures, or dikes as suggested elsewhere in the Ngorongoro area (Deocampo, 2002), or where the  
119 aquifer intersects the surface due to the slope topography (Norton, 2019). Faults were not directly  
120 observed in the area of Kisima Ngeda (Pickering, 1964), but the continued hydrological activity may have  
121 altered fault contacts and fractures and made them hard to see on the surface (Deocampo, 2002). At the  
122 foothills of Oldeani volcano, water table is high, and a dense wooded vegetation belt with tall *Acacia*

123 *xantophloea* and *Hyphaene petersiana* palm trees develops despite the semi-arid climate (Fick and  
124 Hijmans, 2017) (**Figure 1, 2**). Recently, nomenclature of *Acacia* has been revised; the botanical genus is  
125 now separated into *Vachellia* and *Senegalia* for Africa. For consistency with the names of vegetation and  
126 pollen types, *Acacia* will still be used here.

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

131

## 132 **2. Study area**

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

143 In the region encompassing East Eyasi Basin, Ngorongoro Volcanic Highlands, Salei Plains, and  
144 southern Serengeti Plains, the climate is very contracted due to significant relief variations. It is  
145 principally subtropical semi-arid in the lowlands, and warm temperate semi-arid in the highlands  
146 (Holdridge, 1967) with mean annual temperatures (TANN) of 15°–24°C and mean annual precipitations  
147 (PANN) of 500–900 mm/yr (Fick and Hijmans, 2017). At the level of the East Eyasi Basin, the climate is  
148 sub-tropical arid with TANN of 22–24°C and PANN of 550–650 mm/yr. The Ngorongoro Volcanic  
149 Highlands allow the local development of a colder and wetter climate, with TANN between 12°C and  
150 17°C and PANN between 1100 mm/yr and 1200 mm/yr. Moderate to low rainfall and intense  
151 evaporation of about 2500 mm/yr in the lowlands has allowed the development of the alkaline saline  
152 lakes in the region (Deocampo, 2005).

153 In the northeastern edge of Lake Eyasi, six vegetation zones can be defined based on the  
154 literature and our personal observations. (1) The Afromontane zone occurs above *ca.* 1600 m and 2450  
155 m on the eastern and western wall of Mount Oldeani, respectively. It is constituted of Afromontane  
156 forest with trees of *Albizia gummifera*, several *Olea* species, and *Hagenia abyssinica* (Herlocker and  
157 Dirschl, 1972). The lower part of the Afromontane forest is delimited by an *Acacia lahai* high woodland  
158 belt. (2) The xerophytic zone covers most of the landscape below the Afromontane zone, and is  
159 constituted of *Acacia-Commiphora* bushlands. On the slopes of Mount Oldeani above *ca.* 1250 m, the  
160 *Acacia-Commiphora* bushlands include trees of *Commiphora madagascariensis*, *Acacia tortilis*, *A.*  
161 *mellifera*, and *A. senegal* and grasses are common (Herlocker and Dirschl, 1972). Below *ca.* 1250 m,  
162 bushes become more abundant than trees with decreasing elevation, and include *Acacia oerfota*,  
163 *Maerua trichophylla*, *Cordia rothii*, and *Commiphora* species. Grasses are scarce and plants more  
164 adapted to arid conditions are present such as *Adansonia digitata* (baobabs) and *Euphorbia candelabrum*  
165 (cactoid trees) (Herlocker and Dirschl, 1972). (3) The halo-xerophytic zone occurs on Lake Eyasi margins  
166 where salt mudflats bare of vegetation are numerous. Vegetation on the lakeshore is scarce and  
167 exclusively constituted of salt loving species such as *Suaeda monoica*, *Volkensinia prostrata*,  
168 *Neuracanthus scaber*, and *Senecio mesogrammoides* (Rea, 1935). At the foothills of Mount Oldeani,  
169 between the *Acacia-Commiphora* bushlands and Lake Eyasi margin, a discontinuous vegetation belt can  
170 be identified on satellite images by its green color contrasting with the generally pale-yellow color of the  
171 surrounding xerophytic bushlands. This localized vegetation belt is formed by what we call a mesophytic  
172 zone, a halo-mesophytic zone, and an hydrophytic zone. (4) The mesophytic zone is a 0.5 km wide and  
173 *ca.* 7 km long discontinuous strip of groundwater-fed tall *Acacia xanthophloea* and *Hyphaene petersiana*  
174 palm woodland stretching along the north-eastern side of Lake Eyasi. In this part of the landscape,  
175 groundwater does not emerge but is close enough (*ca.* 1 m) to the surface to maintain dense woodlands  
176 with dense grass cover (*in situ* observation). (5) The halo-mesophytic zone is characterized by high  
177 concentration of *Hyphaene petersiana* palm trees (with more or less bare soil); *Hyphaene* favoring more  
178 salty/alkaline water than the *Acacia xanthophloea* trees, the halo-mesophytic zone occupies the edge of  
179 the spring woodland facing the lake margin (*in situ* observations) (**Figure 3**). (6) The hydrophytic zone  
180 corresponds to a complex of water ponds and swamps which develop where groundwater emerges at  
181 ground level. It is located between the halophytic and mesophytic zones. Cattail *Typha* sp. and sedges  
182 such as *Cyperus laevigatus* are present in the swamps along with the small water-loving tree *Sesbania*  
183 *sesban* (**Figure 2**). Short herbaceous swamps with sedges (probably *Cyperus laevigatus*) and grasses (e.g.  
184 *Sporobolus spicatus*, *Diplachne fusca*) and *Sesbania sesban* trees are also present (Hughes, 1992), as well

185 as tussocks of the tall grass *Sporobolus consimilis* mixed with low sedges (probably *Cyperus laevigatus*)  
186 (Figure 3).

187

### 188 3. Materials and methods

189 During the summer of 2011, we collected a 43 cm-long core with a Livingston-Bolivia drive rod  
190 piston corer in a *Typha* wetland of the hydrophytic zone near the groundwater-fed locality of Kisima  
191 Ngeda at 3°29'8.5"S and 35°20'53.5"E (elevation: 1030m a.sl.) (Figure 2). Core KN1A was described as  
192 black peat with plant debris in the upper interval from 0 to 31 cm, and light grey silty clay without any  
193 visible plant debris in the lower interval from 32 cm to 43 cm (Figure 4). The contact of the upper and  
194 lower intervals is not horizontal, and may be the result of coring. Samples of 1 cm-thickness taken every  
195 2 cm from the level 0-1cm to 42-43cm were used for pollen analyses. Level 30-31 cm was taken from the  
196 upper interval of the core.

197 Pollen grains were concentrated by acid digestion using HCl (33%, 4h) to dissolve carbonates, HF  
198 (48%, 12h) and HCl to remove fluosilicates, and KOH (20%, 10') to remove humic acids. Sieving was done  
199 at 150 microns. Pollen were stained using safranin. Identifications are based on the pollen reference  
200 collection available at CEREGE (Aix-en-Provence, France) and pollen atlases (e.g. Bonnefille and Riollet,  
201 1980). Pollen types are based on Vincens et al. (2007). Pollen percentages were calculated excluding  
202 undeterminable pollen grains and spores. In the lower part of the core, all samples have low (<150)  
203 counts due to poor preservation (Table S1). These samples were not excluded from the analysis given  
204 their importance in documenting paleovegetation before the peat inception. However, we calculated  
205 confidence intervals associated with percentages of *Typha* in Figure 7 to consider the potential bias  
206 linked to such low pollen counts. Calculation of confidence intervals follows Suchéras-Marx et al. (2019).

207 Pollen concentrations were not measured and results presented here are uniquely based on  
208 pollen taxa relative abundances. Pollen grains for <sup>14</sup>C dating were obtained by the same chemical  
209 treatment, without using ethanol and safranin to avoid carbon contamination. We chose to date pollen  
210 concentrates rather than bulk organic matter to minimize the reservoir effect (Li et al., 2012). The  
211 radiocarbon age of material was determined by Beta Analytic (Miami, Florida) and ARTEMIS instrument  
212 (Saclay, France) (Table S2), at depths 22-23 cm and 30-31 cm in the upper part of the core, and at 37.5-  
213 38 cm and 42-43 cm in the lower part of the core (Figure 4). Calibration of the radiocarbon ages (Table  
214 S2) and age model (Table S3) were carried out with the R package CLAM (Classical Age-Depth Modelling  
215 of Cores from Deposits) (Blaauw, 2010), using the IntCal20 calibration (Reimer et al., 2020), a linear



216 interpolation between dated levels and 95% confidence ranges, and the option to have the results in cal  
217 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  
218 cm. Based on the sedimentary facies, the lower interval of the core is probably playa lake margin  
219 sediments. We added a hiatus because it is possible that there are erosion surfaces and gaps in this part.  
220 Hence, it is necessary to remain cautious with the age model of this lower core interval.

221 Pollen counts are given along with ecological and physiological information about the plant taxa  
222 they represent (**Table S1**). Information about plant habitus, plant preferred ecological zone, salt  
223 tolerance, life cycle (for herbaceous taxa), and leaf phenology (for arboreal taxa) were obtained from the  
224 literature ("African Plant Database," 2019; Agnew and Agnew, 1994; Dale and Greenway, 1961;  
225 Greenway and Vesey-Fitzgerald, 1969; P. Loth and Prins, 1986). The ecological and physiological traits  
226 indicated for the pollen taxa of KN1A core correspond to plant species potentially present in the study  
227 area. For example, *Albizia* pollen likely represent the deciduous *Albizia anthelmintica*, that is currently  
228 present in the spring woodland at the northern edge of Lake Manyara (Greenway and Vesey-Fitzgerald,  
229 1969). Pollen percentages by ecological zones (cf. Study area) and by plant habitus were calculated  
230 excluding pollen types with undifferentiated ecological zones and plant habitus (**Table S1**). Cyperaceae,  
231 which occur in both the hydrophytic and mesophytic zones (without being able to distinguish the  
232 different species by their pollen morphology) were excluded from synthetic diagrams in Figure 6.  
233 Palaeoenvironmental interpretations inferred by percentage variations of dominant pollen types are  
234 based on the ecology of the different plants and floristic associations presented in the study area. All  
235 taxa were considered for our interpretations (**Figure 5**).

236

## 237 **4. Results**

### 238 **4.1. Pollen preservation, representation and age model**

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

243 Pollen assemblage of the top core (0-1cm) is consistent with the vegetation surrounding the  
244 coring site in 2011. Pollen of *Typha* (54%) and Cyperaceae (34%) are abundant, typical of *Typha* sp. and  
245 *Cyperus* sp. swamps, but pollen of *Hyphaene* are not recorded (**Figure 6**), despite the presence of some

246 palm trees about 50 m from the site (**Figure 2**). The small hydrophytic tree *Sesbania sesban* present at  
247 the site accounts for 0.1% of the total pollen sum. Thus, *Hyphaene* and *Sesbania sesban* are likely under-  
248 represented in the pollen assemblages. Poaceae in the surrounding short herbaceous swamp near the  
249 site only account for 8% of the total pollen sum. The pollen signal of allochthonous plants include *Suaeda*  
250 *monoica*-type (1%) from the salty lake margins, *Acacia* (2%) from the nearby (*ca.* 1 km away) tall *Acacia*  
251 *xanthophloea* woodland, and *Maerua*-type *crassifolia* (0.1%) from the surrounding xerophytic bushland.

## 252 **4.2. Pollen zones and paleoenvironments**

### 253 **4.2.1. Pollen zone A: below 31 cm (cal yrs C.E. 841 to cal yrs C.E. 1282)**

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

262 (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  
263 highest percentages of *Hyphaene* (>37%), which is incompatible with a wetland setting (**Figure 5**).  
264 Instead, it suggests a dense *Hyphaene* palm woodland almost devoid of grasses within a persistent halo-  
265 mesophytic zone. *Typha* indicates the presence of fresh water, but its low percentage (<20%), the high  
266 abundance of *Hyphaene* (>37%) that cannot live in hydrophytic zone, and the silty clay lithology imply  
267 that fresh-water swamps were present not directly at the site. The groundwater discharge activity at the  
268 coring site was likely low at that time.

269 (2) Sub-zone A2, from 36-37 cm to 34-35 cm (cal yrs C.E. 1024 to cal yrs C.E. 1091) shows a  
270 decrease of *Hyphaene* pollen (<21%, but still >10%) correlated with a significant increase of *Typha* pollen  
271 (35%), while lithology remains silty clay (**Figure 5**). This reflects the development of a short-lived wetland  
272 at the detriment of a part of the *Hyphaene* palm woodland. We prefer to talk here about “short-lived  
273 wetland” and not “wetland” or “swamps” because *Hyphaene* pollen is still represented by >10% which  
274 implies a maintenance of the halo-mesophytic zone. This indicates moderate and intermittent  
275 groundwater discharge activity at the coring site.

276 (3) Sub-zone A3, at 32-33 cm (cal yrs C.E. 1157) shows 23% of *Hyphaene* but reduced relative  
277 abundance of *Typha* (<20%), and an important proportion of pollen from the halo-mesophytic zone  
278 (40%) as observed earlier (sub-zone A1) The site reverts to a dense *Hyphaene* palm woodland almost  
279 devoid of grasses within a persistent halo-mesophytic zone with fresh-water swamps present not directly  
280 at on the site. it is likely that the groundwater discharge activity at the coring site became low again.

#### 281 **4.2.2. Pollen zone B: 30-31 cm to 14-15 cm (cal yrs C.E. 1282 to cal yrs C.E. 1911)**

282 This pollen zone corresponds to a major change in lithology. Between 32-33 cm and 30-31cm  
283 (dated cal yrs C.E. 1157 –1282) an organic-rich peat starts developing and pollen composition changes  
284 drastically. Pollen zone B is characterized by very low percentages of *Hyphaene* (<3%), Poaceae between  
285 16% and 30%, and *Typha* between 21% and 32% (**Figure 6**). Compared to pollen zone A, the proportions  
286 of pollen representing the mesophytic zone (24% to 46%) and the hydrophytic zone (22% to 32%) are  
287 higher, at the expense of thoe of the halo-mesophytic zone, which decrease sharply (<5%). This shows  
288 that the coring site, which was previously covered with palm trees within a halo-mesophytic zone  
289 (before cal yrs C.E. 1282, 30-31 cm), became rapidly transformed into a grassy, species-rich woodland  
290 with trees, shrubs, and lianas afterwards. After cal yrs C.E. 1282, various species of *Acacia*, *Albizia*, *Celtis*,  
291 *Combretum*, *Erythrococca*, *Macaranga*, and *Ximения* are recorded. They could thrive likely because more  
292 fresh water became more accessible to the vegetation (**Figure 5** and **Table S1**). This could be due to a  
293 higher lake level or to a higher flow and discharge of fresh groundwater after cal yrs C.E. 1282. We can  
294 rule out the hypothesis of a higher lake level because, if Lake Eyasi were higher, then it is unlikely that  
295 pollen grains of *Hyphaene* palms would have been preserved in greater abundance than pollen of the  
296 salt-loving species such as the Amaranthaceae *Suaeda monoica* and *Volkensinia prostrata*, which thrive  
297 today on the salty lake margins. The hypothesis of a higher flow and discharge of fresh groundwater  
298 above 30-31 cm (cal yrs C.E. 1282) should be favored because when pressure of fresh water on the salt  
299 water aquifer of the lake is high, salty water cannot penetrate inland (e.g., Fan et al., 1997), leading to  
300 less saline soil conditions and, therefore, to the reduction of the meso-halophytic palm zone. All this  
301 implies at least a moderate activity of the flow and discharge of fresh groundwater above 30-31 cm (cal  
302 yrs C.E. 1282). The proportions of pollen from the hydrophytic zone are low (<32%) compared to the  
303 present (>54%) and the proportions of pollen from the mesophytic zone are high (>24%) compared to  
304 the present (<10%) (**Figure 6**). The freshwater swamp was therefore likely smaller than at present. It is  
305 possible to divide this pollen zone B into 5 subsets.

306 (1) Sub-zone B1, at 30-31 cm (cal yrs C.E. 1282), is characterized by high percentages of *Albizia*  
307 (>10%), a species with low pollen dispersing capacity. A grassy *Albizia* woodland with a low arboreal  
308 cover (arboreal pollen ca. 15%). This type of vegetation and the high proportion of pollen from  
309 mesophytic zone (>45%) (**Figure 5**) imply moderate activity of the flow and discharge of fresh  
310 groundwater.

311 (2) Sub-zone B2, from 28-29 cm to 24-25 cm (cal yrs C.E. 1306 to cal yrs C.E. 1362), shows a  
312 significant decrease in the percentage of *Albizia* (<3%) and an increase in percentage of *Typha* (>28%)  
313 compared to B1. This indicates a development of the hydrophytic zone at the detriment of the  
314 mesophytic zone linked to an increase in the activity of groundwater discharge: moderate at 28-29 cm  
315 (*Typha* <25%) and high from 26-27 cm to 24-25 cm (*Typha* >25%). With arboreal pollen <15%, the grassy  
316 *Albizia* woodland becomes a grassland with few trees still present (**Figure 6**).

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

#### 322 **4.2.3. Pollen zone C: 10-11 cm to 0-1 cm (cal yrs C.E. 1721 to cal yrs C.E. 1997)**

323 This pollen zone is in line with the observations made in pollen zone B: organic-rich peat and  
324 *Hyphaene* <3% (**Figure 5**). Consequently, as for pollen zone B, the fresh groundwater had greater  
325 influence on vegetation than the salty water from Lake Eyasi. The pollen zone C differs to zone B by the  
326 percentages of Poaceae and by percentages of *Typha* >37%. The percentage of *Typha* increases from  
327 30% at the end of pollen zone B to 43% at the beginning of pollen zone C. The percentage of *Typha* tends  
328 to increase with time with values around 55% at the core top. There is a significant increase of pollen  
329 from the hydrophytic zone at the detriment of pollen from the mesophytic zone (**Figure 6**). All this shows  
330 that groundwater discharge flow and, consequently, the size of the wetland (the hydrophytic zone) thus  
331 appear to have increased from cal yrs C.E. 1721 to the present, where they are at their maximum. This  
332 marks phases where the activity of groundwater discharge becomes high. In the mesophytic zone, there  
333 is always a grassland with some trees.

#### 334 **4.3. Pollen signal of regional vegetation**

335 The pollen of Afromontane taxa represent <3% in all levels and confidence intervals associated to  
336 the percentages are too high to allow interpreting differences between levels (**Figure 6**). The pollen

337 signal of all xerophytic zones, reflecting the regional aridity in the lowlands, shows high values (>6%) in  
338 pollen zone A, then globally low values in B1 and B2 (<3%). Finally, at the base of B3, values are at 10.5%  
339 and then tend to decrease progressively to the top of C (~1%).

340

## 341 **5. Discussion**

### 342 **5.1. Comparison with other regional records**

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

346 Before cal yrs C.E. 1200, a generally dry interval of ~400 years is recorded at Lake Emakat  
347 (partially) (Ryner et al., 2008), Lake Naivasha (Verschuren, 2001), Lake Edward (Russell and Johnson,  
348 2005), and is also observed in the spring activity of Kisima Ngeda (as inferred from the percentage of  
349 *Typha* pollen in KN1A core). Indeed, this period is characterized at Kisima Ngeda by the presence of  
350 *Hyphaene* palm woodland, a low water table and a flow of fresh groundwater too low to stop the  
351 advance of saltwater intrusion from the lake into the land. We note, however, that this dry period seems  
352 to be interrupted by intermittent decadal wet episodes between cal yrs C.E. 1000 and cal yrs C.E. 1100 at  
353 Kisima Ngeda, with a temporary reduction of the salty influence and the establishment of short-lived  
354 wetlands. Such wet episodes can also be observed at L. Edward and L. Naivasha but rather between cal  
355 yrs C.E. 900 and cal yrs C.E. 1000. (Russell and Johnson, 2007; Verschuren et al., 2009) (**Figure 7**). This  
356 age shift probably indicates that the age model for the lower part of the core (below 31 cm) (Figure 4)  
357 slightly overestimates the true ages. This would not be surprising because the age model of the lower  
358 part is less well constrained than that of the upper part. Altogether this seems to mark a generally dry  
359 period well recognized in the northern hemisphere as the (warmer than normal) Medieval Climate  
360 Anomaly (MCA). In Africa, the MCA (~cal yrs C.E. 950-1200) is characterized by important changes in the  
361 hydroclimate, with strong regional differences. The latest data compilation shows that Eastern Africa was  
362 drier south of the equator and west of a SSW-NNE line separating the drier inland sites (L. Edward, L.  
363 Victoria, L. Masoko, L. Tanganika, Kismia Ngeda included) from the wetter coastal eastern African sites  
364 during the MCA (L. Challa, L. Malawi) (Lüning et al., 2018). The peat inception at Kisima Ngeda at cal yrs  
365 C.E. ~1200 (between cal yrs C.E. 1157 and cal yrs C.E. 1282) is concomitant with the beginning of a wet  
366 (pluvial) episode at L. Emakat, L. Edward, L. Challa, and L. Naivasha around cal yrs C.E. 1200 (Russell and  
367 Johnson, 2007; Ryner et al., 2008; Tierney et al., 2013; Verschuren et al., 2009), and with peat inceptions

368 at other groundwater-fed localities in Kenya such as the Solai (Goman et al., 2017) and Lobo swamps  
369 (Ashley et al., 2004; Driese et al., 2004). This marks the end of the MCA.

370 From ~cal yrs C.E. 1200 to ~cal yrs C.E. 1400-1450, the development of a peat and a wooded  
371 grassland at Kisima Ngeda occurs while all neighboring lakes record high levels (Russell and Johnson,  
372 2007; Ryner et al., 2008; Verschuren, 2004, 2001) and high  $\delta^{18}\text{O}$  is measured at Kilimanjaro (Thompson  
373 et al., 2002), which the authors interpreted as increased rainfall (rather than cooling) (Barker et al., 2001;  
374 Rozanski et al., 1993). Between ~cal yrs C.E. 1400-1600, the groundwater discharge at Kisima Ngeda is  
375 moderate but sufficient to preserve the wetland bordered by grassland. This interval corresponds to low  
376 lake level at L. Emakat and drought inferred at L. Edward (Russell and Johnson, 2007) and at other small  
377 lakes in western Uganda (Russell et al., 2007) and Malawi (Brown and Johnson, 2005; Johnson et al.,  
378 2001; Johnson and McCave, 2008), but to high lake level at L. Victoria (Stager et al., 2005) and L.  
379 Naivasha (Verschuren et al., 2000; Verschuren, 2001). Lake Challa, L. Masoko and L. Tanganika, do not  
380 match any of the pattern cited before, and show contrasting and varying patterns over this ~cal yrs C.E.  
381 1400-1650 time period (Tierney et al., 2013). Hence, at the scale of Eastern Africa the Little Ice Age (LIA),  
382 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  
383 period between cal yrs C.E. 1400 and cal yrs C.E. 1700 (**Table S4**), shows very contrasting patterns. At  
384 Kisima Ngeda, the LIA is marked between 1400 and 1600 by a period of moderate spring activity  
385 between two periods of high spring activity. Later on, between cal yrs C.E. 1650 and cal yrs C.E. 1750,  
386 while drought is recorded in the western rift zone at L. Malawi, L. Masoko, L. Tanganika, and L. Edward, a  
387 pluvial interval is recorded in the eastern rift zone at L. Naivasha, L. Emakat, and in the ice of Kilimanjaro,  
388 which marks the end of LIA in this part of the rift. This interval corresponds at Kisima Ngeda to a period  
389 of high spring activity that marks the beginning of the swamp expansion. After cal yrs C.E. 1750, the  
390 activity of the spring remains high, which correlates with L. Emakat and L. Edward (Russell and Johnson,  
391 2007; Ryner et al., 2008) but is not correlated with L. Naivasha level and Kilimanjaro  $\delta^{18}\text{O}$  record. From  
392 cal yrs C.E. ~1750, spring activity has been increasing at Kisima Ngeda and has not weakened since  
393 (**Figure 7**), despite marked droughts recorded throughout the African continent in the 1820s and 1830s  
394 and since 1990 (Lyon and DeWitt, 2012).

395 As shown by the regional comparison attempted here and more thoroughly elsewhere, trends  
396 between different site archives are rarely shared over the last 1200 years (i.e., over the entire period) in  
397 Eastern Africa (Nash et al., 2016; Tierney et al., 2013). The Kisima Ngeda record of spring activity over  
398 this period is sometimes consistent with sites in the south and west (e.g., Masoko, Tanganika, Edward)  
399 and sometimes with the more coastal sites (e.g., Challa and Naivasha) depending on the time interval

400 considered, but it also shows no signs of any early-19th century drought, and no signs either for other  
401 severe drought events in the final decades of the 19th century like in the Kenya Rift Valley (Nicholson et  
402 al., 2012; Lyon and DeWitt, 2012), or in Ethiopia or elsewhere in northern Tanzania where as much as 40-  
403 75% of pastoralist Maasai may have succumbed (Iliffe, 1987). The climate mitigating effect of the Kisima  
404 Ngeda spring needs to be examined in more details. Nevertheless, the spring activity of Kisima Ngeda is  
405 well correlated with the level of L. Emakat (**Figure 1**). This relatively small 3 km-wide lake enclosed in a 6  
406 km-wide crater on the Ngorongoro Volcanic Highland is hydrological closed and fed directly by rainfall.  
407 The inter-annual level variations of Lake Emakat are directly related to rainfall variability on Ngorongoro  
408 Volcanic Highlands (Frame et al., 1975; Ryner et al., 2008) that feed wetlands of northeastern margin of  
409 Lake Eyasi (Ryner et al., 2008; Thompson et al., 2002; Verschuren, 2001; Verschuren et al., 2000). The  
410 good temporal correlation between the activity reconstruction of KN1A spring and the paleo-levels of  
411 Lake Emakat shows that the response of the KN1A spring (discharge peaks) to regional rainfall variations  
412 in the highlands is very fast (decadal scale). Finally, although spring activity shows general trends that are  
413 inverse to regional lowland aridity (e.g. part 4.3), but the detail of the spring activity cannot be explained  
414 by regional variations of aridity in lowland.

## 415 **5.2. Spring vegetation response to IOD positive events**

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

### 432 **5.3. *Acacia-Hyphaene* palm woodland versus spring forest**

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

### 461 **5.4. Kisima Ngeda, a dual and therefore sustainable groundwater system?**



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

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

#### 489 **5.5. Impact of springs on the geological and paleobotanical records at hominin sites**

490 As mentioned, the hydrological system of Kisima Ngeda seemed to be a potential analog to some  
491 Olduvai sites because of the presence of a (paleo) lake nearby that is saline/alkaline, of palms, and of  
492 (paleo) springs with fresh groundwater whose recharge occurs in the Ngorongoro Highlands. The Olduvai

493 pollen record (Bonnefille, 1984), however, differs from the KN1A pollen record by the abundance of  
494 Poaceae (35-75%), rare *Typha* (0-10%), the absence of *Hyphaene* or other palm taxa, and the abundance  
495 of pollen markers of the *Acacia-Commiphora* bushland. Olduvai pollen data alone suggest open semi-  
496 desert environment comparable to the present-day vegetation with the presence of very reduced or  
497 distant fresh-water swamp, but no spring forest or woodland. Yet, other vegetation proxies ( $\delta^{13}\text{C}$  on  
498 pedogenic carbonates, phytoliths, macro-remains) indicate highly heterogeneous woody cover,  
499 abundant palms, and *Typha* wetlands (Arráiz et al., 2017; Ashley et al., 2010a; Bamford, 2012; Barboni,  
500 2014; Barboni et al., 2010; Cerling and Hay, 1986; Magill et al., 2013b; Sikes and Ashley, 2007), while tufa  
501 mounds are geological evidences attesting for the presence of groundwater discharge areas (springs) at  
502 Olduvai (Ashley et al., 2010a). The absence of "spring indicators" in the Olduvai pollen record despite  
503 evidences in the geology, geochemistry and phytoliths and macro-remains may be explained by the low  
504 pollen production (e.g. *Sesbania sesban*) or low dispersion capacity (e.g. *Hyphaene* or *Acacia*) of spring  
505 plant taxa, which makes them less easily recordable than e.g. grasses. Pollen grains of *Hyphaene*,  
506 however, were recorded in the Pliocene of Laetoli (Bonnefille and Riollet, 1987). Hence, the depositional  
507 context is another factor that could explain the absence of spring pollen markers at Olduvai. As shown in  
508 this study, groundwater discharge areas trigger and maintain a landscape heterogeneity, not only in  
509 terms of vegetation by allowing the development of dense and tall woodlands and wetlands within an  
510 otherwise desert-like vegetation, but also in terms of depositional environments. Indeed, following the  
511 groundwater discharge and level, a given area may alternatively accumulate organic-rich peatland  
512 material (which favor pollen preservation) or become a sandy clay-rich soil (less likely to preserve  
513 pollen). The water table level and spatial position of the discharge areas (spring outlets) likely change  
514 over millennia, and swamps, woodlands, and palm groves (the spring-associated vegetation zones) are  
515 then displaced laterally by few kilometers. Yet, if these local movements have potentially little impact on  
516 the wildlife, they may considerably disturb the geological and paleobotanical records.

517 Groundwater forests and woodlands have a very distinct but also very local pollen signal, which  
518 can go unnoticed (Barboni et al., 2019). Depending on the location of the sampling site, the period  
519 studied and the resolution of the record, this type of spring system can give a very heterogeneous  
520 vegetation signal, often interpreted as mosaic environment with swamps, groundwater woodlands, palm  
521 groves, bushland/wooded bushland, etc. Hence, to characterize hominin habitats in the East African Rift  
522 where springs are common, it is necessary to consider spatial and/or temporal resolution of  
523 paleoenvironmental reconstructions (Behrensmeyer and Reed (2013), and to search for evidences of

524 paleo-springs in both the geological and the biological records (Barboni et al., 2019) to avoid  
525 interpretation biases.

526

## 527 **6. Conclusions**

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

553

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562

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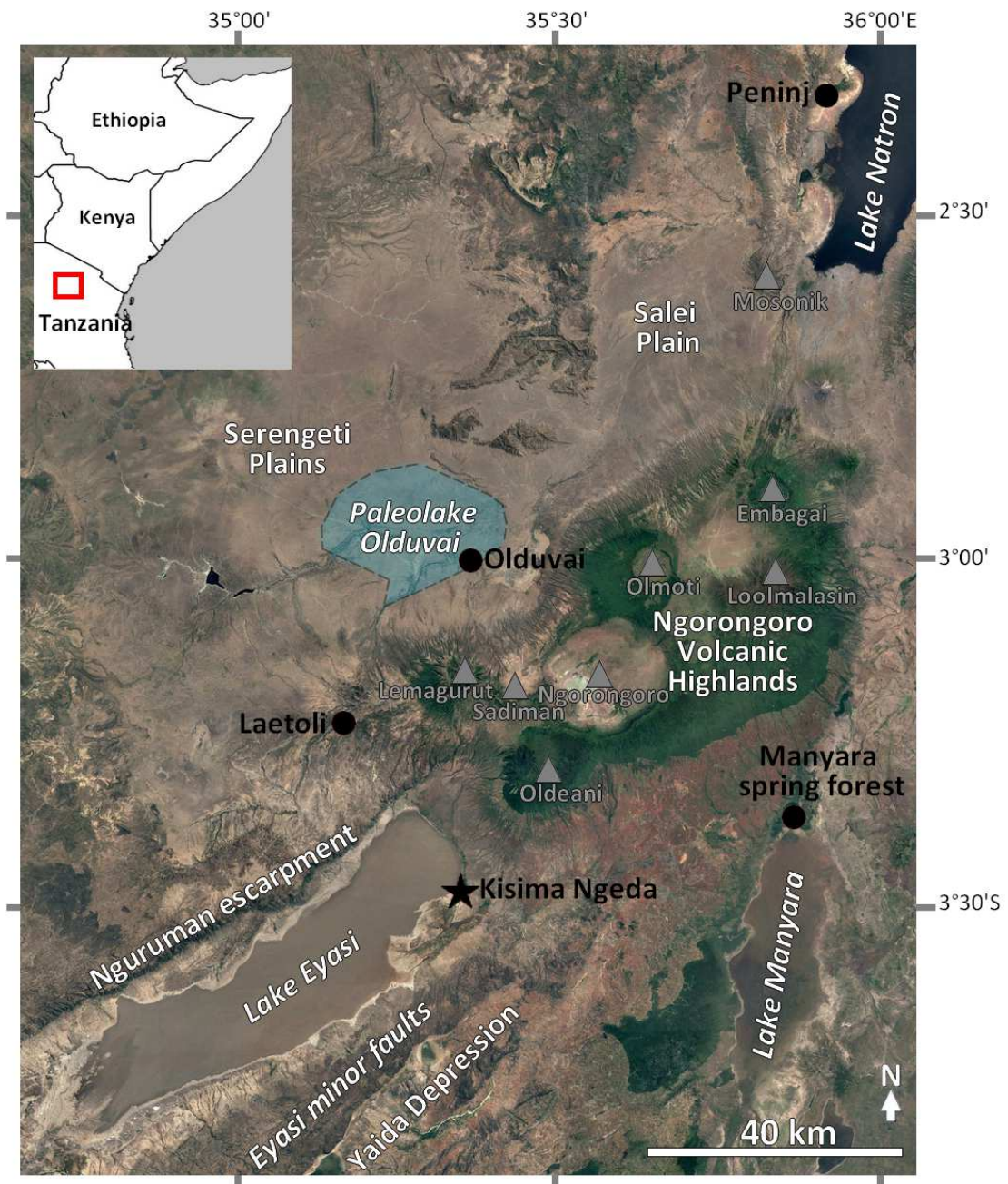
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806 **Figures**

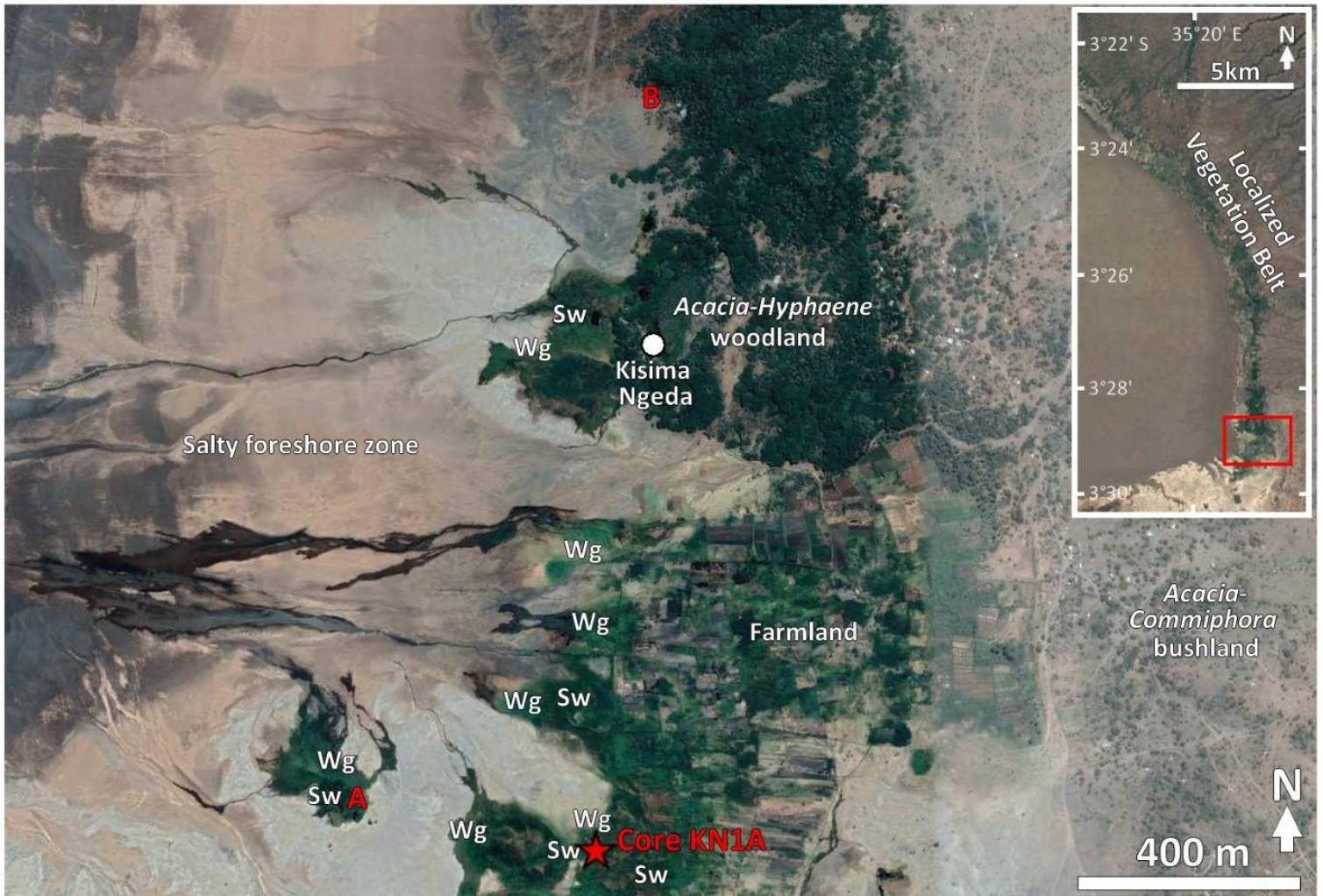
807 **Figure 1:** Satellite image (Google Earth) of sector around the Ngorongoro Volcanic Highlands. Grey  
 808 triangles are volcanoes, black circles are hominin paleontological sites (Ashley et al., 2009 ; Barboni,  
 809 2014) and Manyara spring forest , and black star is our study site. The approximate contour of paleolake  
 810 Olduvai is for 1.75 Ma age. Lake Emakat is the crater lake at Embagai.



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815 **Figure 2:** Satellite images (Google Earth) of the localized vegetation belt on the northeastern margin of

816 Lake Eyasi with a zoom on the Kisima Ngeda area (Tanzania). Sw: swamp, Wg: wet grassland. The letters

817 A and B are respectively the positions of the photo in Figure 3.A and the photo in Figure 3.B.

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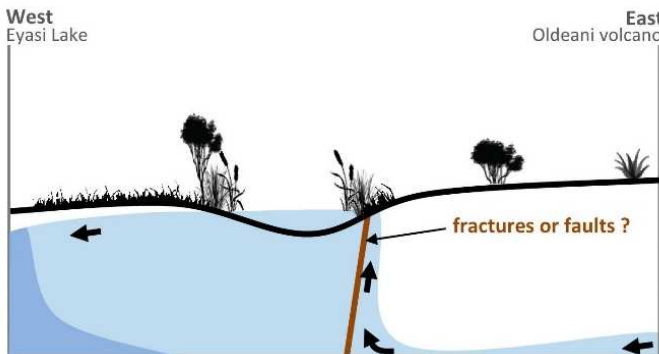
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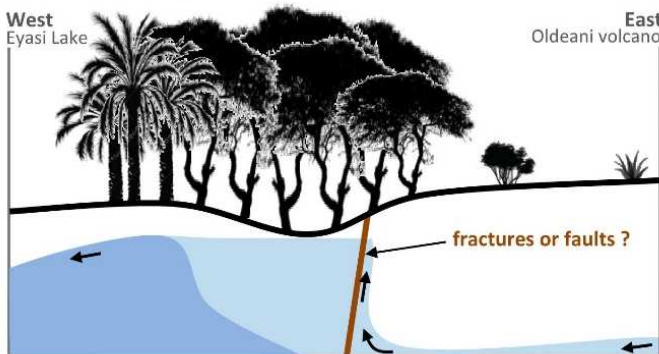
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**A. Hydromorphic zone**



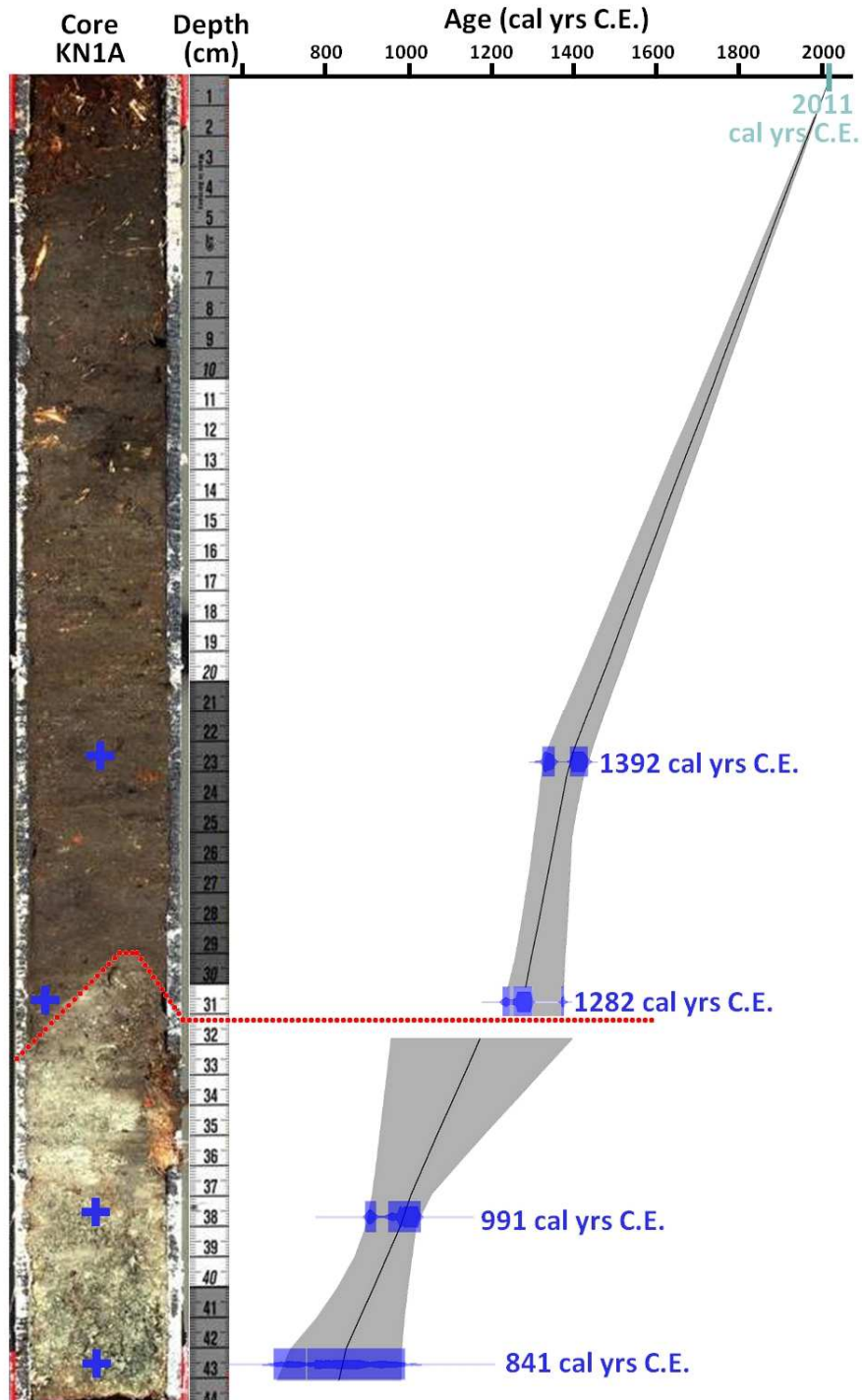
**B. Mesomorphic zone**



824 **Figure 3:** Theoretical drawing showing vegetation according to the groundwater level which controls the  
 825 spatial extent of the hydrophytic (A) and mesophytic (B) zones. Photographs show how the two zones  
 826 may look like in the area of Kisima Ngeda (photographs taken by D. Barboni and G.M. Ashley in 2011).



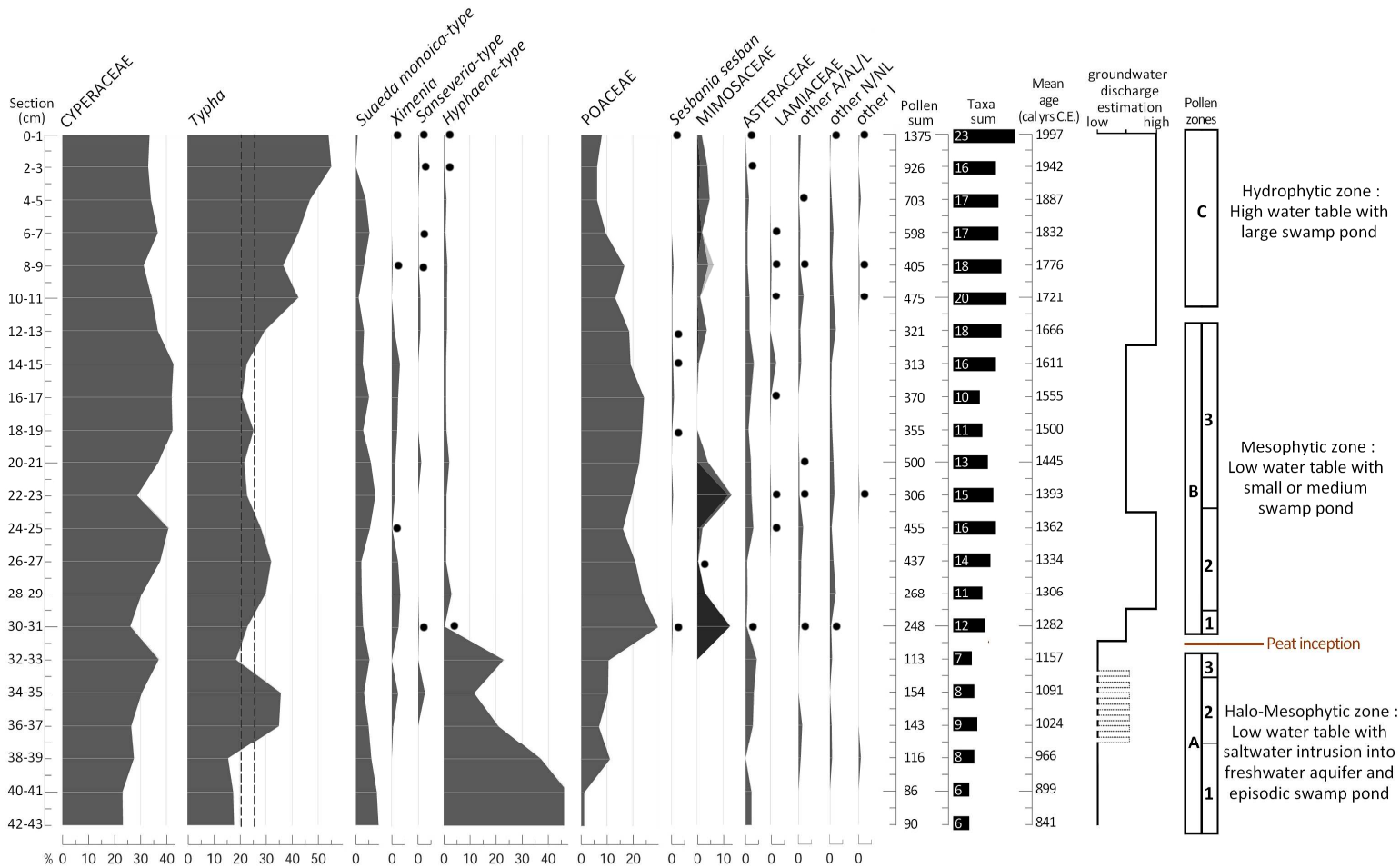
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827 **Figure 4:** Photograph of core KN1A cut in half with age models in cal yr C.E. based on  $^{14}\text{C}$  dating of  
828 concentrated pollen grains. Calibration of the radiocarbon ages and age model were carried out with the  
829 R package CLAM (c.f. Materials and methods). Blue crosses indicate position of samples for  $^{14}\text{C}$  dating.  
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834 **Figure 5:** Pollen diagram with major pollen types, pollen zones, and interpretation of the pollen signal.

835 Mimosaceae include *Albizia*-type in black, *Acacia* in grey and *Calpocalyx*-type *letestui* in light grey. Black

836 dots indicate pollen percentages <0.5%. Groundwater discharge estimation is based on percentage of

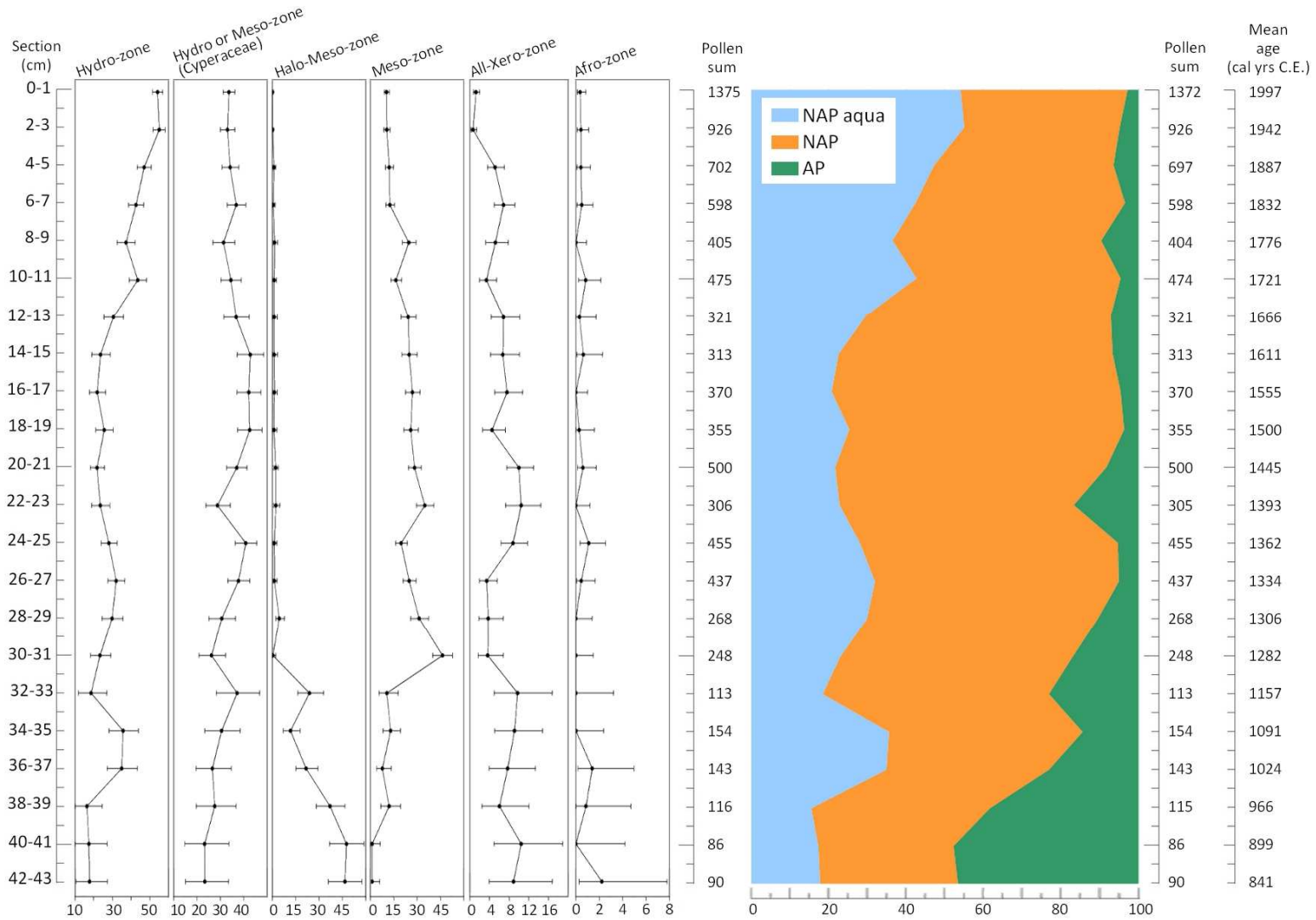
837 pollen.

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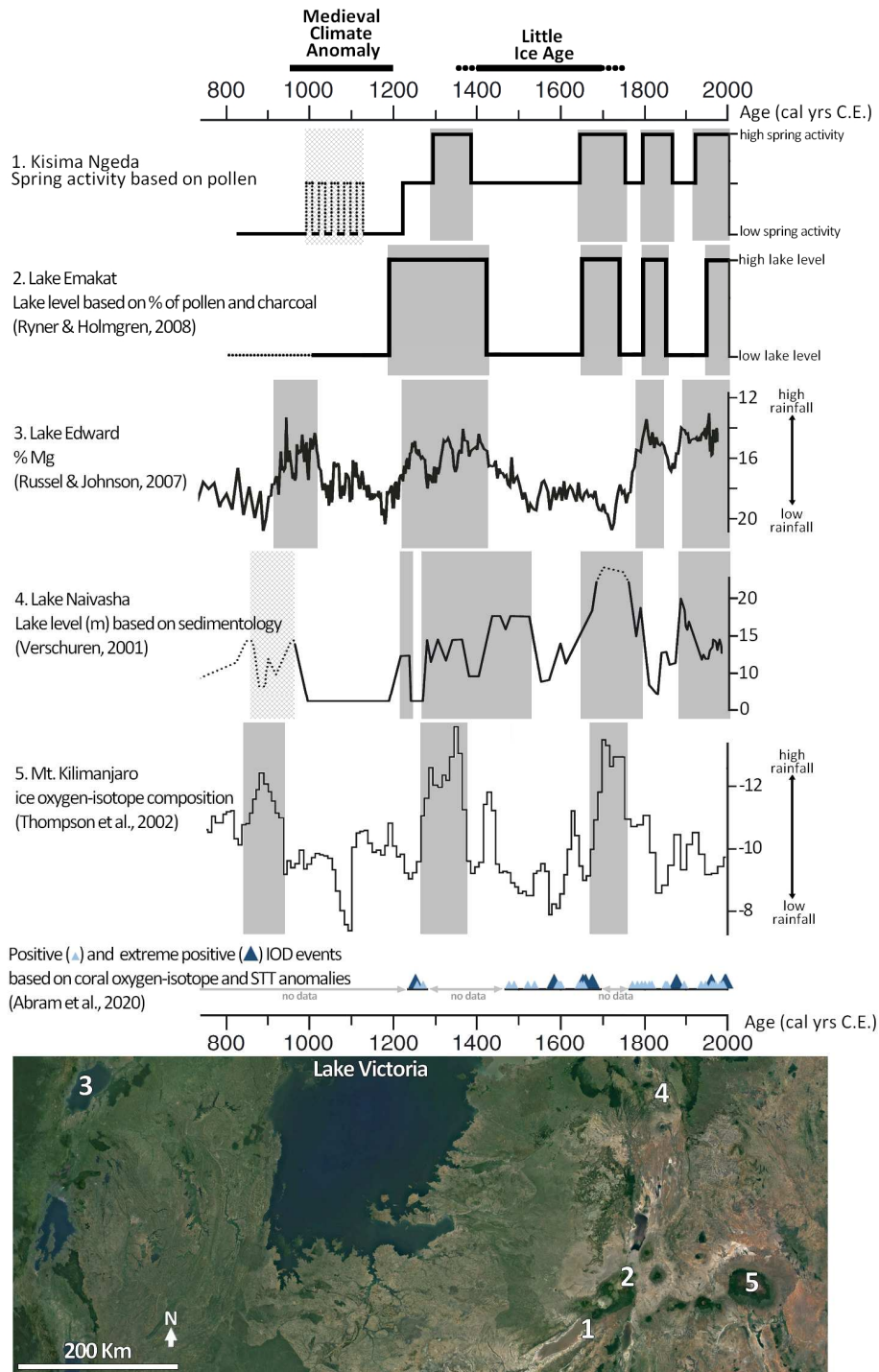
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844 **Figure 6:** Synthetic pollen diagrams by ecological zones (Ubiquist excluded, cf. Table S1) and by pollen  
 845 habitus (undifferentiated excluded, cf. Table S1). AP: arboreal plants; Halo: halophyte; Hydro:  
 846 hydrophyte; Meso: mesophyte; NAP: non-arboreal plants; NAP aqua: non-arboreal aquatic plants; Xero:  
 847 xerophyte.

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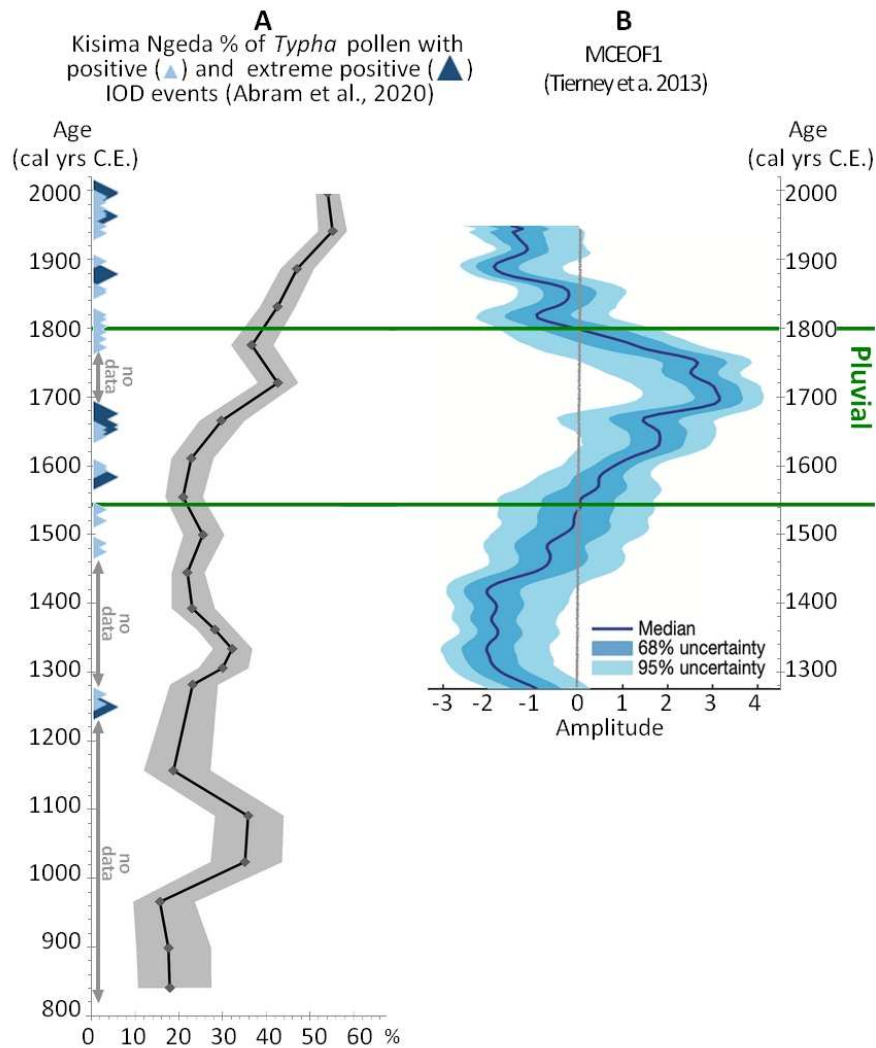
849 **Figure 7:** Spring activity of Kisima Ngeda based on pollen percentages over the past 1200 years  
 850 compared with other regional proxy records reflecting moisture variations and Indian Ocean Dipole (IOD)  
 851 events. Light gray stripes indicate the "wet" phases.



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855 **Figure 8:** Kisima Ngeda spring response (wetland expansions) to mega-regional and regional events. (a)  
856 Relative abundance of *Typha* pollen with 95% confidence interval (dark gray envelope) in KN1A core at  
857 Kisima Ngeda, Lake Eyasi, N Tanzania with positive and extreme positive Indian Ocean Dipole (IOD)  
858 events according to the coral  $\delta^{18}\text{O}$  record of the southern Mentawai Islands, offshore of Sumatra (Abram  
859 et al., 2020). Note that, to date, there is no isotopic record of IOD events older than cal yrs C.E. 1240. (b)  
860 Amplitude of the first Monte Carlo empirical orthogonal factor (MCEOF) showing a coherent statistical

861 signal of rainfall (as inferred by various proxies) in Eastern Africa over the cal yrs C.E. 1300-2000 time  
862 period.