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Benjamin Bourel, Doris Barboni, Andrea Shilling, Gail Ashley. 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. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2021, 580, <10.1016/j.palaeo.2021.110607>. <hal-03353994>

HAL Id: hal-03353994

<https://hal.science/hal-03353994v1>

Submitted on 16 Oct 2023

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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
5 Benjamin Bourel^{1,2}, Doris Barboni¹, Andrea M. Shilling³, Gail M. Ashley³

6 ¹ CEREGE, Aix Marseille Université, CNRS, IRD, INRAE, Coll. France, Technopole Arbois, 13545 Aix en
7 Provence cedex 4, France

8 ² Biogéosciences UMR 6282 CNRS, Université de Bourgogne Franche Comté, 6 boulevard Gabriel, 21000
9 Dijon, France

10 ³ Department of Earth and Planetary Sciences, Rutgers University, Piscataway, 08854, NJ, USA

11

12 Benjamin Bourel (corresponding author) : benjaminbourel1@gmail.com

13 Doris Barboni : barboni@cerege.fr

14 Andrea M. Shilling : shilling.andrea@gmail.com

15 Gail M. Ashley : gmashley@eps.rutgers.edu

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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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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 ¹⁴C 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 *Ximenia* 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 Loboï 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 μS), but high and highly variable at Kisima (640-5600 μS). 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

554 **Acknowledgments**

555 This work was supported by Aix-Marseille University (doctoral fellowship to BB), the Agence
556 Nationale de la Recherche (HADoC Project to DB, ANR-17-CE31-0010-02), and a Waitt Grant/ National
557 Geographic to GM Ashley (Grant # 168-11). Some ¹⁴C dates were determined by accelerator mass
558 spectrometry at Artemis facility, UMS LMC14 Saclay, France, in the framework of INSU national service
559 (grant to DB). We thank Chris and Nani Schmeling for their hospitality and for allowing us to core on the
560 property (Kisima Ngeda Tented Camp), and Joseph Masoy for help with coring logistics. We thank
561 Jonathan Coutaz (CEREGE) for his assistance on the hydrogeological interpretations of this study.

562

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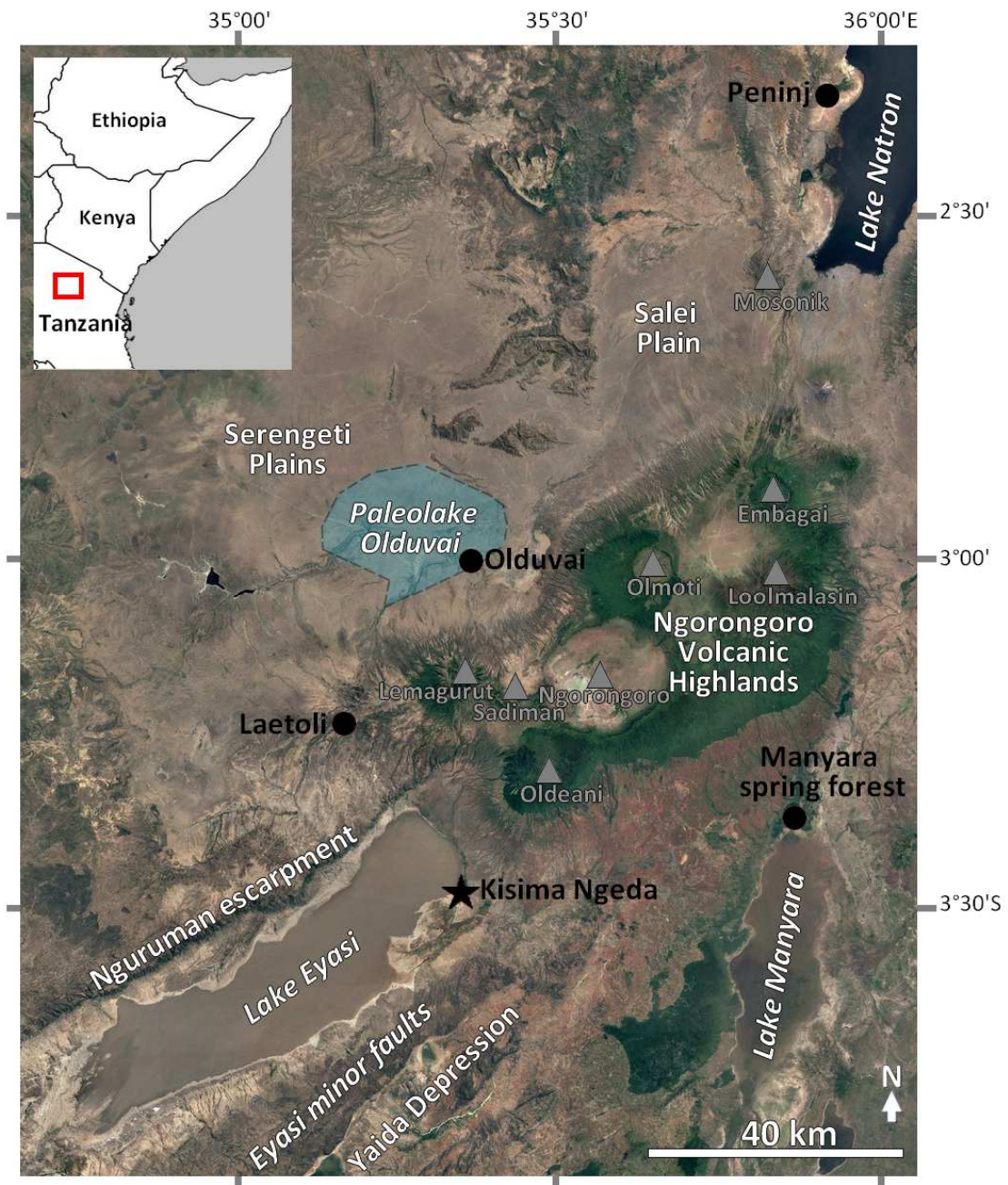
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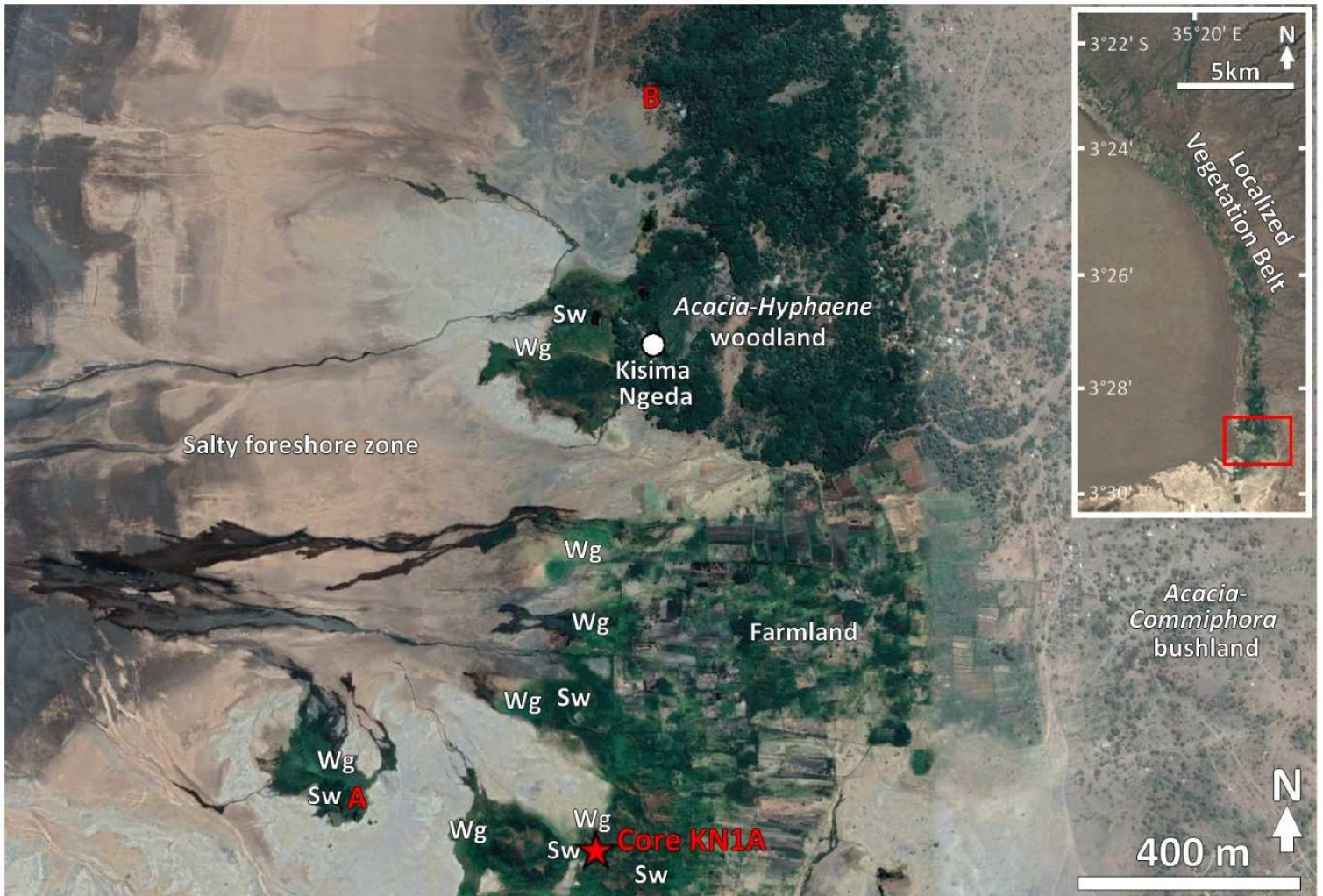
806 **Figures**

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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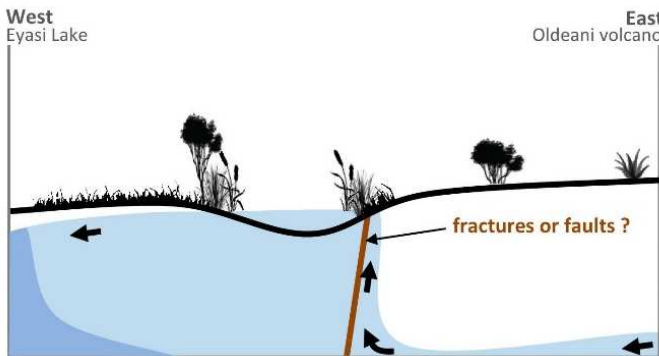
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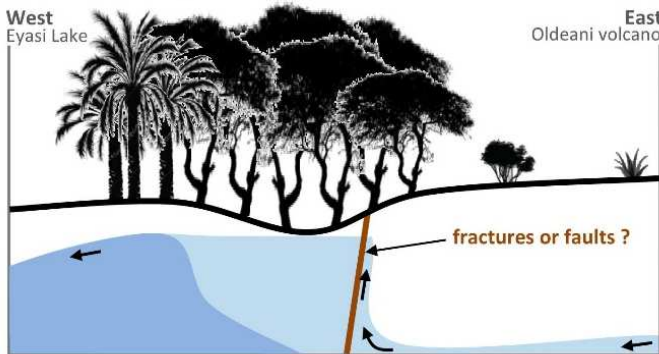
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A. Hydromorphic zone

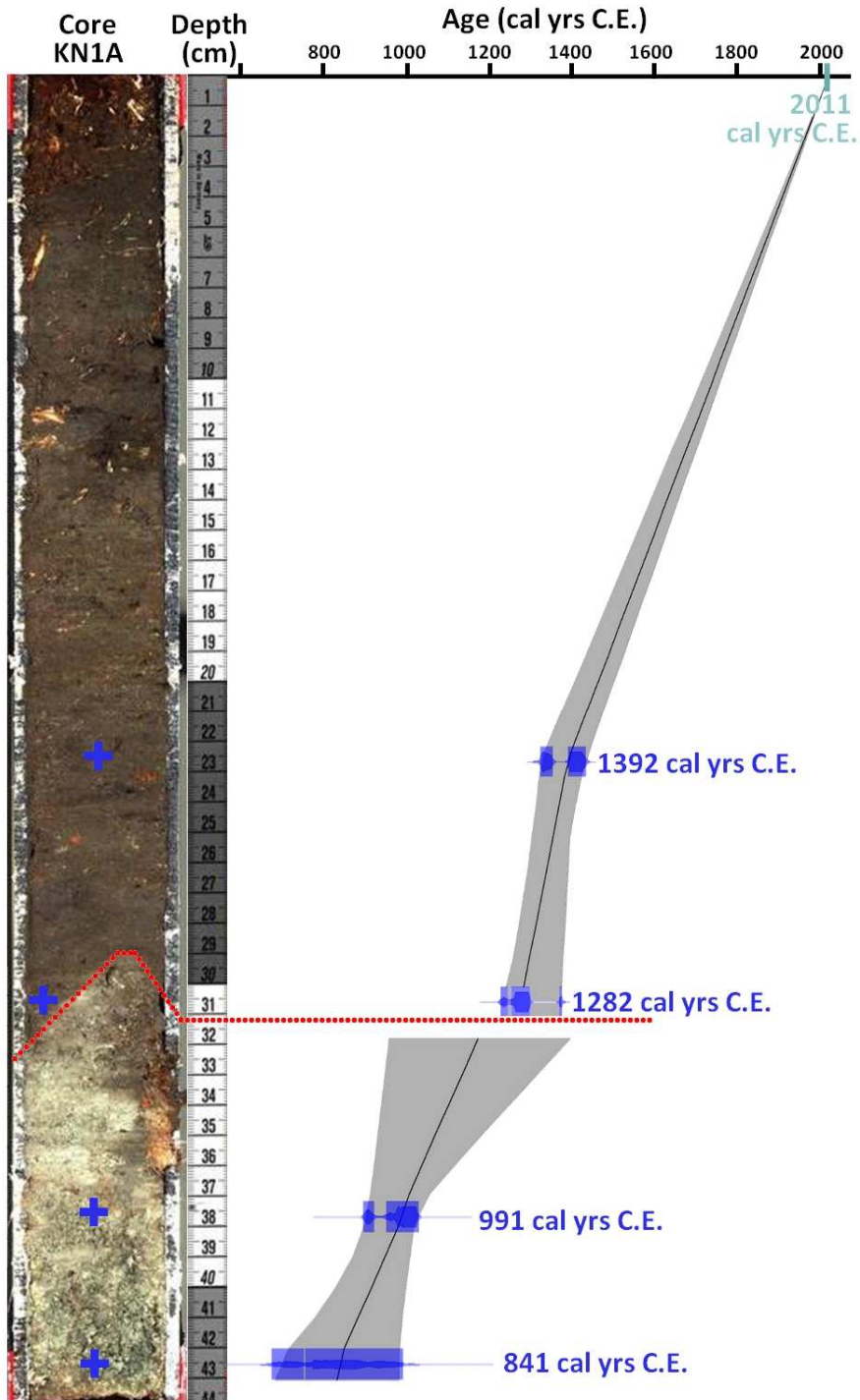


B. Mesomorphic zone



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).

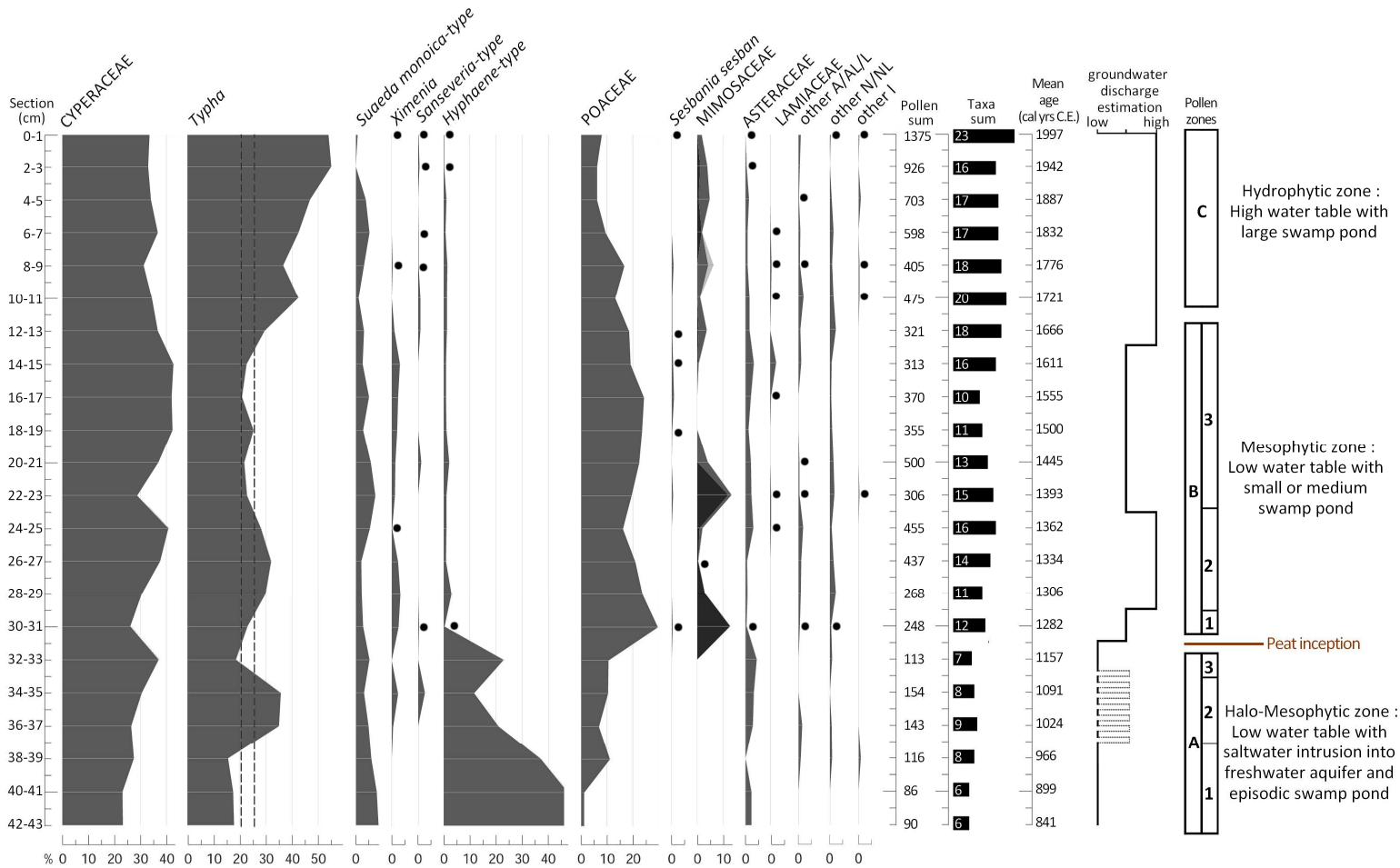
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827 **Figure 4:** Photograph of core KN1A cut in half with age models in cal yr C.E. based on ^{14}C dating of
828 concentrated pollen grains. Calibration of the radiocarbon ages and age model were carried out with the
829 R package CLAM (c.f. Materials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

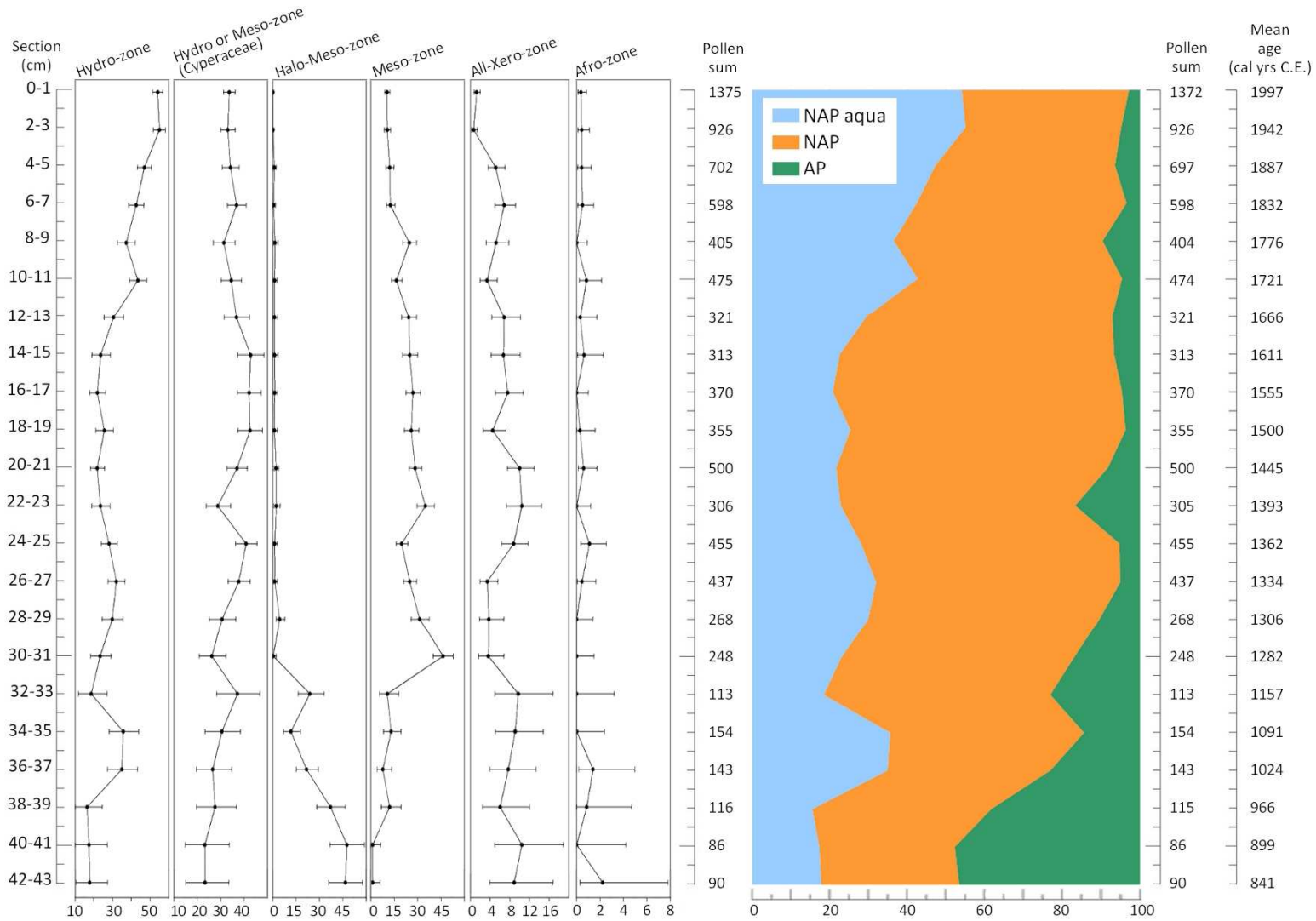
837 pollen.

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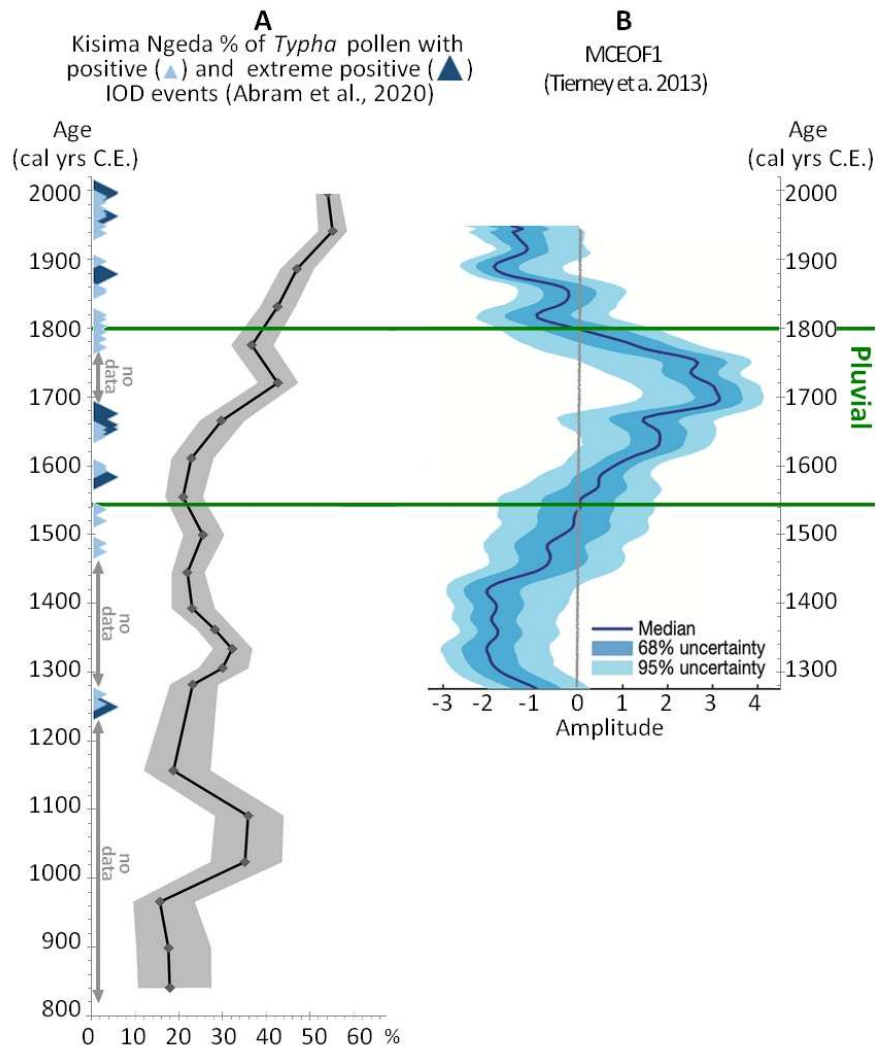
843

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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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.