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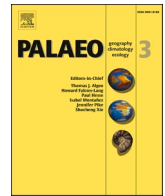
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Long-term ecological successions of vegetation around Lake Victoria (East Africa) in response to latest Pleistocene and Early Holocene climatic changes

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ABSTRACT

Reconstructions of ecosystem dynamics in tropical East Africa during the latest Pleistocene and the Holocene provide important long-term ecological insights, but so far, only a few, sometimes incomplete terrestrial records exist. In this paper, we present a new high-resolution palynological record from the Lake Victoria basin, covering the period from 16,600 to 9000 cal yr BP, when Afromontane forests and tropical rainforests gradually replaced the savanna. We discuss this dataset in the context of published palaeoclimate data, TEX₈₆ inferred temperature and $\delta D_{\text{leaf wax}}$ inferred precipitation records, to assess long-term ecological successions and their potential causes. By ca. 16,500 cal yr BP, the movement of the Afrotropical rainbelt, not only brought an increase in temperature and moisture into the Lake Victoria basin, but also promoted the spread of arboreal taxa, such as *Celtis* and *Podocarpus*, at the expense of the savanna. At that time, fires were prominent in the sparse Afromontane vegetation. Later from ca. 15,500–15,000 cal yr BP, temperature and humidity rose and Afromontane trees such as *Olea* and *Macaranga* spread slightly, while grasses were burning in the savanna. During the period from 13,250 to 10,700 cal yr BP, Afromontane vegetation dominated by *Olea* became more prominent and expanded towards the lowlands where the tropical rainforest or gallery forest established; however, the savanna only marginally retreated. An initial spread of tropical rainforests occurred from ca. 11,500–11,100 cal yr BP during the onset of the Holocene, when temperatures and moisture further increased. Subsequently, between 10,700 and 10,300 cal yr BP the tropical savanna was largely replaced by the tropical rainforest, while the Afromontane forest likely spread to higher elevations, similar to the patterns observed today. Our high-resolution record demonstrates the dynamic response of African tropical ecosystems to major temperature and humidity variations from 16,600 to 9000 cal yr BP, including some of the most important landscape transformations in East Africa in the past 20,000 years.

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1. Introduction

Climate change is expected to significantly impact East African ecosystems in the coming years, including biodiversity and provisioning services in regions such as the Lake Victoria basin (Chapman et al., 2008; Lejju, 2012). The frequency and intensity of rainfall is expected to increase, and temperature is predicted to rise (Luhunga and Songoro, 2020), both of which will consequently impact commercial activities, agriculture, water stress, health, and food security in the region (IPCC, 2022). The climate of the East African region is complex due to the influence of the Atlantic and the Indian Ocean (Liu et al., 2017; Marchant et al., 2007; Nicholson and Kim, 1997). Changes in temperature, rainfall, fire regime, herbivory and human activities are among the most important factors altering the landscape. Some of these environmental drivers have been studied in the Lake Victoria basin since the beginning of the 20th century, with a special focus on the geological history (Wayland, 1929), the lake's water level fluctuations following the late Pleistocene desiccation (Johnson et al., 1996; Kendall, 1969; Stager, 1984; Stager et al., 2011; Stager and Johnson, 2008; Talbot and Livingstone, 1989; Wienhues et al., 2023), and vegetation dynamics revealing important changes since the Pleistocene to modern times (Beuning, 1999a; Colombaroli et al., 2014; Kendall, 1969; Ssemmanda and Vincens, 2002, 2018; Temoltzin-Loranca et al., 2023).

Lake Victoria is the largest tropical lake on Earth; thus, both aquatic and terrestrial habitats in its basin represent important reservoirs of biodiversity (Sayer et al., 2018; UN-Habitat, 2008). One of the most significant impacts for the vegetation on both historical and palaeoenvironmental (Late Quaternary) scales has been the change in precipitation regimes, which results in variable drought frequency, changes in lake water level and changes to the surrounding vegetation (Nicholson and Yin, 2001).

In the past 17,000 years, rainfall and temperature have played an important role in shaping the landscape. In this context, palynological records from Lake Victoria have allowed us to examine general trends in vegetation dynamics and reported considerable biome changes (Kendall, 1969; Temoltzin-Loranca et al., 2023). Namely, the expansion of Afrotropical vegetation at ca. 13,250 cal yr BP, the expansion of the tropical rainforest at ca. 10,600 cal yr BP, and the re-expansion of the savanna after 4500 cal yr BP (Kendall, 1969; Temoltzin-Loranca et al., 2023). While these major biome shifts have been documented in past studies, the temporal resolution of available records remained rather low (for instance, every ca. 340 years in Kendall, 1969 or ca. 410 years in Beuning, 1999a and ca. 700 years in Temoltzin-Loranca et al., 2023), which impeded to thoroughly address the involved ecological processes such as the ecosystem responses to climate change during the savanna-rainforest transition and the fire regimes in the Lake Victoria area.

The timespan analysed here covers some major climate and ecosystem reorganizations during the latest Pleistocene and the Early Holocene, including the onset of the African Humid Period (AHP) – the most notable climatic period for the African continent since the Pleistocene to modern times – which extends from ca. 14,800 to 5500 cal yr BP (deMenocal et al., 2000; Shanahan et al., 2015). More specifically, humidity peaked during the Early and Mid-Holocene, triggering important vegetation changes, such as the decline of savanna and the expansion of forests in East Africa (Ssemmanda and Vincens, 1993; Van Zinderen Bakker and Coetzee, 1988; Vincens et al., 2005). Considering the importance of such ecological reorganizations, in this manuscript we refer to this humid-warm period at ca. 11,500–5500 cal yr BP as the Holocene AHP.

The major biome reorganizations observed in previous palaeoecological investigations opened major questions regarding the precise timing of changes and the ecological processes involved. For instance, the timing of the spread of the tropical rainforest dominated by Moraceae in the surroundings of Lake Victoria was debated, mainly due to differences in the accuracy of the chronologies previously published. While Kendall (1969) reported the expansion at ca. 9500 ¹⁴C yr BP

(10,900 cal yr BP) during the Holocene AHP, Beuning (1999a) suggested it occurred in the Late Pleistocene at ca. 11,200 ¹⁴C yr BP (13,100 cal yr BP). Three independently dated pollen records collected from sediment cores along a transect from the lake shore to the deep water presented in Temoltzin-Loranca et al. (2023) provided robust evidence that the tropical rainforest spread between 11,500 and 10,000 cal yr BP, confirming the Early Holocene age of this important vegetation reorganization. However, the low temporal resolution of that study (ca. 700 years on average in sediment cores LV1, LV2 and LV4) impeded a chronologically and ecologically precise assessment. For instance, it remains unclear whether the tropical rainforest spread solely in response to moisture conditions, or if the Early Holocene warming also played a role. Similarly, the ecological processes that led to the expansion of Afrotropical vegetation at ca. 13,250 cal yr BP are elusive, and the source of fire remained unexplored (Temoltzin-Loranca et al., 2023). Here, we aim to merge this gap by investigating the changes observed during the savanna-forest transition from the latest Pleistocene (16,600 cal yr BP) to the Early Holocene (9000 cal yr BP) at a high temporal resolution (every 40 years).

This study seeks to: (I) provide the first high-resolution pollen record for the Lake Victoria basin during the latest Pleistocene and Early Holocene; (II) to assess the major vegetation and ecosystem changes including the source of the biomass burning; and (III) to elucidate the ecosystem responses to climate, by comparing our palaeoecological time series with independent palaeoclimate proxies, reflecting rainfall amount and temperature (Berke et al., 2012). We are particularly interested in the factors that allowed Afrotropical and tropical rainforest vegetation to gradually replace the savanna during the period from 16,600 to 9000 cal yr BP.

2. Site and methods

2.1. Study site

Lake Victoria is the second-largest freshwater lake in the world (surface area = 68,800 km²). Its formation can be attributed to the reverse flow resulting from the damming of rivers flowing westward, brought about by the uplifting of the western section of the East African Rift System (EARS; Danley et al., 2012; Johnson et al., 2000). Since its formation, the lake has undergone alterations over time, but there is no evidence of further tectonic modifications since the middle Pleistocene (Beverly et al., 2020). It is located at an altitude of 1135 m above sea level (m asl), and it has a maximum water depth of 68 m (Johnson et al., 1996; Fig. 1a). Rainfall is the biggest contributor to Lake Victoria's water balance accounting for ca. 80%, and the remaining ca. 20% comes from 17 tributaries of which the largest is the Kagera River (Yin and Nicholson, 1998). Both rainfall and the wind regime follow a bimodal pattern with two rainy seasons occurring from March to June, and from October to December (Okungu et al., 2005). Today's precipitation ranges from 1000 to 1500 mm/year, mainly controlled by the migration of the Afrotropical rainbelt and the Congo Air Boundary (CAB) across the equator (Colombaroli et al., 2018; Okungu et al., 2005; Tierney et al., 2011; Verschuren et al., 2009). The wind direction from January to March is regulated by the Northeast Monsoon, whereas from August to September it is influenced by the Southeast Monsoon (Nieuwolt, 1979). The times between April and July, and October and December are transitional periods (Okungu et al., 2005).

The three main biomes or vegetation types around Lake Victoria are the tropical rainforests (Elenga et al., 2000; Vincens et al., 2006) that develop in warm-humid conditions, the Afrotropical forests which expand at higher and cooler altitudes at ca. 1200–2500 m asl, and the tropical savanna, rich in evergreen to semi-evergreen bushlands, which extend over warm to arid conditions (Lillesø et al., 2011; Fig. 1b). More specifically, the vegetation types include the Guineo-Congolian rainforest, transitional rainforest, swamp forest, scrub forest, riverine forest, Afrotropical rainforest, Afrotropical undifferentiated forest, evergreen

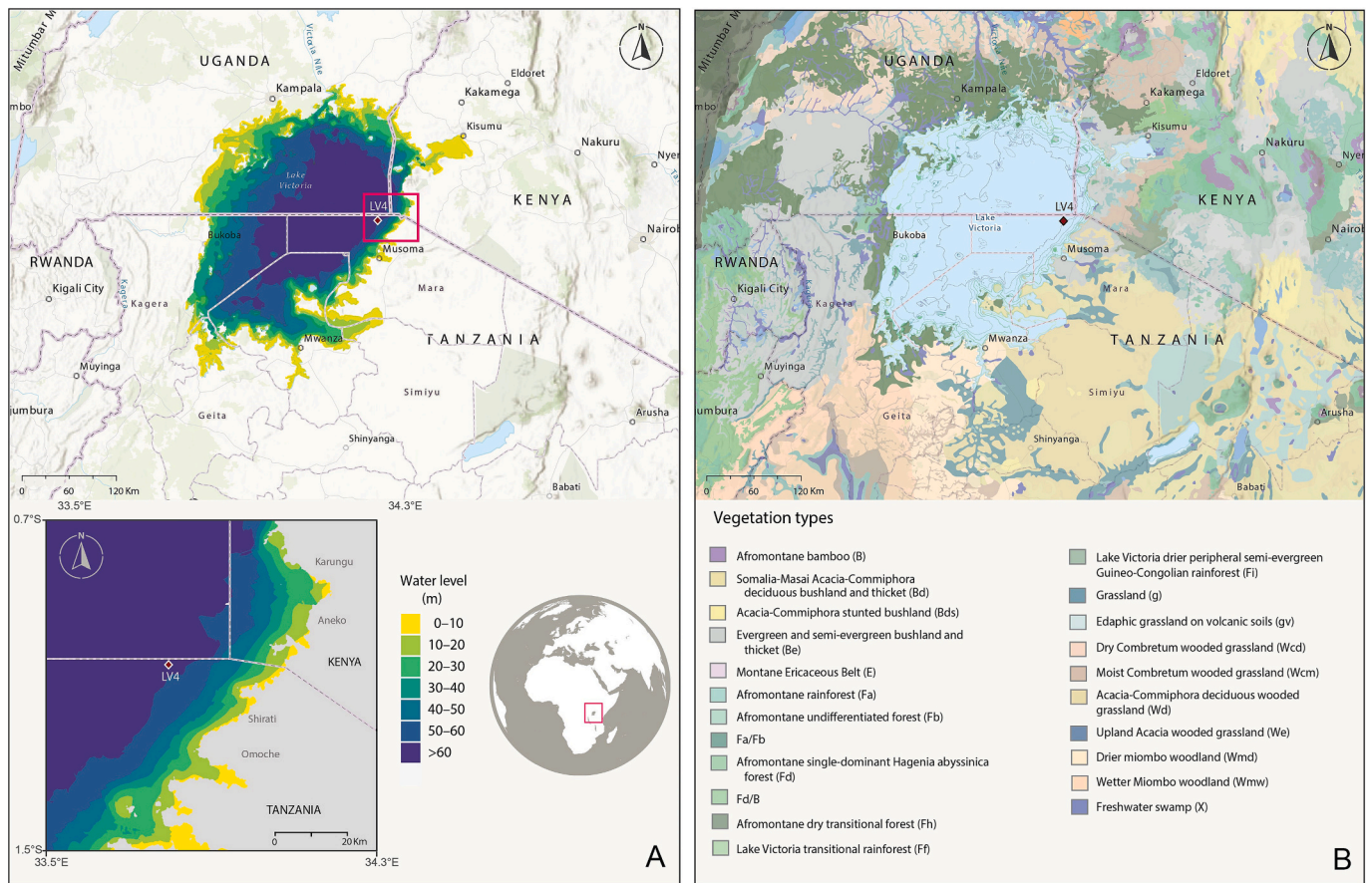


Fig. 1. (A) Bathymetry and location of Lake Victoria and core LV4. The colour chart shows the water depth in 2017. Datapoints for elaborating both maps were extracted from Hamilton et al., 2022. (B) Potential Natural Vegetation (PNV) in the Lake Victoria area, extracted and adapted from Lillesø et al., 2011.

and semi-evergreen bushland, and thicket and derived communities (White, 1983), as well as several transitional plant communities between these major units. In order to allow for a better comparison with the pollen evidence, we have grouped all the rainforest types under the African biome “tropical rainforest” (e.g. Elenga et al., 2000), and the two types of Afromontane forests under Afromontane vegetation (FTEA, 1995–2012). In addition to the zonal vegetation types, azonal vegetation can occur in areas such as wetlands (FTEA, 1952–2012). Today, the lake basin is surrounded by the ecosystems mentioned above, having the closest stands of Afromontane taxa at Mount Elgon (ca. 90 km), the Mau escarpment (ca. 180 km), and the Ngorongoro crater (200 km; Hedberg, 1955). Outside the study region, subtropical to temperate Afromontane forests grow in disjunct zones of the mountains of East, West and South Africa (Allen et al., 2021; Bekele, 1993; Mucina and Geldenhuys, 2016; Powell et al., 2023). Striking floristic (e.g. *Olea*, *Podocarpus*, *Celtis*, *Juniperus*, *Erica*) and faunal similarities, as well as ecological niche models, suggest that these isolated mountain forest communities were connected in the past during cold periods of the Pleistocene that allowed Afromontane taxa to spread to lower altitudes (Allen et al., 2021).

2.2. Sediment cores, chronology and XRF

As part of a campaign organized by the University of Bern and the Tanzanian Fisheries Institute (TAFIRI), four sediment cores (LV1, LV2, LV3 and LV4) located at water depths ranging from 13.4 to 63 m were retrieved near the Shirati Bay. Coring was conducted using the UWITEC Niederreiter coring system from the Institute of Plant Sciences at the University of Bern. This system was modified with the replacement of rubber pontoons for metal floating boxes to adapt to high wave action. In this study, we focus on core LV4, located at 01°02.966'S /

33°47.768'E, ca. 30 km away from the shore at a water depth of 63 m (Fig. 1a). The chronology of LV4 was established using 25 ¹⁴C dates (Table 1) which were crosschecked and validated with additional age-depth models coming from two other coring sites at Lake Victoria (LV1 and LV2). Details of these complex chronologies are provided in Temoltzin-Loranca et al. (2023). Scanning X-ray fluorescence (XRF) was performed at 5 mm intervals with an ITRAX core scanner using a Mo- and Cr- anode X-ray tube at 50 mA, 30 kV and 30 s integration time. Here, we display only 2 elemental ratios, Rb/K as an indicator of chemical weathering (Wienhues et al., 2023) and Zr/Ti as a grain size proxy (e.g. Brown et al., 2007). Rb/Zr typically increases when chemical weathering is high, whereas Zr/Ti shows higher values with an increase in grain size (Davies et al., 2015).

2.3. Pollen and charcoal analyses

We took 153 sediment samples of 1 cm³ which were collected at 2 cm intervals (ca. every 40 years) throughout the lower portion of LV4 (core depths = 463–777 cm). The samples were prepared for pollen analyses following standard procedures using HCl, KOH, HF and acetolysis (Moore et al., 1991). *Lycopodium clavatum* tablets (Batch number 3862 with $n = 9666 \pm 671$ spores per tablet) provided by the University of Lund (Maher, 1981) were added to the samples prior to chemical treatment in order to calculate microfossil concentrations and influx (Stockmarr, 1971). Samples were stained with fuchsine and diluted with glycerine for mounting. The slides were analysed under a light microscope (Leica 2500) at 400× magnification. We used palynological keys, atlases (Gosling et al., 2013; Reille, 1992; Roubik and Moreno, 1991; Schüler and Hemp, 2016) and the pollen reference collection of the Kilimanjaro region located at the palynological laboratory of the

Table 1
Radiocarbon dates of the Lake Victoria core LV4. Extracted and adapted from [Temoltzin-Loranca et al. \(2023\)](#).

Sample #	Laboratory code	Core	Sample ID	Composite core depth (cm)	Material	Carbon mass (μg)	^{14}C age (yr BP)*	Age corrected for ^{14}C reservoir effect for B and P (yr BP)*	Median ages (cal yr BP)	95% C.I. (cal yr BP)	Model ages (cal yr BP)	Model age C.I.
1	BE-16248	LVC18_S4	L2_31-35	116-118	C	32	2890 \pm 100	-	3035	2781-3329	3051	2770-3344
2	BE-16249	LVC18_S4	L2_59-63	144-148	C	71	3290 \pm 70	-	3517	3373-3690	3539	3293-3787
3	BE-16262	LVC18_S4	L2_61-63	146-148	P	968	3400 \pm 25	2830 \pm 410	2972	1932-3980	3557	3344-3787
4	BE-16250	LVC18_S4	L2_85-87	170-172	C	105	3670 \pm 70	-	4004	3777-4233	4043	3832-4268
5	BE-16251	LVC18_S4	L3_03-05	188-190	C	37	3990 \pm 90	-	4463	4156-4814	4404	4155-4649
6	BE-16252	LVC18_S4	L3_23-27	208-212	C	47	4190 \pm 90	-	4706	4440-4959	4774	4488-5151
7	BE-16263	LVC18_S4	L4_18-20	272-274	P	995	5770 \pm 30	5200 \pm 410	5952	4883-6882	6273	5946-6564
8	BE-16253	LVC18_S4	L4_18-22	272-276	C	43	5500 \pm 100	-	6294	6003-6492	6297	5946-6647
9	BE-16254	LVC18_S4	L5_09-11	334-336	C	55	6570 \pm 100	-	7468	7273-7613	7498	7198-7773
10	BE-16255	LVC18_S4	L5_61-65	386-390	C	48	7910 \pm 120	-	8763	8429-9023	8749	8413-9081
11	BE-16256	LVC18_S4	L5_93-97	418-422	C	53	8340 \pm 110	-	9323	9029-9531	9296	8958-9585
12	BE-16264	LVC18_S4	L5_95-97	420-422	P	999	8510 \pm 30	7940 \pm 410	8843	7935-9883	9311	8978-9585
13	BE-16257	LVC18_S4	L6_58-60	484-486	C	62	9270 \pm 120	-	10,459	10,201-10,988	10,325	9829-10,657
14	BE-16258	LVC18_S4	L7_06-08	516-518	C	18	9000 \pm 260	-	10,103	9481-11,058	10,620	10,167-11,084
15	BE-16259	LVC18_S4	L7_36-38	546-548	C	31	9320 \pm 190	-	10,557	9974-11,182	11,056	10,597-11,626
16	BE-16265	LVC18_S4	L7_36-38	546-548	P	775	10,200 \pm 60	9660 \pm 410	11,068	9914-12,476	11,056	10,597-11,626
17	BE-16260	LVC18_S4	L8_30-32	594-596	C	25	10,600 \pm 230	-	12,453	11,755-13,066	12,263	11,581-12,850
18	BE-16261	LVC18_S4	L8_84-86	648-650	C	33	11,500 \pm 200	-	13,379	13,000-13,795	13,447	13,034-13,906
19	BE-15553	LVC18_S4	L9_10-12	674-676	C	50	12,200 \pm 190	-	14,234	13,614-14,974	14,097	13,716-14,565
20	BE-16266	LVC18_S4	L9_10-12	674-676	P	688	13,000 \pm 70	12,300 \pm 410	14,478	13,414-15,667	14,097	13,716-14,565
21	BE-15554	LVC18_S4	L9_20-24	684-686	C	60	12,300 \pm 170	-	14,408	13,808-15,003	14,299	13,866-14,791
22	BE-15555	LVC18_S4	L9_40-42	704-706	C	38	12,000 \pm 210	-	13,920	13,434-14,828	14,738	14,108-15,298
23	BE-15556	LVC18_S4	L10_02-04	762-764	C	194	13,700 \pm 170	-	16,588	16,081-17,056	16,386	15,899-16,826
24	BE-15557	LVC18_S4	L10_12-14	772-774	C	193	13,700 \pm 160	-	16,589	16,121-17,045	16,596	16,106-17,046
25	BE-16267	LVC18_S4	L10_12-14	772-774	P	248	14,100 \pm 110	13,500 \pm 410	16,282	15,046-17,432	16,596	16,106-17,046

*Dates rounded following Stuiver & Polach (1977). C = Charcoal, P = 20-50 μm palynomorph concentrate, C.I. = Confidence Interval.

University of Göttingen, Germany. Pollen sums ranged from 98 (deepest sample of the record where grains were rare to find) to 588 grains per sample (mean = 375 pollen grains, standard deviation = 95). Pollen percentages were calculated with respect to the terrestrial pollen sum excluding pollen of aquatic and wetland plants and spores. Eight samples above the lowermost sample were palynologically sterile (ca. 300 years).

For biomass burning assessment, we analysed macrocharcoal for a total of 389 sediment samples (whole core) of ca. 9 cm³ taken continuously at 2 cm intervals and sieved through a mesh size of 200 µm (see Temoltzin-Loranca et al., 2023). In this paper we only display the samples corresponding to the lower portion of LV4 (depths = 463–777). The samples were analysed under a stereomicroscope (Leica M125) at 40× magnification, and the charcoal was picked. Additionally, charcoal morphotypes (wood vs grass) were determined following Colombaroli et al.'s (2014) approach. Charcoal particles with a length–width ratio ≥ 3:1 and stomata within the rows of epidermal cells (Colombaroli et al., 2014; Jensen et al., 2007) were considered to originate from grass, whereas particles with thicker structure and a length–width ratio of ≤ 3:1 were identified as wood charcoal pieces (Umbanhowar and McGrath, 1998). For the calculation of macroscopic charcoal influx, charcoal particle numbers were standardized to 1 cm³ respectively to 1 cm²/year using the age–depth model from Temoltzin-Loranca et al. (2023).

2.4. Numerical methods

2.4.1. Pollen zonation and ordination

We assigned Local Pollen Assemblage Zones (LPAZ) by using the optimal partitioning approach with a minimum sum of squares (Birks and Gordon, 1985) and determined the number of significant zones with the aid of the broken-stick model (Bennett, 1996). In order to retain the original low-resolution subdivision (LPAZ) of Temoltzin-Loranca et al. (2023), the new significant zone limits, resulting from the additional pollen sample analysis, were used to delimit subzones.

To identify gradients in vegetation composition, we analysed the pollen percentage data with a Detrended Correspondence Analysis (DCA; Legendre and Birks, 2012; Lepš and Šmilauer, 2003; ter Braak and Prentice, 1988) using Canoco 5.10 (ter Braak and Šmilauer, 2018). The gradient length of the first axis of the DCA was 1.71 standard deviations, indicating that Principal Component Analysis (PCA) would be suitable to analyse the data. Since the PCA displayed a marked horseshoe effect, we used a detrended unimodal ordination technique (i.e. DCA) to eliminate the horseshoe effect (Legendre and Birks, 2012; ter Braak and Prentice, 1988). Pollen percentage data was detrended by segments, and we applied a squared-root transformation to stabilize the variance. Additionally, the rare types were down-weighted using the automated down-weight function in CANOCO 5.10 in order to reduce their influence and to emphasize the importance of dominant types. This down-weighting gives low weight to rare species during the calculation of the ordination (ter Braak and Šmilauer, 2018). Therefore, only the 35 taxa with the largest contribution to the total variance explained along axis 1 and 2 are shown in the final figure.

2.4.2. Response curves

In order to explore the response of selected taxa to climate, specifically rainfall and temperature, we fitted generalized additive models (GAMs) (Hastie and Tibshirani, 1990; Šmilauer and Lepš, 2014) assuming a Poisson distribution for the response variables and using a log link function with a maximum of 2 degrees of freedom (DF). Then, we chose the most parsimonious model using stepwise selection based on the Akaike Information Criterion (AIC) value. Response curves were fitted in Canoco 5 (ter Braak and Šmilauer, 2018). In this study we used the previously published data from TEX₈₆ and δD_{leaf wax} (Berke et al., 2012) to represent past changes in temperature and rainfall amount in the study region. Additionally, we tested the response of vegetation to fire

(charcoal); however, as the response curves did not exhibit noteworthy responses, we decided to not pursue further analysis.

3. Results and interpretation

3.1. Vegetation and fire history

The palaeoecological record of Lake Victoria (LV4) starts at 16,600 cal yr BP and the whole examined sequence includes 7600 years (16,600–9000 cal yr BP; Figs. 2 and 3). However, in the bottom part of the core, pollen grains were very rare or absent from 16,600 to 16,300 cal yr BP. We found a total of 128 pollen taxa that were identified to the most detailed taxonomic level possible. Due to the higher temporal resolution of this record, the subzones LV4-1a and LV4-1b previously determined by visual criteria (Temoltzin-Loranca et al., 2023) were now statistically significant. Moreover, LV4-2 resulted in two additional statistically significant subzones: LV4-2a and LV4-2b.

LV4-1a (16,600–13,250 cal yr BP); dominance of the savanna grasslands. Herbaceous pollen is present in the landscape with values close to 90% of abundance. The most frequent taxa are Poaceae, which maintains pollen values between 50% and 60%, as well as Cyperaceae, with values around 10 to 20%. Pollen belonging to the Amaranthaceae, Brassicaceae and Cichorioideae families and taxa such as *Artemisia* and *Senecio* are also important (5–10%). Additionally, our pollen data suggest the presence of savanna trees such as *Acacia*-type, *Combretum*, *Indigofera* and *Lannea* (Figs. 2 and 3). The pollen assemblage also indicates the presence of sparse Afromontane vegetation which, under cooler conditions (Berke et al., 2012) might have formed isolated stands in the surroundings of the lake (e.g. trees and shrubs such as *Podocarpus*, *Celtis*, *Olea*, and *Juniperus*, as well as herbs such as *Coryza*, and *Rumex*; Fig. 4). *Olea* expanded for the first time around 15,000 cal yr BP but remained rather low until ca. 13,800 cal yr BP. During this period, the lake was most likely shallow, the presence of *Typha* (>3%) suggests the proximity of our coring spot (today at 63 m water depth) to a lake shore or wetland, until ca. 13,800 cal yr BP, when aquatic taxa (*Lemna*, *Potamogeton*, *Nymphaea coerulea*, *Nymphaea lotus*) disappeared.

Frequent biomass burning inferred from macrocharcoal influx peaks occurred between 16,600 and 16,000 cal yr BP. The higher influx in woody charcoal particles suggests that most fires occurred in the (pollen-inferred) Afromontane stands (*Olea*, *Podocarpus*, *Juniperus*). Around 15,500 cal yr BP, grassland burning started to increase steadily, resulting in maximum values in the grass charcoal influx around 14,500 cal yr BP (Fig. 3). Towards the end of this zone (around 14,000 cal yr BP), the amount of savanna fires as inferred from grassland charcoal declined to become low (when compared to previous times).

LV4-1b (13,250–10,700 cal yr BP); spread of Afromontane vegetation, first tropical rainforest or gallery forest stands. Pollen of herbs continues to dominate the record (Fig. 4); however, it decreases to ca. 65%. Pollen of woody taxa characteristic of the thicket clumps, such as *Allophylus*, *Trema*, *Scutia*, *Grewia* and *Syzygium* increases (Figs. 2 and 3). Subtropical Afromontane vegetation spread rather abruptly at around 13,250 cal yr BP. Specifically, pollen from *Olea* becomes important (>15%) together with *Podocarpus*, *Celtis* and *Macaranga* (ca. 5%). Moreover, concurrent with the mass expansion of *Olea*, an initial establishment of tropical rainforest or gallery forest taxa occurred. At around 11,500–11,100 cal yr BP the tropical rainforest taxon Moraceae increased to reach a first peak (>10%), while moderate minima of Moraceae occurred around 12,500, 11,700 and 10,800 cal yr BP. From ca. 11,100 to 10,700 cal yr BP, higher macroscopic charcoal influx dominated by woody taxa suggests frequent fire events in the Afromontane and rainforest stands.

LV4-2a (10,700–10,300 cal yr BP), expansion of the tropical rainforest and the vanishing of the savanna. Pollen percentages of herbs (particularly Poaceae and Cyperaceae) decrease markedly (Figs. 2 and 3), while arboreal pollen percentages increase (>60%). Pollen of tropical rainforest taxa such Moraceae (>20%), *Alchornea* (ca. 5%) and

Lake Victoria (LV4)

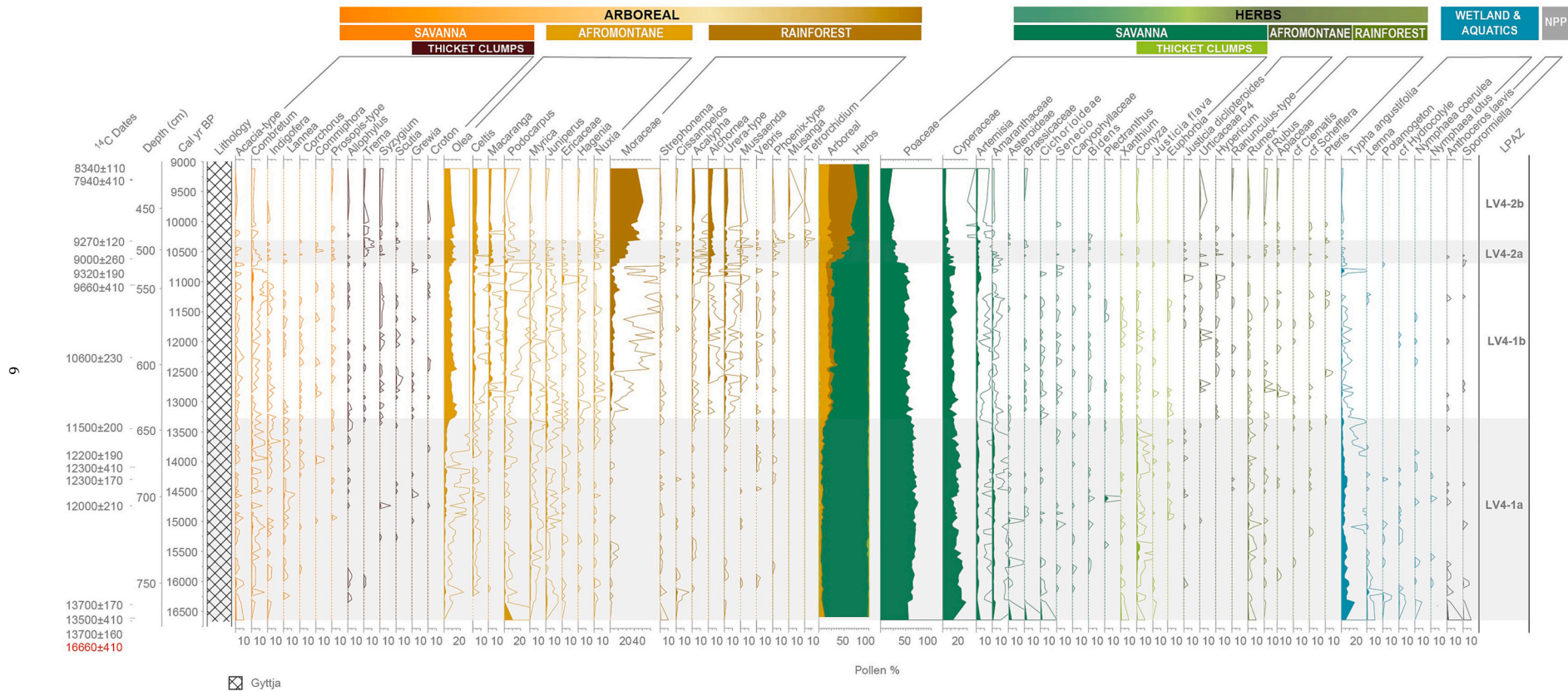


Fig. 2. Pollen record from Lake Victoria (LV4). Arboreal taxa are plotted on the left side in different shades of orange according to each biome indicated by the bands on top. Herb taxa are plotted on the right side in different shades of green according to each biome indicated by the bands on top. LPAZ = Local pollen assemblage zones. Empty curves represent a 10× exaggeration. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

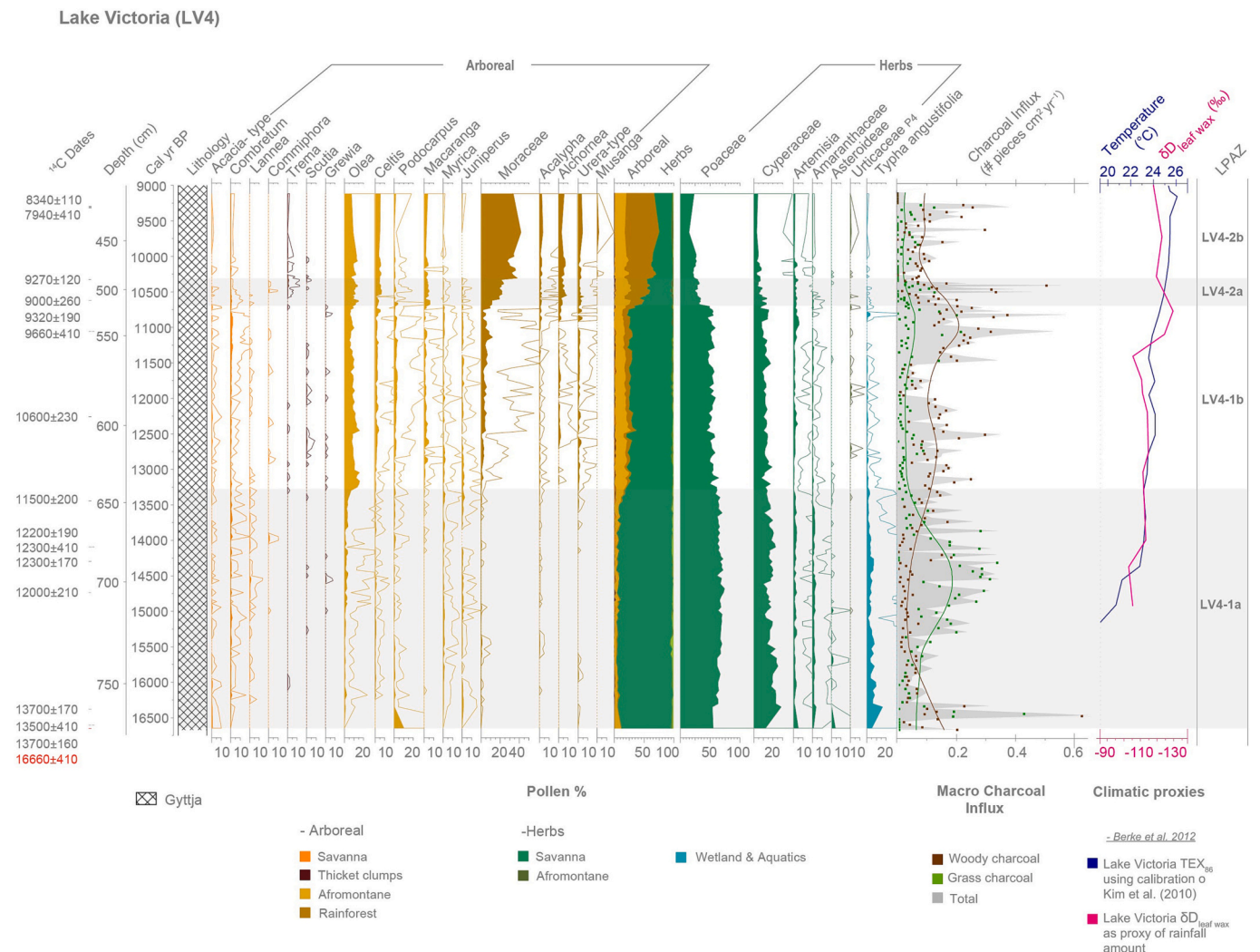


Fig. 3. Selected pollen taxa from Lake Victoria core LV4, charcoal influx, temperature, $\delta D_{\text{leaf wax}}$. For the pollen record, the woody taxa are plotted on the left side of the summary curve, in diverse orange-brown shades representing a different ecosystem: Savanna (orange), thicket clumps (brown), Afromontane (dark gold) and tropical rainforest (dark goldenrod). Herb taxa on the right side of the summary curve are plotted in diverse green shades representing a different ecosystem: Savanna (sea green) and Afromontane (olive green). Wetland and aquatics are represented in blue. LPAZ = Local pollen assemblage zones. Empty curves represent a 10× exaggeration. For the charcoal record, the points represent the herb charcoal influx (lime green) and the woody charcoal influx (brown). Continuous lines superimposed on the charcoal data indicate LOWESS smoothing used only for visualization purposes. The gray curve represents the total charcoal influx. Temperature record of Lake Victoria is plotted in °C inferred from TEX₈₆ using the calibration of Kim et al. (2010), obtained from Berke et al. (2012). $\delta D_{\text{leaf wax}}$ record from Lake Victoria in ‰, used as proxy of rainfall amount (Berke et al., 2012), more negative values indicate more rainfall. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Acalypha (2%) spread around Lake Victoria during this period. Changes in the Afromontane forests comprised the expansion of *Olea*, *Celtis* and *Macaranga*, while *Podocarpus* remained rare and others such as *Myrica*, *Juniperus*, *Ericaceae* and *Hagenia* decreased markedly. A remarkable change in savanna trees and shrub communities and thicket clumps occurred during LV4–2a (Fig. 4), with a shift from *Combretum* to *Trema*, likely indicating the expansion of evergreen *Trema* trees on the costs of drought-adapted *Combretum* shrublands. Subtropical and tropical trees or shrubs such as *Phoenix*-type and *Alchornea* spread during this phase with distinct pollen peaks at around 10,300 cal yr BP at the transition to zone LV4–2b. Interestingly, *Tetrorchidium* appeared for the first time together with *Musanga* in the pollen record, likely pointing to the persistence of canopy openings in a disturbed environment. At the onset of this subzone around 10,700 cal yr BP macroscopic charcoal originating from trees starts to decline after a last peak, suggesting that forest fires became less frequent than before.

LV4–2b (10,300–9000 cal yr BP), further spread of tropical rainforests and persistence of Afromontane vegetation. At ca.

10,300 cal yr BP the dominance of *Moraceae* pollen rapidly increases from 30 to 40% suggesting that tropical rainforests spread abruptly (in <40 years; Figs. 2, 3 and 5f). Around 10,000 cal yr BP *Moraceae* was partly replaced over 100–200 years by tropical rainforest taxa such as *Alchornea* (ca. 5%) and *Acalypha* (ca. 3%). Furthermore, pollen taxa such as *Phoenix*-type and *Tetrorchidium* are lacking during this phase, indicating a decline of these palms, shrubs or trees in the lake catchment. Fluctuations among the tropical rainforest tree taxa may indicate minor reorganizations of vegetation composition and successional processes towards closed forest canopy. Indeed, after 10,000 cal yr BP, arboreal pollen (AP) dominated by *Moraceae*, reaches peak values around 75%, suggesting the occurrence of rather dense forest in the Lake Victoria area. Although declining, the pioneer tree *Musanga* persisted, while *Urera*-type, possibly in the form of lianas reaching the forest canopy, spread. The expansion of tropical rainforest was not at the expense of Afromontane taxa with stable populations of *Olea* (pollen ca.10%) and *Macaranga* (pollen ca. 5%), but rather the savanna vegetation almost collapsed. Specifically, pollen of herbaceous taxa such as *Poaceae* (ca.

Lake Victoria's palaeoecological reconstruction from 16,600 to 9000 cal yr BP

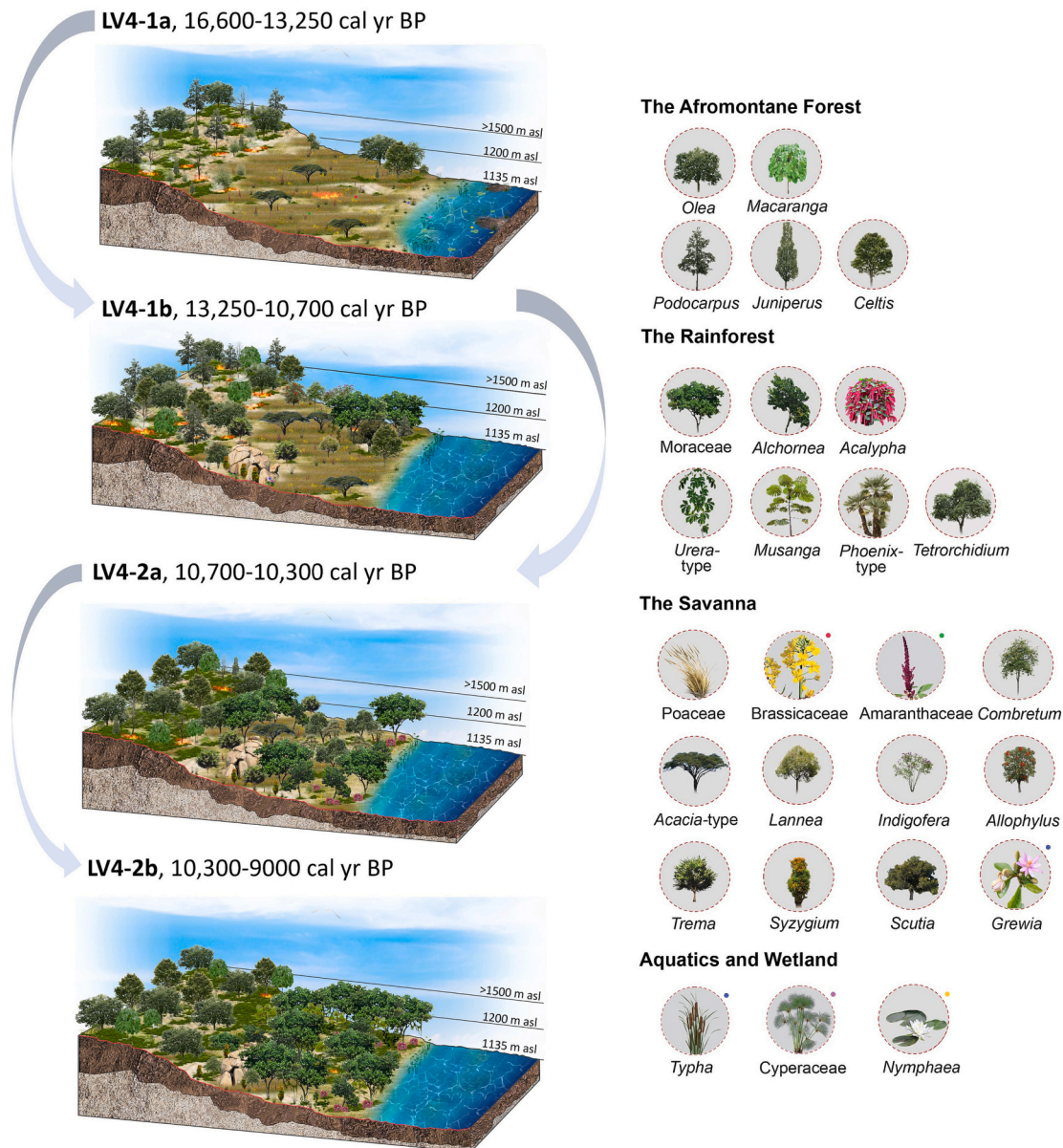


Fig. 4. Lake Victoria's palaeoecological reconstruction from 16,600 to 9000 cal yr BP, considering the 4 significant Local Pollen Assemblage Zones (LPAZ). The images are merely illustrative and show only some of the most important plant genera/families, which are shown in detail on the right side of the image.

20%), *Cyperaceae*, *Artemisia* (ca. 2%), as well as pollen of savanna woody taxa such as *Combretum* and *Indigofera* reached lower abundances. Macroscopic herbaceous and woody charcoal influx suggests fewer fires when compared to previous zones.

3.2. Ordination and response curves

The ordination results are displayed in a taxa and sample scatterplot (Fig. 6a and b), and as variations in DCA axis 1 over time (Fig. 5b). The taxa scores indicate that DCA axis 1, explaining 21.07% of the variance in the taxa data, represents a gradient of temperature and moisture requirements from warm and wet (e.g. *Moraceae*, *Acalypha*, *Urera-type*) to cool and dry (e.g. *Amaranthaceae*, *Rumex*, *Acacia-type*, *Indigofera*). For DCA axis 2, explaining only 4.04% of the variance, taxa scores suggest a weak gradient from eroding habitats (e.g. *Thalictrum*, *Hypericum*, *Lannea*, *Euphorbia*) to more stable landscapes (e.g. *Asteroidae*, *Lemna*,

Acacia-type). In the sample scatterplot, the sample scores are grouped according to the statistically significant pollen assemblage zones LV4-1a to LV4-2b. When plotting variations in DCA axis 1 along time, together with changes in temperature, rainfall amount, and proxy measurements for chemical weathering (Rb/K; Wienhues et al., 2023) and grain size (Zr/Ti; Fig. 5a), axis 1 scores follow changes in climatic conditions from cool and dry to warm and wet. Until ca. 10,700 cal yr BP, before the tropical rainforest dominated by *Moraceae* became prevalent, cool and dry conditions were associated with low or shallow erosion, while warm and wet conditions were associated with enhanced or more deeply incised erosion (Fig. 5). With the mass expansion of the tropical rainforest, the erosion declined.

Although the response curves based on fossil pollen occurrences and palaeoclimatic data (GAMs; Figs. 7, S1, S2) cannot capture the full climatic niches of the taxa, they reveal interesting linkages to climate and moisture. Afromontane taxa such as *Podocarpus*, *Macaranga* and *Olea*

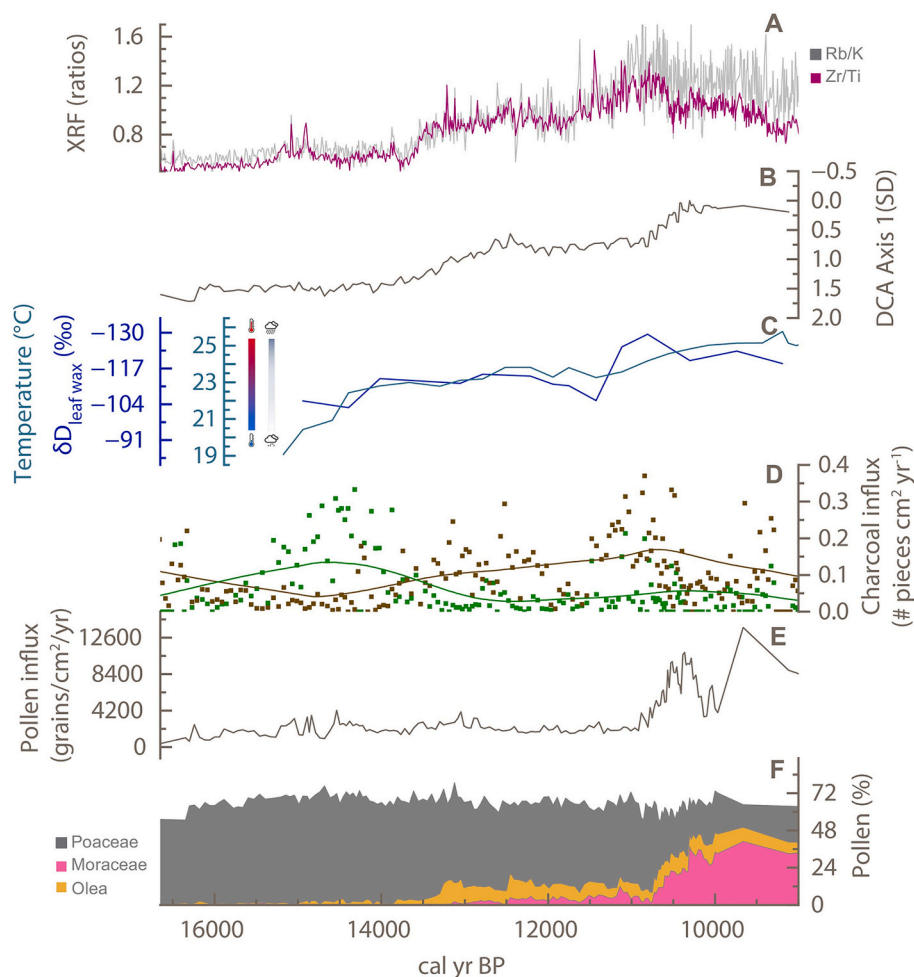


Fig. 5. (A) XRF ratio record of Rb/K (Wienhues et al., 2023) indicating chemical weathering, and Zr/Ti as grain size proxy in Lake Victoria. (B) DCA Axis 1 of the LV4 pollen record from 16,600 to 9000 cal yr BP. (C) Temperature (light blue) and moisture (dark blue) proxies, temperature in °C inferred from TEX₈₆ using the calibration of Kim et al. (2010) according to $\delta D_{\text{leaf wax}}$ record of Lake Victoria from Berke et al. (2012), more negative values indicate more rainfall. (D) Macro charcoal record, the dots represent the herbs charcoal influx (green) and the woody charcoal influx (brown). The brown (woody) and the green (herbs) continuous lines indicate a trend line based on LOWESS smoothing used for visualization purposes. (E) Total terrestrial pollen influx of Lake Victoria (LV4). (F) Pollen percentages of the most dominant taxa in each ecosystem type. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were advantaged by warm conditions and responded positively to high moisture availability. The tropical rainforest and riverine forest taxa (Moraceae and *Urera*-type) responded similarly. In contrast, Afrotropical *Juniperus* was favoured by drier and cooler conditions, similar to savanna taxa such as Poaceae and Amaranthaceae. Moraceae and *Olea* responded most positively to warming, while grasses (Poaceae, Cyperaceae) benefitted mostly from cool conditions. In contrast to the generally positive response to temperature, Moraceae and *Olea* were advantaged by moister conditions only until a certain level, after which they started to decline. Poaceae and Amaranthaceae were strongly advantaged by drier conditions.

4. Discussion

4.1. Causes of vegetation dynamics in the latest Pleistocene

During the latest Pleistocene at around ca. 19,000 cal yr BP (Hughes et al., 2013; Lang et al., 2023), dry and cool conditions prevailed across East Africa over a range of elevations, from the summit of Mt. Kilimanjaro (Schüler et al., 2012) to intermediate and low altitudes such as at Lake Albert (Berke et al., 2014), Lake Tanganyika (Vincens et al., 1993) and Lake Victoria (Berke et al., 2012). The southward shift of the

Afrotropical rainbelt and reorganization of the monsoon circulation, in combination with a weakening of regional rainfall systems at ca. 17,000 cal yr BP, altered the climate at lower elevation sites causing aridity, which played an important role in Tanzania, Ghana, the Niger-Sanaga and Congo watersheds (Stager et al., 2011). At this time, Lake Victoria was experiencing a desiccation phase, as evidenced by seismic data and the presence of a palaeo-vertisol (Beverly et al., 2020; Johnson et al., 1996; Stager et al., 2011). In the surrounding region, grassland savanna became the dominant landscape feature, alongside the coexistence of Afrotropical vegetation, until temperatures started to gradually rise by ca. 2 °C before 15,500 cal yr BP in eastern Africa (Berke et al., 2012; Figs. 7 and S2). Warming associated with the end of Heinrich event 1, at around 16,000 has been also documented in other regions such as the Mediterranean realm (Samartin et al., 2012) and in Europe north of the Alps (Bolland et al., 2020). In our study area, this shift in temperature induced ecosystem changes including increased grassland-savanna fire activity at around 16,000–15,500 cal yr BP (Figs. 3, 5d, S2). In agreement with our evidence (pollen, grassy charcoal), Polycyclic Aromatic Hydrocarbons (PAH) show that biomass burning at this time was dominated by angiosperms in the Lake Victoria area (Karp et al., 2023). It is likely that during this time, *Coryza* benefited from increased burning because of its resistance to disturbance (Schüler and Hemp,

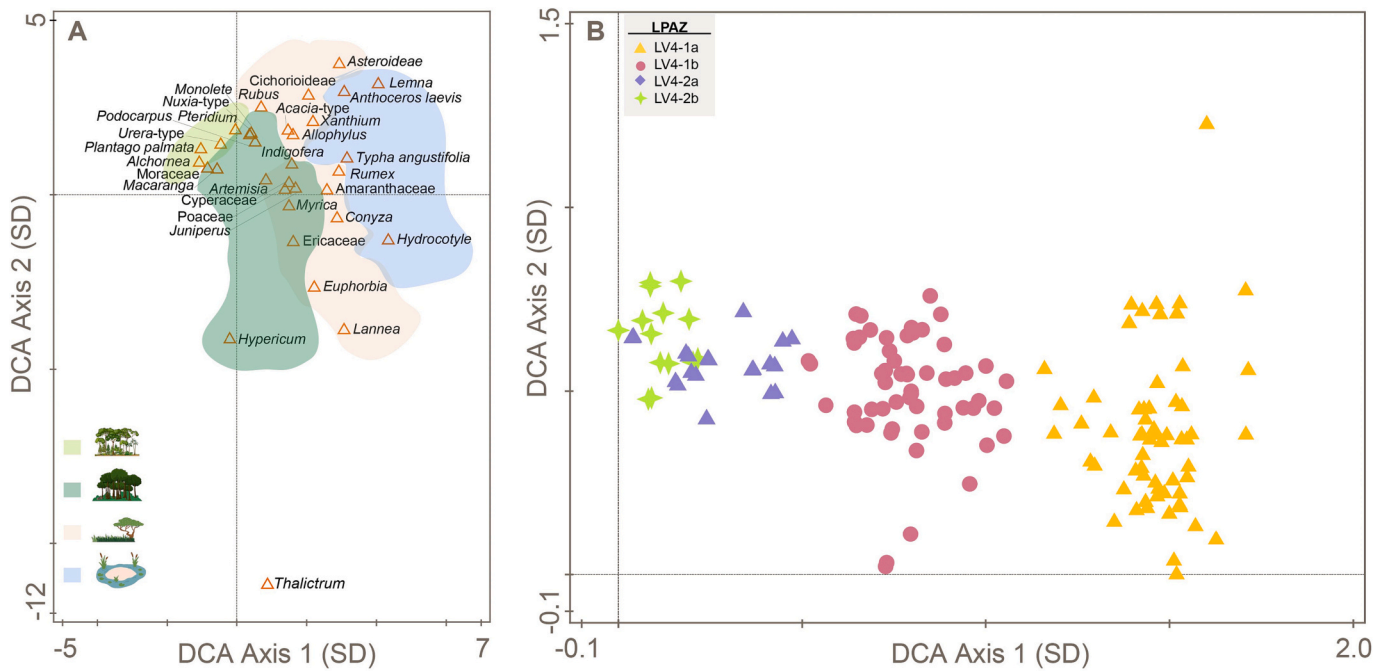


Fig. 6. (A) Detrended Correspondence Analysis (DCA) scatterplots of taxa, and (B) samples scores. In (A) the scatter of taxa scores along DCA Axis 1 (21.07% of variance) indicates a gradient of temperature and moisture, with taxa associated with lower lake levels, dry and cold environments (e.g. *Typha*, *Lemna*, *Amaranthaceae*, *Asteroideae*) with high scores and those associated with warm, moist, and forested environments (e.g. *Moraceae*, *Macaranga*, *Alchornea*) with low scores: Taxa scores along axis 2 (4.04% of variance) suggest a weak gradient between eroding habitats (e.g. *Thalicttrum*, *Hypericum*, *Lannea*, *Euphorbia*, low scores) and more stable landscapes (e.g. *Asteroideae*, *Lemna*, *Acacia*-type, high scores). The shaded area represents the main different biomes: Aquatic (light blue), Savanna (light brown), Afromontane (dark green), Tropical rainforest (light green). In (B) the samples are grouped according to the local pollen assemblage zones (LPAZ). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

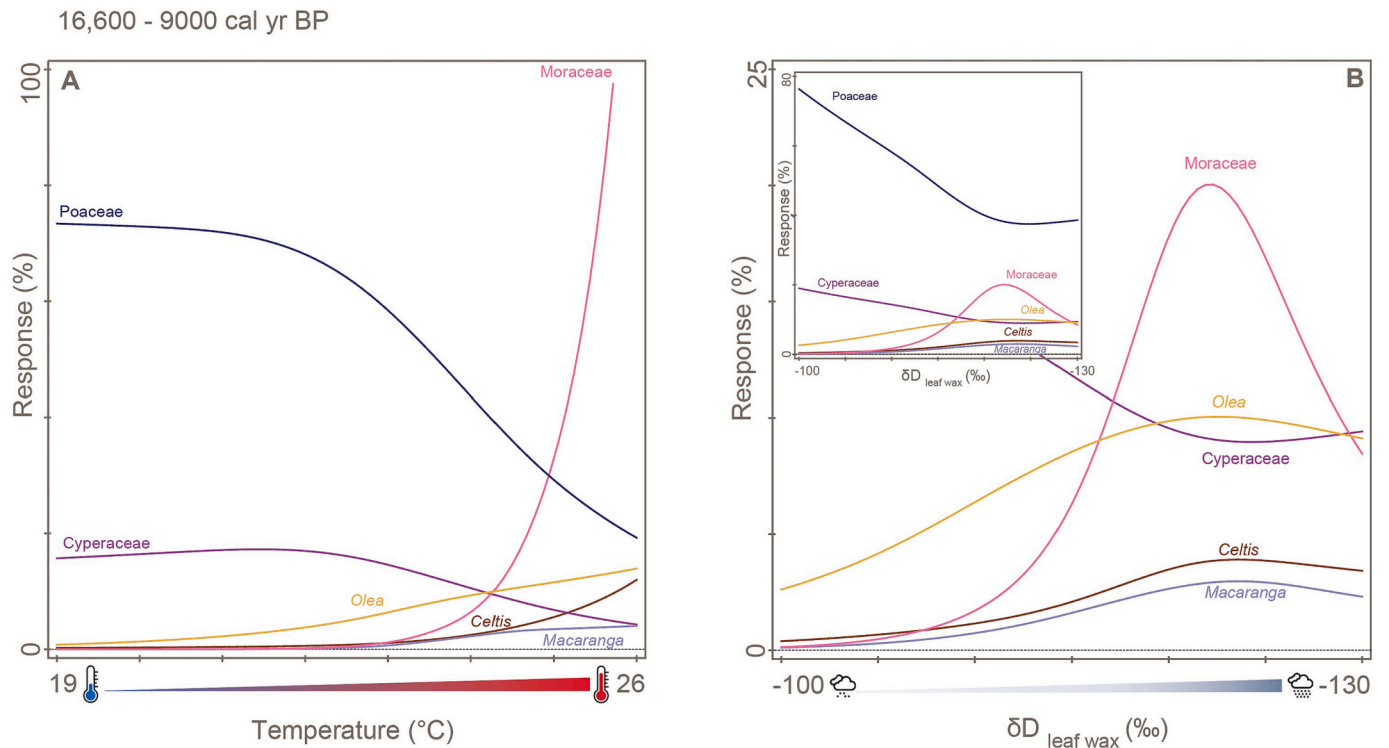


Fig. 7. Response curves of the main taxa in the pollen record to: (A) Temperature in °C inferred from TEX₈₆ using Kim et al. (2010) calibration, obtained from Berke et al. (2012), (B) $\delta D_{leaf\ wax}$ used as a proxy of rainfall amount (Berke et al., 2012), more negative values indicate more rainfall. The smaller image shows a zoom-of the response curves to illustrate the dominant response of Poaceae. Fitted using General Additive Models (GAM).

2016) and could, therefore, spread in the savanna (Figs. 2 and 3).

At Lake Masoko, ca. 700 km south of Lake Victoria, an expansion of semi-deciduous forests took place between 16,000 and 14,000 cal yr BP (Vincens et al., 2007) when precipitation was rather high. It is conceivable that warmer and/or moister conditions caused the minor increase of *Olea* abundances at Lake Victoria around 15,000 cal yr BP (Figs. 3 and 5). However, in addition to higher temperatures (Berke et al., 2012), precipitation regimes must have varied significantly given that some lakes in eastern Africa started to dry out approximately at 15,000 cal yr BP (Lézine, 2007). Indeed, afforestation was interrupted ca. 200 km north-west of Lake Victoria at Lake Albert and further west in western Africa at Lake Bosumtwi (Bonnefille and Riollet, 1988) and herb taxa re-expanded in the surroundings of Lake Magadi ca. 250 km south-east of Lake Victoria (Elmoutaki, 1994).

Afromontane *Olea* spread at ca. 13,250 cal. yr BP (Figs. 3 and 5f), while drought-adapted trees and shrubs declined, the thicket clumps expanded in the savanna. This vegetation shift likely promoted diverse microclimates within the savanna, which helped among others, to retain water. The expansion of *Olea* was followed by other Afromontane trees such as *Podocarpus*, *Celtis* and *Macaranga*, the latter preferring swamp forest habitats (Beuning, 1999a). Our results also show that the savanna herbs contracted slightly, while tropical rainforest taxa such as Moraceae, *Acalypha* and *Alchornea* benefitted, probably forming fringing forests due to the return to more humid conditions, as suggested by Tryon et al. (2016). Indeed, the lake levels of Lake Victoria rose between 14,000 and 13,600 cal yr BP (Wienhues et al., 2023), implying that moisture availability increased. About 300 km south of Lake Victoria, the Miombo flora diversified around Lake Tanganyika, promoting diversity in the savanna with more moisture-loving plants (Vincens, 1991).

The latest Pleistocene increase of Afromontane pollen has led to debates about long-distance transport (e.g. Beuning, 1999a; Kendall, 1969; Ssemmanda and Vincens, 2018). At Lake Victoria the increase of Afromontane pollen is recorded at all coring sites, and over long distances (e.g. LV4 in Temoltzin-Loranca et al., 2023 vs. P2 in Kendall, 1969, and V95–2P, in Beuning, 1999a). Therefore, it is likely that the expansion of Afromontane vegetation at around 13,250 cal yr BP occurred throughout the entire Lake Victoria catchment. Moreover, we propose that due to cooler conditions, the Afromontane stands were growing at lower altitudes and closer to the lake shore than today (Temoltzin-Loranca et al., 2023).

Between ca. 12,800–11,700 cal yr BP water tables dropped at several lakes in East Africa, suggesting arid conditions (Roberts et al., 1993). However, hydroclimatic reconstructions indicate that this was not the case at Lake Victoria (Castañeda et al., 2016; Overpeck et al., 1996). Forest cover remained comparable to the preceding period, when arboreal pollen (AP) reached ca. 20–25%, while pollen influx slightly declined (Fig. 5e). At this time, our data point to minor expansions of tropical rainforest taxa (e.g., Moraceae, *Alchornea*), which occurred at the expenses of Afromontane *Olea* but not *Podocarpus* (Fig. 2). Such a vegetation response would require a minor warming and/or moisture increase, which is indeed recorded in the Lake Victoria palaeoclimatic proxies (Berke et al., 2012, see Figs. 3, 7, S1, S2).

Increasing moisture during the latest Pleistocene prompted changes in aquatic plant communities (Figs. 2, S1). Kendall (1969) had already noticed an increase in *Nymphaea* at ca. 14,500 cal yr BP, interpreting it as a change of water chemistry, probably in pH, resulting from more diluted conditions. This finding agrees well with the inference of a continuous water table rise at Lake Victoria (Temoltzin-Loranca et al., 2023; Wienhues et al., 2023). Our new macrophyte pollen record refines this notion and suggests that *Nymphaea caerulea* and *Nymphaea lotus* formed stands rather close to the coring site, together with other macrophytes such as *Lemna* and *Potamogeton* during the period 16,600–13,800 cal yr BP, when lake-levels were lower than today (Wienhues et al., 2023). Macrophyte populations may have grown next to the *Typha* reed belt, which is unambiguously documented by pollen

percentages reaching 2–15% from 16,600–13,800 cal yr BP (Figs. 2 and 3). After 13,800 cal yr BP aquatics completely disappeared locally and *Typha* declined massively at Lake Victoria, as also documented by Beuning (1999b).

In sum, during the period 16,600–11,500 cal yr BP, prior to the onset of the Holocene, the Lake Victoria basin was characterized by gradually increasing temperatures and precipitation. The grassy savanna was converted into a woodland savanna, and subtropical or warm-temperate Afromontane taxa became more prominent at lower elevations together with rare first gallery or tropical rainforest patches (Fig. 4). Fires occurred regularly throughout the period, with a change in biomass burnt at around 13,800 cal yr BP, from a mostly grass-dominated fuel type during the earliest part of the period to a woody-dominated fuel type after this period.

4.2. Biome reorganizations during the Holocene AHP

Increases in temperatures and moisture were likely caused by the strengthening of the East African Monsoon activity, towards the onset of the Holocene (Tierney et al., 2011). During the Holocene AHP, monsoon activity was higher across East Africa (Dallmeyer et al., 2020; Liu et al., 2017), inducing more mesic conditions. Enhanced trade wind circulation and moisture increase led to two sharp peaks of pollen influx in tropical Africa (Lézine, 1998) as also observed in our record (Fig. 5e). At Lake Victoria, increases in temperature and precipitation caused a rapid transformation from savanna to tropical rainforest (Fig. 7), while Afromontane vegetation probably moved to higher altitudes where temperatures were likely cooler (Kendall, 1969; Temoltzin-Loranca et al., 2023).

Previous studies in Lake Victoria discussed the timing of the spread of the tropical rainforest. For instance, in V95–2P (Beuning, 1999a), an initial phase was recognized in the Late Pleistocene (11,200 ¹⁴C yr BP, ca. 13,100 cal yr BP), after which a discontinuity attributed to a hiatus in sedimentation occurred, preventing any more detailed assessment. In this study we show that, after an initial spread at the earliest Holocene, the main tropical rainforest expansion to >20% occurred at ca. 10,700–10,500 cal yr BP (Fig. 2). This finding is supported by three other sedimentary records with independent chronologies: LV1, LV2; (Temoltzin-Loranca et al., 2023), and by the core P2 (Kendall, 1969), where the tropical rainforest expansion is dated at ca. 9500 ¹⁴C yr BP, corresponding to 10,900 cal yr BP.

The climatic change was more abrupt during the Early Holocene than during the latest Pleistocene, with precipitation increasing more rapidly than temperature at ca. 11,500–10,700 cal yr BP. (Figs. 3 and 5). Concurrently, a simultaneous rise in biomass burning accompanied the biome reorganization. Specifically, at ca. 11,700–11,100 cal yr BP Moraceae increased from ca. 3–5% (at the end of the Younger Dryas), to ca. 5–10% during the Early Holocene. The first Moraceae peak of >10% occurred at ca. 11,200 cal yr BP, when precipitation peaked (Fig. 5). When Moraceae expanded more massively at ca. 10,700 cal yr BP, the Afromontane vegetation spread as well. This spread of the tropical rainforest and Afromontane plants is congruent with similar dynamics at other sites in the region, displaying expansions of Afromontane (mainly *Olea*), and pioneer forest taxa (*Alchornea*, *Macaranga*; Lézine, 2007). At Lake Victoria, increased rainfall promoted the establishment of gap colonizer trees such as *Tetrachidium* and *Musanga*. While the former is well adapted to moist conditions in the understories, the latter is well known for adapting in nutrient-poor or disturbed areas (Akinifesi et al., 2010; De Caluwé and De Smedt, 2005; Vincens, 1991). Kendall (1969) suspected a misidentification of *Musanga* pollen, causing a spurious peak; in our record, we observe the same increase at the same time, so we can infer that its expansion, together with that of *Urera*-type, was real. It is plausible that this marked the initial stage of forest densification, with some canopy openings, as observed in Gabon in more recent times (Ngomanda et al., 2005). Consequently, the incidence of fires likely declined between 10,500 and 9700 cal yr BP.

Later at ca. 10,300 cal yr BP, when high rainfall stabilized (Berke et al., 2012), savanna-herb patches, composed of Poaceae and Amaranthaceae, started to shrink in response to moister environments and Moraceae flourished (Figs. 5, 7 and S1). Similarly, and contemporaneously, at higher elevations in Mt. Kilimanjaro (Schüler et al., 2012), warmer and wetter conditions than today were recorded, allowing the expansion of Afromontane and Ericaceous vegetation at the expense of grasslands. Wetter and warmer conditions promoted biomass production, and thus, fuels that intensified burning, this time mainly of woody taxa (Figs. 3 and 5d). The new high-resolution evidence is in agreement with previous studies (e.g. Temoltzin-Loranca et al., 2023; Karp et al., 2023) that emphasized the role of vegetation for fire incidence. Cross-correlation analyses (see Supplementary material) suggest that fire had a significant impact on some plant taxa during the Early Holocene. For instance, *Olea* and *Trema* were reduced, while *Grewia*, *Myrica* and *Ericaceae* increased in response to burning (Fig. S3). Similar vegetational patterns in response to fire emerged during the latest Pleistocene, with fire-induced reductions of *Trema* and increases of *Grewia* during the period 16,600–12,000 cal yr BP (Fig. S4).

Overall, during the Holocene AHP, temperature and precipitation increased. We propose that the increase of moisture played a major role when compared to the latest Pleistocene, during which temperature changes were probably more important for vegetational reorganizations. Increasing Holocene moisture triggered the transformation of the savanna to the tropical rainforest at lower altitudes and increasing temperatures likely released the expansion of Afromontane vegetation at higher elevations, at or above the altitudinal positions observed today.

5. Conclusions

Our record provides detailed evidence of major shifts in vegetation. We assume that, during the latest Pleistocene and the Early Holocene, vegetation was in dynamic equilibrium with climate, as illustrated by the response curves of plant taxa to climatic change (Figs. 7, S1 and S2). Specifically, our response analyses show that, over the entire study period (16,600–9000 cal yr BP), warm and/or humid conditions favoured both Afromontane and tropical rainforest communities (Figs. 7, S1 and S2). Conversely, colder or drier periods were associated with savanna grassland vegetation. Even minor changes in temperature and/or precipitation likely induced vegetation shifts, arguing for the high climate sensitivity of tropical and Afromontane vegetation. Fire regime changed also according to climate and vegetation, acting as a co-driver in the ecosystem dynamics.

Our newly obtained high-resolution record provides insights into the environmental conditions characterized by shifts attributed to natural climatic changes, in which alterations of vegetation composition and structure took place, with temperature and moisture fluctuations likely acting as the primary driving forces to cause complete biome reorganizations in the area. The high sensitivity of natural ecosystems illustrated here may be used to assess the magnitude and rate of future vegetation responses to warmer and/or moister climate conditions, especially where vegetation conditions are still close to natural. Investigating the subsequent Mid and Late Holocene periods with enough temporal resolution, in combination with the effects of changes in land use, could provide more insights to better assess the human-caused fragmentation of ecosystems.

Declaration of Competing Interest

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

Data availability

The data will be available in Neotoma database

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2023.111839>.

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