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A palaeovegetation and diatom record of tropical montane forest fire, vegetation and hydroseral changes on Mount Kenya from 27,000–16,500 cal yr BP

Colin J. Courtney Mustaphi[a,*], Stephen M. Rucina[b], Lydia King[c], Katherine Selby[d], Rob Marchant[e]

[a] Geoecology, Department of Environmental Sciences, University of Basel, 4056 Basel, Switzerland
[b] Department of Earth Sciences, Palynology and Palaeobotany Section, National Museums of Kenya, P.O. Box 40658, 00100 Nairobi, Kenya
[c] Limnologie-Phykologie-Diatomologie, Freiburg im Breisgau, Baden-Württemberg, Germany
[d] Department of Environment and Geography, University of York, Heslington, York, North Yorkshire YO10 5NG, UK
[e] York Institute for Tropical Ecosystems, Department of Environment and Geography, University of York, Heslington, York, North Yorkshire YO10 5NG, UK

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ABSTRACT

Fire is an important ecological disturbance in moist tropical forests influencing vegetation composition and structure. Contemporary and historical records of forest fires in mountain forests of Kenya are limited to the past decades and have a strong anthropogenic influence for ignition patterns and fire suppression activities. Palaeoenvironmental geoarchives provide the temporal depth to investigate long-term (multidecadal-to-millennial) changes in fire activity. Here we use a sediment record from the Rumuiku wetland, located in a volcanic crater on the eastern flank of Mount Kenya that was radiocarbon dated and analysed for diatom, pollen and charcoal subfossils to produce a highly resolved time series of local hydroclimatic change, vegetation, and fire; respectively. This study focuses on the time during and following the global Last Glacial Maximum, a time of rapid warming and changing regional hydroclimate with relatively stable atmospheric CO_2 and not yet intensive anthropogenic modification of ecosystems. Charcoal and pollen data support associated changes in vegetation-fire centred around 21,500 cal yr BP when Afromontane forests with predominant abundances of *Juniperus*, *Podocarpus* and other montane forest trees changed to *Hagenia*-dominated forests that are relatively more open and adapted to burn more frequently but with less intense fires.

These transitions in ecosystem composition, distribution and structure support the important role of fire in driving and maintaining forest composition in the watershed and contributing to the spatial complexity of forests around the mountain. These changes in composition, structure and biomass occurred during a time of rapid Late Pleistocene climate warming, regional hydroclimatic drying, and slowly rising atmospheric CO_2 from 27,000 to 16,500 cal yr BP, during and following the conditions of the global Last Glacial Maximum. Temperature, hydroclimate and atmospheric CO_2 are well-known drivers of montane vegetation change in the tropics and the role of fire is shown here to be a contributing driver to the spatial heterogeneity of forest patches at long time scales. Vegetation modelling at spatial scales relevant to land management and conservation should include retrospective evidence of the range of drivers of ecological disturbance regimes.

1. Introduction

Fire is a key ecological process influencing vegetation distribution, composition and structure at centennial-to-millennial scales, and is influenced by climatic variability and interacts with local abiotic and biotic processes (Whitlock et al., 2010). Variability of fire causes vegetation change and is also itself varying in response to changing vegetation composition, structure and biomass (Archibald et al., 2013). Fire maintains some montane ecosystem types in eastern Africa mountains, including montane forest ecotones; severe fires are known to regenerate monospecific stands of either *Erica*, *Podocarpus*, *Juniperus*, or *Hagenia* under different conditions (Wood, 1965; Lange et al., 1997;

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* Corresponding author.
E-mail address: colin.courtney-mustaphi@unibas.ch (C.J. Courtney Mustaphi).

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Bussmann, 2001; Hemp and Beck, 2001; Young, 2004). Whether or not fire regime variability maintains a forest type, modifies ecotonal transitions, or facilitates or inhibits forest compositions is spatially complex and only a limited number of studies have focused on the role of fire disturbance ecology in Afromontane forests (Wesche et al., 2000; Wooller et al., 2000; Bussmann, 2002a; Hemp, 2005, 2006). The highly stochastic occurrence of fire makes it difficult to model with certainty at spatial scales smaller than biomes when fire return intervals are longer than multidecadal re-occurrences (Pfeiffer et al., 2013; Rabin et al., 2017; Hantson et al., 2020). Current observational records and satellite monitoring of fires are useful for examining short-term patterns of fire regimes with return intervals of less than multidecadal scales and are limited to a temporal depth featuring a strong anthropogenic signal (Hempson et al., 2018; Henry et al., 2019; Johansson and Granström, 2020). Sediment-based records provide retrospective analyses of multidecadal-to-millennial patterns of fire in tropical montane forests (Sánchez Goñi et al., 2017). A changing fire regime is one of the dominant ecological disturbances controlling forested ecotonal transitions (Supplementary Fig. S1; Hemp and Beck, 2001; Gil-Romera et al., 2019; Courtney Mustaphi et al., 2021) and contributes to the spatially heterogeneous vegetation distributions around the mountains of eastern Africa (Bussmann, 2002a; Hemp, 2005, 2006) including compositional and structural patchiness (Wood, 1965; Xu et al., 2016). Understanding how montane forests and fire regime variability have responded to the warming and varying hydroclimatic conditions following the Late Glacial Maximum (LGM; Marine Isotope Stage II), a time interval of rapid global climate change, provides quantitative mechanistic insights useful for comparing proxy data and climate and vegetation models (Hantson et al., 2016; Marlon et al., 2016). The forest compositions during late glacial and post-glacial interval provide a comparative context for how forests and fire regimes are currently changing rapidly on Mount Kenya (Bussmann, 1996; Gathaara, 1999; Ndegwa Gichuki, 1999), neighbouring mountains (Hemp, 2005; Finch et al., 2017; Said et al., 2019) and across the tropics (Hantson et al., 2017; Probert et al., 2019).

The purpose of this study is to investigate past vegetation change and associated changes and influence of fire on the mountain forests of a mid-montane catchment on Mount Kenya. A sediment core was collected from Rumuiki wetland to analyse diatom composition, aquatic invertebrate remains (presence data), pollen composition, and total charcoal subfossils as proxy indicators of wetland hydrology, vegetation change, and fire activity during the Late Pleistocene (Fig. 1). The age-depth model presented a relatively linear sediment accumulation rate during the Late Pleistocene providing a temporal resolution rarely attainable in Afromontane sites (Rucina et al., 2009; Fig. 2). The combination of pollen, charcoal and diatom data from Rumuiku is used to explore centennial-scale patterns of vegetation change, climate-fire-vegetation interactions, and local wetland conditions on this facet of the mountain in the context of global to regional scale changes in temperature, hydroclimate, and atmospheric CO_2 concentrations. Previous paleoenvironmental analyses of the sediment core provided radiocarbon dates, a pollen record, and pollen slide charcoal data (Rucina et al., 2009) and here we re-use the radiocarbon and pollen data with new sieved charcoal (> 125 μm), aquatic invertebrate and diatom data.

2. Background

Previous studies using Quaternary pollen data show that mountain vegetation distribution patterns of eastern African underwent high turnover through the LGM (~23,000–19,000 cal yr BP; Hamilton, 1982; Van Zinderen Bakker and Coetzee, 1988). Responses were spatially complex (Barker et al., 2003; Bartlein et al., 2011; Tierney and deMenocal, 2013) resulting in spatially heterogeneous vegetation distribution patterns along aspect and elevational gradients around Mount Kenya (Olago et al., 1999; Wooller et al., 2003; Street-Perrott et al., 2007) and neighbouring highlands (Jolly et al., 1997; Schüler et al., 2012; Marchant et al., 2018). Regional temperatures increased by an estimated 4 °C following the LGM (Loomis et al., 2012; Annan and Hargreaves, 2013) and the amount, distribution and seasonality of precipitation were altered by changing monsoonal patterns (Braconnot et al., 2007;

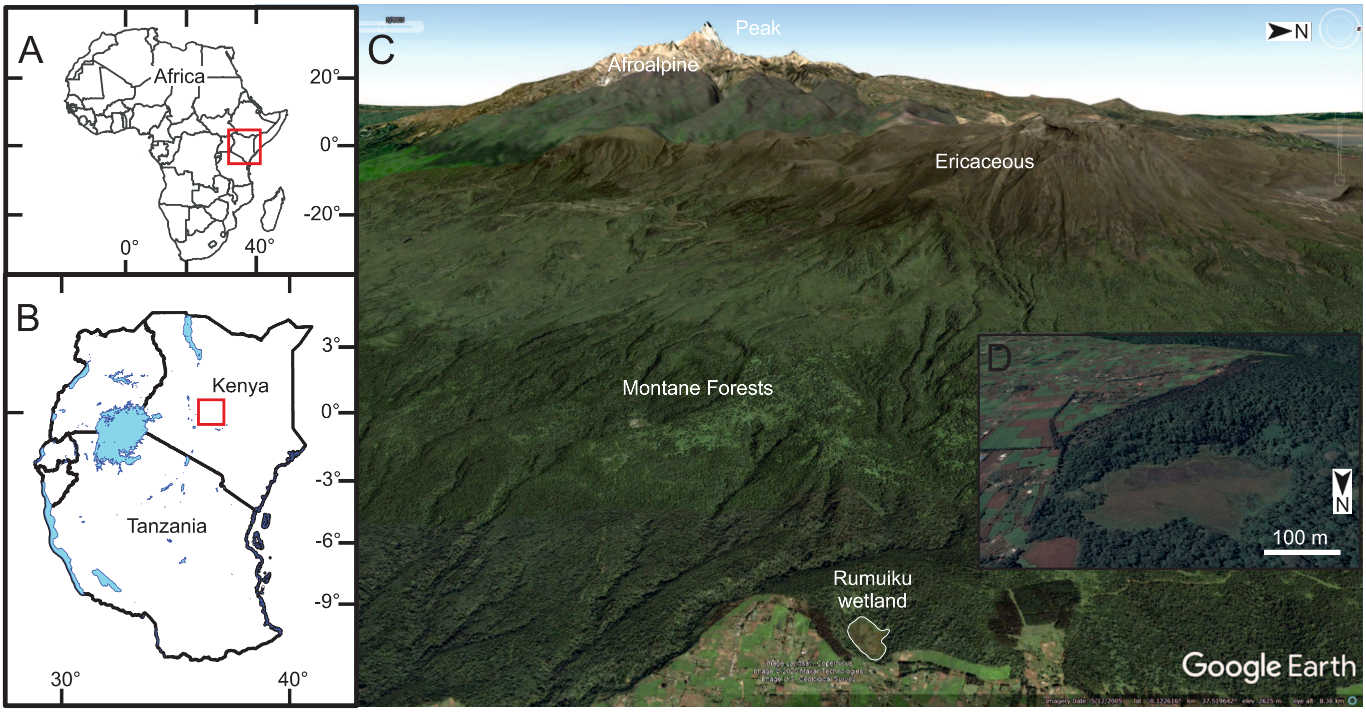

Fig. 1. The study site location inset maps of **A.** Africa **B.** and in central Kenya. **C.** An oblique view perspective facing westward toward the eastern flank of central Mount Kenya showing approximately 2000 m asl to the Uhuru peak (5895 m) and vegetation biomes (Hedberg, 1951, 1955; Bussmann, 2002a) and **D.** a south-facing view of the Rumuiku volcanic crater wetland (0.118583°S, 37.5611°E; 2160 m asl; 8.9 ha; Rucina et al., 2009). Image date 9 February 2020 from Google Earth Pro version 7.3.3.7699 (64-bit) with 2.0× vertical exaggeration to show topographic relief (Google Earth/DigitalGlobe, 2021).

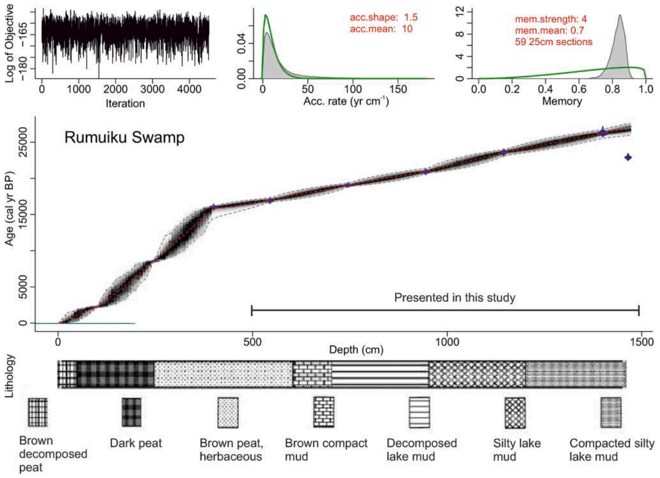

Fig. 2. An age-depth model produced using R scripts (R Development Core Team, 2015) Bacon version 2.2 (Blaauw and Christen, 2011a and b) using the IntCal13 radiocarbon curve (Reimer et al., 2013) and parameterized as shown in red text that used the 9 AMS radiocarbon dates (Rucina et al., 2009). Blue symbols represent the calibrated radiocarbon date probability distributions, the grey areas represent the probability densities of the Markov Chain Monte Carlo (MCMC) iterative random walks through the age probability distributions, and the dashed lines show the 95% confidence intervals. The dashed red line shows the weighted mean of all iterations. The lowermost radiocarbon date (SUERC-17200) was objectively rejected from the age-depth model; and was also rejected in the original study (Rucina et al., 2009). Core lithology with sediment types and legend (Troels-Smith, 1955) shown horizontally below the x-axis (Rucina et al., 2009). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Konecky et al., 2014) and millennial scale moisture regimes were controlled by orbital variations (Verschuren et al., 2009; Wolff et al., 2011). The spatiotemporal moisture patterns of equatorial mountains are complex, involving insolation, atmospheric circulation (Nicholson, 2000; Hemp, 2009), lapse rates (Loomis et al., 2017), cloudiness and fog forest ecohydrology (Los et al., 2019; Cuní-Sanchez et al., 2019), soils and drainage, and the variability and gradients of each influence montane vegetation patterns. Atmospheric CO_2 was relatively stable during the LGM and early postglacial interval until 17,000 cal yr BP (Petit et al., 1999) and subsequently contributed to changing vegetation assemblages across the region, including highlands (Jolly et al., 1997; Boom et al., 2002; Wooller et al., 2003), by modifying competition strategies among C_3 and C_4 plants. Following the LGM on eastern African mountains, alpine glaciers generally retreated and montane vegetation re-expanded to higher altitudes (Coetzee, 1964; Hamilton, 1982; Van Zinderen Bakker and Coetzee, 1988). Forest composition was spatially complex as many individual plant taxa responded differently to changing climatic conditions. Several pollen and paleovegetation studies have been presented for Mount Kenya (listed in Courtney Mustaphi et al., 2017: Table 1) but vary in duration and forest ecosystems and few studies focus explicitly on the fire-vegetation feedbacks (Wooller et al., 2000; Ficken et al., 2002; Wooller et al., 2003). Across eastern Africa, most palaeofire studies present pollen slide charcoal data (Power et al., 2010; Hawthorne et al., 2017; Sánchez Goñi et al., 2017). Sieved charcoal studies have been presented from semi-arid lowland sites (Nelson et al., 2012; Colombaroli et al., 2018; Githumbi et al., 2018a; Githumbi et al., 2018b) and a single montane palustrine site (Githumbi et al., 2021). The spatiotemporal complexity of fire-vegetation interactions has yet to be explicitly analysed and taken into account in pollen-based climate reconstructions for many biomes including those of eastern Africa (Bonnefille and Chalié, 2000) or within analyses of the role of atmospheric CO_2 concentration in shaping montane vegetation distributions (Jolly and Haxeltine, 1997). This is partly due to the paucity of available palaeoenvironmental datasets for data-model comparisons (Marlon et al., 2016) and few fire-vegetation studies focused on catchment scale spatial areas with high temporal resolutions.

During the LGM, the positioning of the East Africa monsoon was compressed due to atmospheric circulation during the high-latitude glaciations (Chiang and Bitz, 2005). Glaciers on Mount Kenya during the LGM covered up to 200 km^2 and reached as low as 3300 m asl (Baker, 1967; Johansson and Holmgren, 1985; Mahaney, 1988; Rosqvist, 1990; Young and Hastenrath, 1991). During the global LGM, Afromontane treelines were approximately 1000 m lower (Van Zinderen Bakker and Coetzee, 1988). Periglacial alpine tundra persisted at higher elevations below the glaciers, Ericaceous zones occupied upper-mid elevations, montane forests on the mid-lower more mesic slopes, and savanna-woodlands across the surrounding lowlands. Vegetation distributions responded to climatic variability and spatially heterogeneous local-scale factors (Mizuno, 1998, 2005; Zech, 2006; Mizuno and Fujita, 2014; Montade et al., 2018) resulting in novel assemblages as ecosystems did not, and do not (Platts et al., 2013), linearly shift across the elevation gradient (Coetzee, 1964; Hemp, 2006; Street-Perrott et al., 2007). Orbitally driven climate variability resulted in regionally drier conditions (Moernaut et al., 2010) in response to changing circulation and ocean-atmosphere interactions as large-scale processes interacted with local environmental processes on the mountain resulting in catchment-scale vegetation variations (Street-Perrott et al., 2007; Verschuren et al., 2009). Limnological and sedimentological changes were not coherent across aquatic ecosystems on Mount Kenya (Street-Perrott et al., 2007). C_4 plants benefited from lower atmospheric CO_2 concentrations, yet, CO_2 variability was not a major interacting factor for mediating vegetation distributions on Mount Kenya (Ficken et al., 2002; Wooller et al., 2003; Street-Perrott et al., 2007) until increasing to over 200 ppmv after 16,500 cal yr BP (Petit et al., 1999; Jolly and Haxeltine, 1997).

At present, the dominant mid-montane forest types occur over relatively wide elevations and hydroclimatic ranges and, currently, *Podocarpus* is found around the mid-montane forests but occurs in high abundances in the northeastern and western forests, and *Juniperus* is locally abundant primarily in the rainshadow northwest area as well as smaller areas in the northeast (Bussmann and Beck, 1995a). The spatiotemporal abundance patterns of forest types vary around the mountain as well as with altitudinal hydroclimatic patterns and disturbance regimes. The upper montane forests at 2700 to 3300 m asl are dominated by *Hagenia abyssinica* (Lange et al., 1997) with *Erica*-dominated forests and heathlands above 3000–3400 m asl (elevation varies around the mountain) up to the tundra zone. Temporal variability of ecological disturbance regimes modify ecosystem composition and structure and result in high spatial heterogeneity on the indigenous mountain forests within the protected areas (Bussmann and Beck, 1995a; Bussmann, 2001, 2002a; Kleinschroth et al., 2013). Although *Hagenia*, *Juniperus* and *Podocarpus* co-occur at similar mid elevation temperature-moisture climate conditions (Niemelä and Pellikka, 2004; Zhou et al., 2018) and recruit in monospecific stands following fire, *Hagenia* germination rates are highest on bare soils following ecological disturbances that open surfaces and canopy (Bussmann, 2001). As the forest develops, *Hagenia* stands maintain wider intertree (bole) distances and are less dense lower and mid canopy (Bussmann, 2001; Grímsson et al., 2021). Recruitment is potentially inhibited by very frequent ground fires and high grazing pressure (Assefa et al., 2010). Fire appears to be an important disturbance among the dominant montane forest types (Schmitt, 1991; Bussmann and Beck, 1995b; Bussmann, 2002a, 2002b), yet there are few sources of long-term evidence of how vegetation-fire interactions have occured around the mountain. Given that several montane forest types occur under similar climatic conditions around the mountain, the spatial and temporal variability of fire may contribute to the heterogeneity of forest compositions and structure on the mountain.

Table 1
Age determinations for the Rumuiku wetland sediment core collected in 2005 CE (−55 cal yr BP) (Rucina et al., 2009; Rucina, 2011). BP, before present 1950 CE. Analytical radiocarbon dating error values are not rounded (sensu Stuiver and Polach, 1977) and presented as reported from the laboratories (SUERC, Scottish Universities Environmental Research Centre Radiocarbon laboratory, University of Glasgow, UK; Wk, Waikato Radiocarbon Dating Laboratory, University of Waikato, New Zealand). The lowermost radiocarbon date (SUERC-17200) was rejected from the age-depth model (Rucina et al., 2009).

Depth (cm)	Age (^{14}C yr BP)	error (± yr BP)	δ^{13}C	Material	Lab ID
0	−55	0		Top of core	Surface of sediments
100	2252	30	−10.7	Bulk sediment	SUERC-22553
245	7763	40	−21.8	Bulk sediment	SUERC-17195
400	13,325	75	−23.1	Bulk sediment	SUERC-22554
545	13,953	59	−24.5	Bulk sediment	SUERC-17196
745	15,759	71	−29.8	Bulk sediment	SUERC-17197
945	17,296	85	−29.6	Bulk sediment	SUERC-17198
1145	19,578	111	−31.5	Bulk sediment	SUERC-17199
1400	22,016	180	−29.7	Bulk sediment	WK-18792
1465	19,006	112	−30.0	Bulk sediment	SUERC-17200
1469					Base of sediments

3. Study site

Rumuiku is a small wetland in an extinct volcanic crater surrounded by montane forests near the Mount Kenya National Park boundary (geographical coordinates 0.118583° S, 37.5611° E; Fig. 1; Supplementary Fig. S2) at 2160 m asl. This elevation was not glaciated during the Pleistocene. The crater is elliptical and approximately 350 × 200 m across and the crater wall is asymmetric with steeper walls on the south and west (Fig. 1, Supplementary Fig. S2). Rumuiku outflows eastward as a tributary of the Tana River. Currently, the local vegetation surrounding the wetland is disturbed montane forest at the edge of the Mount Kenya National Park (Kehlenbeck et al., 2011) with *C. macrostachyus*, *Macaranga kilimandscharica* and *Neoboutonia macrostachys* predominating and other primary montane forest taxa such as *Podocarpus* spp., *Polyscias* spp., *Schefflera* spp. and *Tabernaemontana holstii* and many others, with *Syzygium cordatum* and *Morella salicifolia* found near the wetland margin (Rucina et al., 2009). Wetland vegetation included tussock-forming species of *Carex* spp. with locally abundant *Pennisetum mildbraedii* and *Sphagnum*, similar to other volcanic highland wetlands of equatorial eastern Africa (Salt, 1954; Coetzee, 1967; Hamilton, 1982, 1987; Githumbi et al., 2021).

4. Materials and methods

Fieldwork during 2005 recovered a 1469 cm deep core using a Russian peat corer with a 5 cm diameter by 50 cm long hemicylindrical chamber (Jowsey, 1966). The recovered core sections were wrapped in plastic and aluminium foil and stored in split PVC pipes in a refrigerator at 4 °C and analysed at the National Museums of Kenya, Nairobi, and the University of York, UK. Accelerator mass spectrometry radiocarbon dates (nine total, one rejected from age-depth model; Rucina et al., 2009; Rucina, 2011) produced a nearly linear age-depth model through the Late Pleistocene glacial interval (27,000–16,500 cal yr BP) (Fig. 2; Table 1), a time when the site existed as a shallow lake surrounded by montane forest (Rucina et al., 2009). An age-depth model was generated using the R statistical computer language (R Development Core Team, 2015) and Bacon version 2.2 scripts (Blaauw and Christen, 2011a and 2011b). The age-depth model used nine AMS radiocarbon dates with the SUERC-17200 radiocarbon date being rejected as an outlier (Rucina et al., 2009) (Table 1). Radiocarbon ages were calibrated with the IntCal13 radiocarbon curve (Reimer et al., 2013) and expressed as calibrated calendar years BP (Before Present, calendar year 1950 CE). Because of the consistent linear sediment accumulation rates from 27,000–16,500 cal yr BP (1469–500 cm stratigraphic depth), the site provides a unique opportunity for high-resolution analyses of climate-fire-vegetation interactions on Mount Kenya using subfossil pollen and charcoal as palaeoenvironmental proxy data. This study presents previously published radiocarbon dates ($n = 9$), core lithology, and subfossil pollen data ($n = 32$; Rucina et al., 2009) with new subfossil diatom ($n = 48$) taken from different stratigraphic levels to the pollen, and continuously sampled charcoal data ($n = 969$) collected from the lacustrine sediments of the deeper stratigraphy (1469–500 cm). The sampling offsets between pollen and charcoal ranged from 0 to 19 cm (0 to approximately 200 years of temporal offsets). The continuous charcoal data provided co-located samples with pollen and diatom subsamples, respectively.

Diatom analysis used 1 cm^3 wet sediment subsamples extracted at ~20 cm intervals (range 6–40 cm, n = 48) from 500 to 1460 cm core depth for chemical digestion preparation (Battarbee, 1986, 2000). Frustules were identified using published keys (Gasse, 1986; Krammer and Lange-Bertalot, 1986–1991; Reichardt and Lange-Bertalot, 1991; Lange-Bertalot, 1993; Lange-Bertalot and Moser, 1994; Lange-Bertalot and Metzeltin, 1996; Reichardt, 1997; Reichardt, 1999; Lange-Bertalot, 2001; Krammer, 2000, 2002, 2003; Levkov, 2009; Hofmann et al., 2011) and enumerated to a minimum total count of 300–500 valves per subsample under a Zeiss Axioscope A1 light microscope at 1000× magnification with differential interference contrast (DIC). Diatom assemblages were expressed as relative abundances of total diatoms counted. Taxa were grouped as planktonic, facultative planktonic, and periphytic using ecological associations from Gasse (1986), Krammer and Lange-Bertalot (1986–1991) and Hofmann et al. (2011).

Pollen analysis was previously reported by Rucina et al. (2009) and used wet sediment samples that were sequentially digested using HCl, KOH, HF, and acetolysis. The residue that remained was dehydrated and prepared with 95% ethanol (Fægri and Iversen, 1975). The chemically-digested residual was soaked in glycerol and a droplet was mounted on a microscope slide under a cover slip for identification under optical microscopy at 400× magnification. Pollen relative abundances were calculated using the total sum of terrestrial pollen and the relative abundance of aquatic taxa were calculated using the wetland taxa of *Cyperaceae*, *Myriophyllum*, *Typha* and *Potamogeton*, that influx locally into the sediments (Hamilton, 1982).

Sieved charcoal analysis (Whitlock and Larsen, 2001; Conedera et al., 2009; Hawthorne et al., 2017) was undertaken at a contiguous 1 cm thick sampling resolution (n = 969) using 1–3 cm^3 subsamples of wet sediment and immersed for >24 h with sodium metaphosphate solution. Each subsample was wet sieved through a 125 μm mesh and the retained fraction was transferred to a gridded Petri dish (Bamber, 1982; Tsakiridou et al., 2021). Charcoal pieces were identified and tallied through visual inspection and manipulation with a metal probing needle under a Zeiss Stemi 2000-C optical stereomicroscope at 10-40× magnification (Hawthorne et al., 2017). Aquatic invertebrate remains (>125 μm) were also counted when coincidentally found in the sieved charcoal samples and are presented as presence data. Charcoal concentrations (pieces cm^{-3}) were resampled to the median sampling interval of 10 years creating an even time series and converted to charcoal accumulation rates (CHAR; pieces cm^{-2} yr^{-1}).

Both diatom and pollen assemblage zones were separately delimited using stratigraphically constrained incremental sum of squares (CONISS) technique (Grimm, 1987) and a broken stick plot indicated that three zones were significant (Bennett, 1996; Traverse, 2007; Legendre and Legendre, 2012). For diatoms, the rare taxa with <1% maximum relative abundance throughout the record were not included in the CONISS analysis (34 of 66 taxa; 51.5%). The pollen CONISS zones matched the prior analysis published by Rucina et al. (2009).

5. Results

5.1. Age-depth model

The age-depth model developed for Rumuiku show a nearly linear accumulation rate of lacustrine sediments during the Late Pleistocene with a relatively high resolution median sedimentation rate of 10.3 years cm^{-1} (range of 7.7–14.0 years cm^{-1}) and a basal age estimate of 27,000 cal yr BP (Fig. 2). A conspicuous change in sedimentation rates above 400 cm to the core top was related to a depositional environment change from organic rich lacustrine deposits to palustrine sediments close to the Pleistocene-Holocene transition (Rucina et al., 2009). This study focuses on the sediments from the base at 1469 cm to 500 cm (27,000–16,500 cal yr BP) to analyse the transition after the global LGM (Fig. 2). The average sampling interval for diatom analysis was 250 years, 320 years for pollen analysis, and 10 years for macroscopic charcoal analysis.

5.2. Diatom assemblage

Diatom assemblages were quantified in 46 samples and a total of 66 taxa were identified and 32 (48.5%) taxa occurred with ≥1% relative abundance (Fig. 3). Two of the 48 processed samples, at 796 cm and 1360 cm depth, predominantly contained broken diatoms and assemblages could not be enumerated. The diatom assemblages throughout the core were characterised by abundant facultative planktonic and periphytic taxa. Generally, there are conspicuously low abundances of planktonic taxa throughout the record. Three significant diatom assemblage zones were identified through a CONISS analysis (Fig. 3; Table 2).

5.2.1. Diatom zone A: 27,000–19,800 cal yr BP (1469–826 cm)

The earliest zone was of the longest duration and was largely dominated by facultative planktonic taxa such as *Fragilaria delicatissima* (up to 90%) with subordinate *Staurosira construens* (up to 70%) and moderate abundances of *A. granulata* (25%). Prior to 26,000 cal yr BP, *A. granulata*, a planktonic species, was present in abundances of 2–30% then subsequently was only sporadically present in abundances up to 5% only in Zone A. Periphytic taxa were present with relative abundances >10% and included *Gomphonema elegantissimum*, *Encyonopsis* cf. *subminuta* and *E. minima* that occurred the most frequently. The zone is punctuated by abrupt and short duration increases in periphytic taxa at the relative expense of facultative planktonic. A pronounced peak of the facultative planktonic *A. minutissimum* occurred at the top of the zone.

5.2.2. Diatom Zone B: 19,800–18,800 cal yr BP (826–726 cm)

Zone B was characterised by significant changes within the facultative planktonic taxa assemblages and a conspicuous absence of periphytic taxa. *Fragilaria tenera* and *F. capucina* increased and *F. delicatissima*, *Staurosira construens* and *Pseudostaurosira brevistriata* decreased. The changes in facultative planktonic species occurred gradually over the 1000-year interval. The periphytic species *Encyonopsis* cf. *subminuta* continued to be present throughout Zone B, albeit, at very low abundances <3%. Planktonic taxa were not present.

5.2.3. Diatom zone C: 18,800–16,600 cal yr BP (726-500 cm)

The uppermost diatom assemblage Zone C was marked by gradual increases in the relative abundances of periphytic taxa and significantly increased total periphytic diatoms, which increased to >50% total diatoms. Many rarer periphytic taxa became increasingly abundant in Zone C, such as, *B. brebissonii*, *E. minor*, *Fragilaria gracilis* and *Navicula cryptotenella*, which occurred with abundances up to 2%. The changes within the co-dominant facultative planktonic species were abrupt and prominent. *F. delicatissima* remained below 30% and *S. construens* (≤60%), *Aulacoseira* cf. *distans* (≤10%), and *P. brevistriata* (≤7%). *F. tenera* abruptly vanished from the high abundances found in Zone B.

5.3. Vegetation and fire record

The CONISS zonation of the pollen assemblage confirmed the previous pollen analysis (Rucina et al., 2009) analysis and identified four significant assemblage zones in the deeper sediments of Rumuiku. The assemblage consisted predominantly of montane forest taxa and Poaceae with moderately abundant Ericaceae and Asteraceae (Fig. 4; Table 2).

5.3.1. Pollen Zone I: 26,400-24,000 yr BP (1469–1210 cm)

Pollen Zone I was dominated by Afromontane taxa that comprised ~65% of the relative abundance of terrestrial taxa and included *Podocarpus* (≤40%), *Juniperus* (≤20%) and *Olea* (≤10%). Subordinate abundances of *Alchornea* (<6%) and *Celtis* (<2%) were also present (Fig. 3). Ericaceous taxa totalled (≤13%) and was dominated by *Stoebe* (<13%) and *Erica* increased from <1–3%. Woodland taxa were scarce throughout this zone (<1%). Herbaceous taxa comprised 20–30% of the

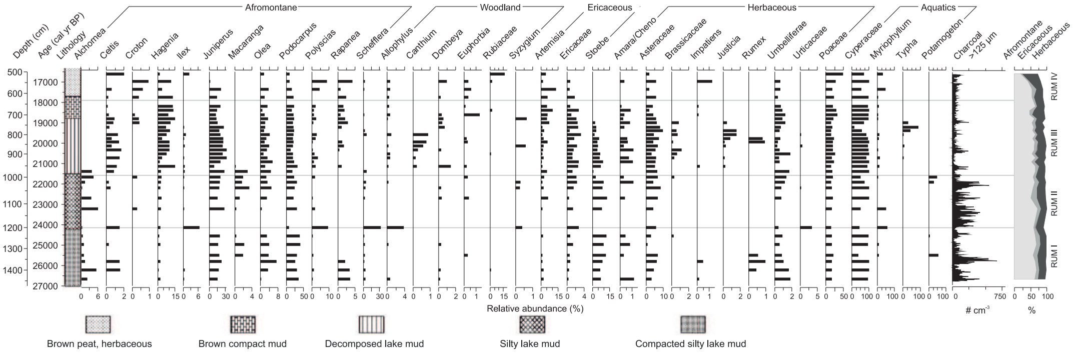

Fig. 3. Relative abundances of diatom taxa grouped by ecological types for the time interval of 27,000–16,500 cal yrs. BP (Gasse, 1986; Krammer and Lange-Bertalot, 1986–1991; Hofmann et al., 2011). Assemblage zones were derived using stratigraphically constrained incremental sum of squares (CONISS) technique and a broken stick plot indicated that three zones were significant (Grimm, 1987; Bennett, 1996; Legendre and Legendre, 2012). Rare taxa with <1% maximum relative abundance (34 taxa; 51.5%) throughout the record were not included in CONISS analysis. Taxa with a maximum relative abundance of ≥1% are shown.

Table 2

Summary of results and interpretation of diatom, pollen and charcoal data at Rumuiku.

Age (cal yr BP)	Diatom zone	Diatom description	Diatom interpretation	Pollen zone	Pollen description	Biomass burning	Vegetation interpretation
16,500 17,000	**Rum C** 726–500 cm 18,800–16,621 yr BP	Dominated by *Staurosira construens* with subordinate *C. placentula*, *E. sorex*, *Gomphonema elegantissima*, *Encyonopsis subminuta* and *E. minima.*	Shallower water likely, possibly nitrogen limited (higher abundance of *Epithemias*) and eutrophic as evidenced by *C. placentula*. The species present were probably living within macrophytes.	**RUM IV** 610–380 cm 17,500–15,500 yr BP	Afromontane taxa. *Hagenia*, *Polyscias*, *Podocarpus*, *Schefflera*. *Juniperus* down, *Rapanea* up. Secondary forest taxa present. Continued increase Poaceae and aquatic Cyperaceae. Ericaceous taxa begin to decrease.	Charcoal low with low variability.	Hydroseral succession, increases in aquatic taxa. Charcoal variability reduced and Poaceae increases significantly. Afromontane taxa decrease as woodland taxa increase. May signify change to less intense fires and lower forest biomass.
17,500 18,000 18,500				**RUM III** 970–610 cm 21,000–17,500 yr BP	*Juniperus*, *Podocarpus*, *Hagenia* high. Afromontane taxa present and drier woodland taxa begin to increase. Non-arboreal taxa, *Artemisia*, Poaceae, Asteraceae stable, *Stoebe* decreased.	Charcoal generally low, with some abrupt increases and subsequent decreases over subsequent 1000 years.	*Juniperus* and lower montane taxa increase; Afromontane taxa remain, Ericaceous taxa moderate except *Stoebe* suggesting changes to high elevation taxa. Charcoal lowest at 21000 cal yr BP concomitant with regional hydroclimatic change. Forest biomass may have been lowest during this time.
19,000 19,500	**Rum B** 826–726 cm 19,800–18,800 yr BP	Dominated by *F. delicatissima* and *S. construens* with increased *F. tenera* toward the top of the zone (up to 80%).	Fluctuations in water level likely represented by changed proportions from taxa with needle-like morphologies (deeper water) to small ovate (shallower water) and represented the species sensitivity to light.				
20,000 20,500	**Rum A** 1469–826 cm 26,826–19,800 yr BP	Dominated by *F. delicatissima* (up to 90%) with subordinate *S. construens* (up to 70%) and notable presence of *A. granulata* (25%).	Deeper water allowed planktonic species to live and longer, needle-like species thrived. *S. construens* probably represented a pioneer species and *A. granulata* suggested eutrophic waters.				
21,000 21,500 22,000 22,500 23,000 23,500				**RUM II** 1210–970 cm 24,000–21,000	*Juniperus* and *Podocarpus* dominant and covary. Afromontane taxa present but not abundant. Ericaceous taxa abundant. Woodland taxa negligible. Poaceae abundant and stable.	Charcoal is highly variable and decreases throughout.	Afromontane and Ericaceous taxa dominate and stable throughout. Forest density may be highest and biomass may have been an important contributor to fire activity.
24,000 24,500 25,000 25,500 26,000 26,500				**RUM I** 1469–1210 cm 26,430–24,000	Afromontane taxa dominate, *Podocarpus*, *Juniperus*. Nonarboreal taxa, Asteraceae, *Stoebe*, *Artemisia* abundant. Poaceae abundant and stable. Few aquatic taxa.	Charcoal accumulation peaks and then decreases over millennial scales.	Afromontane forest with abundance of Ericaceous taxa and *Juniperus*, high forest biomass with intense fires.

total terrestrial pollen and Poaceae (~15%) consistently dominated. Umbelliferae decreased from 1 to 2%. There were few aquatic taxa in this zone but Cyperaceae pollen was consistently observed and likely originated from plants that fringed the wetland.

The range of variability of charcoal concentrations (Fig. 3) and charcoal accumulation rates (CHAR) was highest in Zone I (5–70 pieces cm^{-2} yr^{-1}) (Fig. 5). The qualitative baseline low frequency variability of CHAR generally had values of 5–7 pieces cm^{-2} yr^{-1} and decreased overall throughout the zone. CHAR values conspicuously peaked then subsequently decreased over several centuries before a subsequent abrupt increase. This interval showed the lowest CHAR values of the record (Fig. 5).

5.3.2. Pollen Zone II: 24,000-21,000 yr BP (1210–970 cm)

Afromontane taxa continued to dominate and comprised ~65% of the relative abundance of terrestrial taxa; although throughout the zone the abundance decreased to ~55% (Fig. 3). Taxa were dominated by *Podocarpus* (≤40%) but decreased throughout the zone to <30%, *Juniperus* (≤20%) and *Olea* (≤10%). Subordinate abundances of *Alchornea* (<6%) and *Celtis* (<2%) were also present. At 24,000 cal yr BP, *Juniperus* abruptly decreased and *Polyscias*, *Ilex* and *Schefflera* increased. This zone was marked by the last observations of *Alchornea* and *Macaranga*. *Myrsine* (*Rapanea*) was not found in this zone. Ericaceous taxa abundances ranged from 2 to 18% and were dominated by *Stoebe* (<13%) and *Artemisia* increased to 5% in Zone II. Woodland taxa continued to be scarce (<1%) and the earliest observation of *Syzygium* occurred at 24,000 cal yr BP. Similar to pollen Zone I, the herbaceous taxa comprised 20–30% of the total terrestrial pollen and Poaceae abundances were consistently ~15%. Cyperaceae dominated the aquatic taxa. CHAR values were generally high during Zone II and averaged 11 pieces cm^{-1} yr^{-2} but decreased stepwise throughout the zone.

5.3.3. Pollen Zone III: 21,000-17,500 yr BP (970–610 cm)

Afromontane taxa dominated but had decreased to 55% total terrestrial pollen. *Juniperus*, *Podocarpus*, and *Olea* remained dominant. *Podocarpus* continued to gradually decrease (25–20%), *Hagenia* abruptly increased from 2 to 15% and remained the dominant taxa. *Polyscias*, *Celtis* and Myrsine (*Rapanea)* were present at subordinate abundances. Woodland abundance remained low 0–4% and composition remained unchanged with the exception of presence (1%) of *Canthium* from 21,500–19,000 yr BP. Ericaceous abundances were consistently 5–12% of the terrestrial pollen and compositions were stable, although *Stoebe* steadily decreased and was absent by the end of the zone. Herbaceous abundances were moderate (20–32%) and dominated by Poaceae

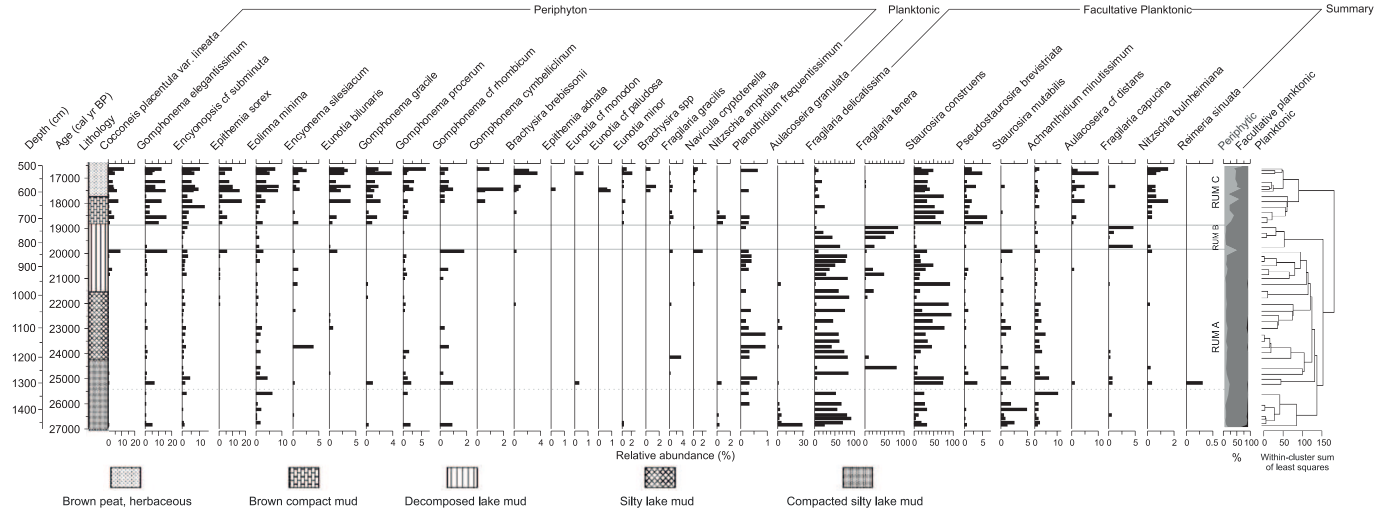

Fig. 4. Relative abundances of selected terrestrial pollen taxa grouped by functional types for the time interval of 27,000–16,500 calibrated years BP (Rucina et al., 2009). Taxa with a maximum relative abundance of ≥1% are shown. Aquatic taxa is presented as a relative abundance of aquatic taxa sum only. Zones delimited by CONISS and a broken stick test of the sum of squares (Grimm et al., 1987; Bennett, 1996; Legendre and Legendre, 2012). The full late Pleistocene to Holocene pollen record is presented in Rucina et al. (2009) and Rucina (2011).

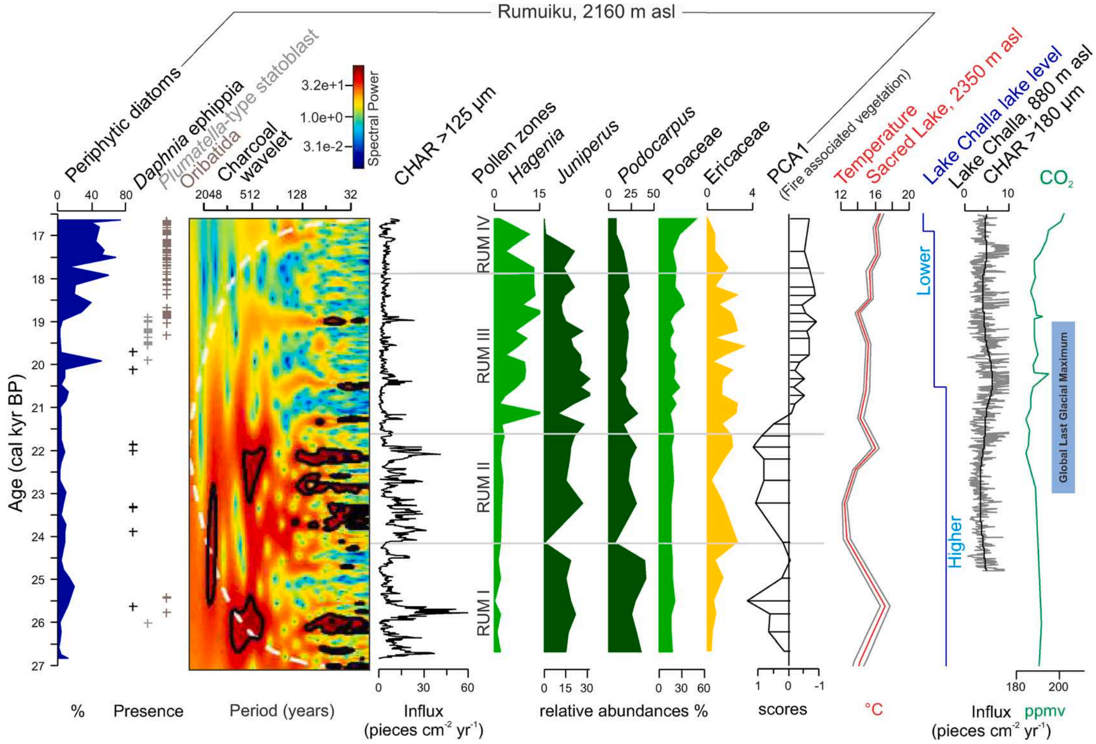

Fig. 5. Palaeovegetation change at Rumuiku and regional environmental change. The periphytic diatom abundances and presence data of aquatic invertebrates track the shallowing of the lake and wetland establishment. Biotic palaeovegetation indicators from Rumuiku (2160 m asl; at left and center) and abiotic environmental controls of vegetation change (at right) over the 27,000–17,000 cal yr BP time interval showing concomitant changes between 21,000–20,000 cal yr BP. Charcoal accumulation rates (CHAR) and wavelet spectrum. Pollen zones delineated through CONISS (Supplementary Fig. 4) and relative abundances of selected key Montane Forest taxa: *Hagenia*, *Podocarpus*, and *Juniperus*, and Poaceae and Ericaceae (Rucina et al., 2009). First principal component axis scores of pollen and charcoal data as an indicator of fire associated taxa (note the reversed x-axis).
A mid-montane elevation temperature reconstruction with error estimates (red and grey lines) using sediments from Sacred Lake (2350 m asl), Mount Kenya (Loomis et al., 2012) and a qualitative lake level reconstruction from Lake Challa representing regional eastern African hydroclimatic variability (blue line; Moernaut et al., 2010) and the sieved charcoal from Lake Challa (Nelson et al., 2012). Global atmospheric CO_2 measured from the Vostok ice core, Antarctica (green line; Petit et al., 1999). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(15–30%) and Asteraceae (2–10%). Cyperaceae continued to be the consistent predominant aquatic taxa.

CHAR was low in Zone III and averaged 3.8 pieces cm^{-2} yr^{-1} and the low frequency variability was very low yet increased slightly throughout the zone. The long-term trend in the charcoal data remained important while short-term intervals were intermittently important and significant.

5.3.4. Pollen Zone IV: 17,500-15,500 yr BP (610–380 cm)

Poaceae increased from 30 to 50% relative abundance and increased continuously until 15,500 yr BP (not presented here; see Rucina et al., 2009). Total Afromontane pollen abundances steadily decreased (50–15%) but at different rates for each taxon as *Juniperus* decreased to minor values and *Podocarpus* continued a gradual decline to <20%. Ericaceous abundance decreased overall and ranged from 2 to 20%. *Artemisia* increased while *Erica* decreased. Woodland abundance was <1–2% with notable consistent presence of *Allophylus*, *Dombeya*, *Euphorbia*, (each <2%) and Rubiaceae (<15%). Cyperaceae were the dominant aquatic taxa.

CHAR remained low in Zone IV (averaged 5.5 pieces cm^{-2} yr^{-1}), CHAR peaks were much lower than in each of the previous zones, and the low frequency variability amplitude was low, yet continued to increase from 4 to 7 pieces cm^{-2} yr^{-1} throughout the zone.

6. Discussion

Significant CONISS zones delimited for the diatom and pollen assemblages showed slight temporal offsets (Figs. 3 and 4; Table 2) and suggested that local catchment vegetation and within-lake ecosystems responded differently to the long-term glacial-interglacial

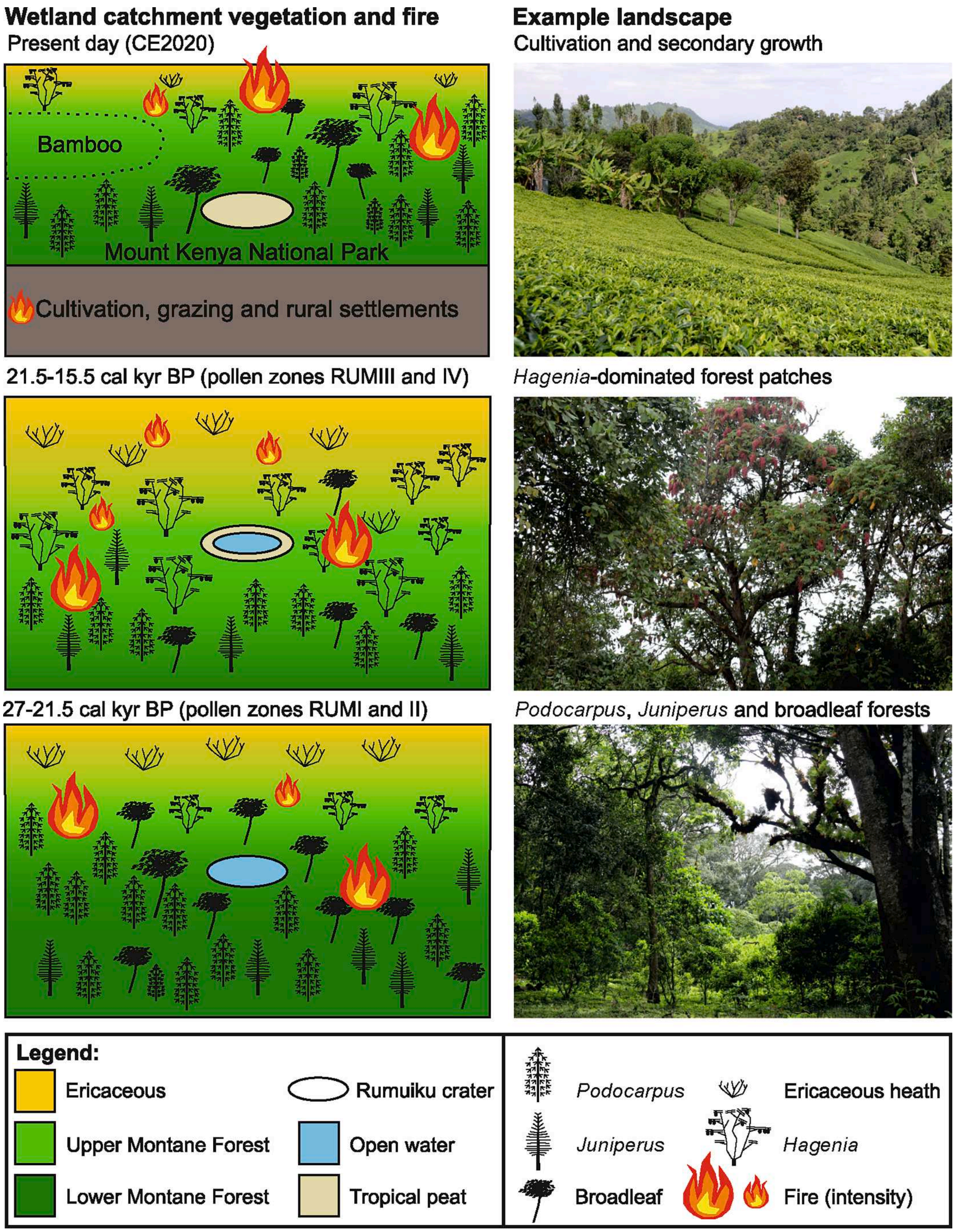

Fig. 6. Summary landscape diagram of Rumuiku on the eastern flank of Mount Kenya. Changes to vegetation and fire in the Rumuiku catchment prior to 21,500 cal yr BP and afterwards, and the conditions at present (2020 CE) are shown for comparison. Pollen taxa are associated with broad forest types and silhouettes represent the tree physiognomy and vegetation structure. Fires are represented with flame symbols among the vegetation zones where larger fires are more intense and severe and smaller flames where fires are less intense, less severe, but more frequent that are associated with Poaceae, Ericaceous, and *Hagenia* forests.

environmental variability that included climatic warming, fire activity, and limnological fluxes of sediments, C and N (Street-Perrott et al., 2007). The major vegetation change occurred at 21,500 cal yr BP when *Hagenia* increased in abundance within the local mid-montane forest with a concomitant decrease in charcoal that indicated a changing vegetation-fire relationship (Fig. 6). Published fire ecology studies of observed disturbances of these forest types have noted that *Juniperus* and *Podocarpus* forests experience infrequent (multidecadal-to-centennial scale), stand-replacing fires; whereas, *Hagenia* forests experience less severe fire types at higher burn frequencies and have a relatively more open forest structure (Wesche et al., 2000; Bussmann, 2002a). In summary, the results from the study site track published evidence of changing regional hydroclimate, montane vegetation change and fire activity prior to the global increase in atmospheric CO_2 toward the end of the Late Pleistocene postglacial, which later contributed to modifying plant compositions and distributions (Jolly and Haxeltine, 1997; Boom et al., 2002; Ficken et al., 2002; Wooller et al., 2003).

6.1. Diatoms, invertebrates and hydroseral succession

The ecosystem was dominated by periphytic taxa throughout and represented a slow succession over the millennia that documented the hydroseral transition from a shallow lake to a wetland (Figs. 3 and 5; Mavuti, 1981; Mavuti, 1992) and the site remained palustrine to present (Rucina et al., 2009). In shallow lakes, periphytic taxa can be detached from sediment and plant surfaces and found within the plankton (tychoplankton). *A. minutissimum* is one of the most common diatoms in many environments. It is attached to substrates by short stalks and cells can grow on top of each other (Krammer and Lange-Bertalot, 1986–1991). All *Gomphonema* species are attached with stalks, some short, some very long. *Stenopterobia delicatissima* is not attached. ong, thin *Fragilaria* taxa predominates the assemblages over much of the record. *F. delicatissima* is mostly planktic, but does also occur as epiphytic. It is light sensitive and may indicate deeper water in the lake. There might be an exchange of diatom frustules from the periphyton into the open water rather than these taxa really growing in the open water. It is likely that Rumuiku existed as a shallow lake with several diatom taxa that are facultative periphytic and/or planktonic with some taxa potentially attached to aquatic vegetation, namely Cyperaceae and hydric Poaceae taxa. Diatom zone C contained less planktonic and more periphytic taxa and indicates that the lake became shallower and the littoral zone would have expanded with more habitat space for aquatic plants and attachment area for epiphytic diatoms. The presence of taxa with N-fixing cyanobacteria as symbionts, such as *E. sorex*, may suggest that the system was N limited or at least close to N limitation (Krammer and Lange-Bertalot, 1986–1991). *E. sorex* also suggests a shallower water column (Gasse, 1986). *C. placentula* is an often epiphytically growing species, which is tightly attached to surfaces.

The diatom assemblage zones divided the record into three time intervals (Fig. 3). Zone A had abundant facultative planktonic and periphytic taxa and suggested a shallow lake ecosystem and the subzone between 25,500 and 23,000 yr BP appeared to be a moderately distinct assemblage found in a single sample with abundant *Gomphonema elegantissimum*, *G.* cf. *rhombicum*, and *Reimeria sinulata* (Fig. 3). Zone B is a short (1000-year) interval of varying abundances of facultative planktonic taxa and a conspicuous reduction of periphytic taxa concomitant with a reduction in Cyperaceae and *Myriophyllum* pollen and increased *Typha* (Fig. 4). These changes could have been promoted by hydrologic stabilization in littoral areas by the continued sediment infilling of the wetland and subsequent water shallowing or nutrient availability changes (Hamilton and Taylor, 1986; Woo and Zedler, 2002) or both because these environmental changes can benefit *Typha* (Bansal et al., 2019). Observations of *Typha* expansion, and dominance, has been associated with rapid sedimentation rates in other wetlands of eastern Africa (Hamilton, 1982: p262) and *Typha* is present in many montane wetlands usually with relatively high pH (Lind, 1956; Hamilton, 1982: p99). Previous analyses of montane lacustrine-palustrine sediment hydroseral sequences in eastern Africa have mainly focused on lithology and pollen data (Hamilton and Taylor, 1986) and there have been relatively few analyses that use aquatic invertebrate remains. The aquatic invertebrate remains observed during continuous charcoal analysis also support the succession of the aquatic ecosystem from a permanent shallow lake to a wetland when *Daphnia* ephippia (no eggs inside) were observed during the permanent lake phase, and continued to shallow with bryozoan statoblast remains consistently observed during 20,000–19,000 cal yr BP, and more oribatid mites during the wetland phase when more wetland vegetation established and periphytic diatoms increased (Fig. 5). The increased concentrations of oribatid mites in the upper zones of Rumuiku may relate to altered littoral conditions or be derived from the surrounding soil organic litter layer in the wetland and catchment area (Knoepp et al., 2000; Solhøy, 2001; Gergócs and Hufnagel, 2009; Fig. 5).

6.2. Vegetation and forest fires

The earlier half (27,000–21,500 cal yr BP) of the vegetation record from Rumuiku suggested that the site was surrounded by dense, moist Afromontane forests with high abundances of *Juniperus* and *Podocarpus* that have a fire ecology that benefits from long intervals between severe fires, which may have resulted in the generally higher CHAR values (Figs. 4 and 5). These taxa occur over a wide hydroclimatic range and *Podocarpus* is found around the mid-montane forests. *Juniperus* is more abundant with slightly drier conditions (Bussmann and Beck, 1995a). Long-term changes in *Juniperus* pollen abundances at Rumuiku may reflect changing hydroclimatic variability by either a reduction in the amount of precipitation or changing contrast between wet-dry seasonality (drier dry seasons). Both taxa benefit from stand-replacing fires at longer fire return intervals (multidecadal-to-centennial scale) in order to establish and grow to mature stands (Bussmann, 2002a). *Hagenia* abundances had already increased by 22,000 cal yr BP at Lake Rutundu (3078 m asl) coincident with changes in the Poaceae taxa assemblages (Wooller et al., 2003) suggesting that fire regimes were changing across the moist montane forest zones around Mount Kenya, at least on the windward western slopes of the mountain. The influence of CO_2 increases and other effects cannot be disentangled from the effects of fire regimes alone and the potential for a drier interval on the mountain based grass cuticle, phytolith and charcoal evidence from the Lake Rutundu sediment record from 25,000 to 13,400 cal yr BP (Wooller, 1999; Wooller et al., 2003). From 21,500–16,500 cal yr BP, the persistent lower intensity fires and likely more frequent fire regime promoted conditions that contributed to a reduction in the Afromontane taxa and maintenance of relatively more open *Hagenia*-Poaceae vegetation on the mountain facet surrounding Rumuiku and consistently lower CHAR (Fig. 5).

The decreased charcoal accumulation rates after 21,500 cal yr BP suggest a transition from the dense Montane Forests to the relatively more open *Hagenia* dominated composition of forests around Rumuiku and maintaining these forests at least 16,500 cal yr BP. The changed fire regime, burning forests with lower tree densities at likely more frequent time intervals; yet with lower fuel loads and lower charcoal production due to the decreased biomass, was an important factor in maintaining *Hagenia*-Poaceae over other Montane Forest taxa (Fig. 5). Both *Podocarpus* and *Juniperus* require longer fire return intervals and more severe fires to compete as dominant tree taxa (Bussmann, 2001, 2002a, 2002b). At 19,000 cal yr BP and afterward, Poaceae increased and both *Podocarpus* and *Juniperus* decreased as the regional hydroclimate continued to warm and dry (Figs. 4 and 5; Loomis et al., 2017). At higher elevations, periglacial conditions continued to ameliorate and Ericaceous cover expanded uphill above Rumuiku catchment, peaking around 20,000 cal yr BP and slowly decreasing to 16,000–13,000 cal yr BP (Wooller et al., 2003; Rucina et al., 2009). Regionally, the palaeoenvironmental records of vegetation and fire on highlands of Kenya

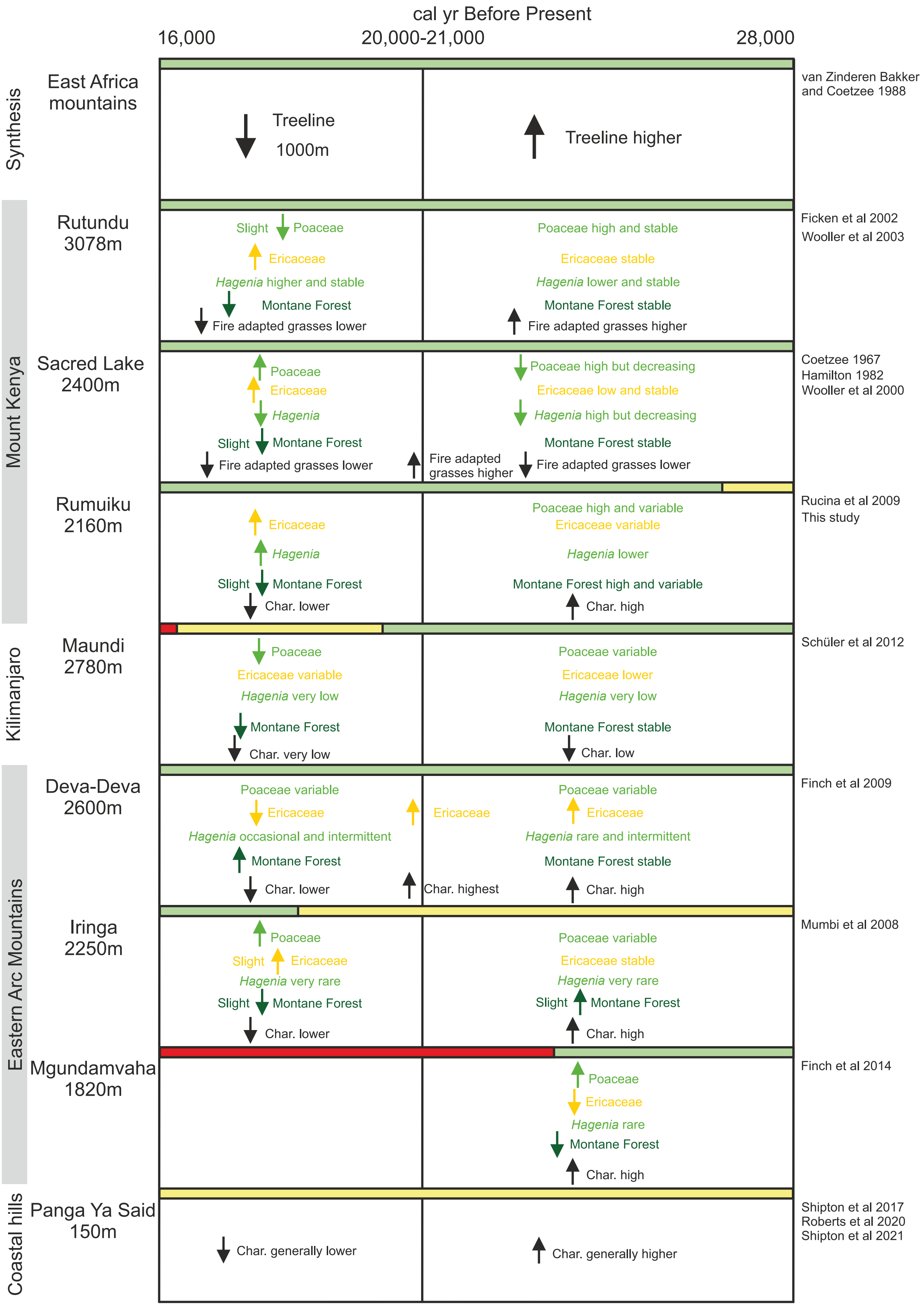

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Fig. 7. Summarized palaeoenvironmental records that analysed pollen and fire from forests in Kenya and Tanzania for comparison with Rumuiku (Coetzee, 1967; Hamilton, 1982; Van Zinderen Bakker and Coetzee, 1988; Wooller et al., 2000; Ficken et al., 2002; Wooller et al., 2003; Mumbi et al., 2008; Finch et al., 2009; Rucina et al., 2009; Schüler et al., 2012; Finch et al., 2014; Shipton et al., 2017; Roberts et al., 2020; Shipton et al., 2021). Geochronological quality of each sediment-based palaeoenvironmental record is represented by the thin horizontal bar above each record: red, poor geochronological control (no dates or very high uncertainty); yellow, few radiocarbon dates and high uncertainty for timing; green, good chronological certainty with several radiocarbon dates and uncertainty. Site elevation in meters above sea level (m asl). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and Tanzania show apparent spatial heterogeneity (Van Zinderen Bakker and Coetzee, 1988) with several study sites suggesting local changes in vegetation and fire around 21,000–20,000 cal yr BP (Fig. 7). This suggests complex climate-vegetation-fire interactions across the region and the importance of regional and local spatial environmental conditions influencing Montane Forest vegetation and fire regimes prior to significant and intensive anthropogenic modifications of mountain forests.

7. Conclusions

These new palaeoenvironmental data document the importance of the role of fire in long-term vegetation change in the moist montane forest ecosystems on Mount Kenya during a time with little to no known evidence of anthropogenic modifications. The data suggest climate-fire-vegetation are temporally complex. The comparison with other published records supports some broad similarities yet spatial complexity in montane forest vegetation and disturbance interactions suggesting that the ecological role of fire and other local-scale factors potentially contribute to spatial patterns. As in other mountainous areas of eastern Africa (Hemp, 2006; Verschuren et al., 2009), these were not solely linear elevation shifts of plant distribution in response to climate change but were complex interactions of local (disturbance regimes, competition, soils, topographic complexity) and large-scale processes (atmospheric CO_2 and moisture-vegetation ecohydrology). Currently there are several pressures modifying the forests of Mount Kenya and these forest palaeoenvironmental and disturbance pattern results provide long-term context on vegetation and fire activity changes for mid-montane forest patches and facets of Mount Kenya.

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.

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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.2021.110625.

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