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Late Pleistocene montane forest fire return interval estimates from Mount Kenya

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ABSTRACT: Past forest fire events and fire frequencies are reconstructed with sediment–charcoal records at lake catchment spatial scales. Few quantitative palaeofire analyses exist in tropical montane forests, where fire return intervals are long (decadal and centennial scales) because of the infrequency of fire weather and fuel conditions. Fire return intervals are a key characteristic of fire regimes and changing fire frequencies rapidly alter land cover compositions and vegetation structure. Charcoal records from small lakes with relatively small catchments covered with dense forest provide an opportunity to reconstruct low-frequency, high-severity fires through a time series decomposition approach to identify charcoal peaks above a varying background rate as a proxy for palaeofire events. The sediment core from Rumuiku wetland on Mount Kenya, equatorial eastern Africa, accumulated a nearly linear age–depth model and provided a high temporal resolution (10 years cm⁻¹) sieved charcoal count record (>125 μm). Pollen analysis showed a significant change in montane forest assemblage occurred at 21 200 cal a BP from a montane forest with abundant *Podocarpus* and *Juniperus* to a forest with more abundant *Hagenia*. This change in forest altered the vegetation composition and structure with concomitant changes to the fire regime. Forest biomass in the *Hagenia* forests decreased and it is likely that fire activity qualitatively changed toward lower intensity and lower severity fires. The quantitative fire event reconstruction focuses on the interval from 27 000 to 16 500 cal a BP and the older montane forest that experienced higher severity fires from 27 000 to 21 200 cal a BP, which reconstructed a temporally heterogeneous fire regime with fire return intervals that ranged from 30–430 years and a mean of 120 years (median 160 years) in the catchment. These are the first estimates of fire return intervals of mountain forests in eastern Africa. We then explore the potential for further comparative research and incremental research contributions to improve quantitative and qualitative palaeofire research in tropical forest ecosystems. We discuss the potential to use these types of data for characterizing variables of fire regimes prior to ostensibly significant modification by anthropogenic activity as well as during the recent past as human land use pressures increased within Afromontane forests. © 2022 The Authors *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: Africa; Afromontane; charcoal; fire frequency; fire regime; mountains

Introduction

Tropical montane forests are important as global hotspots for biodiversity conservation that underpin agricultural livelihoods and a wide spectrum of ecosystem services for both mountain and downstream communities (McClanahan *et al.*, 1996; Bussmann, 1999; UNEP, 2012). Fires in the mountain forests of eastern Africa are commonly featured in the international news media (Henry *et al.*, 2019a; BBC News, 2020; Hemp, 2020) and are driven by human activities, land use changes and meteorological variability. In recent centuries and decades the anthropogenic pressures on montane forest resources and land cover conversions have increased in eastern Africa (Hobley, 1914; Troup, 1932; Ndegwa Gichuki, 1999; Petursson *et al.*, 2013; Heckmann *et al.*, 2014; Finch *et al.*, 2017; Githumbi *et al.*, 2021). For example, the forests of Mount Kenya have been extensively converted to tea and coffee agriculture and agroforestry (Routledge and Routledge, 1910; Bussmann, 1996; Gathara, 1999;

Mugo, 2007; Kleinschroth *et al.*, 2013). The disturbance ecology of ostensibly pre-anthropogenically modified montane forests is important for understanding the vegetation responses to fire and a comparator for current and future forest management (Mahaney, 1986; Bussmann and Beck, 1998; Kindt *et al.*, 2007; Omoro *et al.*, 2010, 2011).

Several palaeoenvironmental studies of palustrine and lacustrine sediment cores collected on Mount Kenya and neighbouring mountains have described the late Quaternary and Holocene vegetation assemblage variability of lower montane forests (Ficken *et al.*, 1998; Olago *et al.*, 1999, 2003), mid-montane forests (Coetzee, 1964, 1967; Cooremans and Mahaney, 1990; Ficken *et al.*, 2002; Wooller *et al.*, 2003; Rucina *et al.*, 2009) and Afroalpine elevations (Hamilton, 1982; Perrott, 1982; Barker *et al.*, 2001; Courtney Mustaphi *et al.*, 2017, 2021a). Despite available studies of long-term dynamics of Afromontane ecosystems, quantitative estimates of past variability for fire return intervals (Landres *et al.*, 1999) in the different moist montane forest ecosystems of eastern Africa are unknown. Forest management plans for ecosystems with decadal- to centennial-scale patterns of fires benefit from a long-term perspective (Marchant *et al.*, 2018;

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Manzano *et al.*, 2020; Marchant, 2021). Management plans in the moist montane forests do not incorporate quantitative estimates of return intervals as there are no detailed analyses of forest disturbance over long time scales beyond the latter past century on Mount Kenya (FAO, 2012; Henry *et al.*, 2019b). Because of the quantitative knowledge gap, fire management plans have tended to focus on ecosystems with observable and measurable fire return intervals (Hempson *et al.*, 2017) and on fire protection in agroforestry and agricultural areas (Phillips, 1965; Wesche *et al.*, 2000; Sang, 2001). Palaeoenvironmental research contributes to our understanding of fire in modern ecosystems (Seddon *et al.*, 2014; Armstrong *et al.*, 2017; McLauchlan *et al.*, 2020) to provide information about disturbance dynamics under different climate conditions and levels of anthropogenic modifications (Keane *et al.*, 2009; Bowman *et al.*, 2011; Archibald *et al.*, 2012).

Fires in dense forests can produce large quantities of burned biomass and a large influx of charcoal occurs during the post-fire years that may be detected as charcoal accumulation peaks in sediment–charcoal records (Whitlock and Millspaugh, 1996; Larsen and Whitlock, 2001; Courtney Mustaphi *et al.*, 2015). The purpose of this study was to reanalyse palaeoenvironmental data from the Rumuiku wetland sediment core to reconstruct estimates of fire frequency in a mid-montane forest of Mount Kenya, Meru County, Kenya, eastern Africa. The sieved sediment charcoal time series (Courtney Mustaphi *et al.*, 2021b) was reanalysed to estimate charcoal accumulation rate time series peaks that represent fire episodes in the geological record (Long *et al.*, 1998; Gavin *et al.*, 2006; Higuera *et al.*, 2009, 2010, 2011a; Blarquez *et al.*, 2013) and was then integrated with previously published pollen data from the same sediment core (Rucina *et al.*, 2009; Courtney Mustaphi *et al.*, 2021b). The lowermost section of the Rumuiku record was dominated by *Podocarpus* pollen and the charcoal was deposited under lacustrine conditions, from 27 000 to 21 200 cal a BP, and produced a charcoal signal with a relatively high mean value and relatively high peaks above the

varying background accumulation rate used for peak analysis. Here we report on the sample selection, analysis and interpretation of the charcoal time series analysis to estimate fire return intervals.

Study area

The Rumuiku stream is part of the Tana River watershed that originates within a small Cyperaceae and Poaceae vegetation-covered wetland in an extinct volcanic crater near the eastern edge of the Mount Kenya National Park and Forest Reserve boundary at 2160 m asl (geographical coordinates: $-0.118583, 37.5611$; Fig. 1 and Supporting Information Fig. S1). The lacustrine and palustrine sediment stratigraphy of the wetland provided an environmental record of the past 27 000 years to the present (Rucina *et al.*, 2009). The elliptical crater is $\sim 350 \times 200$ m across and the crater wall is asymmetric with steeper walls on the south and west (Fig. 1; Fig. S1). The surrounding mid-montane forest is currently composed of *Croton macrostachyus*, *Macaranga kilimandscharica*, *Neoboutonia macrostachyus*, *Podocarpus*, *Polyscias* spp., *Schefflera* spp. and *Tabernaemontana holstii* and others (Rucina *et al.*, 2009). At higher elevation the forests transition to *Juniperus*-dominated forests, then *Podocarpus*-dominated forests, with considerable spatial variability and patchiness in forest stands and compositions (Wimbush, 1937; Coe, 1967; Bussmann, 2001, 2006). A narrow *Hagenia* forest zone exists at the upper montane forests on the western side of the mountain and is much wider along the southern flank (Bussmann and Beck, 1995) (Fig. 1).

Holocene and Pleistocene forest extents were much larger (Hamilton, 1982; van Zinderen Bakker and Coetzee, 1988) and allowed for more genetic connectivity among highland vegetation (Hamilton and Taylor, 1991; Jump *et al.*, 2014; Hemp and Hemp, 2018). Montane forest extents have been reduced during, at least, the past millennium (Finch *et al.*, 2017) and further reduced during the past century (Hutchinson, 1907; Cranworth, 1912; Hobley, 1914; Troup, 1932; Castro, 1991a)

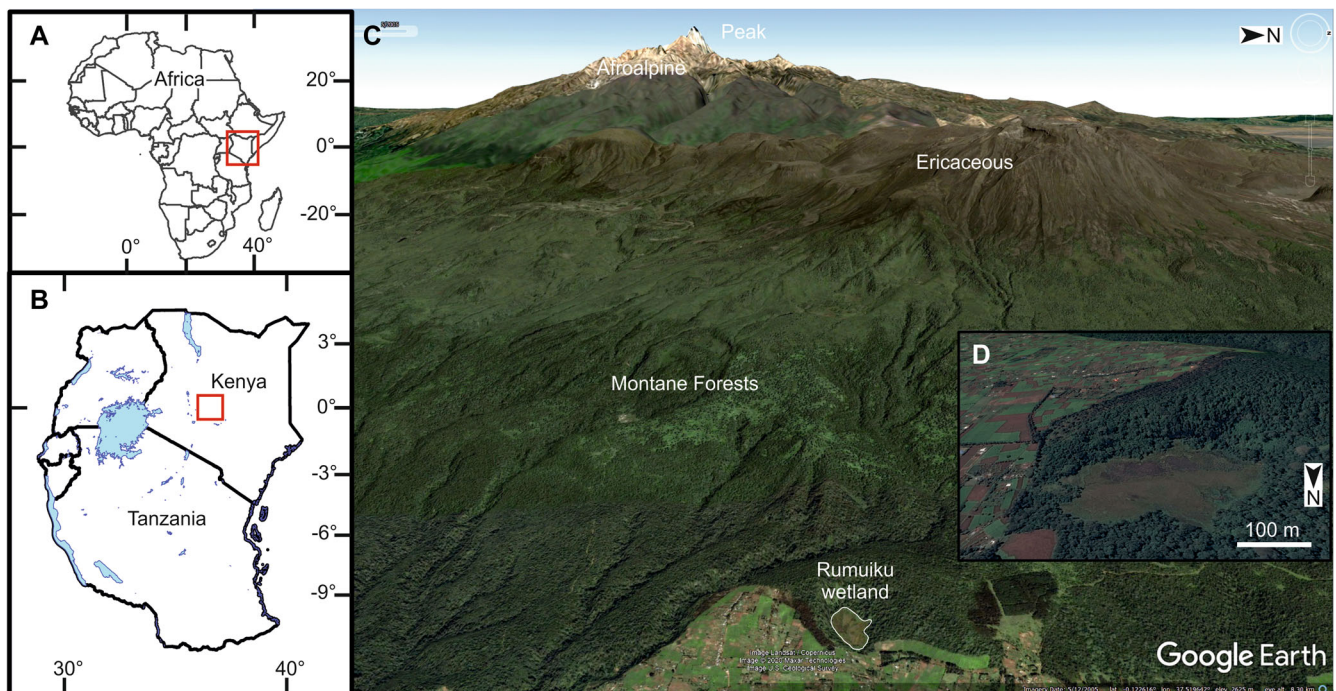


Figure 1. The Rumuiku wetland study site location inset maps of (A) Africa and (B) in central Kenya. (C) An oblique perspective of the eastern flank of Mount Kenya from the edge of Mount Kenya National Park and forest reserve to Batian peak (5199 m asl) with generalized vegetation biomes (Hedberg, 1951; Hedberg, 1955; Bussmann, 2002) and (D) a southward-facing view of the Rumuiku volcanic crater wetland ($-0.118583, 37.5611$; 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 2.0x vertical exaggeration to show topographic relief (Google Earth/DigitalGlobe, 2021).

and recent decades (Castro, 1991b; Fanstone, 2016), but with some stable forestlines and reforestation areas (Gathaara, 1999; Hansen *et al.*, 2013; Eckert *et al.*, 2017). At present on Mount Kenya, fires occur most frequently in the Ericaceous vegetation, along trail routes, along protected area boundaries and on the drier leeward northwestern flank (Fig. 2) (Vacik *et al.*, 2018; Henry *et al.*, 2019b). In the relatively more fire-prone northwestern area of the mountain, most observed fires since 1980 occurred during February–March and a secondary mode during August–September (Poletti *et al.*, 2019). Montane vegetation has the potential to burn at any time of the year if the fire weather conditions occur (Wesche, 2003) and small-scale fires ignited by people occur even under moist conditions. Fire ignitions occur naturally, commonly by cloud-to-ground lightning, and purposefully or accidentally by people using forest resources (KFS, 2010; Nyongesa and Vacik, 2018; Nyongesa and Vacik, 2019). Fires in Mount Kenya National Park and Forest

Reserve together make the area one of the most frequently burned protected areas of Kenya, as observed by satellite products from 2003–2014 (Karanja, 2016). The long-term fire and disturbance ecologies of the different montane forest types have yet to be fully characterized across the highlands of eastern Africa. Changing fire frequencies on mountains of eastern Africa are key processes that influence vegetation composition and structure (Wesche, 2003) with many effects on patchiness and ecotonal transitions (Hemp and Beck, 2001; Hemp, 2005; Gil-Romera *et al.*, 2019; Courtney Mustaphi *et al.*, 2021a). It is unknown what disturbance ecology processes promote the persistence or hindrance of the spatial and temporal patterns of tree stand compositions over multidecadal, centennial and millennial time scales, and how these processes interact with other ecological processes. Stand-replacing fires have been proposed as a disturbance ecology mechanism to explain the spatial vegetation patterns in highland forests across eastern Africa (Wimbush, 1937; Lange *et al.*, 1997; Wesche, 2000), yet there are few datasets available for analysis.

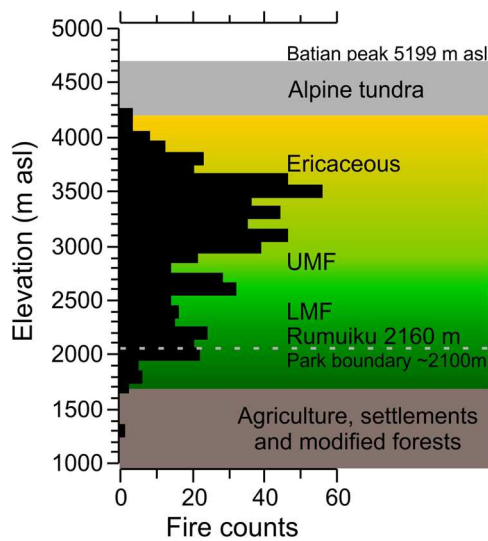


Figure 2. The total number of observed fire events from 2001 to 2013 on Mount Kenya binned by 100-m elevation bands. Fires with >50% detection confidence from the satellite-based Earth observation MODIS active fire product MCS14ML (years: 2001–2013) around the entire mountain (also see Henry *et al.*, 2019). Generalized vegetation on the eastern flank of Mount Kenya are shown in horizontal bands: brown, agriculture; greens, montane forests; yellow, ericaceous; grey, Afroalpine and tundra (Hedberg, 1951; Hedberg, 1954; Coe, 1967; Zhou *et al.*, 2018). Note the boundary for Mount Kenya National Park and the forest reserve varies in elevation around the mountain from ~1500 to 2200 m asl.

Material and methods

Sampling and previously published data

A 1469-cm-long sediment stratigraphy was collected in 2005 from the Rumuiku crater wetland surface with a Russian peat corer (Jowsey, 1966) from parallel boreholes by overlapping 50 cm long, 5 cm diameter hemicylindrical cores. Nine accelerator mass spectrometry (AMS) radiocarbon dates provided a 27 000-year chronology to the present (–55 cal a BP; Table 1; Rucina *et al.*, 2009; Rucina, 2011) and we reused the radiocarbon calibrations (IntCal13, Reimer *et al.*, 2013; Table 1; Fig. 3) and age–depth model presented in Courtney Mustaphi *et al.* (2021b). Select pollen taxa have been presented in this study from the previously published pollen relative abundance data and pollen zones from the same sediment core (Rucina *et al.*, 2009; Sánchez Goñi *et al.*, 2017). Charcoal analysis used continuous 1-cm-thick subsamples ($n = 969$) of 0.5–3 cm³ wet sediment that were immersed for >24 h in a sodium metaphosphate solution and manually wet sieved through a 125- μ m mesh (Bamber, 1982). The retained material was visually inspected with a metal probing pick under a Zeiss Stemi 2000-C optical stereomicroscope at 10–40 \times magnification and the charcoal pieces were diagnostically identified and counted (Whitlock and Larsen, 2001; Hawthorne *et al.*, 2018).

Table 1. Age determinations for the Rumuiku wetland sediment core collected in 2005 (–55 cal a 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). NA, not applicable.

| Depth (cm) | Age (¹⁴ C a BP) | 1 σ error (\pm a BP) | δ^{13} C (‰) | Material | Laboratory code or description |
|------------|-----------------------------|--------------------------------|---------------------|---------------|--------------------------------|
| 0 | –55 | 0 | NA | 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 |

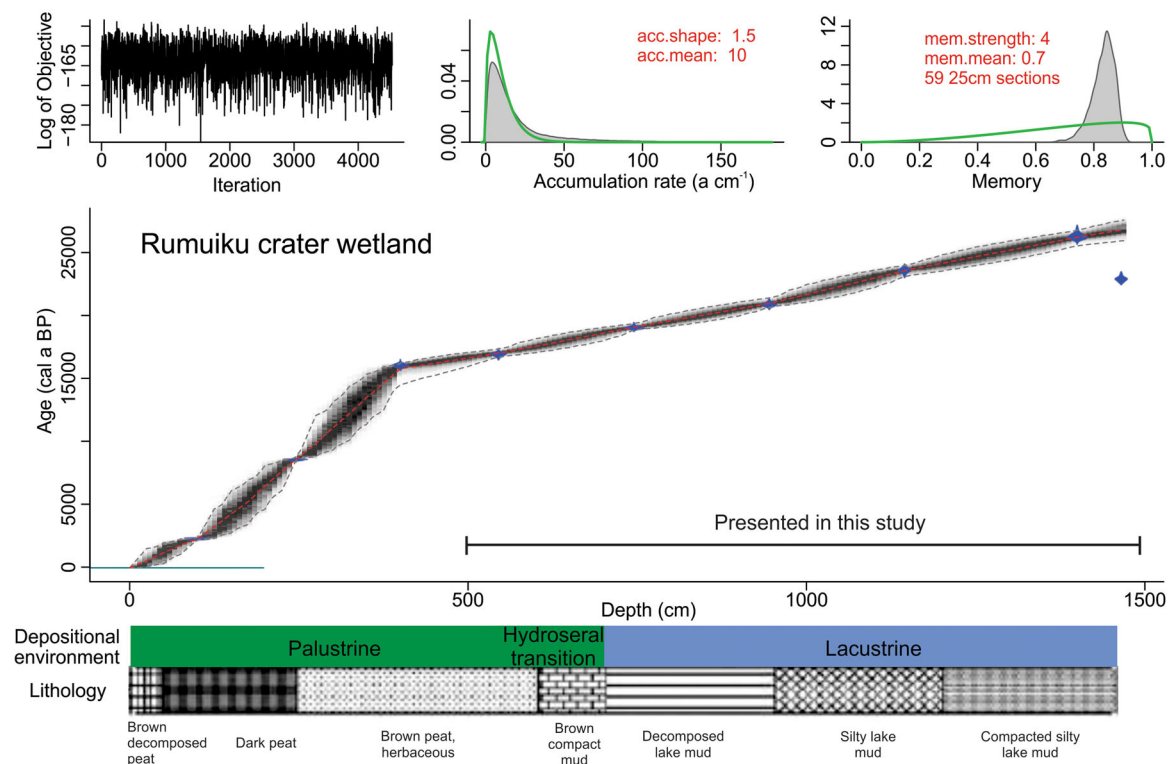


Figure 3. An age–depth model produced with the R package Bacon version 2.2 (Blaauw and Christen, 2011a, 2011b; R Development Core Team, 2015) that used nine AMS radiocarbon dates (Rucina *et al.*, 2009) and the IntCal13 radiocarbon curve (Reimer *et al.*, 2013) and parameterized as shown in red text. Blue symbols represent the calibrated radiocarbon date probability distributions, the grey shaded 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 (age–depth model applied to the charcoal and palaeoenvironmental data). The lowermost radiocarbon date (SUERC-17200) was objectively rejected from the age–depth model and was rejected in the original study (Rucina *et al.*, 2009). Core lithology with sediment types and legend (Troels-Smith, 1955) and hydroseral interpretation shown horizontally below the *x*-axis (Rucina *et al.*, 2009).

The weighted mean age–depth model results (Blaauw and Christen, 2011a) were applied to the palaeoenvironmental data and charcoal concentrations (pieces cm^{-3} of wet sediment) were resampled to a median temporal sampling interval of 10 years (mean = 10.6, median = 10.3, range 7.8–14 a cm^{-1}) to create an even interval time series and converted to charcoal accumulation rates (CHAR; pieces $\text{cm}^{-2} \text{a}^{-1}$) (Courtney Mustaphi *et al.*, 2021b). CHAR was analysed using the CharAnalysis Matlab script as implemented through an ensemble-member strategy for decomposing the charcoal series to identify charcoal peaks (Higuera *et al.*, 2009, 2010) that represent robust fire events, RFEs (Blarquez *et al.*, 2013), above the variable background CHAR (Gavin *et al.*, 2006). RFEs were determined and supported through consensus between the ensemble member iterations of multiple smoothing window lengths and smoothing techniques (LOWESS smoother, LOWESS smoother robust to outliers, moving average, moving median and moving mode) (Blarquez *et al.*, 2013). Smoothing window durations of 100–1500 years at 50-year increments were implemented for each of the five smoothing techniques creating a total of 470 runs for each of the five smoothing techniques. Fire return intervals (FRIs) were obtained from each member and fire frequencies were calculated from the identified fire dates within each member using a kernel density function. The final RFEs were obtained from the ensemble of fire events through consensus, defined as the 75th percentile of the distribution as a threshold for the minimum number of members identifying the same peak (minimum agreeing iterations cutoff $n = 463$). The times between the detected charcoal peaks were used as estimates of FRIs. The signal-to-noise ratio of the CHAR time series was also calculated for all iterations (Higuera *et al.*, 2009; Blarquez

et al., 2013). For visualization on graphics, a minimum threshold value of 3.0 was applied for data interpretation of the CHAR time series that used the LOWESS smoother with a 750-year window duration and implemented in CharAnalysis (Higuera *et al.*, 2009; Kelly *et al.*, 2011).

First, we analysed the charcoal time series available from 27 000 to 16 500 cal a BP (1500–500 cm). We then focus on the section from 27 000 to 21 200 cal a BP that spanned Rumuiku pollen zones I and II with *Podocarpus*-dominated mid-montane forests. We argue that the results from this section are the most representative because of the taphonomic effects of the palaeolake shallowing and hydroseral succession to a wetland and potentially the very different fire regime under the *Hagenia*-dominated pollen zones (RUM III and IV, 21 200–16 500 cal a BP) that led to a charcoal signal with a lower mean charcoal accumulation rate and much smaller peaks. We present the distribution of FRI results for the two palaeofire regimes of the *Podocarpus*-dominated mid-montane forests (27 000–21 200 cal a BP) and the *Hagenia*-dominated zones (21 200–16 500 cal a BP), as well as the entire duration of 27 000–16 500 cal a BP.

Results

The Rumuiku wetland sediment record presents a high temporal resolution and relatively stable depositional environment with a near-linear pattern of sediment accumulation rates from 27 000 to 16 500 cal a BP (1469–500 cm depth; Fig. 3 and Table 1). The Rumuiku crater lake then accumulated organic-rich deposits through a hydroseral succession to a wetland (palustrine sediments) characterized by increased relative

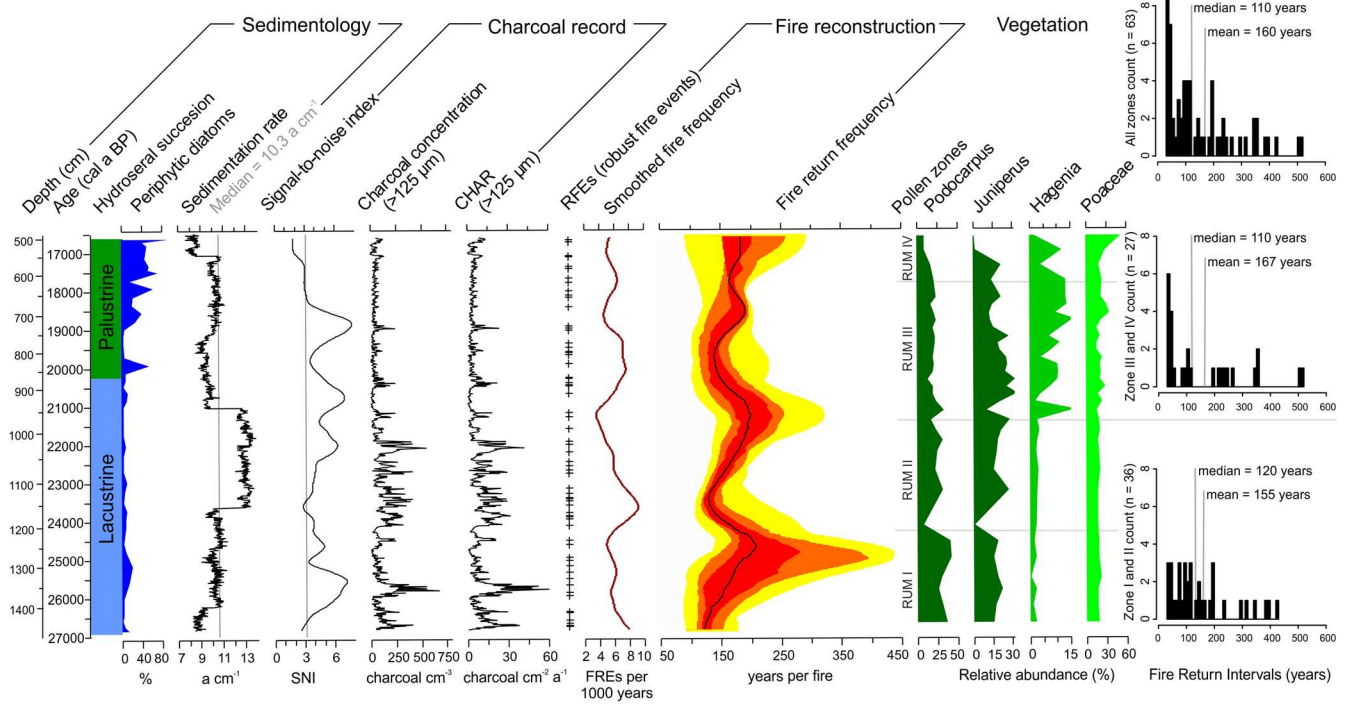


Figure 4. The hydroseral succession of the palaeolake Rumuiku to wetland conditions in the crater are summarized at left based on diatom assemblages, aquatic invertebrate remains, aquatic pollen types and lithology data (Rucina *et al.*, 2009; Courtney Mustaphi, 2021b). The charcoal accumulation rate (CHAR) record of the Rumuiku sediment core and the portion analysed for peak detection to reconstruct fire events ('+' symbols) and fire frequency (brown curve). Signal-to-noise index values are shown (black curve at left) with >3.0 cut-off detection (grey line; Kelly *et al.*, 2011). Range of fire return frequencies (yellow envelope), 10th percentiles (orange), 25–75th percentiles (red) and the median (black line) estimated by the ensemble RFE approach. The calculated fire return intervals (FRIs) that used the robust fire events reconstructed from the sediment charcoal record of the entire record (at right, top) and for each pollen taxon-dominated assemblage zones (at right).

abundances of epiphytic diatom taxa (Courtney Mustaphi *et al.*, 2021b) and more rapid sedimentation rates (Rucina *et al.*, 2009). The hydroseral transition occurs just after the significant transition from pollen zone II to III, from *Podocarpus*-dominance to *Hagenia* forests (Fig. 4). Sedimentation rates ranged from 7.8 to 14.0 years cm^{-1} throughout the record analysed with a median rate of 10.3 years cm^{-1} (mean = 10.6 years cm^{-1}) (Fig. 4 at left). Charcoal concentration values averaged 82 pieces cm^{-3} throughout the record, with lower magnitudes following the forest transition. The analysis presented here is focused on the two fire regime zones based on the charcoal record between the *Podocarpus*-dominated pollen zone and forest type section from 27 000 to 21,200 cal a BP (Rumuiku pollen zones I and II) and the *Hagenia*-dominated zone (after 21 200 cal a BP, pollen zones III and IV) based on the pollen zonation and amplitude differences of peaks and varying background rates observed in the charcoal record.

The record was divided at 21 200 cal a BP by pollen zones and charcoal with a pollen assemblage change from *Podocarpus*- to *Hagenia*-dominated, lower mean charcoal and lower charcoal peak amplitudes, and the onset of hydroseral succession from lake to wetland. Even with no significant change in sedimentation rates after 21 200 cal a BP (Fig. 4), the charcoal record has a nearly stepwise decrease in mean and variance amplitudes that are concomitant with the abrupt and persistent increased *Hagenia* pollen abundances that suggested a changed forest type in the catchment (Rucina *et al.*, 2009). We explored peak analysis (RFEs) that used both the entire charcoal record of 1469–500 cm (27 000–16 500 cal a BP; Supporting Information Figs S2–S5) and then focus on two subset records divided at 21 200 cal a BP. The apparent stepwise change in CHAR cannot be disentangled from the influence of taphonomy or vegetation and fire ecology

changes, and the techniques used should be robust to significant ecosystem changes (Blarquez *et al.*, 2013).

A total of 64 RFEs were estimated for the entire record analysed (27 000–16 500 cal a BP) that produced 63 FRI estimates (Fig. 4, top right) with a median FRI of 110 years (mean = 160 years). The *Podocarpus*-dominated zone had a median FRI of 120 years (mean = 155 years) and the *Hagenia*-dominated zone had a median FRI of 110 (mean = 167 years). We did not fit a model distribution to the FRI distribution and instead we present the arithmetic descriptive statistics because there is no evidence for whether the performance of Weibull or negative exponential distributions (or another distribution) are appropriate models of the FRIs of Afromontane forests (compare with other forest types: Johnson and Wagner, 1985; Moritz *et al.*, 2009). The FRI distributions for the *Podocarpus*- and *Hagenia*-dominated zones are both right-skewed but are different (Fig. 4 at right). The smoothed fire frequency suggests there were 4–8 fires per 1000 years, with the highest frequency centred at 23 500 cal a BP (Fig. 4).

The palaeofire reconstruction approach of RFEs was applied to the older sediments that have the properties of a stable sediment accumulation rate of ~10 years per sample (contiguous 1-cm intervals), stable montane forest assemblage (pollen zones I and II; Rucina *et al.*, 2009), and relatively high charcoal concentrations and accumulation rates (range of 3–672 pieces cm^{-3} , mean = 120, standard deviation = 102 pieces cm^{-3} , $n = 504$ of the 969 samples analysed for charcoal content) (Fig. 4). The calculated signal-to-noise index (SNI) values for this section were generally >3.0, with the exceptions of when SNI reached 2.8 during 23 710–23 460 cal a BP ($n = 26$ samples, 5.2% of the analysed record) and an edge effect at the very beginning of the time series (Fig. 4), which supported that the signal was appropriate for a time series peak component analysis for the duration of pollen zones I and II

(Kelly *et al.*, 2011). SNI values are moderate (>3.0) because of the relatively high-amplitude peaks and standard deviation of the charcoal record in the older section of the core, under the catchment charcoal transport and preservation of palaeolake Rumuiku conditions. To our knowledge, this is the first record used for a quantitative palaeofire reconstruction in Africa and that closely fits the assumptions developed for the CHAR peak analysis approach (Higuera *et al.*, 2009; Blarquez *et al.*, 2013; Crawford and Vachula, 2019).

Discussion

Palaeofire reconstruction and uncertainties

The vegetation record of Rumuiku has a major compositional change at 21 200 cal a BP from pollen zone II to III (Fig. 4) and this change to *Hagenia*-dominated vegetation cover probably produced changes in total forest biomass within the catchment, different fire–vegetation interactions and potentially different charcoal taphonomic processes (Whitlock *et al.*, 1997; Marlon *et al.*, 2006; Courtney Mustaphi *et al.*, 2015). The FRIs reconstructed from the Rumuiku crater palaeolake sediments from 27 000 to 21 200 cal a BP (Fig. 4) show a temporally heterogeneous distribution with short multidecadal return intervals (<100 years), intermediate duration return intervals (100–200 years) and longer return intervals (200 to a maximum of 490 years) (Fig. 4). The temporal heterogeneity of FRIs (Johnson and Gutsell, 1994) reconstructed at Rumuiku suggest that FRI variability is one of the disturbance ecology mechanisms that contribute to the patchy mosaic of montane forest subtype associations and stand structures around Mount Kenya. Multidecadal-scale burning evident in agroforestry stands in northwestern Mount Kenya produced estimates of fire rotation durations of 87–92 years (Poletti *et al.*, 2019). Northwestern Mount Kenya, which included some patches of indigenous forests, has a drier hydroclimate, is highly modified by human land uses and the total area is significantly larger than the Rumuiku wetland catchment. At present, there are few additional sources of palaeoenvironmental evidence to compare with these results. It is difficult to assess whether the shorter FRIs (<100 years) could be related to secondary peaks caused by continued erosion of post-fire surface soil charcoal on the Rumuiku catchment or if the peaks are true relatively rapid reburns. The variability in fire weather, the vegetation regrowth patch conditions and ecohydrological feedbacks could promote drier conditions and thus increased flammability as the forest stands regenerated. To date, there are no publications that provide support for these mechanisms or occurrences. Reconstructed mean annual temperatures at neighbouring Sacred Lake on the mountain (2350 m asl) varied between 13 and 17 °C from 27 000 to 21,200 cal a BP (Loomis *et al.*, 2017), but a quantitative reconstruction of local hydroclimate has not been developed. Qualitative evidence from the Rumuiku record derived from the aquatic plant pollen, diatom and presence data of aquatic invertebrates (*Daphnia* ephippia, Bryozoa statoblasts, oribatid mites) suggest a hydros-eral succession from shallow lake to wetland well after 21 500 cal a BP (Courtney Mustaphi *et al.*, 2021b); but the sampling resolution for the pollen data limited further precision for interpretation of the pattern of change at.

At present, there are no additional proxy data or available palaeofire techniques to independently corroborate the peak analysis and the estimates potentially underestimate past FRIs (Finsinger *et al.*, 2014). Observations (Pisaric, 2002) and charcoal source area and transport studies (Woodward and Haines, 2020; Vachula, 2021) from temperate ecosystems

have shown the spatial fidelity of charcoal records is influenced by fires from beyond the watershed (Lynch *et al.*, 2004; Adolf *et al.*, 2018; Vachula *et al.*, 2018; Hennebelle *et al.*, 2020), with implications for the interpretation of sediment–charcoal data (Ohlson and Tryterud, 2000; Tinner *et al.*, 2006; Leys *et al.*, 2015, 2017). Indeed, single fragments of grass charcoal from burned savannas have been observed to be transported 10 km across relatively flat areas during the evening by the authors. The contribution of long-distance transport of charcoal to background charcoal accumulation rates on mountain areas has yet to be assessed (Courtney Mustaphi *et al.*, 2021a, 2022). Future studies should incorporate quantification of charcoal transport and deposition in tropical mountain areas, similar to approaches for pollen (Schüler, 2012; Ssemmanda *et al.*, 2014; Schüler and Hemp, 2016) and charcoal in temperate ecosystems (Adolf *et al.*, 2018). The fire weather and convection patterns for lofting charcoal particles into the atmosphere have not been explored and remain an emerging study area for tropical mountains and lowland source areas of charcoal (Courtney Mustaphi *et al.*, 2022).

Although *Juniperus*, *Podocarpus* and *Hagenia* co-occur under similar climate conditions and recruit in monospecific stands following fire, *Hagenia* germination rates are highest in bare soils following ecological disturbances that open surfaces and canopy, and as the forest develops, *Hagenia* stands maintain a less dense canopy (Bussmann, 2001). These mid-elevation montane forest types occupy similar temperature–moisture climatic conditions on Mount Kenya (Niemelä and Pellikka, 2004; Zhou *et al.*, 2018) and variability in FRIs may contribute to the interspecific competition of the dominant tree taxa and promote the spatial heterogeneity of forest stands (Fig. 5; and see supplementary information in Courtney Mustaphi *et al.*, 2021b). The fire ecology of the moist forests of Mount Kenya has not been fully documented, including information on fire weather and climatology, ignition sources and rates, and the conditions and effects of multiple ecological disturbance interactions (e.g. windfall, wildlife interactions, plant diseases, plus fire) (White, 1979), and notably, prior to significant modification by human agency. Fire regimes in the mixed-species broadleaf forests that are *Podocarpus*- or *Juniperus*-dominated experience low-frequency (not quantified in previous studies), high-severity, stand-replacing fires that have been observed to be replaced by even-aged stands (Wimbush, 1937; Bussmann, 2001). Fire frequency distributions and quantifications of ‘low-frequency’ fires, with return intervals longer than several decades, have not been published in previous studies. Fire statistics of the past few decades at lower elevation agroforestry areas in the leeward northwestern area of Mount Kenya provide some insight into spatiotemporal patterns (Poletti *et al.*, 2019). Fires can benefit both *Podocarpus* and *Juniperus* forests, leading to nearly monospecific stands, and dominance may also relate to seed germination conditions or local site factors (Sharew *et al.*, 1996). Other forest type associations with abundant *Ocotea* or *Hagenia* have overlapping hydroclimatic ranges and elevational distributions on the highlands of eastern Africa, supporting the importance of non-climatic ecological controls on forest compositions of the co-dominant trees (Bussmann, 2001).

Hagenia forests benefit from disturbances that cause open canopies with abundant light to establish and maintain and *Hagenia* seeds, which are easily wind-blown in large numbers to open areas (Fetene and Feleke, 2001; Lange *et al.*, 1997; Young *et al.*, 2017; Grímsson *et al.*, 2021). Mature *Hagenia* trees are fire-adapted with relatively flakey, resistant bark (Fetene and Feleke, 2001) and bole architecture that reduces fuel laddering from the ground surface to canopy. In *Hagenia*

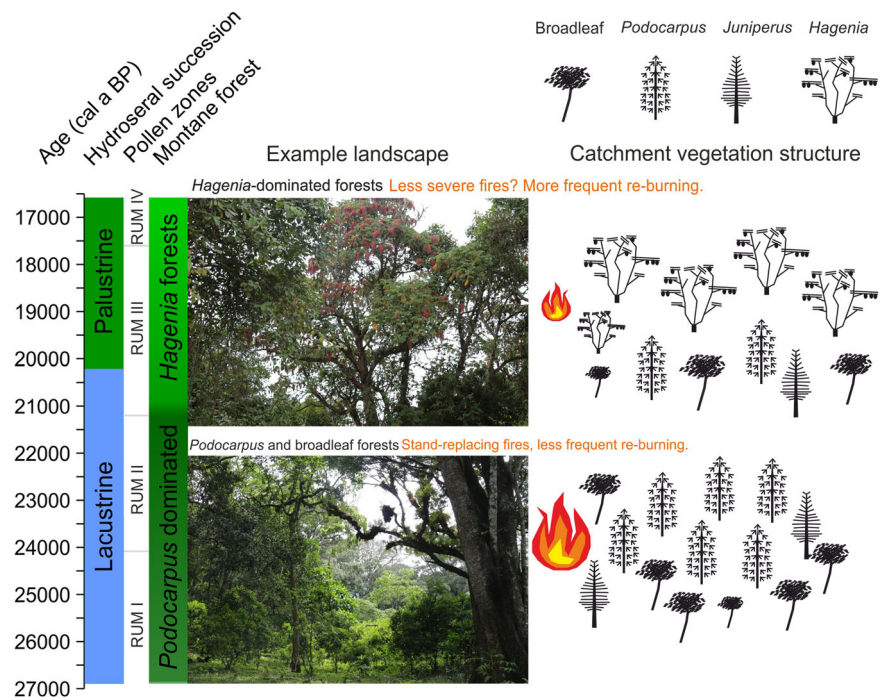


Figure 5. Pollen zones and data are summarized into forest type, inferred forest structure and fire type schematics at middle and right of the diagram. Photographs by Colin Courtney Mustaphi.

forests, fire regimes may be characterized by lower intensity burns that are more frequent, and potentially, surface fires if graminoid and detrital fuels (litter) accumulate in less dense forests (Fig. 5). Even in relatively dense *Hagenia* stands, grazing–fire interactions in modern forests of Ethiopia inhibited surface fire activity (Johansson and Granström, 2020), but herbivore grazing pressures prior to African defaunation during the Pleistocene and Holocene would have been different from what is observed today (Phelps *et al.*, 2020; and see Hempsom *et al.*, 2017). In some cases, very large individual *Hagenia* trees tower above the surrounding canopy, such as on some slopes in Ethiopia (Umer *et al.*, 2007) and some of the northern Tanzania highlands. An example is along the Themí River catchment, Mount Meru, although this could be due to conservation interventions and not solely abiotic ecological disturbance regimes. *Hagenia* at its upper elevation limit can persist in fire-sheltered areas among Ericaceous vegetation, but may be reduced by short-duration (not quantified) FRIs (Johansson and Granström, 2020) if the fire severity is sufficient enough to cause mortality (see also Gil-Romera *et al.*, 2019). The establishment of *Hagenia* stands modifies surface fuels through the seasonal accumulation of large numbers of shed flower parts and anemophilous seeds and may modify soil nutrients over the long term (Habtemariam and Woldetsadik, 2019) (Fig. 5).

Challenges and opportunities for future research

Previous observations and explanations have suggested the role of stand-replacing fire and complex fire–vegetation interactions for some of the spatial vegetation patterns in highland forests across eastern Africa (Wimbush, 1937; Lange *et al.*, 1997; Wesche, 2000). Re-analysis of the Rumuiku sediment–charcoal record presented here generated the first quantitative estimates of forest fires in tropical Afrotropical forests. Charcoal-based fire reconstruction methods have been developed for lacustrine deposits in ecosystems with long FRIs that experience high-severity fires, for example boreal forests (Higuera *et al.*, 2009; Clear *et al.*, 2015), temperate mixed conifer-dominated forests (Long *et al.*, 1998; Gavin *et al.*, 2006; Morris *et al.*, 2013; Courtney Mustaphi and Pisaric, 2013, 2014a; Davis *et al.*, 2016) and forests with mixed-severity fire regimes (Courtney Mustaphi and Pisaric, 2014a). Aggregating sediment charcoal records is

also useful for comparisons between different sites (Daniau *et al.*, 2010) at intermediate and larger spatial scales (Baker, 1989; Falk *et al.*, 2007). Sediment–charcoal studies in temperate ecosystems have the potential to be compared with dendrochronological palaeofire evidence (Brossier *et al.*, 2014; Barhouni *et al.*, 2019) and observational records (Courtney Mustaphi and Pisaric, 2018). Dendrochronological sources of paleofire evidence have yet to be applied to tropical montane forest of eastern Africa (Henry *et al.*, 2019b). Remote sensing products, such as Royal Air Force air photography (from the 1940s and 1950s), early satellite observations (1960s–1980s), in combination with modern earth observations and fire detection satellites could provide some additional evidence for decadal-scale fire activity in the mountain forests. These additional tools are limited by temporal and spatial resolutions, and data aggregation challenges, and still lack the long duration for centennial-scale FRIs (Marchant *et al.*, 2018; Courtney Mustaphi *et al.*, 2019). Archival sources also supplement historical knowledge of fire activity, yet available sources have focused on fires in savannas and shrublands (ex. Sinclair, 2012), whereas fires in the moist montane forests have less frequently been presented (Wood, 1965a, 1965b; Spinage, 2012; Aleman *et al.*, 2018).

Recent observational fire records are limited for exploring past fire regimes as the recent history reflects the significantly altered direct and indirect anthropogenic effects, such as accidental or purposeful burning, introduced plant taxa, and forest wildlife defaunation. Local-scale modelling provides another source of evidence for fire regimes in wet tropical forests, but many studies have focused on regional, continental and global scales (Hantson *et al.*, 2016, 2017, 2020). Modelling fire at smaller spatial extents would be more applicable for national, subnational and land management institutions for characterizing and planning ecosystem management. Exploring fire models, both heuristic (Van Wagner, 1978; Johnson and Gutsell, 1994; McCarthy *et al.*, 2001; Iglesias *et al.*, 2015) and computational (Pfeiffer *et al.*, 2013; Lasslop *et al.*, 2014, 2018; Hantson *et al.*, 2020), for relatively small spatial areas have yet to be developed for the montane forests of eastern Africa (Lasslop *et al.*, 2016).

Analysing the potential of other palaeoenvironmental research approaches, or combined approaches, for palaeofire

records and disturbance ecology has yet to be a major focus in tropical ecosystems. Use can be made of other palaeoenvironmental archives (tree rings, soils, cave, marine sediments, glacial ice) (Marlon, 2020), other sediment analyses of fire proxies such as pyrogenic chemicals (Battistel *et al.*, 2017; Karp *et al.*, 2020), subfossil charcoal morphologies (Courtney Mustaphi and Pisaric, 2014b; Courtney Mustaphi *et al.*, 2022; Hubau *et al.*, 2015) and historical ecology (Phillips, 1965; Fanstone, 2016). Dendrochronological techniques for establishing past FRIs have yet to be developed for these tropical forests and have not been used to establish estimates (Higuera *et al.*, 2011b; Brossier *et al.*, 2014; Barhoumi *et al.*, 2019). In the tropics, there has been some use of long-lived trees for investigating stand age distributions (Swart, 1963; Coughenour *et al.*, 1990; Patrut *et al.*, 2013) and stand ages (Wyant and Reid, 1992; Martin and Moss, 1997; Maingi, 2006; Patrut *et al.*, 2020), including applications for fire histories by analysing fire scars on trees (Richardson, 1988; Verlinden and Laamanen, 2006; Patrut *et al.*, 2010). Only a handful of dendroclimatological records exist for eastern Africa and their potential has yet to be fully investigated (Trouet *et al.*, 2006). Analyses of soil profiles using sedimentological, palaeobotanical and palaeofire techniques add additional evidence on past fire activity (Kasin *et al.*, 2013; Montade *et al.*, 2018). In soil stratigraphies, temporal resolution and uncertainties are rarely as constrained as lacustrine and palustrine sediment records, such as Rumuiku (Rucina *et al.*, 2009). Anthropological studies in eastern Africa have investigated purposeful human use of fire on savannah landscapes in eastern Africa (Anderson and Lochery, 2008; Butz, 2009; Kamau and Medley, 2014), coastal forests (Ming'ate and Bollig, 2016), and in the foothill forests of mountain areas (Nyongesa and Vacik, 2019). Newspaper reports of forest fires, early European documents and Forest Service archives have not been fully analysed to develop historical and archival records of past fire activity (for examples see Spinage, 2012; Nyongesa and Vacik, 2018; Henry *et al.*, 2019b). Fire and vegetation modelling studies focused on the catchments of Mount Kenya would be useful for exploring biodiversity, forest structural diversity and human–environment interactions relevant to land management and policy.

The spatial and temporal patterns of ecological disturbances deserve particular attention in the moist Afromontane forests, to explore and analyse disturbance effects on the spatial distribution of forest types and biodiversity and ecosystem resilience of managed forests of high conservation and societal value. Few palaeoenvironmental studies have investigated multiple ecological disturbance interactions, and records such as Rumuiku offer some potential for multi-proxy single study site analyses using the potential of high-resolution subsampling designs and geochronologies (see Courtney Mustaphi and Pisaric, 2018; Rey *et al.*, 2019). Disturbance dynamics have been shown to be important in nearby wooded tropical ecosystems (Anderson *et al.*, 2008). For example, the combination of elephant damage plus fires has been shown to be an important contributor to savannah tree demographics and mortality in parts of the Serengeti (Dublin *et al.*, 1990; Sharam *et al.*, 2006; Morrison *et al.*, 2016; Rugamalila *et al.*, 2016). The interaction of several ecological disturbance types in forests would be a useful avenue for investigating the legacy effects of multiple processes and for conservation.

Prospects

Quantification of fire regimes is a shared knowledge gap among the research agendas of palaeoecological research, ecology, conservation sciences and land management

(Veblen, 2003; Rull, 2010, 2014; Gillson and Marchant, 2014; Courtney Mustaphi *et al.*, 2019). Archival and observational data should be collated and analysed to estimate historical fire frequency regimes around Mount Kenya. The results presented here are the first estimations of FRIs using one palaeofire technique applied to a single mid-montane catchment on the western side of the mountain. This example presents a record of past ranges of FRI variability of montane forests prior to significant (or evident) anthropogenic modification and a geological period with lower atmospheric CO₂. As climate change, introduced species, CO₂ increases and human population pressures increase on the remaining forested areas of the mountain, knowledge of fire regimes helps define priority forest stands and stands experiencing more frequent fires. Fire regime changes facilitate ecological changes and could be a consideration for allocating forest fire suppression effort, fire prevention or areas for non-intervention on the mountain. Changing fire regimes at the interfaces of primary forests and agroforestry causes changes at the ecotonal edges (Thijs *et al.*, 2014; Wekesa *et al.*, 2019; Cardoso *et al.*, 2021) as well as at indigenous ecotonal zones within protected areas (Wesche, 2000; Wesche *et al.*, 2003; Hemp and Beck, 2001). Future projects investigating palaeofire in Afromontane forests should be co-produced with land users, and land management and academic stakeholders to align priority research questions (Seddon *et al.*, 2014; Chazdon *et al.*, 2017) and facilitate the longer-term deployment of sediment and charcoal traps in the field to improve the calibration of sediment–charcoal studies to the level of development available in temperate forests (for an example see Adolf *et al.*, 2018). Studies quantifying ecological disturbance regimes are necessary for the long-term management of Afromontane forests, to understand spatially heterogeneous patterns of compositions and structure and the influence on biodiversity on ecosystem functioning. Rehabilitation of montane forest areas requires knowledge of disturbance ecologies to manage wildlife habitat spaces, fog forest ecohydrology (Omoro *et al.*, 2010; Aerts *et al.*, 2011; Thijs *et al.*, 2014; Los *et al.*, 2019), and riparian (Thijs *et al.*, 2012) and wetland areas (Wesche *et al.*, 2003; Macharia *et al.*, 2010; Githumbi *et al.*, 2021) crucial to the 'water tower' ecosystem functioning of Mount Kenya (Funnell, 2003; Liniger *et al.*, 2005; Notter *et al.*, 2007) and to the communities around central Kenya (Bussmann, 1999; Wiesmann *et al.*, 2000; Aeschbacher *et al.*, 2005).

Conclusions

The Rumuiku wetland palaeoenvironmental record provided an opportunity to develop a first-order estimation of past ranges of FRIs for this small mid-montane catchment. The montane forest assemblages represented in the Rumuiku record still persist on the mountain today, but have been modified by climate variability, land use and forest resource pressures and introduced species throughout the Holocene to present. The charcoal record shows a stepwise change in forest type at 21 200 cal a BP, and we used the charcoal record from 27 000 to 21 200 cal a BP, during Rumuiku pollen zones I and II, to reconstruct fire events and frequencies during the *Podocarpus*- and *Juniperus*-dominated montane forest. The results show a temporal heterogeneity in a single catchment area, showing that fires potentially may be relatively rapid reburns (<100 years), of moderate duration (100–200 years), and infrequently very long (200–430 years). Future work should make more use of collating and interpreting observational records complemented with archival research, computer models and the development of

conceptual heuristic models for fire in moist montane forests to improve tropical palaeofire investigations. Research should garner multistakeholder co-produced perspectives on forest management to improve the longevity and success of research outputs. Alignment of research agendas with land management and local land users and improved dissemination promotes research insights that inform land management options and decisions (Capitani *et al.*, 2016; Courtney Mustaphi *et al.*, 2019; Kariuki *et al.*, 2021). The observed pattern toward larger fires in tropical latitudes and tendency for anthropogenic activities to homogenize forest fire regimes could put forest biodiversity at further risk on Mount Kenya. Quantifying the spatial and temporal distributions of FRIs and other fire regime components (fire sizes, seasonality, intensities, severities; Maezumi *et al.*, 2021) are important for long-term management of these moist montane forests with relatively long durations (decades to centuries) between fires but with a degree of spatial heterogeneity that remains unquantified.

Supporting information

Additional supporting information can be found in the online version of this article.

Supplementary Figure 1. View of Rumuiku wetland from the eastern edge facing southwest (0.118583°S, 37.5611°E; 2160 m asl), Mount Kenya National Park and forest reserve, Kenya (Courtney Mustaphi *et al.*, 2021). Photographs taken in 2014 by Colin Courtney Mustaphi.

Supplementary Figure 2. Signal to Noise Index (SNI) and Kolmogorov-Smirnov Goodness of Fit (GOF) p values of the Rumuiku wetland charcoal concentration data using five techniques to define the varying background rate of charcoal accumulation across variable moving window lengths. The median of the ensemble runs (black lines), the 25th and 75th percentiles (red lines), and the 5th and 95th percentiles (blue lines), are shown for SNI and GOF. Window lengths shaded in grey were rejected and the zone in white was retained during the analysis and the number is shown at top (N). Output designs and code by Blarquez *et al.* (2013) and incorporated Higuera *et al.* (2009) and Gavin *et al.* (2006).

Supplementary Figure 3. Ensemble sums of reconstructed fire events that contributed to establishing robust fire events (RFEs; '+' symbols) (Blarquez *et al.*, 2013).

Supplementary Figure 4. Fire return interval (FRI) distributions of each of the five techniques for background charcoal accumulation rate estimation techniques (Blarquez *et al.*, 2013). Weibull distributions (black line) were fitted and parameters and number of fire events shown.

Supplementary Figure 5. The ensemble of fire frequency reconstructions (Blarquez *et al.*, 2013). Warm colours show the mid percentiles 25–75, cool colours show higher percentiles >75 and <25, the median (black line), and dashed black lines show a filtering of the CHARraw using a rLOWESS with a 700 year window width (the bootstrapped 90% confidence intervals are displayed using dashed lines).

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Abbreviations. asl, above sea level; BP, before present (1950 calendar year); CE, Common Era; CHAR, charcoal accumulation rate; FRI, fire return interval; LOWESS, locally weighted scatterplot smoothing; RFE, robust fire event; SNI, signal-to-noise index.

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