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Highland forest dynamics across equatorial East Africa during the end of the African humid period

Sarah J. Ivory [a,b,*], Elizabeth MacDougal [c], Andrea Mason [d], Eleanor Pereboom [e], Sloane Garelick [d], Katherine Ficken [f], Matthew J. Wooller [g], Bob R. Nakileza [h], James Russell [d]

[a] Departmentof Geosciences, Penn State University, State College, PA, USA
[b] Earth and Environmental Systems Institute, Penn State University, State College, PA, USA
[c] Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA, USA
[d] Department of Earth, Environment, and Planetary Sciences, Brown University, Providence, RI, USA
[e] Department of Human Evolutionary Biology, Harvard University, Cambridge, MA, USA
[f] Department of Geography, Swansea University, Singleton Park, Swansea SA2 8PP, UK
[g] Water and Environmental Research Center, University of Alaska Fairbanks, Fairbanks, AK, USA
[h] Department of Environmental Management, Makerere University, Kampala, Uganda

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ABSTRACT

Tropical mountain ecosystems hold immense ecological and economic importance, yet they face disproportionate risks from shifting tropical climates. For example, present-day montane vegetation of East Africa is characterized by different plant species that grow in and are restricted to certain elevations due to environmental tolerances. As climate changes and temperature/rainfall zones move on mountains, these species must rapidly adjust their ranges or risk extinction.

Paleoenvironmental records offer valuable insights into past climate and ecosystem dynamics, aiding predictions for ongoing climate change impacts. In particular, warming and wetting in tropical East Africa during the mid-Holocene resulted in both lowland and highland forest expansion. However, the relative impacts of rainfall and temperature change on montane ecosystems along with the influence of lowland forest expansion on montane communities is not completely understood. We use fossil pollen to study the vegetation changes in two lakes at different altitudes in the Rwenzori Mountains, Uganda: Lake Mahoma (Montane Forest belt) and Upper Kachope Lake (Afroalpine belt). Further, using the newly relaunched African Pollen Database and recent temperature reconstructions, we provide a regional synthesis of vegetation changes in the Rwenzori and then compare this with changes observed from other equatorial East African montane sites (particularly Mt Kenya).

In the early to mid-Holocene in the Rwenzori Mountains, trees common today in lowland forests dominated, driven largely by warmer temperatures. After 4000 years ago (4ka), Afromontane forest trees along with grasses progressively replaced lowland trees. Not all sites experienced identical transitions. For instance, at Lake Rutundu on Mt Kenya at the same elevation as Lake Mahoma, bamboo expansion preceded Afromontane forest growth, likely influenced by variations in fire. Variance partitioning indicates that each site responded differently to changes in temperature and rainfall. Therefore, these site-specific ecological responses underscore the importance of considering biogeographic legacies as management strategies are developed, despite similarities in modern ecology.

1. Introduction

The biogeography of African vegetation is strongly shaped today by legacies of human land-use and climate (Ellis et al., 2008; Marchant et al., 2018; Mottl et al., 2021). Although broad geographic zones are largely related to hydroclimate, non-climax vegetation such as forest-savanna mosaics and relict patches of dense forest within bushland are thought to be a result of the interacting impacts of drying of climate during the late Holocene as well as anthropogenic alteration (White, 1983; Verschuren et al., 2002; Ivory and Russell, 2016, 2018;

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* Corresponding author.
E-mail address: sarah_ivory@psu.edu (S.J. Ivory).

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Colombaroli et al., 2018; Marchant et al., 2018; Aleman et al., 2020). There is also evidence that montane vegetation distributions have been shaped by interacting climatic and anthropogenic forces, such that previously continuous low elevation distributions of some taxa now limited to the mountains have been fragmented only since the last ~13kyrs (Dupont et al., 2011; Tocheri et al., 2016; Ivory et al., 2018; Casas-Gallego et al., 2023), but records of climate and vegetation from African mountains remain limited.

Understanding the processes that have shaped the structure, composition, and biodiversity of this complex vegetation is becoming increasingly important within the context of ongoing climate change. For example, the most recent report from the Intergovernmental Panel on Climate Change (IPCC) has suggested that Africa is likely to warm to temperatures not currently observable in the region (IPCC AR6, 2023). Dahinden et al. (2017) demonstrated that climates within the Afromontane ecosystem, in particular, are categorized as areas of "disappearing climate," and modeling studies suggest that these forests are likely to undergo an ~80% loss of range (Ivory et al., 2019). However, intriguingly, these same studies show uneven sensitivity to climate across species within this biodiversity hotspot, as some taxa may be less sensitive to temperature than previously expected (Ivory et al., 2016). However, there are few direct observations of montane forest taxa responses to temperature.

During the early Holocene, increased global temperatures and an insolation maximum in the northern hemisphere resulted in an invigorated hydrological cycle in much of the tropics (Ritchie et al., 1985; DeMenocal et al., 2000; Marcott et al., 2013). In Africa, temperature reconstructions from microbial membrane lipids suggest that temperature rose from the late Pleistocene until the mid-Holocene, when they were 1–2.5 °C warmer than today (Powers et al., 2005; Tierney et al., 2008; Loomis et al., 2017; Dee et al., 2021; Garelick et al., 2021). In addition, records based on the hydrogen isotopic composition of leaf waxes (δD_{wax}) indicate that rainfall was higher than the present day from the early to mid-Holocene (Tierney et al., 2008; Konecky et al., 2011; Berke et al., 2012; Shanahan et al., 2015; Garelick et al., 2022). Evidence from pollen records suggests a reduction in rainfall seasonality in some regions as monsoons extended further into central and western Africa, reducing the length of the dry season and therefore increasing seasonal moisture availability during this time (Vincens et al., 2007; Ivory et al., 2012). However, unlike the homogeneity of temperature change, increases in rainfall and decreased rainfall seasonality likely varied greatly over short distances, particularly in areas of topographic complexity such as equatorial East Africa. During this time, closed-canopy semi-deciduous forests expanded across much of equatorial East Africa (e.g. Livingstone, 1967; Kendall, 1969; Jolly et al., 1997; Ivory et al., 2018; Phelps et al., 2020). In particular, evidence for expansion of forests with Guineo-Congolian affinities eastward from the Congo Basin and over the western rift is observed at Lake Edward and Lake Victoria as well as farther south in Lake Tanganyika (Kendall, 1969; Vincens, 1991; Ivory et al., 2018).

Although this lowland forest expansion during the Holocene is relatively well understood, what is less clear is how climate change and forest expansion interacted with montane communities. For example, increased temperatures may have facilitated upslope migration of some lowland and submontane forest taxa into areas now occupied by Afromontane and Afroalpine plants. There is some evidence that such migrations disrupt the frequently-described zonation of montane communities, creating both novel combinations of forest taxa and resulting in the shrinking of some key high elevation ecosystems that have nowhere to migrate (Livingstone, 1967; Lézine, 2017; Ivory and Russell, 2018). In the Western Rift in particular, one of the seminal pollen records from the East African mountains, that of Livingstone (1962, 1967) from Lake Mahoma, has indicated upward dispersal of some lowland forest taxa into the highlands alongside extant Afromontane taxa created forest communities that do not co-exist today. However, the climatic and ecological controls driving this change in community assembly and its timing are highly uncertain due to the relatively few age constraints on this record and the lack until very recently of local, high-elevation quantitative temperature reconstructions.

Given the threats by climate to Afromontane ecosystems, it is important that we use long-term datasets to allow us to understand how species respond to climate both as individuals and how that shapes communities. For example, reconstructions of mid-Holocene temperature suggest that this was a time of warmer than modern temperatures in East Africa and thus may serve as an analog to future warming. Therefore, mid-Holocene to present paleoecological records from different elevations and across different mountains in equatorial East Africa allow us to evaluate the character and the similarity of ecological responses to the same climatic forcing. In this way, they may provide an essential stop gap for linking modern studies to future ecological trajectories required for developing management strategies.

Here, we present new and previously-published paleoecological data from the Rwenzori Mountains of western Uganda in order to evaluate ecosystem reorganization in response to climate change over the last 20kyrs. We also conduct a synthesis of pollen records from equatorial East Africa across an elevational gradient on two key equatorial mountains (Rwenzori Mountains and Mount Kenya). These records are integrated with quantitative reconstructions from paleoclimate studies, providing insights into the climatic context of biogeographic change and the sensitivity of major forest communities to climate variations from the mid-Holocene to the present. Despite the significance of this region, synthetic research focused on change across broad geographic regions and elevations is currently lacking. Our study aims to contribute to narrowing this gap, enhancing our understanding of Holocene geographic connections and the impacts of recent warm periods on these African highland forests.

2. Regional setting

The Rwenzori Mountains sit in the western arc of the East African rift system and lie directly on the equator at the border between the Democratic Republic of Congo and Uganda (0.3858°N, 29.8717°E; Fig. 1). The highest peak, Mt. Stanley, rises to 5109m asl. Modern climate in the region is dominated by high rainfall which varies between 2000-3000 mm/yr, with higher values on the eastern slopes occurring in two rainy seasons from mid-March to May and from September to mid-December with no true dry season (Osmaston, 1965; Eggermont et al., 2009). Temperature at high altitude varies more diurnally than seasonally, and freezing occurs occasionally above 3000m asl and regularly above 4000m asl (Rundel, 1994). Lake Mahoma (0.3456°N 29.9684°E; 2990m asl) is a moraine-dammed lake with a maximum depth of 25m that sits adjacent to the last glacial age terminal moraine (Livingstone, 1967; Russell et al., 2009; Kelly et al., 2014). The lake is generally circular and has no inlet. It is surrounded by a mixture of montane and bamboo forest. Upper Kachope Lake (0.3322°N, 29.8761°E; 3961m asl) is a moraine-dammed lake with steeply sloping sides surrounded by Ericaceous and Afroalpine vegetation.

3. Materials and methods

Afromontane communities across equatorial East Africa found in the Rwenzori, Mount Elgon, and Mount Kenya are presented in Fig. 2 as they have been described by Osmaston (1968), Hedberg (1970), White (1983), and Bussmann (2006). Elevational zonation in the Rwenzori follows a similar organization to most mountains across equatorial East Africa (Bussmann, 2006). In the lowlands below ~1800m asl, vegetation is dominated by mosaics of Somali-masai bushland, grassland, and wooded grasslands dominated by *Acacia*. Closed-canopy, lowland forests with Guineo-Congolian affinities do occur in small relict patches, such as the Bwindi Impenetrable Forest, and include semi-deciduous and evergreen trees such as *Myrica*, *Macaranga*, Ulmaceae (*Celtis africana*,

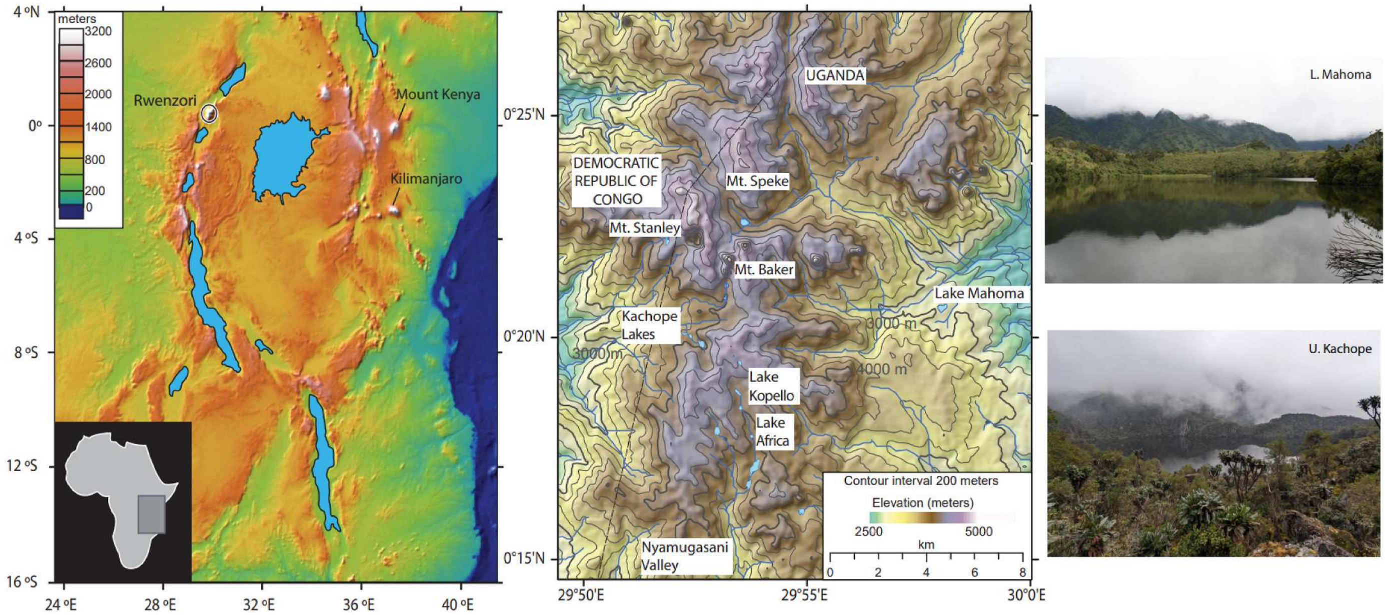

Fig. 1. (Left to right) Map of the elevation of East Africa showing with inset map with grey rectangle showing the region. Map of the Rwenzori Mountains showing the locations of key lakes, including Lake Mahoma and Upper Kachope Lake. Photos of Lake Mahoma and Upper Kachope Lake.

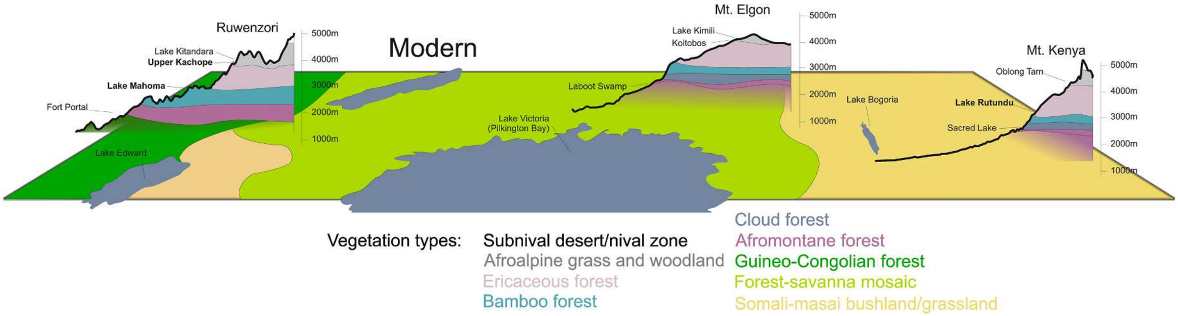

Fig. 2. Modern vegetation of equatorial East Africa including vegetation belts of the Rwenzori Mountains, Mt Elgon, and Mt Kenya. Sites indicated are those referred to in the text and bold text indicates data is presented in figures from these sites (Lakes Mahoma and Upper Kachope – this study; Livingstone, 1967; Garelick et al., 2022; Lake Rutundu – Wooller et al., 2003; Urban et al., 2015; Garelick et al., 2021).

Trema spp.), and Moraceae (Polhill, 1982; White, 1983). The transition from lowland to highland vegetation occurs as a gradient from these lowland forests to those that begin to include Afromontane forest species, such as *Podocarpus*. Above 1800m asl until ~2400m asl, Afromontane forest occurs which includes *Olea*, *Podocarpus*, *Dombeya*, and *Prunus africana*. Above this, on the wettest slopes, is a zone of bamboo forest reaching an upper limit between 2600-3000m asl and is dominated by *Sinarundinaria alpina*. Above the bamboo forest is a zone of dense Ericaceous forest which include *Erica arborea* and *Hagenia abyssinica*. Afroalpine communities are above 3900m asl, and herbaceous cover dominated by sedges (Cyperaceae) is common; however, iconic species of grounsels (*Dendrosenecio*) and giant lobelias (*Lobelia deckenii)* also occur. Beyond this elevation is the nival and sub-nival zone with little vegetation cover. The exact position of these zones on other mountains throughout equatorial East Africa varies to some degree. In particular, cloud forest replaces some of the bamboo zone in some places on Mounts Elgon and Kenya, however, species distributions largely follow this organization throughout the region (Bussmann, 2006).

Two new fossil pollen records are presented here from different elevations in the Rwenzori from Lake Mahoma (0.3456°N 29.9684°E; 2990m asl; Fig. 1) and Upper Kachope Lake (0.3322°N, 29.8761°E; 3961m asl; Fig. 1). At Lake Mahoma, a total of 24 pollen samples were analyzed covering the last 20kyrs with the highest sampling density in the Holocene (average Holocene temporal resolution 556 yrs, average overall resolution 833 yrs). These samples were taken from cores collected during two different field seasons. Core Maho08 (0.3449°N, 29.9680°E; water depth 13.2m) was collected in January 2008 using a Bolivia corer, and Core MAHO19 (0.3451°N, 29.9682°E, water depth 11.8m) was collected in January 2019 using a modified Livingstone square rod piston corer. Both cores were logged using a GeoTek multisensor core logger at Brown University. Logs of the magnetic susceptibility and core images were used to correlate sediment features, and a composite section was developed for Lake Mahoma as described in Garelick et al. (2022). From Upper Kachope Lake, 8 pollen samples were taken every 46.5–81.5 cmblf on core UPKAC08 (0.3310°N, 29.8775°E; water depth 10.9m). This core was collected in January 2008 using Bolivia and modified Livingstone square rod piston corers. Age models were constructed for both sites using the *bacon* age modeling package in R which calibrated the dates using IntCal20 (Blaauw and Christen, 2011; Reimer et al., 2020). The age model for Lake Mahoma is based on 16 accelerator mass spectrometer (AMS) radiocarbon dates on bulk organic carbon. This age model was developed by Garelick et al. (2022; Table 1; Supplemental Material). The age model for Upper Kachope Lake is based on 11 AMS radiocarbon dates on bulk organic carbon (Table 2; Supplemental Material).

All pollen samples were processed using standard methods for pollen

Table 1
Radiocarbon dates for Lake Mahoma. Accelerator mass spectrometry (AMS) radiocarbon dates for composite core from Lake Mahoma calibrated using IntCal20 (Reimer et al., 2020), adapted from Garelick et al. (2022).

Composite Depth (cm)	^{14}C Age (radiocarbon years BP)	^{14}C Age 1-σ error	Median Calibrated Age (calibrated years BP)	Calibrated Age 1-σ error
9.5	665	15	589	570–659
73.0	1840	20	1738	1710–1780
109.0	2890	30	3023	2964–3066
186.0	3930	20	4365	4299–4419
209.5	4630	30	5411	5313–5445
233.5	5430	30	6236	6205–6284
265.5	7290	45	8102	8029–8169
290.5	8800	50	9831	9693–10108
300.0	9390	60	10618	10515–10695
332.0	10750	80	12727	12677–12763
352.0	12050	65	13923	13809–14030
364.0	13700	95	16583	16389–16734
378.5	13800	65	16751	16622–16886
388.0	14200	100	17248	17108–17360
404.0	16000	130	19306	19157–19471
420.0	17600	160	21287	20953–21470

Table 2
Radiocarbon dates for Upper Kachope Lake. Accelerator mass spectrometry (AMS) radiocarbon dates for core UPKAC08 from Upper Kachope Lake calibrated using IntCal20 (Reimer et al., 2020).

Composite Depth (cm)	^{14}C Age (radiocarbon years BP)	^{14}C Age 1-σ error	Median Calibrated Age (calibrated years BP)	Calibrated Age 1-σ error
58.0	2290	30	2318	2184–2347
98.0	1550	25	1436	1383–1511
138.5	2990	25	3173	3080–3214
185.0	3340	40	3560	3487–3619
245.0	3040	30	3249	3182–3331
251.0	3180	30	3405	3374–3445
287.0	4110	30	4632	4531–4797
321.0	9240	40	10405	10300–10497
335.0	9090	35	10238	10211–10251
401.0	9000	35	10196	10178–10227
440.0	8230	40	9197	9038–9280

extraction (Faegri and Iverson, 1989). *Lycopodium* spores were added for calculation of pollen concentrations, and all samples were sieved at 10 μm to remove clays. Lake Mahoma pollen counts ranged from 339-425 grains per sample, and Upper Kachope Lake pollen counts ranged from 313-484 grains per sample. Taxon names and pollen habits were assigned in accordance with the nomenclature of the African Pollen Database (Vincens et al., 2006; Lézine et al., 2021). Pollen atlases (Maley, 1970; Bonnefille and Riollet, 1980), the photo library of the online African Pollen Database, and a reference collection at Penn State University were used to identify the pollen grains. In order to calculate percent abundance for each terrestrial pollen type in a given sample, the pollen counts for each taxon were divided by the total pollen sum less aquatics for that sample and multiplied by 100.

The software Tilia v3.0.3 was used to create pollen stratigraphic diagrams, after which, constrained sum of squares cluster analysis (CONISS) was used to determine the zonation (Grimm, 1987, 1990). The abundance values presented in the results represent the relative abundance of each pollen category averaged within each zone, unless otherwise specified. The pollen diagrams (Figs. 3 and 4) present select individual taxa and a summary of pollen habits (trees, herbs, indeterminate [may be trees, shrubs, or herbs], aquatics). The criteria for including an individual taxon were that it either represented more than 5% of the total pollen sum in at least one sample, or that it was an indicator of specific environmental or ecological conditions.

One key motivation for this study was to use pollen analysis on the new, well-dated Lake Mahoma sediment record of Garelick et al. (2022) to better constrain in time the Livingstone (1962, 1967) pollen record. Livingstone (1962, 1967) presented pollen data from a core taken from Lake Mahoma (0.3500°N; 29.9667°E; water depth 9.5m) in July 1960. These data were retrieved from the African Pollen Database on the Neotoma Paleoecology Database (Lézine et al., 2021; Williams et al., 2018). We will refer to this data throughout the text as the "Mahoma 1967" pollen data, and we will refer to the new pollen data presented here from the well-dated, composite record as "Mahoma composite". The Mahoma 1967 record includes 54 pollen samples taken every ~10 cm from the 570 cm core. The record is constrained in time by only three conventional radiocarbon ages on bulk organic matter (Livingstone, 1967). A new age model was made for this record in order to compare directly with the Mahoma composite record using the *bacon* age modeling package in R which calibrated the dates using IntCal20 (Blaauw and Christen, 2011; Reimer et al., 2020; Supplemental Material). Based on this age model, the Mahoma 1967 pollen samples span an

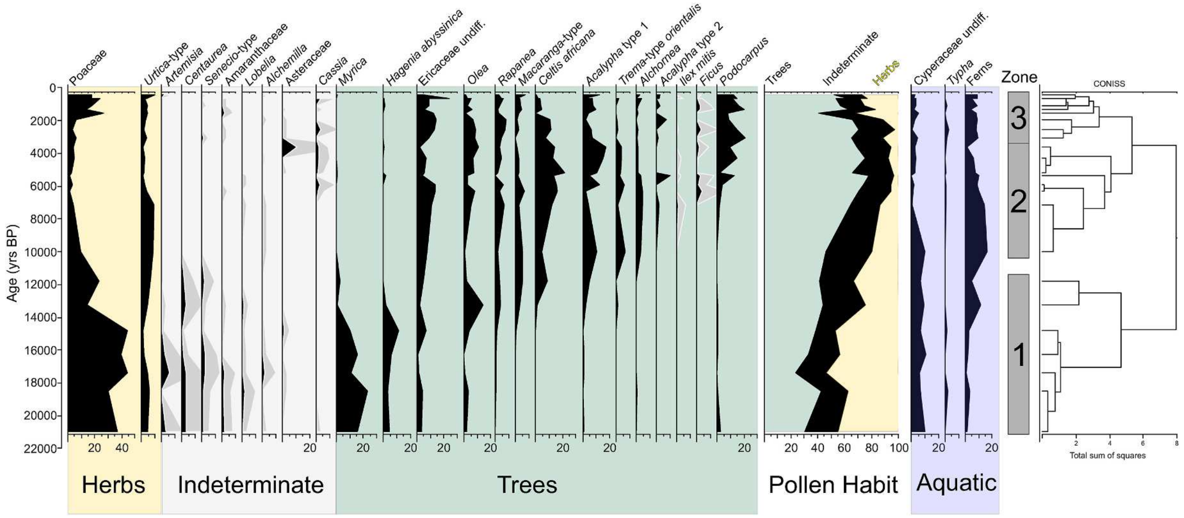

Fig. 3. Pollen percentage diagram from the composite core from Lake Mahoma (MAH008, MAHO19-3A, MAHO19-1B). Pollen abundances are relative to the pollen sum for all terrestrial taxa, aquatics calculated separately. Pollen taxa are color coded based on pollen habit (trees, herbs, indeterminate [may be trees, shrubs, or herbs], aquatics), zones were determined using a constrained cluster analysis (CONISS). Grey curves for some pollen taxa represent a 5% exaggeration.

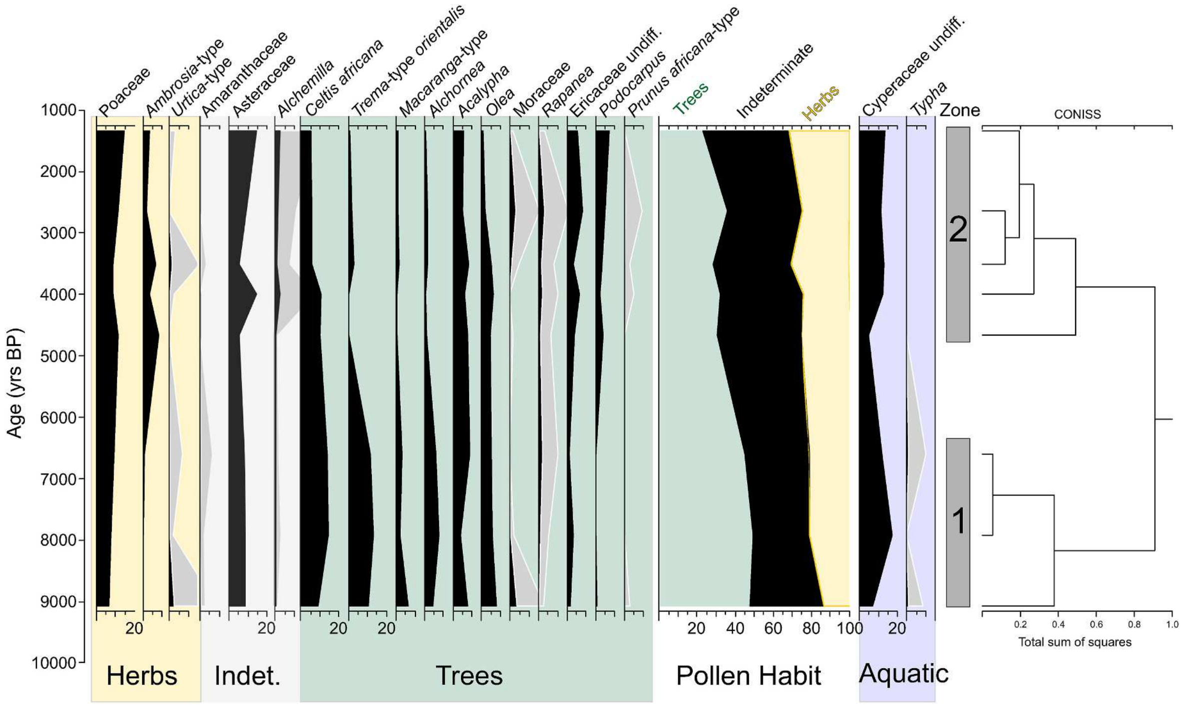

Fig. 4. Pollen percentage diagram from the core UPKAC08 from Upper Kachope Lake (MAH008, MAHO19-3A, MAHO19-1B). Pollen abundances are relative to the pollen sum for all terrestrial taxa, aquatics calculated separately. Pollen taxa are color coded based on pollen habit (trees, herbs, indeterminate [may be trees, shrubs, or herbs], aquatics), zones were determined using a constrained cluster analysis (CONISS). Grey curves for some pollen taxa represent a 5% exaggeration.

age range of 19165-461 years BP with an average temporal resolution of 370 years. Relative abundances were calculated using the same method as described above.

In order to evaluate vegetation change in relation to climate across elevations during the Holocene in the Rwenzori Mountains, the pollen records from Lake Mahoma and Upper Kachope were compared with pollen data from the lowlands at nearby Lake Edward (0.3723°S, 29.6098°E, 912m asl; Ivory et al., 2018). These data were retrieved from the African Pollen Database on the Neotoma Paleoecology Database (Williams et al., 2018; Lézine et al., 2021). Additionally, paleoclimate reconstructions from the region were accessed through the National Centers for Environmental Information (NCEI) Paleoclimatology archive. These included δD_{wax} values from Lakes Victoria (Berke et al., 2012) and Tanganyika (Tierney et al., 2008) as well as a reconstruction of mean annual temperature (MAT) from branched glycerol dialkyl glycerol tetraethers (brGDGTs) from Lake Mahoma (Garelick et al., 2022).

Further, to identify how the changes observed in the Rwenzori Mountains fit into the regional context of vegetation change in equatorial East Africa, published data from other sites in equatorial East Africa were selected for comparison. This comparison focuses on the pollen and climate records from Lake Rutundu (0.0333°S, 37.4333°E, 3078m asl) on Mount Kenya, as it sits at a similar elevation to Lake Mahoma. Pollen data from Lake Rutundu was presented in Ficken et al. (2002) and Wooller et al. (2003), and microcharcoal is presented in Urban et al. (2015); however, they are not available in any open access database. Therefore, the pollen and microcharcoal data were digitized using the online platform *DigitizeIt*. A brGDGT reconstruction of MAT and δD_{wax} values also are available from Lake Rutundu (Loomis et al., 2017; Garelick et al., 2021) and were also accessed through the NCEI archive.

In order to compare the vegetation and fire trends between Lakes Mahoma and Rutundu, several analyses were performed. To compare the timing of relative percentages of key ecological taxa from the pollen records, pollen data for Poaceae, *Podocarpus*, lowland forest taxa (*Celtis africana*, *Macaranga*-type, Moraceae, *Trema*-type *orientalis)*, and all other tree taxa from Lake Rutundu was resampled to the same time points as the Lake Mahoma composite record. This was chosen as the Lake Mahoma composite record has a lower sampling resolution. All of the highland sites analyzed in this study come from small lakes which receive no inputs from major rivers of streams. Therefore, we interpret the pollen signals from these sites to represent pollen input mostly from the airsheds around the lakes and therefore relatively local signals. Finally, in order to determine the relative influence of climate factors on the vegetation change at each site since the late Pleistocene, variance partitioning was conducted on the original data from each site. For each site, abundance data for key pollen taxa (Poaceae, Asteraceae, *Hagenia abyssinica*, Ericaceae undifferentiated (undiff.), *Podocarpus*, *Olea*, lowland forest, other trees) was Wisconsin-transformed prior to redundancy analysis in the *vegan* package in R (Oksanen, 2022). Partial models were created using the temperature reconstruction from each site and δD_{wax} values from Lake Rutundu as predictor variables in the redundancy analysis. δD_{wax} values from Lake Rutundu were used to constrain the influence of rainfall for the redundancy analysis at both sites over the last 20kyrs, because there is no published information about past rainfall from Lake Mahoma. However, the broad trends from Lake Rutundu are similar to those from a new, unpublished record from Lake Mahoma (Mason et al., in review) and other regional records (Tierney et al., 2008; Berke et al., 2012). Garelick et al. (2021) noted depletion in δD_{wax} values prior to ~19ka due to fractionation associated with LGM changes in lapse rate. This should not substantively change the analysis, which includes only one sample from this interval from Lake Mahoma. The variance explained in the partial models was then used to calculate the adjusted R^2 for each unique predictor variable as well as for their overlap (Borcard et al., 1992).

4. Results

4.1. *Lake Mahoma composite pollen record*

The Lake Mahoma composite fossil pollen concentrations are very high (on average 960,229 grains/cm^3), and pollen preservation in the core sediments is very good. The pollen record from Lake Mahoma comprised 122 pollen taxa, two types of freshwater algae, one category of fungal spores, and microcharcoal particles. The abundance of broken grains was never more than 3.5% and is on average 0.6%. The record has been divided into three zones, numbered chronologically, and pollen type abundances reported reflect the average abundance within that zone (Fig. 3).

Zone 1 (426.0–302.0 cmblf; 20.9-11.8ka) was characterized by high abundances of herbaceous pollen taxa. In particular, Poaceae pollen abundances (max = 44.5%) were at their maximum during this zone, along with other shrubby Afroalpine plants such as *Senecio*-type (1.4%), *Artemisia* (1.8%), *Lobelia* (0.75%), and *Alchemilla* (0.5%). Tree pollen was relatively low in abundance with two notable exceptions; *Myrica* (max = 23.3%) and *Hagenia abyssinca* (max = 4.6%) were at a maximum in this zone. Microchracoal influxes were on average 14,443.2 pieces/cm^2/yr.

Zone 2 (302.0–140.5 cmblf; 10.0-3.6ka) was characterized by increasing abundances of arboreal pollen taxa such as *Celtis africana* (13.7%), Ericaceae (8.1%), *Acalypha* (9.8%), *Trema*-type *orientalis* (4.0%), *Macaranga*-type (3.2%), *Olea* (5.5%), *Rapanea* (3.3%), and *Alchornea* (3.0%), as well as the understory herb Urticaceae (7.0%). Fern spore abundances (9.3%) also increased in this zone. Herbaceous pollen was sparse, with Poaceae pollen abundances at 4.1%. Microcharcoal influxes were on average 10,060.1 pieces/cm^2/yr.

Zone 3 (140.5–14.0 cmblf; 3.0-0.4ka) was characterized by declines in some of the tree pollen taxa dominant from zone 2 and increasing abundances of other arboreal pollen types, including *Podocarpus* (14.1%), Ericaceae undiff. (11.2%), and *Rapanea* (4.5%). Most arboreal pollen types decreased in abundance, including *Celtis africana* (4.7%) and *Acalypha* (6.4%), along with *Olea* (4.7%), *Trema*-type *orientalis* (0.4%), and *Macaranga*-type (2.8%). Urticaceae pollen also decreased (4.1%). Poaceae increased in pollen abundances to 14.8%. Microchracoal influxes increased to, on average, 16,061.0 pieces/cm^2/yr.

4.2. Upper Kachope

Upper Kachope fossil pollen concentrations were high (on average 88,629 grains/cm^3), and pollen preservation in the core sediments is very good: the abundance of broken grains is never more than 1.2% and is less than 1% in seven of the eight samples. The pollen record from Upper Kachope Lake is comprised of 85 pollen taxa, one type of freshwater algae, and microcharcoal particles. The record has been divided into two zones, numbered chronologically, and pollen type abundances reported reflect the average abundance within that zone (Fig. 4). For microcharcoal for Upper Kachope, only concentrations are presented given the low resolution of the sampling.

Zone 1 (440.0–330.0 cmblf; 9.0-6.6ka) was characterized by high percentages of arboreal pollen, particularly from *Celtis africana* (13.2%), *Acalypha* (7.2%), *Olea* (6.5%) *Alchornea* (6.4%), and *Macaranga*-type (4.1%). Also present in lower abundances were Ericaceae undiff. (2.3%), Moraceae (2.0%), *Rapanea* (1.3%), and *Podocarpus* (0.2%). Urticaceae pollen contributed 1.8% of the pollen in this zone. Other herbaceous pollen types were much less abundant and diverse. These included Asteraceae (16.0%, of which 6.7% represents *Senecio*-type), Poaceae (8.3%), and Amaranthaceae (0.5%). Aquatics included Cyperaceae (13.1%) and *Typha* (0.6%). Charcoal concentrations are on average 5411 pieces/cm^3.

Zone 2 (330.0–17.5 cmblf; 4.7-1.3ka) showed a decrease in arboreal pollen abundances such as *Celtis africana* (9.7%), *Olea* (5.7%), *Alchornea* (1.4%), and *Macaranga*-type (1.0%). However, there was an increase in the pollen abundances of some trees, such as *Acalypha* (7.9%), Ericaceae undiff. (5.0%), *Podocarpus* (3.6%), and *Rapanea* (1.8%). *Alchemilla* pollen abundances also increased (1.3%). For herbs, Urticaceae pollen abundance decreased slightly (1.6%). Asteraceae pollen increased to 30.7% of the pollen sum, of which *Senecio*-type comprised 14.8%. Poaceae increased (10.3%), while Amaranthaceae abundances decreased (0.1%). Pollen abundances of aquatic taxa declined: Cyperaceae (11.1%) and *Typha* (0.1%). The charcoal concentration was 15,5205 pieces/cm^3.

4.3. Variance partitioning at Lakes Mahoma and Rutundu

Variance partitioning was performed using redundancy analysis on the pollen datasets for Lakes Mahoma and Rutundu using the brGDGT temperature reconstruction (hereafter called mean annual temperature [MAT]) from each site and the δD_{wax} record from Lake Rutundu as predictor variables (Fig. 5). For Lake Mahoma, the first axis of the redundancy analysis (RDA1) explained 37.0% of the variance, and the second axis (RDA2) explained 24.0% of the variance in the pollen dataset. The biplot shows a strong temporal pattern with the oldest samples plotting in the upper left quadrant and youngest samples in the lower left quadrant. The vectors represent the unpartitioned importance of the paleoclimate information on the biplot as constraints on the pollen spectra in the redundancy analysis. In this case, MAT explains variance along RDA1, with positive loadings corresponding to increases of MAT. In contrast, Rutundu δD_{wax} values explain variance along RDA2 with negative loadings corresponding to increased values of Rutundu $\delta D_{wax.}$ Variance partitioning of the RDA suggests that unique effect of MAT for explaining variance in the pollen dataset at Lake Mahoma is large (36% variance explained in comparison to the unique effect of Rutundu δD_{wax} values [4% variance explained]). In contrast, the covarying effects of MAT and Rutundu δD_{wax} values explain 22% of the variance.

For Lake Rutundu, RDA1 explained 79.8% of the variance, and RDA2 explained 8.9% of the variance in the pollen dataset. The biplot of the redundancy analysis also shows a strong temporal signal with the oldest samples plotting in the upper right quadrant and the youngest samples plotting in the upper left quadrant. The constraining vectors of unpartitioned variance explained by the paleoclimate information suggests that MAT explains much of the variance along RDA1, with negative loadings corresponding to an increase in MAT. Rutundu δD_{wax} values explains much of the variance along RDA2 with positive loadings corresponding with increased values of δD_{wax}. Variance partitioning suggests that the unique effect of MAT again explains the majority of variance in the Rutundu pollen data (55% variance explained), while the unique effect of $\delta D_{wax.}$ values explain 15% of the variance.

5. Discussion

5.1. Age correlation of Lake Mahoma pollen records

The first in-depth investigation of the ancient flora of the Rwenzori Mountains was completed by Livingstone (1962, 1967), including a record from Lake Mahoma. This record covered the last ~20kyrs and strongly supported the idea that tropical climate change does not drive a simple lowering or raising of intact vegetation belts on tropical mountains as a function of temperature. Instead, Livingstone (1967) showed that the assembly of modern vegetation zones is of recent origin, and that the Holocene was a time characterized by a mixture of pollen taxa in an association that today characterizes different vegetation zones. However, this seminal record was constrained in age by only three conventional radiocarbon ages and was produced long before the development of more recent quantitative reconstructions of climate to test relationships between climate drivers and vegetation change. These two factors combined add a lot of uncertainty to the interpretation of Livingstone (1967) regarding the timing of dispersal and extirpation of certain taxa relative to other regional paleoecological records as well as the role of climate forcing.

Through comparison of the Mahoma 1967 pollen record with the well-dated Mahoma composite record presented in this study, we can anchor major vegetation transitions from Lake Mahoma in time and test the older chronology (Fig. 6). Due to the lower sampling resolution and change in sedimentation rates noted in the Mahoma composite record

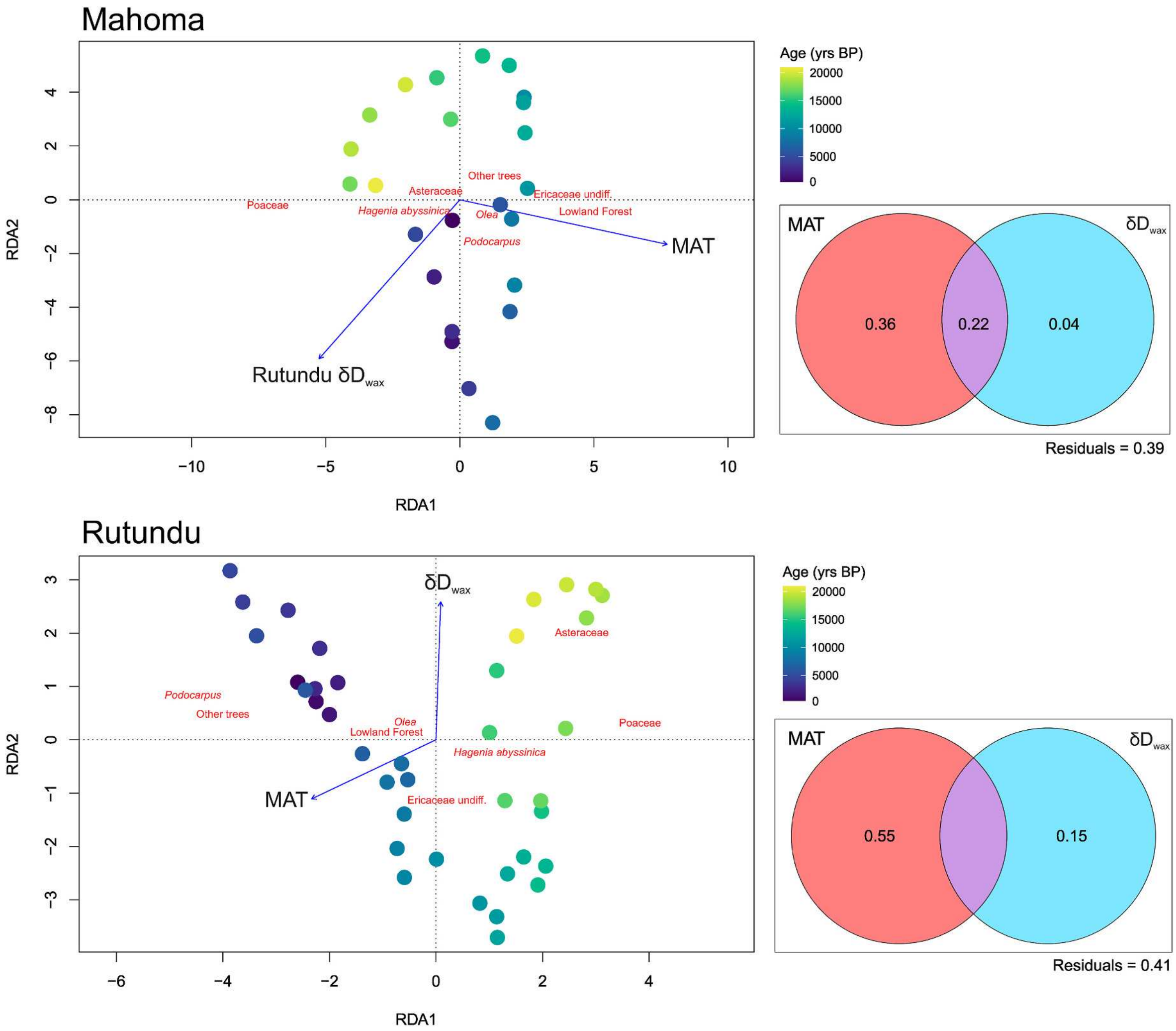

Fig. 5. Left panels are biplots of redundancy analysis on pollen assemblages for each site including temperature reconstructions and dD wax as predictor variables (Lake Mahoma-top; Lake Rutundu – bottom). Right panels are variance partitioning of temperature reconstructions (MAT) and dD as predictors of patterns in the pollen assemblages. The numbers in the Venn diagrams represent the partitioned variance explained by each separately or together.

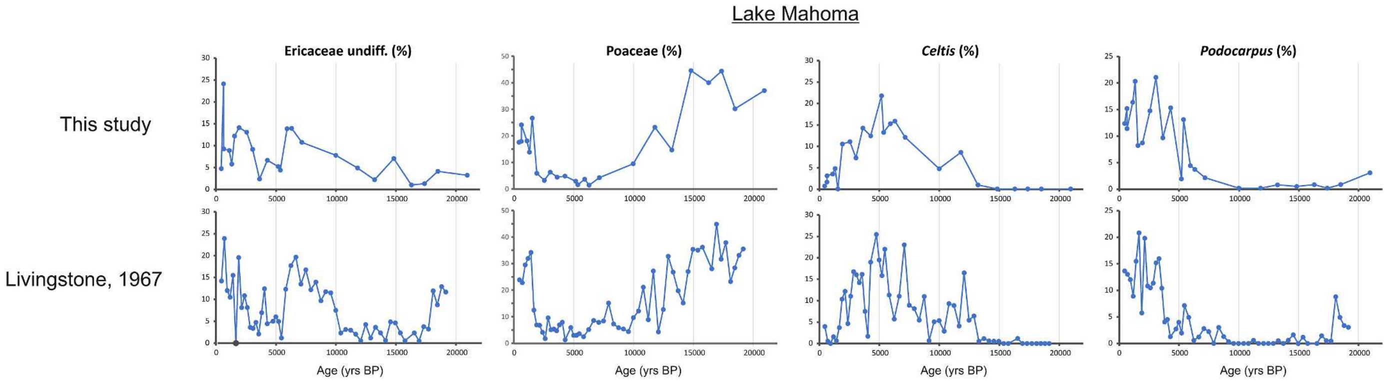

Fig. 6. Comparison of pollen abundances of key taxa from Lake Mahoma from this study as well as historical pollen data from Livingstone (1967).

during the Pleistocene-Holocene transition, correlation prior to 12ka is more challenging and we instead focus on the Holocene for much of the paleoenvironmental interpretation in this paper. However, we observe remarkable similarity between the timing and magnitude of key events in both pollen records, particularly during the Holocene. This suggests that although the Mahoma 1967 chronology is based on fewer constraints, it accurately characterizes the timing of Holocene events within the uncertainty of the Mahoma composite age model and allows for direct comparison to other paleoecological and paleoclimate records regionally after 12ka.

Abundances of key pollen taxa (Ericaceae undiff., Poaceae, *Celtis africana*, and *Podocarpus*) showed similar trends in the two records over the last ~12kyrs (Fig. 6). Of particular interest are a few notable excursions and transitions that help anchor the relative timing of the records. For example, abundances of Ericaceae undiff. showed low values (<5%) in both records until a gradual increase to 15–20% after 10ka, which preceded an abrupt decline during the mid to late Holocene. This final transition is dated to 5927-5361 years BP in the Mahoma composite record, and it occurred between 5822-5460 years BP based on the new *bacon* age model produced using the Mahoma 1967 chronology (Supplementary Figure). Further, a sharp increase in Poaceae to 20–30% occurred in both records in the late Holocene. This transition is dated to 1549-1317 years BP in the Mahoma composite record; in comparison, this same transition occurred between 1665-1422 years BP using the Mahoma 1967 chronology. Therefore, despite the weaknesses of the Mahoma 1967 chronology, there does not appear to be a consistent >120 year offset, within the limit of our sampling, in the timing of important transitions during the Holocene.

5.2. Holocene vegetation of the Rwenzori

Pollen records from the Rwenzori Mountains suggest a reorganization of vegetation at different elevations over the last 20kyrs. Sediments from the last deglacial period come only from Lake Mahoma, as dates on sediment cores and moraines suggest that the higher elevation lakes were glaciated until much later and lakes had not yet established (Livingstone, 1967; Osmaston, 1989; Jackson et al., 2020). Vegetation during this time at Lake Mahoma was characterized by high abundances of grass and other herbs as well as shrubs common above the tree line today *(Senecio*-type, *Artemisia*, *Lobelia*, *Alchemilla;* Fig. 3). This suggests that the elevation of forest was lower than 2900m asl at this time, and that the area hosted open, Afroalpine vegetation suggestive of frequent nighttime freezing temperatures.

The transition from late Pleistocene to Holocene stands out as a particularly dynamic period across elevations. This is characterized by a reorganization of forest tree taxa that today are constrained to different elevational belts, suggesting the modern-day organization into belts has only recently emerged. Above modern tree line in the Afroalpine zone (>3900m asl), the pollen record from Upper Kachope shows high abundances of tree pollen at its base at ~9ka, providing evidence that tree line moved upslope by the early Holocene (Fig. 4). Given the low pollen production of many alpine plants, pollen samples often are overrepresented with respect to tree pollen, even when trees are not locally present (10.4% average, range = 1.4–27.6%; Hedberg, 1954); however, the values observed prior to ~3ka at Upper Kachope greatly exceed this (often >40%), suggesting that tree line was at least near the elevation of the site (3961m asl). Further, higher abundances of understory herbaceous plants which do not travel far from parent plant, such as *Urtica*-type, support the idea that forests expanded further upslope.

The Lake Mahoma pollen records support the idea of forest expansion and reorganization from 10-4ka (Fig. 3), with changes in two phases. The early Holocene is characterized by a distinct increase in Ericaceae undiff. from 10-7ka. Lake Mahoma sits today at the transition between the Afromontane and Ericaceous forests, and similar values of Ericaceae undiff. pollen occur in modern sediments, suggesting heather forest nearby as today. However, the lack of other taxa common at Lake Mahoma today, such as bamboo (Poaceae), *Hagenia abyssinica*, and *Podocarpus*, implies a different forest community.

The second phase occurred during the mid-Holocene from ~7-4ka and was characterized by the decline of Ericaceae undiff. and increasing abundances of submontane/lowland Guineo-Congolian semi-deciduous forest trees (*Macaranga*-type, Moraceae, *Trema*-type *orientalis,* and *Celtis africana*) as well as some Afromontane rainforest taxa (*Olea, Rapanea*). Many of these trees are not locally present above 2000m asl (Bussmann, 2006). While some of these taxa, including *Rapanea* and *Olea*, occur in the mountains near Lake Mahoma today, the continued low abundances of *Podocarpus* (~7%) until ~5-4ka suggests that this important component of the montane forest flora was much less common until the late Holocene. Another interesting feature is the lack of *Poaceae,* which accounts for only about 3% of the pollen spectra from 10-4ka. Although Poaceae is often interpreted as an indication of openness and aridity in lowland pollen records, in this environment it could also be an indication of mesic graminoids such as bamboo. The low values of Poaceae, which is common at this elevation today, suggests that no grasses, whether bamboo or other graminoids, were an important component of the regional flora until the late Holocene.

Evidence of Holocene forests with a different community composition also comes from Upper Kachope (Fig. 4). Typical tree pollen taxa observed in modern Afroalpine lake sediments are Afromontane or Ericaceous forest trees (*Podocarpus*, Ericaceae undiff., *Prunus africana*). Instead, tree pollen taxa represented at this time are more common in moist montane forest (ex. *Olea*) and submontane/lowland forest (ex. *Celtis africana*, *Trema*-type *orientalis*). It is only after 3ka that abundances of Ericaceous and Afromontane trees, such as Ericaceae undiff. and *Prunus africana*, increased despite an overall decrease in tree pollen at the site in favor of Afroalpine pollen taxa, such as Asteraceae undiff. Overall, this suggests that at least some lowland/submontane forest taxa, including *Celtis africana*, *Trema*-type *orientalis,* expanded greatly upslope to near this elevation until the late Holocene when forest taxa retreated to modern elevations.

Together, these records imply changes in the structure of vegetation zonation as well the composition of the communities that make up highland forests in the Rwenzori. For example, the modern Afromontane forest limit sits today around 3000m asl (Lake Mahoma), followed by a bamboo zone and Ericaceous forest until the tree line at ~3900m asl (100m lower than Upper Kachope). The increase in Afromontane forest taxa at Upper Kachope and Lake Mahoma suggests that, during the mid-Holocene, both the forest limit and the treeline were expanded upwards in elevation in comparison to today. The low values of Poaceae and Ericaceae undiff. pollen at both sites from 7-4ka also implies that these zones may have been less important during the mid-Holocene. Instead, the Afromontane forest and lowland forest pollen taxa dominated up to the elevation of Upper Kachope. Although we have no direct constraint between the elevations of the two sites (3000–4000m asl) as to where the upper limit of forest may have been, it must have extended much higher in elevation of Lake Mahoma (3000m asl) and may have been as much as 1000m higher than modern. This is supported by pollen data from another Afroalpine lake, Lake Kitandara (3989m asl; Livingstone, 1967), which recorded similarly high abundances of tree pollen in the mid-Holocene. Particularly striking in this record are the high abundances of Ericaceae undiff. from ~7.5-5.5ka suggesting the presence of the Ericacecous forest near but not present at Upper Kachope (3990m asl). This supports the idea that the upper limit of Afromontane forest was near Upper Kachope, and that Ericaceous forest was likely restricted and also found at higher elevations during the mid-Holocene. The location or even presence of a bamboo zone, which occurs on the mountain today, is still unclear. The lack of abundant Poaceae pollen in any of these sites across elevations in different locations on the mountain suggests that perhaps bamboo was largely replaced by other mesic trees at this time.

Regional pollen data from lower elevation sites near the Rwenzori such as Lake Edward (920m asl; Ivory et al., 2018) noted a marked expansion of lowland semi-deciduous forest during the mid-Holocene (Fig. 7; Ivory et al., 2018). The coeval presence of these same pollen taxa at Lakes Edward, Mahoma, and Upper Kachope from 10-4ka suggests that some lowland trees were regionally very expansive across low and high elevations. Today, *Celtis africana* occurs in both lowland semi-deciduous forest as well as in lower montane rainforests which reach about 1700m asl (White, 1983). Recent studies of modern pollen transport in West African mountains have suggested that upslope winds may carry *Celtis africana* pollen to elevations higher than its actual position due to high pollen production (Verlhac et al., 2018). However, in eastern Uganda, modern pollen samples only record *Celtis africana* pollen in high abundances (max = 20%) below 1000m asl where it currently is found (Hedberg, 1954). The presence of *Celtis africana*

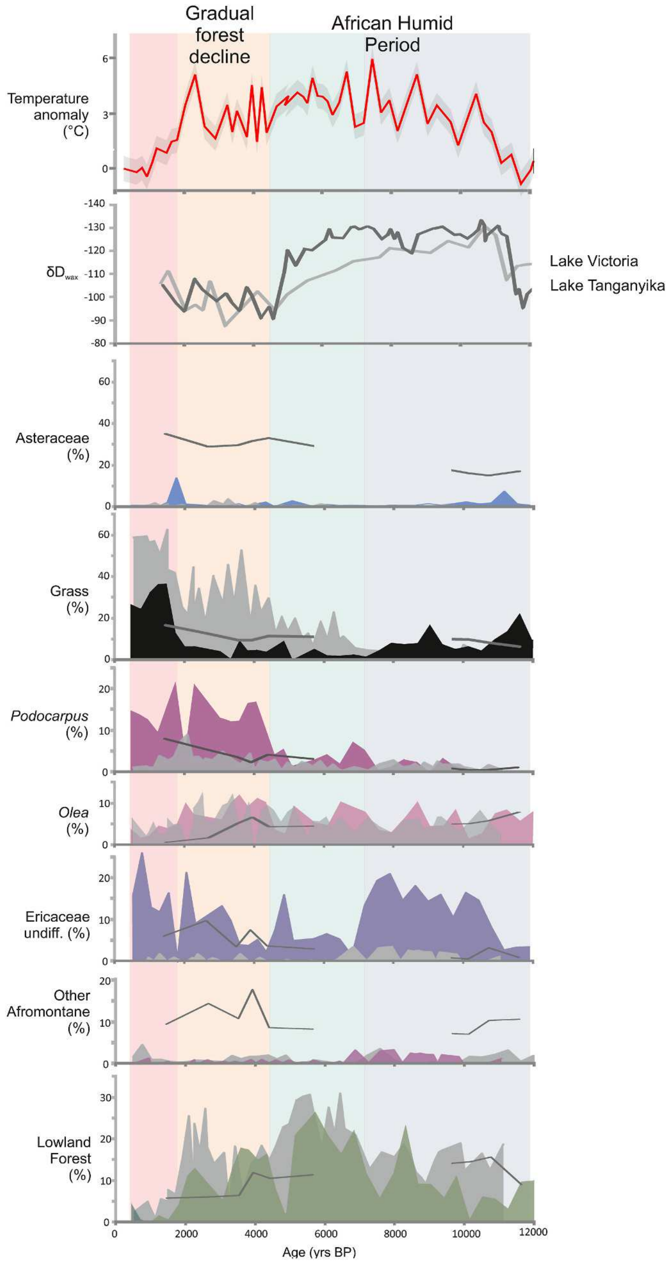

Fig. 7. Climate and vegetation of the Rwenzori Mountains across an elevantional transect for the last 12ka years. Paleoclimate reconstructions from top to bottom: Lake Mahoma mean annual temperature reconstructed from brGDGTs (Garelick et al., 2022) and δD$_{wax}$ from Lakes Victoria and Tanganyika (Berke et al., 2012; Tierney et al., 2008). Pollen abundances for key taxa from three sites at different latitudes: Lake Edward (920m asl; grey curves), Lake Mahoma (2990m asl; colored curves), and Upper Kachope (3961m asl; black lines).

pollen may be recorded today as high as ~3000m asl, but abundances are extremely low (<1%). Thus, we conclude that average pollen abundances of 15.7% from 10-4ka at Lake Mahoma suggest local presence of *Celtis africana* at the elevation of the lake. Additionally, we observe higher abundances of other lowland tree taxa which do not occur outside of the lowland forests today (ex. *Trema*-type *orientalis*) at Lake Mahoma during the early to mid-Holocene. In summary, this means that although tree line itself may have moved upslope by as much as 1000m, many lowland trees expanded much further upslope (~1500–2000m) during the mid-Holocene. This suggests that lowland and lower montane tree taxa were particularly successful at dispersing to higher elevations under mid-Holocene climate conditions and grew in association with Afromontane trees that resulted in the assembly of a no-analogue communities.

The late Holocene was characterized by the emplacement of the modern vegetation at each site in the Rwenzori, albeit in a gradual stepwise manner related to the arrival or extirpation of individual taxa. Although the sampling is coarse in this interval at Upper Kachope, lowland forest trees decreased, while Ericaceae undiff. and Afromontane forest trees, such as *Podocarpus*, increased moderately (Figs. 4 and 7). However, tree pollen overall decreased, and shrubby and herbaceous Afroalpine taxa arrived gradually between 5-4ka, including Poaceae, Asteraceae, *Alchemilla*. This pattern implies that vegetation similar to modern arrived at Upper Kachope by ~4ka, even as the Ericaceous and Afromontane forest taxa continued to decline, indicating a gradual downslope retreat. At Lake Mahoma, the transition of forest from a mid-Holocene no-analogue mix of lowland and montane forest trees to the modern Afromontane community was protracted (Figs. 3 and 7). The forest transition was characterized by the arrival of modern Afromontane trees, including *Olea*, Ericaceae undiff., and *Podocarpus*. Lowland trees continued to remain abundant despite a gradual decline until after 3.6ka. Finally, Poaceae pollen abundances increased very recently at 1.8ka. The high abundances of grass pollen are likely indicative of arrival of bamboo, rather than indicating lowland C4 grasses and forest opening, as the lake today sits within bamboo forest.

5.3. *Vegetation responses to Holocene climate*

Overall, Holocene vegetation responses in the Rwenzori Mountains do not appear to result from a simple raising or lowering of vegetation belts as intact assemblages responding uniformly to climate, in agreement with the interpretation of Livingstone (1967). Instead, some degree of mixing of lowland and highland plants occurred in forests in conjunction with a marked decline of important modern taxa (*Podocarpus*) and vegetation zones (bamboo and Ericaceous forest) as tree line migrated upwards. At the time of the publication of Livingstone (1967), significantly less was known about regional climate as no independent climate information existed in the region, leaving the role of climate versus other factors in driving these changes unclear.

Nevertheless, the paleoclimate information available today in western equatorial East Africa helps contextualize what may have driven the vegetation changes. Early to mid-Holocene (10-4ka) climate was characterized by both an increase in rainfall and temperature. Values of δD$_{wax}$ at Lake Rutundu on Mt Kenya as well as from nearby sites such as Lake Victoria and Lake Tanganyika show an ~40‰ depletion relative to modern, suggesting increased rainfall (Tierney et al., 2008; Berke et al., 2012). An unpublished record of δD$_{wax}$ values from Lake Mahoma itself also shows notable depletion at this time (Garelick, 2022; Mason et al., in review). Within the Rwenzori, organic geochemical reconstructions of temperature from Lake Mahoma based on brGDGTs suggest that MAT at this time were ~2–3 °C higher than today (Garelick et al., 2022).

It may seem plausible that changes in regional rainfall explain the expansion and subsequent decline of lowland and submontane forest over the Holocene in the Rwenzori. This may have been the case in some sites, particularly warmer, more seasonal, low elevation sites like at Lake Edward (Ivory et al., 2018) or many other sites in East Africa (e.g. Taylor et al., 1990; Bonnefille and Chalie, 2000; Kiage and Liu, 2006). However, rainfall seems unlikely to have been the sole driver of vegetation change in the mountains. For example, changes in rainfall alone cannot easily explain the migration of lowland forest trees into the mountains in the mid-Holocene. Variance partitioning to understand the most likely climatic drivers of the vegetation patterns in the Lake Mahoma pollen record suggests a strong relationship between MAT and the pollen assemblages, with δD$_{wax}$ values playing a role only when combined with the influence of MAT (Fig. 5). The Rwenzori Mountains currently receive very high values of yearly rainfall (>2000 mm/yr; Eggermont et al., 2009). This amount is well within, and in some locations on the mountain larger than, rainfall in the Congo basin where lowland trees are prevalent (Ivory et al., 2018). Therefore, we suggest that while an increase in rainfall alone may have driven lowland forest expansion around Lake Edward at the base of the Rwenzori, it is not the sole driver of forest expansion upslope.

Instead, we suggest that increased temperatures resulted both in reduction of freezing and frost days on the mountain that limit lowland species. This seemingly small increase in temperature appears to have resulted in the successful expansion and colonization of frost-intolerant trees, such as *Trema*-type *orientalis* and *Macaranga*-type (White, 1983), in places where even irregular freezing limits warm-adapted trees, such as at Lake Mahoma. This interpretation is supported by a reconstruction of the elevational thermal gradient in the Rwenzori by Garelick et al. (2022), who placed the mid-Holocene 0°C isotherm ~500m further upslope than today. It may be that the current distribution of most submontane trees is strongly controlled by frost elevation on the flanks of mountains, such that the movement upslope of the elevation of frequent frosts resulted in increased competitive ability of lowland trees with montane trees at elevations where many trees are currently excluded by cool temperatures. This could also explain why many common montane trees today (*Podocarpus*, Ericaceae undiff.) were not common during the mid-Holocene, as they were less competitive at the same elevations under warming, persistently moist climates.

Vegetation change at the end of the mid-Holocene also likely can't be explained by decreases in moisture alone. Reconstructions of rainfall using δD_{wax} values from Lakes Victoria and Rutundu show drying occurred gradually between ~9-4ka (Berke et al., 2012; Garelick et al., 2021). Although the gradual pace of drying is similar to the gradual decline of several forest taxa at Lake Mahoma and at Upper Kachope, major structural turnover occurred later at both sites. Forest taxa decline happened earlier at Upper Kachope than at Lake Mahoma, with most forest taxa already gone from the pollen record by between 7-5ka (Fig. 4). At Lake Mahoma, compositional change was centered around 4ka and unfolded slowly. Several individual taxa arrived near 6ka (*Podocarpus*) or decline only after 4ka (*Celtis africana*).

Further, although the decline of semi-deciduous forest taxa in favor of *Podocarpus*-dominated forest has been interpreted as an indication of drying (e.g. Bonnefille and Chalie, 2000), the replacement of one forest type by another, rather than a collapse of forest, does not intuitively correspond to an ecological response to marked drying. In fact, there is very little evidence for an increase in drought-tolerant taxa at the end of the mid-Holocene. Although some species of podocarps grow on drier sides of African mountains, most are drought-intolerant and slow-growing, which makes them less competitive in drier climates relative to angiosperm trees (Brodribb and Hill, 1998). In the Rwenzori, *Podocarpus mijanianus* is the species present today, and in fact prefers extremely moist environments (Twala et al., 2023). These inferences combined with the variance partitioning results from the Lake Mahoma pollen record support the idea that the decline in forest at Upper Kachope and the change in forest type at Lake Mahoma are related to changes in temperature in conjunction with drying. It is likely that during the late Holocene, the 0°C isotherm moved back downslope, and gradually frost intolerant trees no longer had an advantage. This idea is supported by Garelick et al. (2022) who suggest that the modern temperature gradient in the Rwenzori was established in the last few thousand years.

However, this result stands in contrast with the typical interpretation of the influence of moisture decline at the end of the African Humid Period on ecosystems in Africa (Hamilton, 1982; Vincens, 1986; Bonnefille and Chalie, 2000; Demenocal et al., 2000; Wooller et al., 2003; Kiage and Liu, 2006; Tierney et al., 2011; Shanahan et al., 2015; Ivory et al., 2018; Marchant et al., 2018). Within tropical Africa, the literature is full of examples of forest decline and desertification associated with reduced monsoon intensity by 4.5ka. For example, tropical plant taxa extended as far north as 25°N during the early Holocene but declined as rainfall no longer penetrated as far into the Sahel and Sahara after 4.5ka (Lézine, 2017). In East and West Africa, woodland and forest expanded in the lowlands until 4-3.5ka, when rainfall declined and more seasonal climates emerged (Vincens, 1986; Bonnefille and Chalie, 2000; Thompson et al., 2002; Kiage and Liu, 2006; Ivory et al., 2018; Marchant et al., 2018). Even as nearby as Lake Edward (<50 km) at the base of the Rwenzori, forest expansion and collapse appeared to follow a pattern of connectivity with the more stable forest of the Congo basin related to increased rainfall (Elenga et al., 1994), such that during the African Humid Period, a continuous bloc of forest extended out of central Africa into the rift valley (Russell and Johnson, 2005; Ivory et al., 2018). Decreased rainfall and increased fire after 4ka resulted in forest fragmentation and retreat westward, away from Lake Edward as the modern savanna and mosaic developed.

Why then is temperature such an important ecosystem driver in the Rwenzori? We suggest that in lowland, tropical Africa, frost is never a limiting factor on plant growth, and therefore competitive advantage is instead primarily related to adaptations of moisture, seasonality, and fire. In contrast, in the mountains, the migration of isotherms that determine frost duration and intensity result in a strong control on environmental suitability for lowland taxa, such that the relative impact of temperature and rainfall trade off along a gradient from mountain to lowlands. Thus, in this key region of ecosystem interchange between central Africa and East Africa, the increase in rainfall coupled with the increase in temperature during mid-Holocene allowed lowland forest taxa to migrate, not just into the rift, but far up the mountain. Then, at the end of the African Humid Period, cooling and drying had differential impacts, such that cooling resulted in retreat of lowland taxa off the mountains, but more intense drying resulted in further fragmentation of lowland forest and retreat back to central Africa.

5.4. *Climate and vegetation of Equatorial East African mountains*

Climate change during the late Pleistocene-Holocene follows broad regional patterns in East Africa (Tierney and deMenocal, 2013). As at Lake Mahoma, temperature records from sites throughout tropical Africa (including Lakes Tanganyika, Malawi, Rutundu, Sacred Lake) show a gradual warming during the late Pleistocene and early Holocene to a maximum of 2–3°C warmer than today at ~6ka, followed by gradual cooling (Powers et al., 2005; Tierney et al., 2008; Loomis et al., 2017; Garelick et al., 2022). The evolution of deglacial and Holocene hydroclimate was more spatially variable in timing and magnitude across the continent (Shanahan et al., 2015); however, some general trends agree within East Africa. For example, by 15-14.5ka, evidence of increased moisture comes from a number of studies showing rift lakes at highstand (Demenocal et al., 2000; Williams et al., 2006). δD_{wax} records mostly agree that rainfall increased at ~15ka. A δD_{wax} record from Lake Tanganyika suggested that this period of increased moisture was followed by an abrupt decline by 4ka (Tierney et al., 2008; Berke et al., 2012). However, δD_{wax} records from Lakes Rutundu, Victoria, and Challa as well as off the Congo basin instead suggest a more gradual decline in rainfall beginning by 8-7ka and reaching values similar to modern by ~3.5ka (Garelick et al., 2021; Tierney et al., 2011; Weijers et al., 2007). Therefore, while the pace of the drying is still unresolved, the trend and general timing of the end of the African Humid Period by 4-3.5ka is regionally similar.

Although at a continental scale vegetation patterns are very complex, the timing of ecosystem responses across the highlands of equatorial East Africa regionally also largely agrees. A complete review of tropical paleoecology in Africa is outside of the scope of this work and can be found elsewhere (Marchant et al., 2018; Runge et al., 2021), thus, we focus on mid-elevation, equatorial sites (1°N-1°S, >2500m asl). Similar to the vegetation pattern in the Rwenzori, moist forest increased across elevations by 13ka (Coetzee, 1967; Livingstone, 1967; Kendall, 1969; Hamilton, 1987; Jolly et al., 1997; Olago et al., 1999; Kiage and Liu, 2006; Rucina et al., 2009). Forest decline occurred between 5-3.5ka and differed in the highlands and lowlands. In the lowlands, forest opened and was replaced by savanna or woodland, while in the mid-elevations

(2500–3500m asl), early to mid-Holocene forests transitioned to modern Afromontane forest by 4-3.5ka (Livingstone, 1967; Kendall, 1969; Perrott, 1982; Hamilton, 1982; Rucina et al., 2009; Ivory et al., 2018). In particular, a rise in *Podocarpus* occurred near the end of the African Humid Period in a number of records across eastern Africa including from Mount Elgon, Mount Kenya, and the Rwenzori Mountains (Livingstone, 1967; Coetzee, 1967; Hamilton and Perrott, 1978; Perrott, 1982; Olago, 1995).

However, despite the coeval timing, the specific pattern of ecosystem responses, in particular, the assembly of early to mid-Holocene forest in the mid-elevations >2500m asl across equatorial East Africa mountains, was remarkably unique from west to east. In particular, colonization of mid-elevations by moist lowland and submontane forest appeared to be a feature only observed in the western section of the equatorial highlands, such as at Lake Mahoma (Livingstone, 1967). A similar community type is also observed in some records from lower elevations in this region (Taylor, 1990; Beuning et al., 1997; Ivory et al., 2018), but it is notable at the elevation of Lake Mahoma. In contrast, at Laboot Swamp (2880m asl; Hamilton and Perrott, 1978) on Mount Elgon as well as at Sacred Lake (2440m asl; Coetzee, 1967) and Lake Rutundu (3078m asl; Ficken et al., 2002; Wooller et al., 2003) on Mount Kenya, an increase in grass pollen rather than trees was observed (Lake Rutundu in Fig. 8). At Sacred Lake, high grass pollen abundances were accompanied by high values of *Hagenia abyssinca* pollen, a tree that sits today near the treeline (Coetzee, 1967). At Lake Rutundu, the presence of bambusoid and pooid cuticle along with depleted $\delta^{13}C$ values likely indicates an increase in the presence of an open bamboo zone from 9-4ka (Wooller et al., 2003).

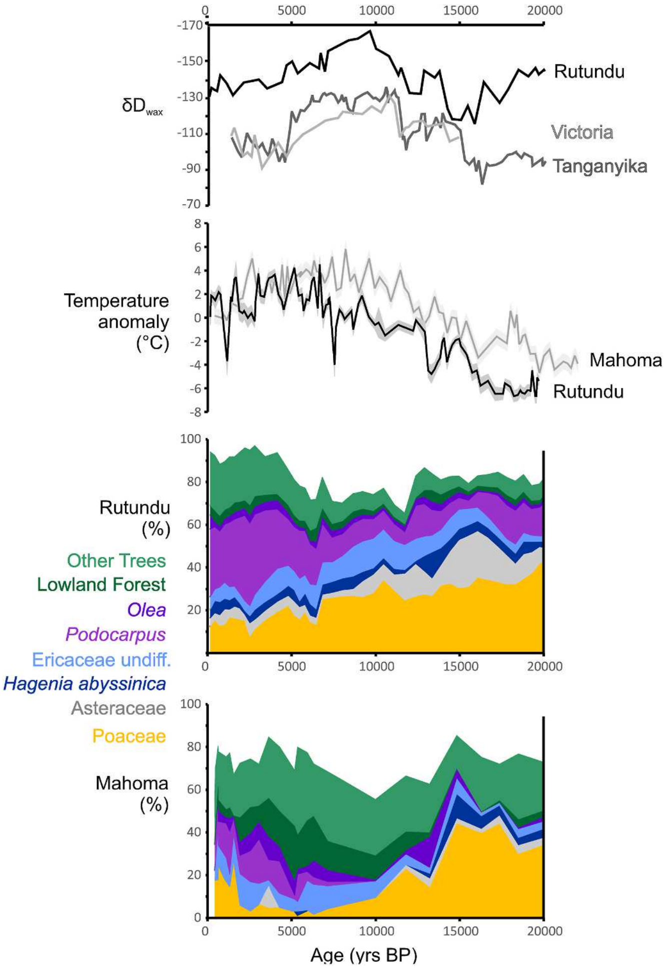

Fig. 8. Climate and vegetation of two Equatorial East African montane sites over the last 20kyrs. Paleoclimate reconstructions from top to bottom include Dwax from Lakes Rutundu (Garelick et al., 2021), Victoria (Berke et al., 2012), and Tanganyika (Tierney et al., 2008) and mean annual temperature anomaly relative to modern from Lakes Mahoma (Garelick et al., 2022) and Rutundu (Loomis et al., 2017). Lower two panels are stacked pollen abundances for key Afromontane groups or taxa (colored filled curves) from Lakes Rutundu (Wooller et al., 2003) and Mahoma (this study).

A direct comparison of the pollen records from Lake Mahoma and Lake Rutundu further highlights the difference in assemblages during the early to mid-Holocene on western versus eastern highlands in the region (Figs. 8 and 9). For example, at Lake Mahoma, lowland and all other trees increased in pollen abundances at ~10-4ka (Fig. 9). This interval had considerably lower charcoal influxes relative to the late Pleistocene, suggesting that these dense forests suppressed fire (Fig. 10). In contrast, at Lake Rutundu, there is no evidence of increased lowland or Afromontane forest. Instead, Poaceae pollen remained comparatively high throughout the deglaciation and increased at ~12ka (Fig. 9). Prior studies of plant cuticle have identified bambusoids and pooids near the lake at 6ka, supporting the interpretation that the pollen signal implies a more open zone of bamboo expansion rather than a C4 dominated grassland environment (Wooller et al., 2003). Further, charcoal influxes at Lake Rutundu were higher during the mid-Holocene from 10-5ka than at Lake Mahoma (Fig. 10). This is likely related to the fire ecology of bamboo which encourages fire through the creation of flammable biomass, but shows marked fire-tolerance as it regrows quickly following burning (Masiga et al., 2001). Overall, in eastern equatorial Africa, mid-elevation vegetation demonstrated less migration upslope of lowland taxa, which may potentially have been limited by frequent fire.

Variance partitioning using the Lake Rutundu pollen record also supports the idea that temperature played an important role in vegetation change as at Lake Mahoma (Fig. 9). However, in contrast, at Lake Rutundu, δD_{wax} values also independently explain a large amount of variance. Thus, it seems likely that one explanation for the difference between sites is the role of moisture as a control on vegetation. In the Rwenzori, rainfall is very high and aseasonal today (2000–3000 mm/yr) and therefore not limiting to mesic taxa. Thus, increased values during the mid-Holocene had little impact on promoting forest expansion independently. In contrast, although quite wet in comparison to the surrounding lowlands, Mount Kenya is generally much drier than the Rwenzori. Rainfall on the northwestern flank near the lake is ~1500 mm/yr and with more pronounced seasonality (Ficken et al., 2002). While this value is already within the range for *Arundinaria alpina* (1200–1800 mm/yr; Masiga et al., 2001), an increase in rain during the mid-Holocene likely played a larger role in the expansion of such mesic taxa. Therefore, the gradient in hydroclimate across the equatorial tropics in eastern Africa also played a role in determining vegetation change in the past.

Today, in much of the Afromontane region, there is a remarkable similarity in forest composition across this discontinuous phytogeographic region (White, 1983). These similarities appear to have largely emerged only within the last few thousand years as highland vegetation converged into its modern pattern through the expansion of *Podocarpus* and other montane trees. Figs. 9 and 10 show a comparison of pollen abundances of key taxa and microcharcoal from both Lakes Mahoma and Lake Rutundu. We observe that while the two sites show strongly opposing signals for all of these taxa over the Holocene, abundances converge to similar values along a 1:1 line only very recently. Therefore, we suggest that the similarity in modern ecology observed today is not a product of long-term stability but rather long-term instability.

We suggest that this gradient in ecological responses to climate regionally across the equatorial highlands is related to interactions between climate, ecology, and biogeographic setting. The Rwenzori Mountains and Lake Mahoma sit closer to the Congo basin, which has hosted more stable communities of tropical lowland forest (Elenga et al., 1994). This nearby source of lowland forest trees means that dispersal distance to the Rwenzori is less than to eastern equatorial mountains. In contrast, Mount Kenya was surrounded in the lowlands by more open landscapes for much of the Holocene. Therefore, when rainfall and

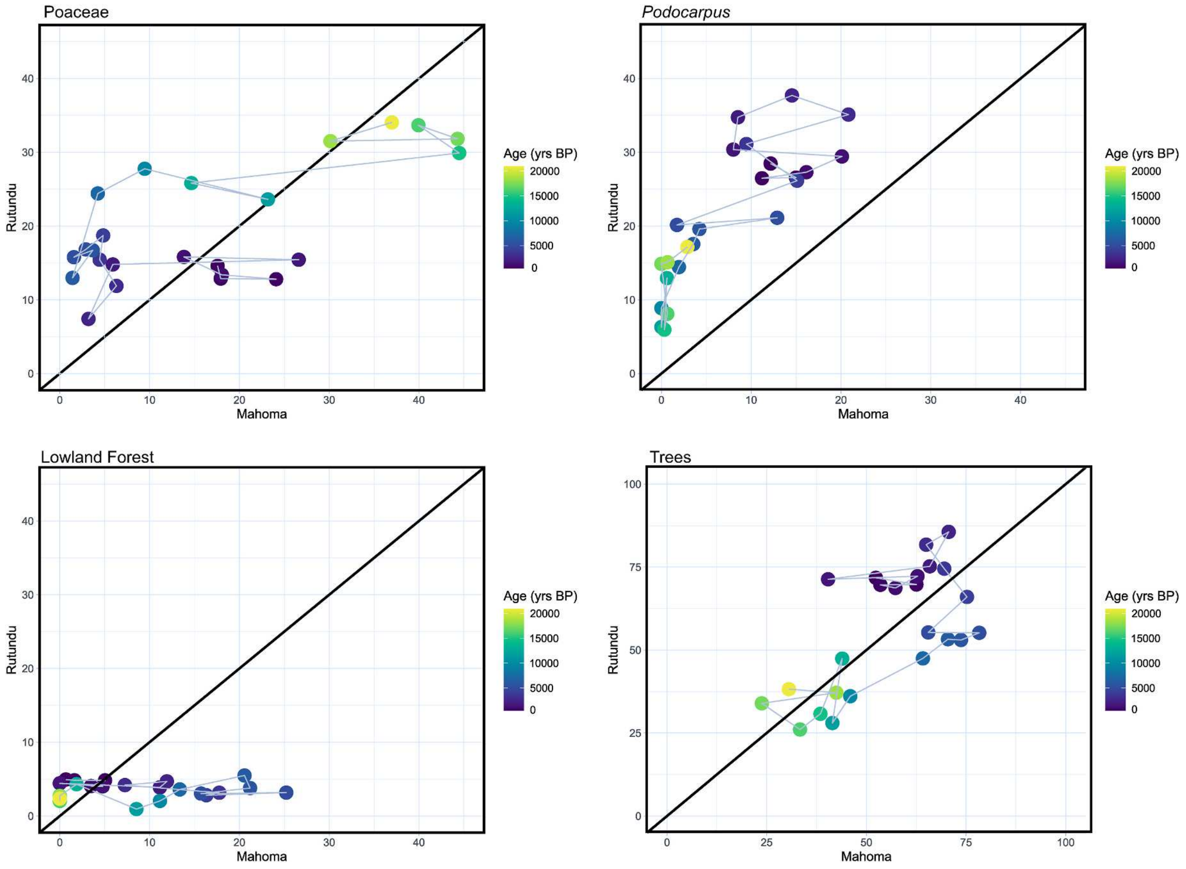

Fig. 9. Timing of vegetation changes at Mahoma versus Rutundu. Plots show the abundances of key pollen taxa from both sites sampled onto timesteps from Lake Mahoma (this study). Color of the dots indicates the age of samples and the arrows show the order of samples in time. Black line is the 1:1 line, so samples plotting above the line show higher relative abundances of each taxon at Lake Rutundu in comparison to Lake Mahoma at a particular time.

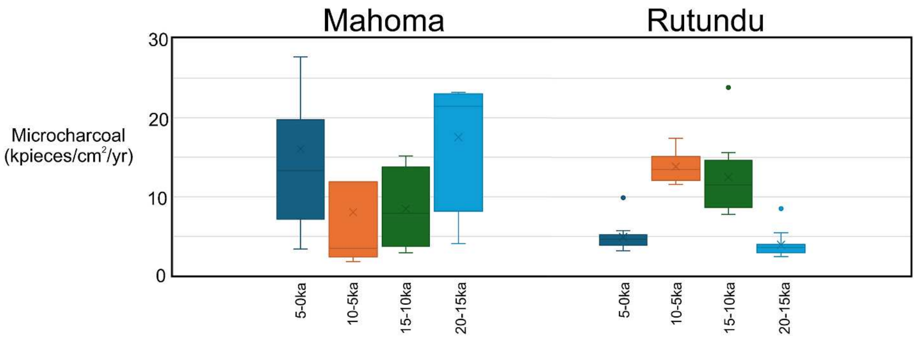

Fig. 10. Microcharcoal influxes for Lakes Mahoma and Rutundu (Urban et al., 2015). Influx values were binned every 5kyr due to the difference in data resolution in order to compare relative values across intervals.

temperature increased in the mid-Holocene inducing upwards migration of montane forest taxa, no source of lowland forest was near enough to colonize the wet mid-elevations. Instead, this led to the expansion of a fire-disturbed bamboo zone at Rutundu which prevented establishment of other forest taxa.

6. Conclusions

Two new pollen records from Lake Mahoma and Upper Kachope Lake in the Rwenzori Mountains of Uganda are presented. The new well-dated core from Lake Mahoma allows us to better constrain in time the seminal record of Livingstone (1967) as well as to, for the first time, compare this data to quantitative paleoclimate reconstructions of climate and temperature. An improved chronology also allows us to confidently make regional comparisons of vegetation and climate interactions in order to look at the spatial heterogeneity of ecosystem responses to climate change over the last deglacial period and Holocene.

Patterns of vegetation change across equatorial East African highlands occurred synchronously related to synchronous changes in climate but vary substantially in character due to gradients in climate and biogeography across the region. At Lake Mahoma, increased temperature drove marked upslope migrations, which were variable in their magnitude on a taxon-specific level. In particular, lowland and submontane forest trees migrated very far upslope. In contrast, at Lake Rutundu, a highly flammable, bamboo zone developed. The differences in the responses of each site to temperature and rainfall change provides an important lesson for management and adaptation planning in two of East Africa's national parks (Rwenzori National Park and Mount Kenya

National Park) as well as across the Afromontane biogeographic providence. That is that similar modern ecology may have emerged from very different past responses to change and may in turn lead to very different responses to future changes. In this way, biogeographic context and history must be taken into account in conservation planning.

CRediT authorship contribution statement

Sarah J. Ivory: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Elizabeth MacDougal:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Andrea Mason:** Writing – review & editing, Formal analysis, Data curation. **Eleanor Pereboom:** Writing – review & editing, Resources, Data curation. **Sloane Garelick:** Writing – review & editing, Resources, Formal analysis, Data curation. **Katherine Ficken:** Writing – review & editing, Resources, Data curation. **Matthew J. Wooller:** Writing – review & editing, Resources, Data curation. **Bob R. Nakileza:** Writing – review & editing, Writing – original draft, Resources, Project administration, Funding acquisition, Conceptualization. **James Russell:** Writing – review & editing, Writing – original draft, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Data availability

Pollen data generated for this paper is available in the supplement of this paper and on the African Pollen Database. Organic geochemical data is available in the online supplementary materials of Loomis et al. (2017), Garelick et al. (2021), and Garelick et al. (2022).

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Sarah Ivory reports financial support was provided by National Science Foundation. If there are other authors, they 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.quaint.2024.10.007.

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