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Research Article

A 3000-year record of vegetation changes and fire at a high-elevation wetland on Kilimanjaro, Tanzania

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Abstract

Kilimanjaro is experiencing the consequences of climate change and multiple land use pressures. Few palaeoenvironmental and archaeological records exist to examine historical patterns of late Holocene ecosystem changes on Kilimanjaro. Here we present pollen, phytolith, and charcoal (>125 µm) data from a palustrine sediment core that provide a 3000 year, radiocarbon-dated record collected from a wetland near the headwaters of the Maua watershed within the alpine and ericaceous vegetation zones. From 3000-800 cal yr BP the pollen, phytolith and charcoal record show subtle variability in ericaceous and Montane Forest assemblages with apparent multicentennial secular variability and a long-term trend of increasing Poaceae and charcoal. From 800-600 cal yr BP, Montane Forest taxa varied rapidly, Cyperaceae abundances increased and charcoal remained distinctly low. From 600 yr BP to present, woody taxa decreased and ericaceous taxa and Poaceae dominated with a conspicuously increased charcoal influx. Uphill wetland ecosystems are crucial for ecological and socioeconomic resilience on and surrounding the mountain. The results are synthesized with the existing palaeoenvironmental and archaeological data to explore the high spatiotemporal complexity of Kilimanjaro and to understand historical human-environment interactions. These palaeoenvironmental records create long-term context for current climate, biodiversity and land use changes on and around Kilimanjaro.

Keywords: Africa, archaeology, ericaceae, mires, mountain, palynology, palustrine

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INTRODUCTION

Tropical wetlands are key for biodiversity, carbon cycling, and hydrological ecosystem services (Kamukala and Crafter, 1993; Kolka et al., 2016); yet wetlands are rapidly changing across Africa due to land use management regimes, hydroclimatic variability, defaunation, and introduced taxa (MEMR, 2012; Davidson, 2014). Given the current rapidity and magnitude of environmental transformations driven by global climate change and intensifying anthropogenic pressures on landscapes that threaten biodiversity (Stévart et al., 2019), the utility of long-term socio-ecological insights are increasingly used for contextualising land management dialogues and supporting public policy decisions (Marchant and Lane, 2014; Courtney Mustaphi et al., 2019; Said et al., 2019). High-elevation wetlands accumulate sediments over geologic timescales and are important geoarchives of past environmental conditions - especially in environments with few lake sediment deposits (Marchant et al., 2018). Wetland sediment stratigraphies from subalpine and montane wetlands provide palaeoenvironmental histories across highland areas of equatorial eastern African (Hamilton, 1982a and b; Perrott, 1982a; Umer et al., 2007; Gil-Romera et al., 2019). For example, palustrine sediments records of vegetation change have been developed from wetlands on the Cherangani Hills (van Zinderen Bakker, 1962; 1964; Opiyo et al., 2019), the Pare Mountains (Heckmann et al., 2014; Finch et al., 2017), Eastern Mau (Courtney-Mustaphi et al., 2016; Githumbi, 2017), Mount Kenya (Olago et al., 2004; Rucina et al., 2009) and the Eastern Arc Mountains (Mumbi et al., 2014; Finch et al., 2009, 2014, 2017; Finch and Marchant, 2011).

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On Kilimanjaro, high elevation palaeoenvironmental studies have characterised late Pleistocene and Holocene vegetation and climate change derived from soils (Zech, 2006; Zech et al., 2011; Montade et al., 2018), sediments (Coetzee, 1967; Schüler et al., 2012; Schüler, 2013), and glacial ice (Thompson et al., 2002; Gabrielli et al., 2014) and are also informed by records from nearby Lake Challa (Table 1) (Verschuren et al., 2009; Barker et al., 2011; Nelson et al., 2012; Martin-Jones et al., 2020). Archaeological evidence and oral tradition summaries show a long and varied history of land use on and around Kilimanjaro (Fosbrooke and Sassoon, 1965; Odner, 1971; Mturi, 1986; Clack, 2007, 2009); though as of yet, there are no published archaeological sites above 2000 m asl.

Highland-lowland connectivity is an important climatic, ecological, and socioeconomic dynamic of the mountain. Rapid changes to thermal and hydroclimatic regimes have modified the cloudiness, precipitation and glacial dynamics at high elevations of Kilimanjaro (Mölg and Hardy, 2004; Chan et al., 2008; Thompson et al., 2002; 2009; Park et al., 2012) and the areal extent of glacial ice has reduced over the past century (Geilinger, 1936; Downie, 1964; Hastenrath and Greischar, 1997; Cullen et al., 2006; Mote and Kaser, 2007). Hydroclimatic variability modifies the upper montane soils and vegetation of eastern African mountains (Coe, 1967; Spence, 1989; Young and Peacock, 1992; Mizuno, 1998; 2005; Mizuno and Fujita, 2014), which influences downslope ecosystems (Munger, 1952; Mathooko and Mavuti, 1992) and links highland-lowland ecosystems (Maro, 1988; Chuhila, 2016; de Bont, 2018; Kilungu et al., 2019). Montane Forest hydroclimate is also influenced by anthropogenic land use and land cover changes at lower elevations due to vegetation-atmosphere interactions (Fairman et al., 2011).

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This highland-lowland connectivity creates cascading effects on ecosystem functions and services and amplifies human-environment feedbacks with socioeconomic and political ramifications (Tagseth, 2008; Mahonge, 2010; Sébastien, 2010; Komakech and de Bont, 2018; Kilungu et al., 2019).

Here we present a 3000 year sediment record of vegetation change established from a wetland located at the ericaceous-alpine vegetation ecotone on the south-facing slope of Kilimanjaro. Centennial scale sampling resolution for proxy vegetation and fire change throughout the late Holocene has not been explored in detail in previous palaeoenvironmental studies on the mountain. Pollen, phytolith and charcoal analysis from the Maua sediment record contributes to this knowledge gap and we present a discussion of the results contextualized with available data on the climatic and ecological drivers of vegetation change on Kilimanjaro, including the known history of land use and land cover change summarised from published archaeological reports, historical texts, and oral traditions. The results focus on a temporal knowledge gap of vegetation change in a fire-prone ecosystem that is susceptible to future rapid ecological change due to climatic variability and anthropogenic land use pressures.

Study region

Kilimanjaro (5895 m asl) is a composite of several dormant stratovolcanoes and satellite craters with an eruptive history beginning during the Early Quaternary (Schlüter, 1997; Nonnotte et al., 2008) and consists of volcanic and pyroclastic rocks flanked by an apron of mixed epiclastic sedimentary rock with airfall tuffs and reworked pyroclasts (Pickford, 1986; Schlüter, 1997). At

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alpine elevations, interbedding of glacial and volcanic extrusive deposits present a long history of variable glacial conditions (Downie, 1964; Osmaston, 1989) and the ice records around Kibo suggest that ice cover has remained since at least the early Holocene (Thompson et al., 2002). The mountain is an important source of orographic precipitation supplying surficial and groundwater flows to several surrounding watersheds including the Pangani and Galana River networks that drain to the Indian Ocean, as well as the endorheic drainage systems of Lakes Challa, Jipe and Amboseli (Meijerink and van Wijngaarden, 1997). Moisture is primarily derived from the Indian Ocean by easterly circulation that varies with seasonal monsoon fronts and interactions with teleconnected climatic modes such as the Indian Ocean Dipole (IOD) (Rodhe and Virji, 1976; Saji et al., 1999; Nicholson, 2000; Marchant et al., 2007). Precipitation is modally concentrated during the rainy seasons of March-June and November-January (Coutts, 1969; Hemp, 2001; Oettli and Camberlin, 2005). The mountain experiences strong diurnal patterns: warmer daytime temperatures transition to cold nights with minimum temperatures below freezing and the possibility of night-time snowfall. Similar to other mountains of eastern Africa, Kilimanjaro experiences complex ecohydrological feedbacks between vegetation and the atmosphere that vary by plant communities, elevation, aspect, and topography (Hemp, 2001; Hemp, 2009; Fairman et al., 2011; Cuní-Sanchez et al., 2019; Los et al., 2019).

Biodiversity is high and vegetation distribution patterns are complex due to intermittent habitat connectivity between Kilimanjaro, Mount Meru, and the older and highly endemic Eastern Arc Mountains (Burgess et al., 1998, 2007; Platts et al., 2011; Jump et al., 2014; Hemp and Hemp, 2018; Burger et al., 2019). The alpine zone (>3900 m asl) of the southern flank has a

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mean annual temperature ranging from 0.7-4.2 °C and mean annual precipitation of 500-700 mm year^{-1} (Schüler et al., 2014a; Schüler and Hemp, 2016) where short alpine plants have patchy coverage (Hedberg, 1951; Hemp and Beck, 2001). The subalpine zone (2800-3900 m) experiences frost and at the upper limits are dominated by ericaceous vegetation that is continuous-to-patchy Ericaceae and Poaceae heathland vegetation with short woody shrubs and microphyllous species, and the vegetation distributions are strongly influenced by fire disturbance patterns (Hemp and Beck, 2001; Hemp, 2005a; Hemp, 2005b; Hemp, 2009; Detsch et al., 2016). Precipitation reaches a maximum of 1800 mm year^{-1} around 2200 m (Wood, 1965a; Røhr and Killingtveit, 2003; Schüler and Hemp, 2016), supporting Montane Forests from 1600-2800 m with a complex continuum of trees and epiphytic species distributions (Hemp, 2006a; 2006b; 2011) that are crosscut with distinct riverine gallery forests (Hemp, 2006b). Submontane forests persist <1600 m, where the vegetation is often modified by cultivation (between ~1000-1800 m asl) with settlements and coffee-banana plantations, agroforestry, and forest gardens (Maro, 1988; Hemp, 2008; Mathew et al., 2016a and b).

Fire is key among the ecological disturbances, interacting with and modifying high elevation plant communities (Hemp, 2005a; Hemp, 2009; Finch and Marchant, 2011; Detsch et al., 2016). Fires are both naturally occurring and anthropogenically ignited with a long history as a land management tool (Archibald et al., 2012; Kamau and Medley, 2014). Fire return intervals, an important variable for maintaining fire-adapted ecosystems, are shorter in grassy and ericaceous ecosystems (<decadal to decadal frequencies) (Hempson et al., 2017) and are much longer in moist montane forests that are dominated by woody fuels (subcentennial to centennial

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frequencies) and have different ecohydrological interactions; yet, there are no studies quantifying fire return intervals in montane forests of eastern Africa. Fire regimes modify vegetation ecotones on mountains at both lower and upper elevations (Wood, 1965b; Hemp and Beck, 2001; Hemp, 2005a; Heckmann et al., 2014) and fire regime variability is associated with climate change (Wood, 1965b; Hemp, 2005a; Hemp, 2009) and anthropogenic activities in forests on the adjacent Pare Mountains (Heckmann, 2014; Finch et al., 2017).

Study site

Maua wetland (-3.129586, 37.431179; 3930 m asl; Fig. 1) is a sloping depression, approximately 75 m wide and 250 m long (0.35 ha), in the basaltic rock of 'The Saddle' of Kilimanjaro (Fig. 2). *Maua*, a Kiswahili word translating as 'flower', is a toponym also associated with a stream catchment down the southeastern flank of the mountain. The wetland is nested between lateral moraine deposits (Downie, 1964; Osmaston, 1989; Rosqvist, 1990; Shanahan and Zreda, 2000) and has an outflow that drains southward. Hydric edaphic conditions are maintained by rain, snow and occult precipitation into the depression.

The alpine vegetation zone (3900-4600 m) around the wetland is characterized by shrubby *Erica* heathlands and *Helichrysum* cushion vegetation (Schüler and Hemp, 2016; Fig. 2a and b) with thin soils and patchy barren areas of glacial deposits. Vegetation in Maua wetland is dominated by Poaceae with Cyperaceae and Asteraceae, pteridophytes, and localized clusters of *Dendrosenecio*, which reach 1-2 m in height (Fig. 2c). The continuous low-lying vegetation grows on the hummocks and hollows that define the wetland microtopography (Fig. 2c and d).

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Current land uses near the wetland include ecotourism, as there are nearby mountaineering trails and camps, and occasional honey collecting at high elevation by subsistence collectors within the Mount Kilimanjaro National Park.

METHODS

Fieldwork

On 29 January 2009, the Maua wetland sediment catena was probed using 1 m long, connectable rods to locate the central basin with the deepest sediment deposit. A sediment stratigraphy of 165 cm deep was collected from the deepest accumulation using a hand pushed Russian peat corer with a 50 cm long, 5 cm diameter hemicylindrical chamber (Belokopytkov and Beresnevich, 1955; Jowsey, 1965) from parallel core holes with ≥10 cm overlap for each drive. The sediment cores were wrapped in plastic and aluminium foil for transportation from the site and later stored in refrigerators at 4 ^{o}C. Pollen and phytolith analyses on the cores were performed at the National Museums of Kenya in Nairobi and charcoal analysis at the University of York, United Kingdom.

Geochronology and age-depth model

Accelerator mass spectrometry (AMS) radiocarbon dating of six bulk sediment subsamples provided a geochronology for the Maua sediment core. Samples were submitted to either Waikato Radiocarbon Laboratory, Waikato, New Zealand, or DirectAMS, Bothell, WA, USA; and were alkali-acid-alkali pretreated, combusted to CO_2 and reduced to graphite on a catalyst

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prior to AMS. Measured ^{14}C ages were corrected for isotopic fractionation with $\delta^{13}C$ values. These dates were used to develop a BACON version 2.2 age-depth model in the R statistical programming language version 3.4.0 (Blaauw and Christen, 2011a and b; R Development Core Team, 2017). Radiocarbon ages (^{14}C year BP) were calibrated using a Southern Hemisphere calibration curve (SHCal13; Hogg et al., 2013) and expressed as calibrated years before present (cal yr BP) relative to the Common Era calendar (CE1950). To provide age estimates for all subsampling depths within the core, ages were interpolated using the weighted mean within a 95% confidence envelope of the densities of ~8 million *t*-walk iterations using the Markov chain Monte Carlo algorithm through the probability densities of the calibrated radiocarbon dates (Blaauw and Christen, 2011a).

Pollen analysis

Thirty three wet sediment samples of 1 cm^3 were taken from 1-cm-thick levels spaced at 5-cm intervals down the core from 5 to 165 cm for pollen analysis. To remove carbonate, organic matter, and siliceous materials from the subsamples, pollen preparations followed a sequential chemical digestion using NaOH, HCl, HF and acetolysis (Erdtman, 1960; Fægri and Iversen, 1989). Between acid and base digestion steps the samples were rinsed with deionized water and decanted, or rinsed with glacial acetic acid for acetolysis, and finally with ethanol (95%) to prepare the pollen residues for microscopy. The samples were not sieved during processing and were not stained with a staining medium. The pollen residue was suspended in glycerol gel for storage and a small volume was mounted on microscope slides with coverslips for microscopy.

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Pollen grains were enumerated under an Olympus CX21FS1 microscope at 400x magnification to a minimum count of 430 grains. Two exceptions occurred: 1) a single sample at 5 cm depth was counted to 342 grains and was retained in the numerical analyses, and 2) another sample at 45 cm depth was excluded from the pollen diagram and other analyses as it anomalously contained 125 grains. Pollen identifications were aided by using the pollen microscope slide reference collection at the Palynology and Palaeobotany Section, National Museums of Kenya, Nairobi, the online African Pollen Database (APD; Lézine, 2001; Hély et al., 2006; Vincens et al., 2007), as well as published reference keys (Assemien et al., 1974; Bonnefille and Riolet, 1982; Retief and van Wyk, 2001; van Geel et al., 2011). For challenging identifications, particularly cf. *Ehretia* (Boraginaceae), fresh pollen reference material was collected from herbarium samples at the National Museums of Kenya and compared directly to the pollen residues extracted from Maua wetland sediments. Relative abundances were calculated from the total pollen sum. *Spirogyra* algal remains and spores of the coprophilous fungus *Sporormiella* were also enumerated during pollen counts and used as presence data (van Geel et al., 2011).

Pollen groupings

Pollen taxa assignments to ecological groups was done by harmonizing several published classifications of montane pollen records in the region (Rucina et al., 2010; Rucina, 2011; Schüler et al., 2012, 2014; Schüler, 2013; Schüler and Hemp, 2016; Finch et al., 2017).

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Macroscopic charcoal analysis

A total of 153 samples of 1 cm^3 were extracted at nearly complete contiguous 1-cm intervals from 0 to 165 cm stratigraphic depth for macroscopic charcoal analysis. Each sample was soaked for >24 hours in a labelled glass beaker of sodium hexametaphosphate solution of varying concentrations to disaggregate the sediments and deflocculate ionic clays from organic detritus (Bamber, 1982). Samples were then wet sieved through a 125 μm mesh and the retained content was examined under a Zeiss Stemi 2000-C stereomicroscope between 10-50x magnifications. Individual charcoal pieces were manipulated with a metal probe, identified with visual and haptic diagnostics (Hawthorne et al., 2017), and tallied (Whitlock and Larsen, 1991; Scott, 2010; Marlon et al., 2016). Subsequently, charcoal concentrations (pieces cm^{-3} wet sediment) were converted to charcoal accumulation rates (CHAR, pieces cm^{-2} yr^{-1}) using the age-depth model estimates (Whitlock and Larsen, 1991; Conedera et al., 2009).

Phytolith analysis

A total of 46 samples of 1 cm^3 of wet sediment were taken from 1-cm-thick levels at sampling intervals varying between 1-5 cm down the core from 1 to 165 cm. Phytolith extraction followed a heavy liquid floatation procedure (Albert et al., 1999) with a few modifications (Mercader et al., 2009). The procedure involved digesting approximately 3 g of sediment with a 10 mL solution of equal volume hydrochloric and nitric acid (3 molar HCl and 3 molar HNO_3) to remove carbonates and organic components respectively. The acidified samples were placed in a hot water bath until bubbling ceased, then washed with distilled water, vortexed and centrifuged

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for 5 minutes at 3000 rpm. Five mL of sodium polytungstate ($Na_6[H_2W_{12}O_{40}]$) with a relative density of 2.4 was added to the decanted residues and samples were vortexed, sonicated and centrifuged for 5 minutes at 3000 rpm (Munsterman and Kerstholt, 1996). The supernatants holding the phytoliths were transferred to 10 mL vials. An aliquot of approximately 1 mg was placed on a 25.4x76.2 mm microscope slide and was mixed with 2-3 drops of Entellen New® Rapid Mounting Medium before overlaying a 22x40 mm rectangular coverslip. Phytolith counts and identifications were done at 400X magnification using an Olympus BX52 optical light microscope. A target of at least 200 phytoliths were counted for morphological classification. In samples with very low phytolith counts, at least 50 phytoliths were counted to obtain as much information as possible following Albert and Weiner (2001), except for two samples that yielded less than 50 phytoliths.

Phytolith morphological classifications and identifications were based on various sources including the International Code of Phytolith Nomenclature (IPCN) 2.0 (ICTP, 2019), published studies (Twiss et al., 1969; Tieszen et al., 1979; Piperno, 1988; Rapp and Mulholland, 1992; Twiss, 1992; Albert, 1999; Fredlund and Tieszen, 1999; Piperno, 2006; Barboni and Bremond, 2009; Mercader, 2009, 2010; Rossouw, 2009; Madella et al., 2015; Neumann et al., 2017), and a modern reference collection created and housed at the Palynology and Paleobotany Section, National Museums of Kenya, Nairobi (Kinyanjui, 2013; 2018).

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Phytolith assemblage groupings

Based on taxonomic associations, phytoliths were grouped into four categories. 1) Poaceae included both diagnostic and non-diagnostic grass short cell phytoliths (GSCP) such as saddles, bilobates, crosses, rondels, trapezoids, polylobates, fan-shaped bulliforms and infilled trichomes. 2) Woody plants included spheroid variants (ornate, echinate, and verrucate), tracheids and sclereids. 3) Cyperaceae included achenes, papillae and cylindroid crenate morphotypes. 4) Generalists included all other discernible morphotypes that have yet to be diagnostically assigned to known taxonomic affiliations in the literature. To understand grassy vegetation cover dynamics, we further categorised morphotypes into their respective taxonomic affiliations as follows: bilobates, crosses and polylobates (Panicoideae), true and squat saddles (Chloridoideae), bilobates with long shanks (Aristidoideae) and collapsed saddles (Bambusoideae).

Data analyses

A stratigraphically constrained cluster analysis (CONISS; Grimm, 1987) was applied to the pollen assemblages and a broken stick model (Bennett, 1996) was used to test zones for significance using the rioja package version 0.9-15 (Juggins, 2017) with scripts in R version 3.4.0 (R Development Core Team, 2017) and plotted with C2 software (Juggins, 2007). To estimate turnover, a rate of change (RoC) analysis of the dissimilarities between each pollen assemblage was done through functions from the PaleoMAS package version 2.0-1 (Urrego et al., 2009; Correa-Metrio et al., 2011).

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We analyzed phytolith data with two commonly used approaches, the general and indices approaches (Neumann et al., 2009). First, the general approach wherein all the identified morphotypes were plotted as abundance diagrams using C2 (Juggins, 2007) to view the data and CONISS zonation. Secondly, the indices approach used well-defined taxa-diagnostic morphotypes to calculate indices that reflect grassland composition and vegetation structures known to correlate with climate variables such as temperature and moisture gradients (Bremond et al., 2005; 2008). Morphotypes used here include: true and squat saddles (Chloridoideae); bilobates, crosses, polylobates (Panicoideae); and spheroid ornates (woody dicots) (Bremond et al., 2005; 2008). The indices approaches first required the use of Principal Component Analyses (PCA) on the square-root transformed relative abundances in order to determine the significance of various morphotypes with regards to identifying vegetation structure types. The following three indices were explored to trace changes in canopy openness/closedness and climatic associations: 1) the Aridity (Iph) index, which uses the ratio of Chloridoideae to Panicoideae diagnostic morphotypes (both C_4 grasses) to infer the preponderance of short or long C_4 grasses along an aridity-humidity gradient (Bremond et al., 2005); 2) the Tree density (D:P) index, which uses the ratio of the sum of spheroid ornate (cf. spheroid granulate) morphotypes diagnostic of woody dicotyledons versus the diagnostic GSCP (Panicoideae and Chloridoideae) morphotypes to estimate canopy openness (Alexandre et al., 1997; Bremond et al., 2008); and 3) the Climate index (Ic), which estimates the proportion of C_3 grasses using the ratio of diagnostic morphotypes produced by Pooideae and Bambusoideae subfamilies versus C_4 Panicoideae and Chloridoideae (Bremond et al., 2008). The selection of the GSCPs was guided by Neumann et al.

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(2015): bilobates, polylobates and crosses were selected to represent Panicoideae; squat and true saddles were selected to represent Chloridoideae; bilobates with a very long shank were representative of Aristidoideae; while trapeziform and rectangular/oblong rondels were grouped as Pooideae C_3 grasses.

RESULTS

Stratigraphy and age-depth model

The sediments of Maua wetland were dense organic-rich deposits from 165 cm to the surface, with a few rootlets visible in the top 50 cm. Radiocarbon date determinations are presented in Table 2 and the age-depth model is presented in Figure 3. The uppermost radiocarbon date at 31–33 cm depth (D-AMS011826) was objectively discarded from the age-depth model and the near modern radiocarbon date at 55–56 cm (Wk-25720) was assigned a skewed student's *t* distribution to account for the long distribution tails of young calibrated radiocarbon ages (Christen and Pérez, 2010) creating a more linear and parsimonious age-depth model. Alternative exploratory models with a more normal distribution for this specific date at 55–56 cm forced a resulting age-depth model with a rapid recent accumulation of sediment, though the core stratigraphy had no visible evidence of such rapid accumulation, as would be seen with a transition to peat, for example. Arguably the uppermost radiocarbon date at 31–33 cm depth does suggest movement of older carbon into the wetland, though there is no conspicuous visual evidence that this was the result of a rapid mass movement of sediments along the relatively gentle slopes proximal to the wetland.

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Pollen and charcoal record

A total of 32 samples were retained for plotting the pollen diagram and for numerical analysis. A total of 94 pollen types were identified (Table 3), including two aquatic plant taxa (*Typha* and *Potamogeton*). Aquatic taxa were infrequent (<1.5% total pollen relative abundance) and were not used to create a separate aquatic pollen sum. *Spirogyra*, a filamentous and often epiphytic green algae common to lentic freshwaters (Ross, 1953; Denny et al., 1978) were observed only at 30-31 cm (393 cal yr BP). Spores of *Sporormiella*, a coprophilous fungus, were observed in 10 subsamples, reaching its highest counts at 85-86 and 80-81 cm (1122-1040 cal yr BP). Pollen analysis at 5 cm intervals averaged 100 years between samples with a range of 75-155 years, permitting interpretations of variability in vegetation cover on centennial and millennial scales. Charcoal analysis at 1 cm sampling intervals averaged 19 years between samples with a range of 12-31 years allowing for analyses at the multidecadal level. Twelve charcoal samples (7.3%) were missing values because of limited sediment material and were linearly interpolated using nearest neighbours for graphing (at 0-1, 4-5, 10-11, 15-16, 18-19, 27-28, 33-34, 34-35, 52-53, 57-58, 60-61, and 164-165 cm). The pollen taxa groups are presented in Figure 4 and Table 3.

The pollen assemblage consisted of three zones Maua1a, Maua1b and Maua2. CONISS cluster analysis identified two statistically distinct pollen assemblage zones in the core: Maua1, from 3000-600 cal yr BP and Maua2, from 600 cal yr BP to present. A statistically insignificant subzone was identified from 800-600 cal yr BP (Maua1b; Fig. 4) with relatively high variability that is evident on visual examination of the data (Fig. 4).

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Zone Maua1a (3000-800 cal yr BP) was predominated by Cyperaceae (20-60%), Asteraceae (<25%), cf. *Ehretia* (Boraginaceae, <30%) and Poaceae (10-35%). Montane Forest taxa are also present, including high and consistent abundances of *Podocarpus* (8-25%), *Olea* (2-6%), and *Hagenia* (2%). Charcoal influx is relatively low and appears correlated with Cyperaceae and cf. *Ehretia*, though values increase at 1200-800 cal yr BP.

The statistically insignificant subzone Maua1b (800-600 cal yr BP) was characterized by conspicuously low charcoal influx. *Podocarpus*, Ericaceae, Asteraceae and cf. *Ehretia* decreased to the lowest values of the record though both Cyperaceae and Poaceae decreased only slightly. In contrast, abundances of *Myrsine*, *Hagenia*, *Nuxia*, Amaranthaceae/Chenopodiaceae, *Phyllanthus* and *Stemodia* increased during Maua1b (Fig. 4).

Zone Maua2 (600 to -59 cal yr BP) was dominated by ericaceous taxa (Ericaceae, *Anthospermum*, *Artemisia*, and *Stoebe*) that increased in abundance from Maua1. In comparison to Maua1, Maua2 features higher peaks and higher mean accumulation rates of charcoal. Montane Forest taxa (*Cordia*, *Ilex*, *Lasianthus*, and *Myrica*) are also more consistently present, and there are relatively high abundances of *Podocarpus*. *Hagenia*, *Macaranga*, *Nuxia* and cf. *Ehretia* are absent from Maua2. Poaceae, Rubiaceae and *Stemodia* increase to their highest abundances while Asteraceae and Cyperaceae are lower than during Maua1a.

Phytolith record

A total of 29-621 phytoliths were counted per sample, with an average of 272±160 (1σ standard deviation). Indeterminable phytolith counts per sample ranged from 0-55, with a mean of 17. The

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phytolith morphology groups are presented in Figure 5 and Table 4. Samples with total counts below 100 (n=9 of 45 samples) were removed from statistical analyses. CONISS zonation of the phytolith assemblage did not identify statistically significant zonal boundaries but did delimit a single statistically insignificant boundary at 550 cal yr BP. The calculation of phytolith-based indices (Bremond et al., 2008) was hampered by several 0 count values and thus division by zero created high overall noise within the phytolith assemblage record. This suggests that the phytolith assemblage at Maua has a high amount of noise or that the assemblage was very different from those derived from previous investigations in montane environments in eastern Africa. Both options are conceivable given the source plant types present, the paucity of existing phytolith studies examining high-elevation vegetation, and also the possibility of syn- and post-depositional taphonomic processes.

The phytolith record was dominated by woody and generalist morphotypes. Woody morphotypes included spheroid ornate (cf. spheroid granulate) (up to 80%), spheroid plicate (cf. spheroid rugose) (<25%) and spheroid verrucate (<25%). Generalist morphotypes, which are present across various taxonomic groups including grasses, included spheroid psilate (<50%), parallelepiped psilate (<50%) and cylindroid psilate (<30%). The phytolith assemblage is characterised by high levels of variation, within both the Poaceae and woody taxa present throughout the record. In terms of relative abundance, morphotypes classified as Poaceae (GSCP) contributed on average 20% to the total phytoliths in each sample. Woody types have a consistently high occurrence until around 800 yr BP and subsequent decrease to present. Poaceae types were consistently higher over the past 300 years only (Fig. 5).

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Review of late Holocene land use histories on Kilimanjaro

The literature review collated and categorised published archaeological research from Kilimanjaro and is informed by regional patterns of livelihood change over the late Holocene. Current prominent land uses on Kilimanjaro include commercial crop cultivation, forestry, urban settlements, conservation, and ecotourism. Archaeological and historical evidence indicates that land use on and around Kilimanjaro since the mid Holocene featured hunting and gathering (continuously throughout this time), pastoralism (c. 4000 cal yr BP) and agriculture (c. 2000 cal yr BP). It is important to note that the mountain has not yet been archaeologically surveyed using systematic methods. Despite Kilimanjaro being an UNESCO World Heritage Site, remarkably little archaeological work has been done to explore the full history of late Holocene human occupation. Despite the lack of published material evidence across the landscape, highland-lowland connections are remembered by current inhabitants as being of both great antiquity and cultural significance. For example, oral traditions refer to the earliest people on the mountain as *Wakonigo*, whose presence in montane forests is marked by old shrines, broken pots, and sacred Chagga plants such as *masala* (*Dracaena*) (Stahl, 1964:53; Clack, 2009). Some of the oldest known clan histories from Kilimanjaro speak of how the ancestors first settled high-elevation areas such as the Shira Plateau (3600-3800 m asl) before descending the mountain (Stahl, 1964:58-59). The known published archaeological sites are notably absent at high elevations (none above 2000 m asl) and the northeastern slopes of the mountain (Fig. 6), but, this spatial

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pattern must be interpreted with caution given the uneven degree of archaeological sampling effort across the landscape (Marchant et al., 2018).

It is not possible to state with certainty that people avoided occupying high elevation areas of Kilimanjaro in the past, and thus the prospect remains that anthropogenic modifications to vegetation and fire regimes may have occurred around the Maua wetland. There are physiological challenges posed by traveling to altitudes as high as Maua. For one, humans accustomed to living at sea level experience hypoxia when they ascend to elevations in excess of 2500 m asl (Beall, 2014). Furthermore, temperature and rainfall conditions at Maua would make the cultivation of African staple crops around the site unrealistic. Livestock also suffer when residing at moderate to high elevations and cattle in particular are susceptible to altitude induced pulmonary hypertension (Pauling et al., 2018). Livestock that have developed adaptations are however able to thrive at impressive elevations and have been known to live at 4000 m asl (Claxton and Ortiz, 1996). Questions remain as to how common the physiological capacity for life at extremely high elevations is across eastern African human and livestock populations. 'Pastoral Neolithic' sites on the Mau Escarpment located above 2500 m asl, such as Remnant site (2800 m asl; Bower et al., 1977), indicate that early herders were capable of occupying areas of considerable elevation, a skill no doubt encouraged by their habitation adjacent to the Rift Valley, a region with intense topographic relief. Still, Maua is much higher than these known comparable sites on neighbouring highlands and the availability of resources, including altitudinal oxygen, is appreciably different. Livestock herding is thus likely to have been a highly marginal practice above 4000 m asl on Kilimanjaro. The available evidence does not however

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allow us to discount the possibility of humans engaging in other activities at Maua, including ceremonial or hunting and gathering practices. The recent discovery of obsidian outcrops in the Bale Mountains of Ethiopia at 4200 m asl that were being used as early as the Middle Stone Age by people living at 3469 m asl is especially intriguing (Ossendorf et al., 2019) and highlights the need for further archaeological exploration of past utilizations of African highlands, including Kilimanjaro. Ethno-archaeological investigations of current and recent historical high elevation land uses on Kilimanjaro, and the ecological legacies of such activities, are also needed.

With respect to interpreting the palaeoenvironmental records at Maua, it is necessary to state that the degree to which pollen and charcoal in the Maua sediment records are derived from lower elevation gradients, where there is more concrete evidence of human land use and land cover change occurring, is also relatively uncertain. The upslope transport of pollen can overrepresent arboreal taxa at high-elevation sites (Markgraf, 1980; Solomon and Silkworth, 1986; Urrego et al., 2011). Modern pollen rain studies on the southern slope of Kilimanjaro along an elevational gradient between 1900 and 3200 m asl (from the submontane forest to upper montane forests) indicate that pollen and spore deposition are representative of the surrounding vegetation, though their dispersal is strongly influenced by regional wind patterns, and even in closed canopy sites there is representation from high and low pollen producing, nonlocal (>100 m distance) taxa (Schüler et al., 2014b). As Table 3 indicates, the Maua sediments do contain pollen that has been transported from lower elevations, and are thus assumed to be capturing, to an extent, signatures of anthropogenically driven vegetation transformation occurring downslope.

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Age determinations for archaeological site occupations are more often inferred from associated ceramic ware assemblages because few of the known sites have been radiocarbon dated (Supplemental Material Table 1). 'Early Iron Age' sites were designated as any recorded presence of Kwale ware ceramics, a pottery tradition roughly dating from the first century to the mid-first millennium CE (Soper, 1967; Helm, 2000). 'Middle Iron Age' sites mark the occurrence of Maore ware, dating to around the later first millennium and early second millennium CE (Soper, 1976; Odner, 1971; Walz, 2010). 'Later Iron Age' sites indicate the presence of either Odner's (1971) Kilimanjaro Group C, D, or E, Lanet ware, or Soper's (1967) Group D ware from Usambara, all of which are thought to have been in use in the second millennium CE (Posnansky, 1967; Helm, 2000:68). Considering the paucity of archaeological investigation here, there is certainly scope to re-evaluate and further refine ceramic typologies for Kilimanjaro. To support our interpretation of human-environmental interactions we plot the archaeological finds that exist in four broad time intervals; these extend from the early food producing Pastoral Neolithic through to the Late Iron Age (Fig. 6).

DISCUSSION

Vegetation assemblage changes at Maua

Maua1a (3000-800 cal yr BP)

During the early Maua record, ericaceous and Montane Forest pollen types decrease slightly while Poaceae and Cyperaceae increase (Figs. 4 and 7). Charcoal also increased slightly throughout Maua1a and positively correlated with variations in Cyperaceae pollen. This

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correlation suggests Cyperaceae made much of the fuel source for the locally-created charcoal, and that there were increased abundances in Cyperaceae within the wetland during Maua1a. Peak pollen abundances of *Podocarpus* in the Maua record occur from 2300-2000 cal yr BP, concomitant with peak abundances at Lake Rutundu, Mount Kenya (3140 m asl; Coetzee, 1967; Hamilton, 1982a), and with increasing relative abundances from 2600-1600 cal yr BP at Oblong Tarn, Mount Kenya (Courtney Mustaphi et al., 2017). A previously studied wetland sediment pollen record from Kilimanjaro (2650 m asl; Coetzee, 1967) shows an increase in *Podocarpus* from approximately 4000-1800 cal yr BP, although the sampling resolution is rather low and the relative change is due to large variations in *Ilex* in that record. It is challenging to examine variability in anemophilous pollen taxa in mountainous areas (Birks and Birks, 1980; Markgraf, 1980; Solomon and Silkworth, 1986), but these coincidental variations in *Podocarpus* could be related to the expansion of montane *Podocarpus*-dominated forests driven by hydroclimatic changes and/or changing fire disturbance regimes.

The wetland was probably ice free by the Holocene transition (Shanahan and Zreda, 2000; Mark and Osmaston, 2008) and glacial ice on Kilimanjaro was greatly reduced and varied slightly during the late Holocene before experiencing significant reductions over the past century (Hastenrath and Greischar, 1997; Thompson et al., 2002). The wetland was dominated by Cyperaceae-Poaceae vegetation throughout the Maua1a zone. Increased abundances of charcoal and Cyperaceae appear to be correlated with wetter intervals (less negative $\delta^{18}O$ values) associated with the composite of isotope records of Kilimanjaro ice fields (Fig. 7; Thompson et al., 2002) potentially supporting the argument that local wetland biomass and burning was

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influenced by high-elevation hydroclimate during this interval. The charcoal is most likely created locally from the wetland and its watershed, although it was not assessed if charcoal is transported uphill by convection from lower elevation fires (Pisaric, 2002; Tinner et al., 2006; Adolfe et al., 2018), highlighting a topic for further research on tropical mountains (Vachula and Richter, 2018).

The pollen record from Small Momela Lake at 1440 m asl on Mount Meru shows centennial-scale variability in the relative abundances of Poaceae and Cyperaceae from 3000-1200 cal yr BP (Bolick, 1991). The increased charcoal accumulation at Maua from 1100-800 cal yr BP coincided with increased charcoal accumulation from 1300-900 cal yr BP at Lake Challa (Nelson et al., 2012), large increases in Poaceae from 1400 to 800 cal yr BP at Namelok wetland (Rucina et al., 2010), and increased charcoal at Enkongu wetland, Amboseli (Githumbi et al., 2018b). All of those sites are located in the lowlands surrounding Kilimanjaro (Fig. 7) and it is difficult to disentangle regional climate and/or anthropogenic drivers of environmental change to explain these variations. Varying relative importance of fire regime drivers at each site may explain some of the spatiotemporal variability (Gillson, 2004). Ericaceous pollen is relatively low during this initial burning interval (1200-800 cal yr BP); while *Hagenia*, *Podocarpus*, Cyperaceae and cf. *Ehretia* abundances are relatively high (Fig. 4).

Phytolith data between 3000 and 2500 cal yr BP represents local input consisting largely of Cyperaceae morphotypes indicating the wetland was relatively moist during this interval. Between 2500 and 800 cal yr BP the phytolith assemblage reflects both local and watershed-area inputs derived from woody dicots - particularly the spheroid morphotypes (Fig. 5). There is a

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notable presence of the Pooideae morphotypes mainly derived from the tussock grass types common upon hummocky alpine periglacial ecosystems. This suggests that the water level in the wetland was generally very low and the absence of aquatic vegetation pollen types supports the interpretation that the wetland was covered by terrestrial vegetation.

People practicing hunting and gathering were almost certainly living on Kilimanjaro throughout the Holocene, and may have even preferred higher elevation areas as the savanna-montane forest ecotonal zone retreated at the termination of the African Humid Period (Ambrose and Sikes, 1991). The oldest archaeological remains suggestive of livestock keeping on Kilimanjaro were deposited around 4000 cal yr BP on the western side of the mountain, just below 2000 m asl in the lower Montane Forest zone (Mturi, 1986). Material remains affiliated with the 'Savanna Pastoral Neolithic' archaeological group, and thus specialized pastoralism, are also present here and date to between 3000-1500 cal yr BP. Faunal remains from these sites are predominantly of cattle and sheep or goat, though wild animals are also present, suggesting a mixed livelihood of pastoral activity and subsistence hunting. Indeed, regional archaeological records indicate that hunting and gathering modes of production would have overlapped and persisted with pastoralism and agriculture over the last three millennia, rather than been displaced through time (Lane, 2004). The possibility of intensive 'wild' resource management by hunter-gatherer and livestock herding populations on Kilimanjaro during the last three millennia and prior also merits further consideration as there is clear evidence for the careful management of morphologically undomesticated plant species in other regions of sub-Saharan Africa (Lane and Shoemaker, 2017). Yet despite Kilimanjaro being one of eastern Africa's 'islands of

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intensive agriculture' (Widgren, 2004), the early history of human-vegetation relationships remains almost entirely unknown. Farming in the wider region is typically thought to have become established after 2000 cal yr BP however, accompanied by Bantu language speakers, agropastoralism, and iron-working (see Crowther et al., 2018 for a review). This date is probably best considered a *terminus ante quem* for the origins of farming in the area as finger millet (*Eleusine coracana*) was very likely cultivated in eastern Africa before the so-called 'Bantu expansion' (Fuller, 2003; Fuller and Boivin, 2009). Some have suggested that Asian domesticates such as taro (*Colocasia esculenta*), chicken (*Gallus gallus domesticus*) and banana (*Musa* spp.) were also being farmed in eastern Africa prior to 2000 cal yr BP (De Langhe, 2007; Mbida et al., 2000; 2001; 2004; 2006; Lejju et al., 2005; 2006; Chami, 2001), and Kilimanjaro may have been an early locus for banana cultivation, though the evidence is inconclusive (Sinclair, 2007; Neumann and Hildebrand, 2009; Shipton et al., 2016). Coastal archaeological records could suggest that the widespread adoption of Asian domesticates by eastern African farmers did not occur until the last millennium (Walshaw, 2015; Crowther et al., 2018). Iron smelting may have also been occurring on Kilimanjaro over the last two thousand years, though archaeologists have yet to document iron working remains here, suggesting it was extremely limited in scope compared to operations underway in the Pare Mountains from the second half of the first millennium (Iles et al., 2018; Iles, 2020). It is possible that people used high-elevation areas of Kilimanjaro during the Maua1a zone, potentially for herding, hunting and gathering, transportation routes or ceremonial activities, though direct evidence is lacking. Certainly the

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surrounding lower elevation areas were being modified by human activities, including pastoralism, hunting and gathering, and agriculture by 2000 cal yr BP (probably increasingly so).

Maua1b subzone (800-600 cal yr BP)

The pollen assemblage subzone is dynamic and represents an assemblage transition between Maua1a and Maua2 with distinctively low charcoal, high Cyperaceae abundances, increasing turnover rates in the pollen assemblage (Fig. 7), highly variable phytolith assemblages, negative values in pollen PCA axis 2 scores (Fig. 7), and the samples from this zone cluster together on the PCA biplot (SM Fig. 1). Low charcoal accumulation rates could be due to several factors. The local hydroclimatic regime could have become too wet and reduced flammability; or decreased ignitions (anthropogenic, lightning, or spontaneous) may have limited fires; fuel connectivity could have also been interrupted as vegetation became more sparse or increasingly dissected by, for example, animal trails; and lastly, productivity changes could have affected total above ground biomass (fuel availability). Above ground biomass varies due to vegetation productivity and herbivory regimes, the latter has been linked to the consumption of the potential fuels for carrying fires and fragmenting the grass canopy (Archibald et al., 2005; Bond and Keeley, 2005; Hempson et al., 2015; Donaldson et al., 2018). There are very few studies of high-elevation herbivory on Afroalpine vegetation by domestic or wild animals (Mulkey et al., 1984; for subalpine effects see Wood, 1965b; and Kikoti et al., 2015) or information to explain reduced fire ignitions; thus, it remains difficult to explore the equifinality of the observed low charcoal accumulation rates. During this subzone, the wetland transitioned from a Cyperaceae-Poaceae

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dominated to more Cyperaceae dominated habitat (see high abundances in Fig. 4), having lower fuel flammability and connectivity and also lower grazing desirability. The Maua1b subzone also has concomitant changes within both the Montane Forest and ericaceous taxa assemblages (Fig. 4; SM Fig. 1). Several Montane Forest taxa, such as *Nuxia*, *Hagenia* and *Schefflera* increase and then decrease during the subzone and there is a conspicuous decrease in *Podocarpus* abundances (Fig. 4). During Maua1b, Kilimanjaro ice field $\delta^{18}O$ values are markedly more negative, as is the Lake Challa BIT index and reconstructed mean annual air temperatures at Lake Rutundu (Fig. 7; Sinninghe Damsté et al., 2011; Loomis et al., 2017), suggesting that - at least at middle and lower elevations - the region was cooler and drier.

Maua2 (600 to -59 cal yr BP)

This zone is significantly different from Maua1 and has more positive scores on PCA axis 1, suggesting further rapid changes in the mountain flora in and around the wetland following the Maua1b transition (Fig. 7). Pollen assemblage turnover remains highest during this most recent interval and the uppermost samples are characterised by very different pollen assemblages (Fig. 7). The phytolith assemblage shows a trend of decreasing forest indicators and woody dicots. Cyperaceae-morphotypes also decrease, though Poaceae morphotypes increase; Chloridoideae C_4 short grasses in particular become more prominent. Overall, the phytolith evidence suggests either drier conditions or clearing of woody plants - and possibly both (Fig. 5). From 500 cal yr BP to present, there is a general decrease in or total absence of forest indicators, dicots and Cyperaceae morphotypes while Chloridoideae C_4 grasses are notably present during Maua2. The

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charcoal record suggests a very different fire regime of increased burning since the onset of Maua2, indicating more fire-adapted taxa (Poaceae and Ericaceae) with consistently higher Poaceae phytolith morphotypes (GSCP) and higher local biomass (Figs. 4 and 5). Increased charcoal during Maua2 could be related to increased vegetation biomass available to burn (Courtney Mustaphi and Pisaric, 2014) in response to increased moisture availability at the wetland. The site may have thus transitioned from a Cyperaceae to a Poaceae tussock dominated wetland, as it remains at present. The data does not make it possible to examine if the wetland itself was ever covered by ericaceous vegetation, as is the case for some high-elevation mires (Salt, 1954), or if it remained consistently dominated by Poaceae throughout the entirety of Maua2. While charcoal accumulation rates showed decreasing values during Maua2 to present, counts are nonetheless predominantly much higher in comparison to previous intervals. Presently on Kilimanjaro, herbaceous biomass increases from the mid-montane forest to alpine elevations, an increase linked to changing moisture availability (Ensslin et al., 2015), potentially suggesting a link between surface moisture, productivity, and fire.

The epiphytic filamentous green algae *Spirogyra* was observed in very low abundance (3 individual remains with a count of 650 pollen) at 393 cal yr BP, which suggests the potential for puddling in the wetland among the vegetation (Ross, 1953; Denny et al., 1978). *Spirogyra* dominated the phytoplankton community in the Lower Kitandara Lake (4020 m asl), Ruwenzori Mountains (Richardson, 1964), and was also found in late Pleistocene peaty sediments at a swamp in the Udzungwa Mountains (Mumbi et al., 2008). *Spirogyra* is frequently present in aquatic ecosystems with high thermal and radiation variability (Gelorini et al., 2011), diurnal

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conditions which prevail at Maua wetland. If occasional puddling within the wetland occurred during the past few hundred years, it suggests that multiannual alternation between wet and dry conditions would be an important characteristic of the climate-vegetation-fire relationship during Maua2, a situation markedly different than during Maua1.

The pollen and charcoal records indicate that local vegetation during this zone becomes predominantly ericaceous with high abundances of *Erica*, *Artemisia*, *Anthospermum* and *Stoebe*. Taxa in both the Ericaceae and Poaceae families likely benefited from increased fire, as has been described in other Holocene records from high elevation *Erica* heathland sites in eastern Africa (Gil-Romera et al., 2019). The associations between charcoal, ericaceous taxa and Poaceae at Maua suggest a more fire-adapted vegetation community at the wetland during a time of regionally drier high-elevation climate (Thompson et al., 2002) and decreasing reconstructed daytime relative humidity (Hepp et al., 2017) and higher ericaceous pollen abundances at Maundi Crater (Schüler et al., 2012). This suggests a more nuanced study of the complex local ecohydrology is needed to explain these patterns to further understand hydroclimate, vegetation and fire and grazing interactions.

The lacustrine sediment record from Small Momela Lake does not cover this time interval in detail but the low elevation sites of Lake Challa (Fig. 7; Sinninghe Damsté et al., 2011) and Lake Duluti, both show evidence of change during Maua2. At Lake Duluti, significant changes to diatom assemblages occur within the past 700 years, both within the relative abundances of planktonic and periphytic taxa and with respect to an overall decrease in periphytic diatoms toward present, suggesting more open water (Öberg et al., 2013). The stable

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carbon-isotopic composition of fossil plant leaf waxes from sediments in Lake Challa increase and remain at their highest values (averaging -30‰) from the past 3000 years (average -31‰; Sinninghe Damsté et al., 2011; Fig. 7) suggesting relatively wet conditions at least at low elevations. Lake Challa is groundwater fed and it has been noted that there is a negative relationship during the late Holocene between $\delta^{18}O$ values in Lake Challa diatoms (Baker et al., 2011). Similar to Maua, an onset of increased fire activity occurred at Kwasebuge, North Pare Mountains, though it has been more directly attributed by Finch et al. (2017) to changing human activities in the forests. Evidence of vegetation and erosion changes from colluvium and palustrine deposits in the Pare Mountains suggest increasing land use intensities, increased erosion, and changing vegetation cover (Heckman, 2014). It has been hypothesized that this intensification of soil erosion over the last five centuries occurred due to wood use for increased iron smelting and smithing (Schmidt, 1989; Hakansson, 2008a) or alternatively, to intensification in agricultural production to meet the demands of an increasingly international landscape as trade caravans became larger and more frequent, particularly in response to global market demand for ivory (Biginagwa, 2012; Iles et al., 2018). Furthermore, large changes to charcoal accumulation rates are evident in several palustrine records from surrounding Kilimanjaro and show high spatial variation in fire histories (Gillson, 2004; Githumbi et al., 2018a, 2018b). Charcoal accumulation rates increase after 500 yr BP at Kimana and Enkongu wetlands, Amboseli, although the geochronological uncertainty is high at Kimana (Githumbi et al., 2018a), and the Namelok wetland record shows increased charcoal content after 300 yr BP-present (Rucina et al., 2010). Charcoal accumulations are lower from 400-500 yr BP to present at both Kanderi, Tsavo

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(Gillson, 2004); and Esambu, Amboseli (Githumbi et al., 2018b). The differing signals in charcoal accumulation highlight local-scale fuel and fire responses, and the spatial heterogeneity of savannah fire regimes, the understudied complexities of fire regimes at the savannah-wetland edges (Kirby et al., 1988; Kirkman, 1995; Casanova and Brock, 2000; Cassidy, 2007; Nielsen et al., 2013; Saintilan and Rogers, 2015) and more broadly the role of human activities in and around wetlands (Seki et al., 2018).

National-scale models estimate that populations and agricultural land use were expanding during this time (Fig. 7), tentatively supporting the hypothesis that anthropogenic drivers of land cover change intensified (Klein Goldwijck et al., 2010; Kaplan and Krumhardt, 2011; Kaplan et al., 2011). Suggestions that intensifications in land use were escalating during the last five centuries should be interpreted with caution however, as evidence for anthropogenically induced environmental change in the form of written records, detailed oral histories and more conspicuous archaeological remains become increasingly accessible toward the present time, potentially leading to underestimations of the magnitude and intensity of earlier land use. Nonetheless, several lines of evidence suggest a diversity of human-environment modifications during this time (Fig. 6), including: the remains of terraced irrigation infrastructure at highlands in the region (up to 1200 m; Sutton, 2004; Stump, 2006; Lang and Stump, 2017); the remains of caves, dugouts and bolt-holes used to shelter people, cattle and valuables during conflicts (Clack, 2009; Silayo, 2016); oral histories for *mfongo* irrigation systems on the slopes of Kilimanjaro (Tagseth, 2010); the cultivation of crops introduced from the Americas (including maize and tobacco; Miracle, 1965; Cherniwchan and Moreno-Cruz, 2019); Chagga forest gardens

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(Fernandes et al., 1985); historical records of elephant hunting, especially using game-pits dug in the upper cultivation zone, c. 2000 m (Meyers 1891:126); records of ivory trade involvement (Coutu et al., 2016); historical records of apiary operations in the heathland vegetation zone, c. 2900-3550 m (Meyers, 1891: 133); limited scale iron-smelting at Uru, Mamba and Marangu (Wimmelbücker, 2002:62) and oral histories of other mountain forest uses (Stump and Tagseth, 2009). On the lower southeastern slopes of Kilimanjaro, stream fed furrow networks known as *mfongo* together with water storage ponds (Kimaro et al., 2019), and irrigation systems have likely contributed significantly to modifying local ecologies. *Mfongo* networks are recognized to be central to the cultural heritage of the Chagga people (Tagseth, 2010:16). Oral traditions, historical references, and linguistic evidence allow for us to conclude that irrigation features on Kilimanjaro were being built by at least the seventeenth century (Stump and Tagseth, 2009), though irrigation systems had emerged in the wider region from as early as the fourteenth century CE (Sutton, 2004; Lang and Stump, 2017; Kabora, 2018; Thornton-Barnett, 2018; Kabora et al., 2020; Fig. 7). The emergence and intensification of irrigation agriculture is linked to a complexity of societal, ecological and climatic factors (Håkansson, 2007; Boserup, 1965; Börjeson, 2007; Davies, 2015). Furrow expansion and defensive constructions during the nineteenth century (Kusimba et al., 2005; Clack, 2007, 2009), does however, seem to coincide with a time of political centralization, conflict, slave raiding (Wimmelbücker, 2002) and intensified long distance caravan trade (Stump and Tagseth, 2009: 111). Kilimanjaro was a major node along multiple caravan trade routes and high-elevation trails above the forest zone crossed the upper slopes of Kilimanjaro during this time, allowing people to avoid potentially hostile

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confrontations (Stahl, 1964: 344); and perhaps increasing the intensity of anthropogenically induced change at elevations closer to Maua.

The uppermost sediments at Maua show moderately high ericaceous pollen, high Poaceae pollen and phytolith relative abundances, and moderately high charcoal (Fig. 7). European descriptions of the mountain emerged during the mid-to-late nineteenth century (Krapf, 1858; Meyer, 1890, 1891, 1900). Further explorations in the early twentieth century, including ascents of the mountain (e.g. Uhlig, 1904; Jaeger, 1909; Klute, 1920; Gillman, 1923), contributed to the written documentation of the diversity of human land use modifications and observations of vegetation, wildlife and glaciers of Kilimanjaro (Alluaud, 1908; Sjoestedt, 1910; Engler, 1925; Cotton, 1930; Humphries, 1959). Increasingly after CE1900, colonialists also annexed large areas of Kilimanjaro for farmlands and a forest reserve (Swynnerton, 1949; Sunseri, 2003; Mwakikagile, 2006). A sharp rise in coffee (*Coffea* spp.) cultivation exacerbated issues of land distribution and scarcity (Tagseth, 2008:475). More detailed descriptions of flora and fauna at the upper elevations were not published until the mid 1900s (Salt, 1954) and systematic air photography began in the mid 1900s (McGrath, 1976); but in the interim years there had been a steady decline in millet production in favor of newer commercial cultivars such as maize, wheat and coffee, and a decrease in investment in irrigation in the uplands concomitant with a major expansion in agricultural activity on the lower slopes of Kilimanjaro (Tagseth, 2006; Chuhila, 2016; Bender, 2016). Satellite observed remote sensing products available since the 1970s support observations that decadal-scale variability at the ecotonal gradients between montane forest and Ericaceous vegetation cover are highly dynamic and are driven by fire (Wood, 1965b;

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Hemp, 2005a; 2005b; Chuhila, 2016; Detsch et al., 2016; Kilunga et al., 2019). Several lines of evidence support rapid (decadal scale) changes to vegetation cover on Kilimanjaro slopes. Future work should integrate several lines of evidence from palaeoecology, archaeology, history, and social sciences (Courtney Mustaphi et al., 2019) to further examine the relative importance of hydroclimatic, fire, plant competition strategies, local topography, herbivory and anthropogenic interactions that influence spatial heterogeneity in vegetation biogeography on Kilimanjaro.

Summarising long-term human-environment interactions

Several factors have long been observed as annual-to-decadal scale drivers of spatial complexity in vegetation on the mountain, including interannual rainfall variability, fuel accumulation, and fire frequency, seasonality and type (Wood, 1965b). Abiotic and biotic factors both explain the spatiotemporal complexity of vegetation on the mountain, including geology and the development of soils (Little and Lee, 2006; Zech et al., 2011; Montade et al., 2018), topographic interactions with cold katabatic air masses and humidity regimes, the large and deep radial ravines (Hemp, 2006a), plant competition, and large mammal wallowing and trampling (Wood, 1965b). Amongst the factors that must be considered when examining ecosystem functioning are long term and legacy effects of anthropogenic activities. For example, plant biogeographers on the mountain have long found it difficult to explain some distribution patterns, such as that of the 'missing' bamboo cover (Moreau, 1944; Hemp, 2006a), and there is some speculation that such distributions were potentially modified by anthropogenic activity (Grimshaw, 1999), including selective logging (Bjørndalen, 1992) or sparing of sacred taxa/space, cultivation (Hemp, 2006a)

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and influences on homogenising and diversifying fire regimes (Archibald et al., 2012; Beale et al., 2018; Coughlan et al., 2018).

Anthropogenic activities, notably grazing, hunting, metallurgy, settlement, agriculture and burning (e.g. for honey hunting, agricultural field preparation, grazing resource management, animal viewing spaces in parks) all significantly modify vegetation patterns (Wood, 1965b; Archibald et al., 2012; Vehrs and Feller, 2017; Boles et al., 2019). The potential of either increased natural or anthropogenic-driven burning (or both) influencing the increased apparent biodiversity in the pollen taxa assemblage during Maua2 is particularly interesting among investigations of relationships between fire and biodiversity (Parr and Andersen, 2006). Wood (1965b) reported that honey collecting and fire use above the forest line contributed to fire occurrences in ericaceous vegetation cover; although this reference was missed in global syntheses of fire use by hunter-gatherer societies (Binford, 2001; Coughlan et al., 2018) and has yet to be corroborated with oral histories. Moreover, fire activity (or specific components of fire regimes) including the development of fire plans in conservation management, have yet to be studied for their role in promoting homogeneity or heterogeneity in high elevation Afromontane ecosystems (e.g. Kelly et al., 2015; Trauernicht et al., 2015; Beale et al., 2018). Further research combining palaeoecology, archaeology, historical ecology, and ethnobiology would advance knowledge of historical human-environment interactions on the mountain. Human induced defaunation on the mountain, both in terms of biodiversity and biomass, cascades and alters plant-animal-soil dynamics (Child, 1965; Wood, 1965b; Lundgren and Lundgren, 1972; Newmark, 1991; Grimshaw et al., 1995; Newmark, 1996). The disruption of persistent land-use

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practices that have unknown historical provenance and durations remain unassessed in both terms of potential negative consequences and beneficial legacy effects on the environment and socio-ecological systems.

An estimate of the number of people living on Kilimanjaro (Meyers, 1891: 114), prior to the disastrous outbreaks of famine, smallpox and rinderpest beginning in the 1890s, suggests that over the last century the population has increased to roughly 30 times its former size. Historically, and still today, there are concerns that human practices such as water extraction (Stump and Tagseth, 2009: 117; Bender, 2016), burning (Hemp, 2005a), and logging (Hemp, 2006a) on the mountain are unsustainable leading to forms of environmental degradation. Of further concern are declines in rainfall indicated in precipitation records and observed by people living on Kilimanjaro's slopes (Ngana, 2002; Hemp, 2005a; Tagseth, 2010:17). The need for appropriate resource management regimes in the face of these challenges warrants research on long-term trends in regional climatic variability and land use histories.

Holocene chronologies of land use changes have relatively high temporal uncertainties, high spatial complexity, and patchworked knowledge gaps. The history of Kilimanjaro is no less complex and there is abundant evidence of diverse livelihood practices and dynamic cultural exchanges occurring throughout the past millennia. The archaeological record (e.g. Lane et al., 2007; Prendergast, 2008; de Maret, 2013; Crowther et al., 2018; Shoemaker, 2018) suggests that livestock herding, metallurgy, agriculture and hunter-gatherer-fisher modes of production were introduced, maintained, abandoned, and reproduced at highly variable temporal and spatial scales (Lane, 2004, 2009; Kusimba and Kusimba, 2005). In addition, we must recognize that the so-

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called 'traditional' practices have not been immune to innovation and change (de Bont et al., 2019). The legacies of land-use activities such as honey gathering, hunting, and grazing, as well as delineating sacred spaces to preserve them from resource extraction, have, however, had influences on vegetation cover patterns of the mountain (Kikoti et al., 2015). More recently, ecotourism has become a major industry in northern Tanzania (UNCTAD, 2002; Kilungu et al., 2019) and is currently the main high elevation land use activity on Kilimanjaro, increasing the risk of introducing new exotic and invasive plant species (Hemp, 2008). Evidence from nearby savannah ecosystems suggests that introduced plant species often radiate from roadsides and refuse areas that service the ecotourism industries (Bukombe et al., 2015a and b).

Knowledge summaries of sustainable and unsustainable uses and human-environment impacts need to be investigated holistically to combat misunderstandings and miscommunications about desirable and less desirable resource management practices and to also assess chronocentric biases (Adams and Anderson, 1988:522; Magliocca et al., 2018). The high biodiversity and relatively lower degree of mountain endemism that characterises the flora of Kilimanjaro is hypothesised to have been driven in part by millennia of anthropogenic activity (Hemp, 2006a) but further archaeological and historical ecology research is required if we wish to elucidate how people have used mountain resources over time and how anthropogenic activities have been modifying Kilimanjaro ecosystems during its long history of human-ecosystem interaction. As for much of eastern Africa, the potential consequences of land use on mountain areas remain unexplored and will require linked and co-located archaeological,

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historical, ethnographic and palaeoenvironmental enquiry (Marchant et al., 2018; Capitani et al., 2019; Courtney Mustaphi et al., 2019; Cuní-Sanchez et al., 2019).

CONCLUSIONS

Previous palaeoenvironmental studies on Kilimanjaro had not analysed high elevation vegetation change during the late Holocene. The Maua palustrine sediments provided a 3000 year record with a relatively high temporal sampling resolution within the alpine-ericaceous ecotone. The Maua record shows a relatively recent and rapidly occurring change in vegetation to more abundant ericaceous land cover and increased fire activity that may be linked to a drier local climate and/or anthropogenic influences on fire regimes at high elevation. Anthropogenic ignition sources at moderate-to-high elevations for honey collecting, pasture management, and ecotourism may have promoted fire activity at the ericaceous vegetation zones in recent centuries and decades. Further analyses focusing on the archaeological record of high elevations and new high resolution palaeoenvironmental records should be integrated with analyses of oral histories and historical records to better understand human-environment interactions in the wetlands and montane vegetation of Kilimanjaro. In general, there has been more research and policy-relevant dialogue focused on large tropical wetlands and those of international importance (Gardner, 2008); yet given the rapidity of change, additional focus on small wetlands and those on highland water towers would contribute to our understanding of the environmental processes and ecosystem services linked to Protected Areas and surrounding communities. The late Holocene is an important temporal context for understanding ranges of historical variability relevant to land

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management (Willis et al., 2010). The Maua record shows the rapidity of vegetation change at ecotonal edges on Kilimanjaro and provides long-term context for biodiversity and resource management dialogues across the mountain.

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FIGURE CAPTIONS

Figure 1. A) Study site location map in Africa and B) equatorial eastern Africa. C) Map of Kilimanjaro area showing Maua study site (black square), glacial ice records, palustrine and lacustrine sediment palaeoenvironmental study sites (black circles, see Table 1) and soil profile studies (black outlined boxes, see Table 1). Basemap: Google Earth, 2019, http://earth.google.com/web/

Figure 2. (a) The high elevation alpine zone. (b) the surrounding landscape of Maua wetland showing the alpine-ericaceous ecotone. (c) a view within the study site showing tussock vegetation. (d) Using a Russian corer to collect the palustrine sediments of the wetland. Photographs by Rob Marchant.

Figure 3. BACON R script age-depth model (red dotted line), random walks (greyscale), and 95% CI (dotted grey lines) of six SHCAL13 calibrated radiocarbon dates (distributions in blue) and parameter settings (top right red font) for the Maua wetland sediment stratigraphy (Table 1; Blaauw and Christen, 2011a; R Development Core Team, 2017). Ages reported as calibrated year BP (before present, 1950 CE).

Figure 4. Selected pollen taxa relative abundances and CONISS-based zonation showing significant changes in the assemblage composition (solid horizontal line) and not significant changes (dashed horizontal line). CHARs shown at the far right.

Figure 5. Phytolith assemblage with CONISS zonation. No significant zone boundaries were identified and a single insignificant boundary is shown (dotted horizontal line), which occurs slightly after the Maua2 pollen zone (see Figure 4).

Figure 6. Topographic maps of Kilimanjaro showing published archaeological finds across the mountain. The sites are organised into four material culture groupings. A list of sites, radiocarbon dates and references are presented in Supplemental Material Table 1.

Figure 7. Cumulative relative abundances for pollen groups, rate of change (turnover, RoC; Urrego et al., 2009; Correa-Metrio et al., 2011) and principal components analysis axes 1 and 2 are shown with the pollen based CONISS zonation (horizontal solid and dashed lines, see Figure 4). The ratio of the relative pollen abundances Poaceae:Cyperaceae (log transformed for visualisation) and the total relative abundance Poaceae phytolith morphotypes (Fig. 5). Other local datasets included: are an oxygen isotope record from South Ice Field Kilimanjaro (black curve) and smoothed mixed composite record (red line) (Thompson et al., 2002); and macroscopic charcoal (>180 µm; Nelson et al., 2012), a branched versus isoprenoid tetraether (BIT) index of monsoon promoted sediment transport into the lake (low BIT=drier conditions; Buckles et al., 2016), and stable carbon isotope record derived from sediment total organic carbon (TOC, Sinninghe Damsté et al., 2011) from the Lake Challa sediments (Moernaut et al.,

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2010; Blaauw et al., 2011). A mid-elevation temperature record derived from the sediments of Lake Rutundu, Mount Kenya (Loomis et al., 2018). Land use modeled outputs for what is now the United Republic of Tanzania: human population density estimates (Kaplan and Krumhardt, 2011; Kaplan et al., 2011) and total cropland area (Klein Goldwijck et al., 2010). Summarised livelihood strategies on and around Kilimanjaro (Odner, 1971a; Mturi, 1986; Tagseth, 2008; Stump and Tagseth, 2009; Chuhila, 2016; de Bont, 2018; and see Supplemental material Table 1): HG, hunter-gatherer; P, pastoralism (and agropastoral); Ag, agricultural; Irr, furrow irrigation for agriculture on lower slopes of Kilimanjaro and the blue dotted line shows potential regional onset of terraced agriculture (Sutton, 2004; Stump, 2006); M, mercantile (Euro., increased European connections and Colonialism). Calibrated radiocarbon age ranges using OxCal 4.2 (n=14 dates, 95.4% confidence intervals shown, SHCal13; Bronk Ramsey, 2009; Hogg et al., 2013) converted to calibrated year BP (before present, CE1950) associated with iron production and iron working in Mwanga region (<1400 m asl), North Pare (Iles et al., 2018; Iles, 2020).

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Tables

Site	Region	Latitude	Longitude	Elevation (m asl)	Age range (cal yr BP)	Distance from Kibo(km)	Archive	Proxies and measurements	References
Kilimanjaro									
Kibo ice fields	glacial alpine	-3.08000	37.35000	5500+	11700-recent	1 to ~4	ice	dust, $\delta^{18}O$	Thompson et al., 2002; Barker et al., 2011
Maua	ericaceous	-3.129586	37.431179	3930	3100 to -59	9	mire	pollen, charcoal	This study
Maundi Crater	ericaceous	-3.17431	37.51828	2780	~90000 to -57	21	lacustrine	pollen, charcoal, TOC, PSD	Schüler et al., 2012; 2014b
Wereweru 26	montane forest	-3.12169	37.27158	2670	52000	10	soil	pollen	Schüler, 2012
Kilimanjaro	montane forest	SE flank*	see note**	2650	5000 to ~-15	unknown	lacustrine	pollen	Coetzee, 1967; Hamilton, 1982b
south slope	montane forest	-3.15404	37.24496	2090-3150	60000 to 6000	10 to 15	soil	palaeopedology	Zech, 2006
north slope	montane forest	-2.91928	37.21667	2200-2800	52000 to 2500	20 to 23	soil	palaeopedology pollen, NPP, phytoliths, charcoal	Zech et al., 2011
Surrounding region									
Lake Challa	Challa Crater	-3.31667	37.70000	880	(max. 140 000?) 25000 to -49	46	lacustrine	charcoal, organic chemistry, fish teeth	Blaauw et al., 2011; Nelson et al., 2012; Sinninghe Damsté et al., 2012; van Bree et al 2014; Villanueva et al 2014; Dieleman et al 2015; Buckles et al 2016
					2700 to -49			pollen	Rucina et al., unpublished
Namelok	Amboseli area	-2.70691	37.45620	1160	2650 to -55	45	palustrine	pollen, microcharcoal	Rucina et al., 2010
Esambu	Amboseli area	-2.71191	37.55436	1190	5000-present	46	palustrine	pollen, NPP, charcoal	Githumbi et al., in press a
Enkongu Narok	Amboseli	-2.70466	37.26078	1135	2200-present	43	palustrine	pollen, charcoal, LOI	Githumbi et al., in press b
Ziwani	Tsavo West	-3.39018	37.78807	880	1000-present	60	palustrine	pollen, microcharcoal	Gillson, 2006
Kanderi	Tsavo East	-3.36317	38.67250	488	1400-present	150	palustrine	pollen, microcharcoal	Gillson, 2004
Lomwe	North Pare	-3.71472	37.67278	1330	1500-present	80	palustrine, colluvium	pollen	Heckmann et al., 2014
Small Momela Lake	Mount Meru	-3.22745	36.896035	1441	6800-1200	55	lacustrine	pollen	
Lake Duluti	Mount Meru	-3.38506	36.78813	1275	1000 to -57	72	lacustrine	diatoms	Öberg et al., 2009; 2012; 2013
Kwasebuge	Mount Shengena	-4.292015	37.92284	1330	1340 to -57	150	mire	pollen, charcoal (>125 µm)	Finch et al., 2017

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Table 1. Late Quaternary palaeoenvironmental studies on and near (<200 km) Kilimanjaro discussed in this study. Acronyms: TOC, total organic carbon; PSD, particle size distributions; LOI, loss-on-ignition analysis; NPP, non-pollen palynomorphs; microcharcoal, pollen slide charcoal counting (Clark, 1988); charcoal, charcoal analysis by wet sieving. Symbols: ~, approximately. * Precise location is not known to the authors (see: Coetzee, 1967; Hamilton, 1982b).

**Additional note for the University of Basel edoc self archive repository version of this article: Coetzee (1967, page 62) states that, in reference to this study site location, "The boring was made in a small crater lake, 30 x 50 m, at an altitude of 2650 m in the Montane Forest Belt on the south-east side of the mountain near Bismarck Hut."

Coetzee, J. A., 1967, Pollen analytical studies in East and South Africa: Palaeoecology of Africa, v. 3, p. 1-146.

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Table 2. Uncalibrated date determinations from 6 bulk sediment AMS radiocarbon dates from Maua wetland sediment core collected on 29 January 2008 (-58 yr BP). The radiocarbon analytical errors are shown as reported from the laboratory and not rounded (Stuiver and Polach, 1977). The measured modern carbon fraction is presented as *p*MC. *Date objectively excluded from BACON age-depth model. **This nearly modern radiocarbon age was treated with long tapering tails on the calibrated age distributions (Blaauw and Christen, 2011b).

Reference	Depth (cm)	Radiocarbon age (^{14}C yr)	Error 2σ (± yr)	$\delta^{13}C$ (‰)	*p*MC (%)	*p*MC 1σ error
core top	0					
D-AMS 011826	31–33	2030*	25	–23.2	77.67	0.24
Wk-25720	55–56	11**	30	–23.7±0.2	99.9	0.1
D-AMS 011825	70–72	1031	25	–15.9	87.96	0.27
Wk-25719	100–101	1522	30	–24.3±0.2	82.7	0.1
D-AMS 011824	130–131	2195	26	–14.2	76.09	0.25
Wk-25721	150–151	2718	30	–25.9±0.2	71.3	0.1
sediment base	165					

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Table 3. Pollen taxa assignments to biomes for vegetation interpretation through harmonizing published pollen records in the area (Rucina et al 2010; Rucina 2011; Schüler et al., 2012; Schüler 2013; Schüler et al., 2014; Schüler and Hemp, 2016; Finch et al., 2017). Plant taxonomic groupings are listed as used in this study. Alp, alpine; Er, ericaceous; MF, montane forest; LF, lower forest; W-Sav, woody savannah; Wet, wetlands. Symbols: X, predominantly occurs; x, present; (x), occasionally present. Taxa in bold font are presented in the pollen diagram (Fig. 3).

Family	Pollen Taxon	Synonym	Alp	Er	MF	LF	W-Sav	Wet
Asteraceae			x	x	x	x	x	x
Commelinaceae	*Commelina*		x	x	x	x	x	
Cyperaceae			x	x			X	X
Boraginaceae	**cf. *Ehretia***				x	x	x	
Euphorbiaceae	***Phyllanthus***				x	x	x	
Poaceae			x	x	x	x	X	x
Rubiaceae	**Rubiaceae**		x	x	X	x	x	
Plantaginaceae	***Stemodia***		x	x	x	x	x	
Umbelliferae			x	x	x	x	x	
Valerianaceae	***Valeriana***		x	x	x	x	x	
Caryophyllaceae	*Cerastium*		**x**					
Iridaceae/Liliaceae			**x**					
Rubiaceae	***Anthospermum***			**X**			x	
Asteraceae	***Artemisia***			**X**				
Ericaceae				**X**	x			
Geraniaceae	*Geranium*			**X**	x	x		x
Primulaceae	***Myrsine***	*Rapanea*		**X**	x			
Asteraceae	***Stoebe***			**x**				
Euphorbiaceae	*Acalypha*				**X**	x	(x)	
Cornaceae	***Afrocrania***				**x**	x		
Euphorbiaceae	***Alchornea***				**X**			
Sapindaceae	*Allophylus*				**x**	x		
Brassicaceae	Brassicaceae	Cruciferae		x	**x**	x	x	
Rubiaceae	*Canthium*				**X**			
Ulmaceae	*Celtis*				**x**	x		
Rosaceae	*Cliffortia*				**X**			
Boraginaceae	***Cordia***				**X**			
Euphorbiaceae	*Croton*				**x**	x		
Ebenaceae	*Diospyros*				**x**			
Sterculiaceae	*Dombeya*				**X**			

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Dracaenaceae	***Dracaena***				**X**			
Rosaceae	***Hagenia***				**X**			
Aquifoliaceae	***Ilex***				**X**			
Balsaminaceae	*Impatiens*				**X**			
Cupressaceae	*Juniperus*				**X**	x		
Anacardiaceae	*Lannea*				**X**	x	(x)	
Rubiaceae	***Lasianthus***				**x**	x		
Euphorbiaceae	***Macaranga***				**X**			
Myricaceae	***Myrica***	*Morella*			**X**			
Euphorbiaceae	*Neoboutonia*				**x**			
Mimosaceae	*Newtonia*				**X**	x		
Loganiaceae	***Nuxia***				**x**			
Oleaceae	***Olea***				**X**			
Podocarpaceae	***Podocarpus***				**X**			
Araliaceae	***Polyscias***				**X**			
Rubiaceae	***Psychotria***				**x**	x		
Araliaceae	***Schefflera***				**X**			
Myrtaceae	*Syzygium*				**x**			x
Combretaceae	*Terminalia*				**x**	x	x	
Moraceae	*Trilepisium*	*Bosquiea*			**X**	X	x	
Urticaceae/ Moraceae					**x**	x	x	
Cyatheaceae	*Cyathea*				**x**	x		
Thelypteridaceae	*Thelypteris*				**x**	x		
	Reniform				**x**	x		
	Monolete				**x**	x		
	Trilete				**x**	x		
Pteridophyte	undifferentiated				**x**	x		
Malvaceae	*Abutilon*					**x**		
Metteniusaceae	*Apodytes*					**x**		
Meliaceae	*Ekebergia*				x	**X**		
Rutaceae	*Fagaropsis*				x	**x**		
Convolvulaceae	*Hildebrandtia*				x	**x**	x	
Acanthaceae	*Justicia*					**x**	x	
Anacardiaceae	*Rhus*					**x**		
Rutaceae					x	**x**		
Talinaceae	*Talinum*					**x**	x	
Mimosaceae	*Vachellia*	acacia				x	**x**	(x)

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Acanthaceae			x	x			**X**	
Mimosaceae	*Albizia*				x	x	**x**	
Amaranthaceae/ Chenopodiaceae							**X**	
Capparaceae	**Capparaceae**						**x**	
Caryophyllaceae	Caryophyllaceae		x	x	x	x	**x**	
Asparagaceae	Cf. *Asparagus*						**x**	
Combretaceae	*Combretum*				x	x	**x**	
Burseraceae	*Commiphora*					x	**X**	
Cucurbitaceae							**x**	
Euphorbiaceae	*Euphorbia*					(x)	**x**	
Moraceae	*Ficus*					x	**x**	
Fabaceae	*Indigofera*						**x**	
Convolvulaceae	*Ipomoea*					x	**x**	
Fabaceae	undifferentiated					x	**x**	x
Lamiaceae	*Leonotis*						**x**	
Lamiaceae	*Leucas*					x	**x**	
Convolvulaceae	*Merremia*						**x**	
Malvaceae	*Pavonia*					x	**x**	
Polygonaceae	*Polygonum*						**x**	X
Polygonaceae	*Rumex*						**x**	x
Scrophulariaceae	Scrophulariaceae						**x**	
Fabaceae	*Senna*						**x**	x
Solanaceae	*Solanum*						**X**	x
Boraginaceae	*Trichodesma*						**x**	
Typhaceae	***Typha***							**X**
Potamogetonaceae	*Potamogeton*							**X**
Onagraceae	*Ludwigia*							**x**

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Table 4. Phytolith morphologies (ICPT, 2019) and groupings (as presented in Figure 5).

Phytolith morphology	**Assigned plant groups**	**Group (Figure 5)**
Bilobates, crosses, polylobate	Panicoideae	Poaceae sum
True saddles, saddles squat	Chloridoideae	Poaceae sum
Collapse saddle	Bambusoideae	Poaceae sum
Bilobate convex, long shank	Aristidoideae	Poaceae sum
Crenates, trapeziforms	Pooideae	Poaceae sum
Fan-shaped bulliforms, rondels, trichomes	Poaceae non-diagnostic	Poaceae sum
Tracheids	Forest indicators	Woody sum
Sclereids	Forest indicators	Woody sum
Polyhedral ornate	Forest indicators	Woody sum
Polyhedral/polygonal	Forest indicators	Woody sum
Spheroid verrucate	Forest indicators	Woody sum
Spheroid ornate	Forest indicators	Woody sum

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Spheroid echinate	Forest indicators	Woody sum
Spheroid ornate/granulate	Forest indicators	Woody sum
Spheroid plicate/facetate	Forest indicators	Woody sum
(Elongate) Facetate	Forest indicators	Woody sum
Blocky echinate	Forest indicators	Woody sum
Tabular ornate	Dicots	ungrouped
Blocky ornate	Dicots	ungrouped
Blocky crenate	Dicots	ungrouped
Irregular verrucate	Dicots	ungrouped
Sub-spheroid echinate	Dicots	ungrouped
Tabular echinate	Dicots	ungrouped
Sub-spheroid ornate	Dicots	ungrouped
Irregular echinate	Dicots	ungrouped
Irregular ornate	Dicots	ungrouped
Tabular verrucate	Dicots	ungrouped
Sub-spheroid psilate	Generalist	Generalist sum

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Spheroid psilate	Generalist	Generalist sum
Tabular psilate	Generalist	Generalist sum
Tabular dentate ciliated	Generalist	Generalist sum
Tabular dendritic	Generalist	Generalist sum
Irregular psilate	Generalist	Generalist sum
Tabular entire	Generalist	Generalist sum
Elongate echinate	Generalist	Generalist sum
Elongate ornate	Generalist	Generalist sum
Elongate dendritic	Generalist	Generalist sum
Elongate sinuate	Generalist	Generalist sum
Elongate baculate	Generalist	Generalist sum
Honeycomb polyhedral	Generalist	Generalist sum
Honeycomb spheroids	Generalist	Generalist sum
Honeycomb elongates	Generalist	Generalist sum
Epidermal cells	Generalist	Generalist sum
Acicular	Generalist	Generalist sum

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Cuneiform	Generalist	Generalist sum
Blocky psilate	Generalist	Generalist sum
Cyperaceae	Cyperaceae	Cyperaceae sum

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Embedded figures

Fig 1

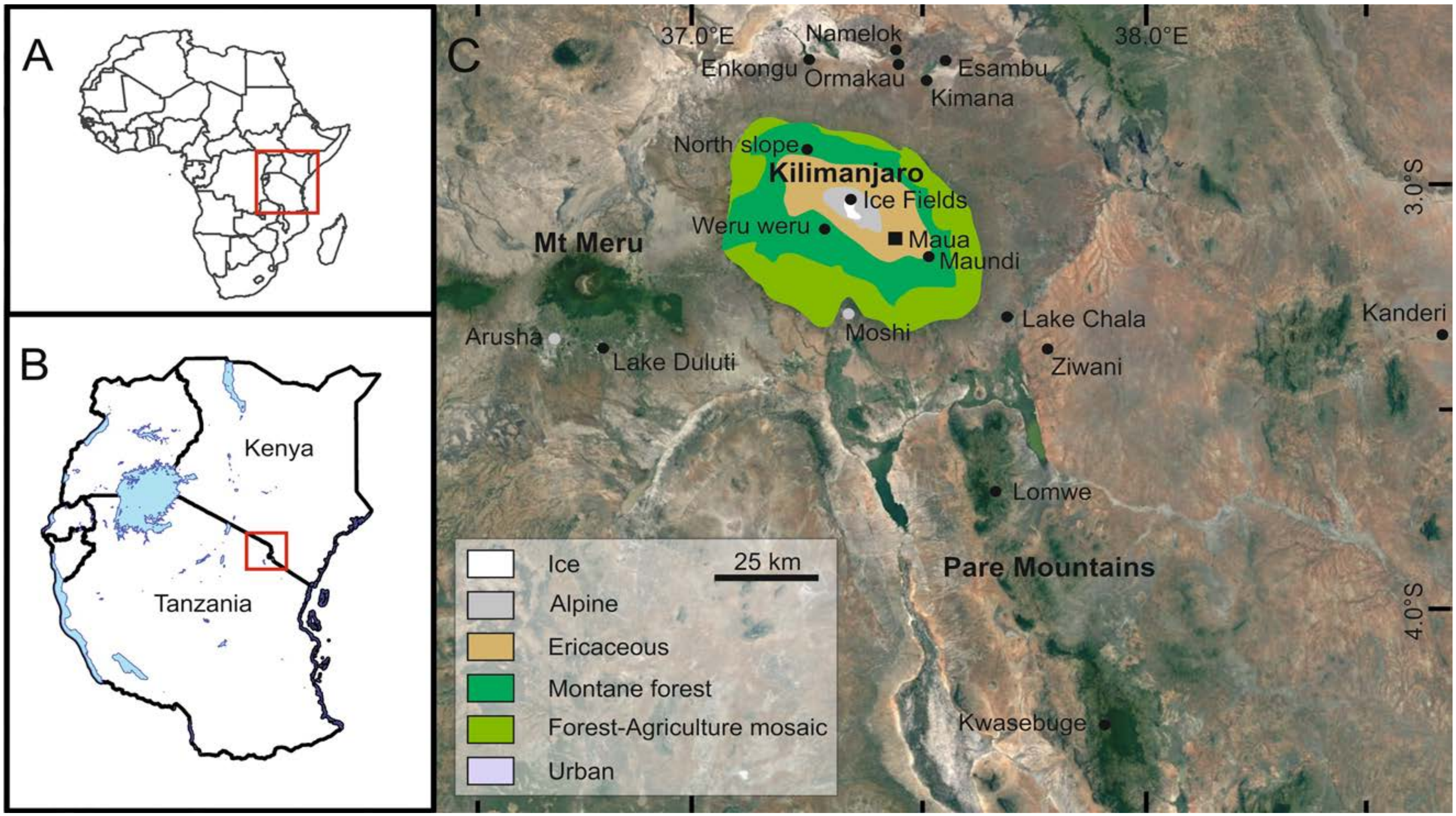

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Fig 2

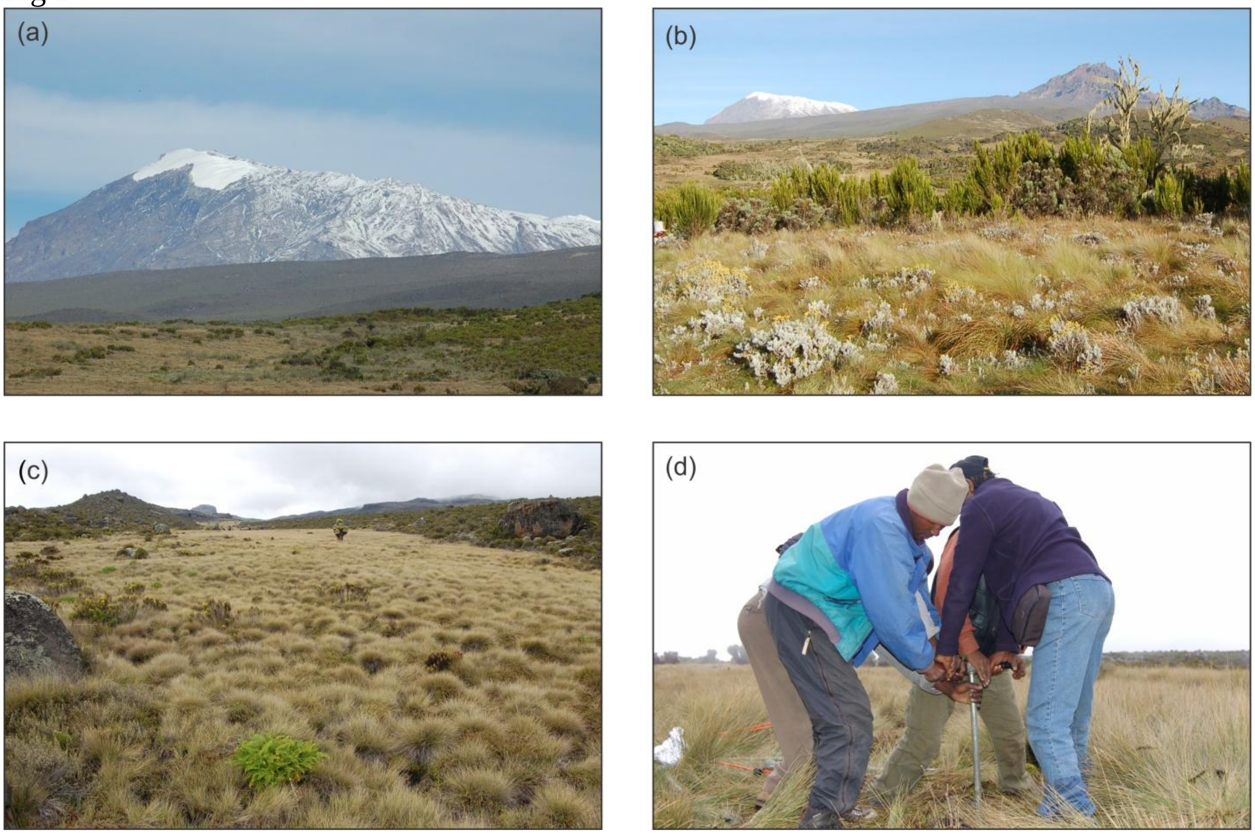

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Fig 3

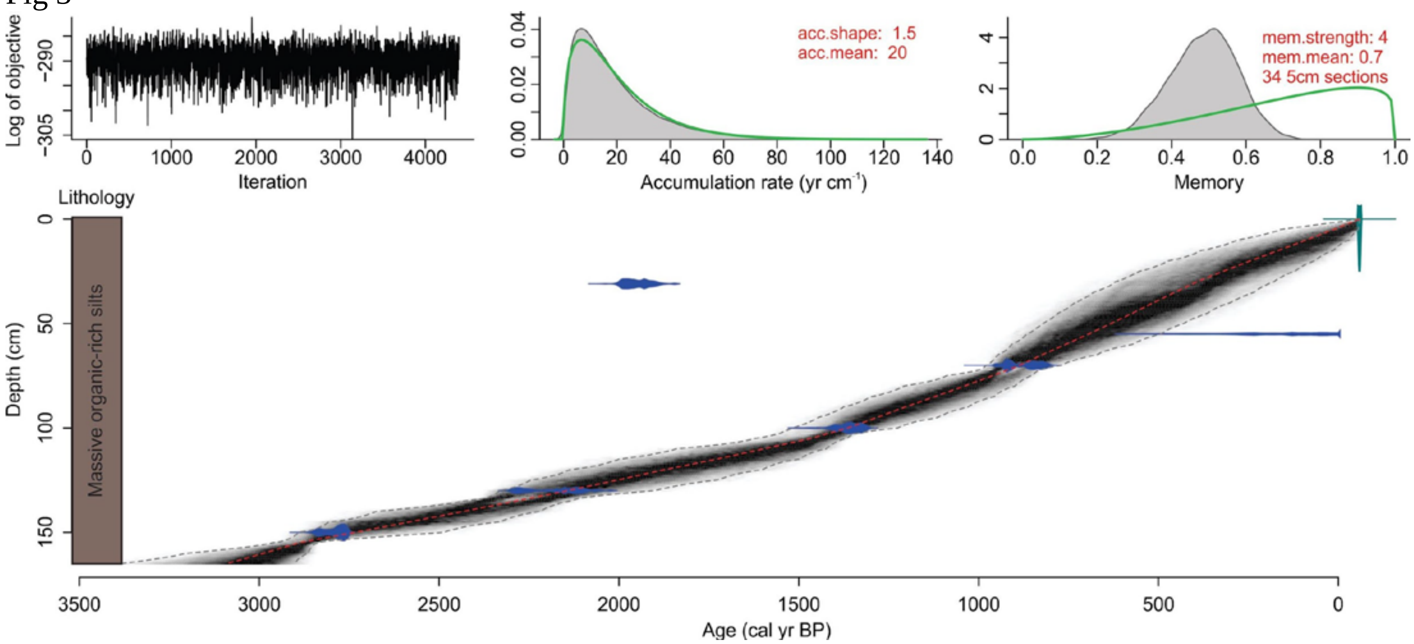

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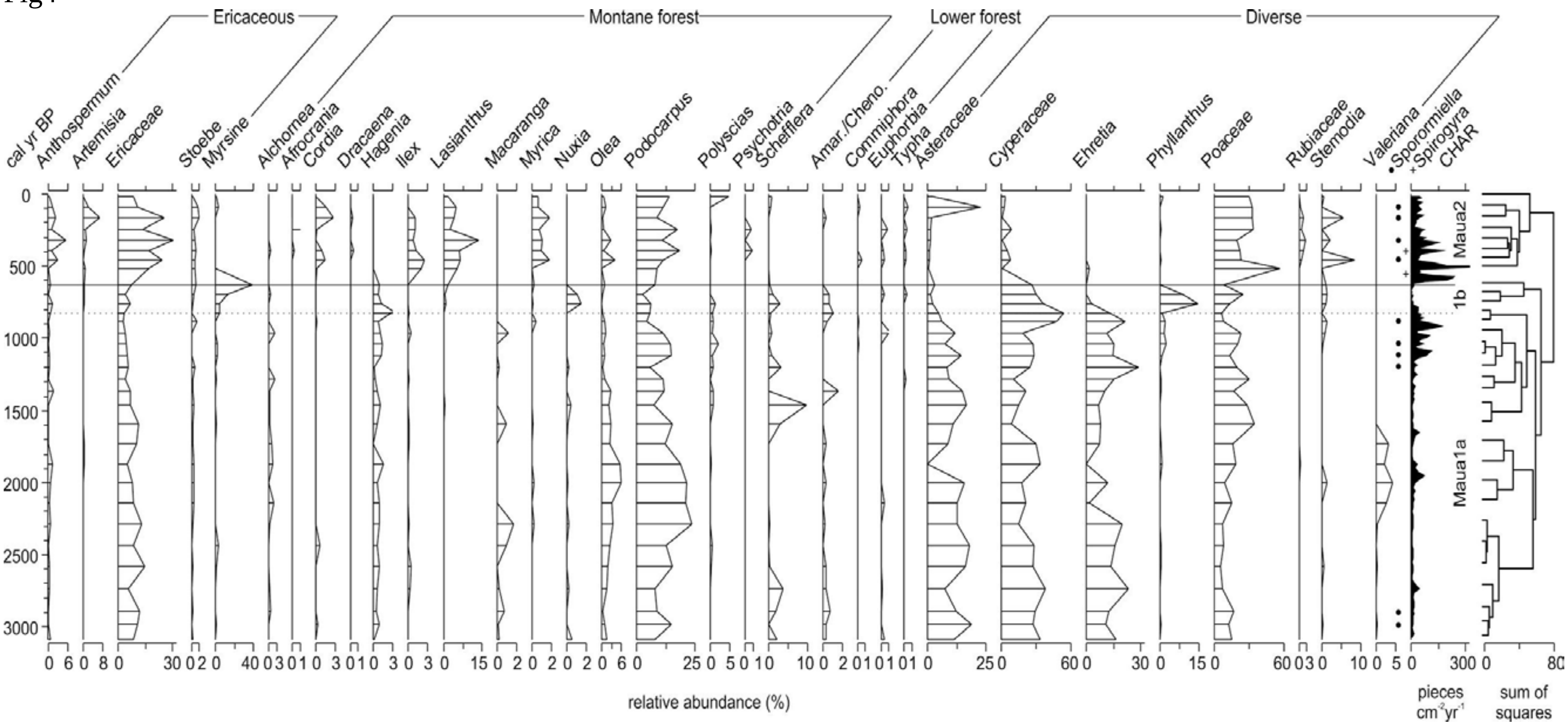
Fig4


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Fig 5

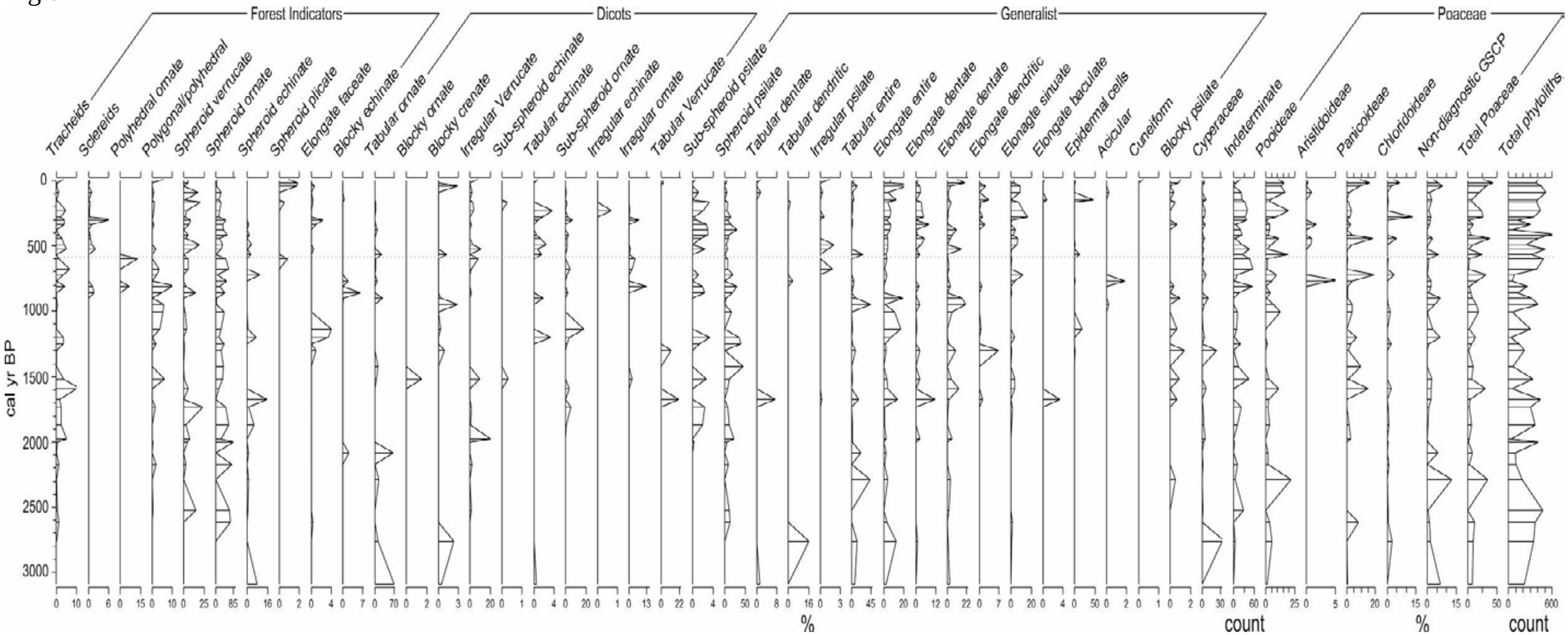

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Fig 6

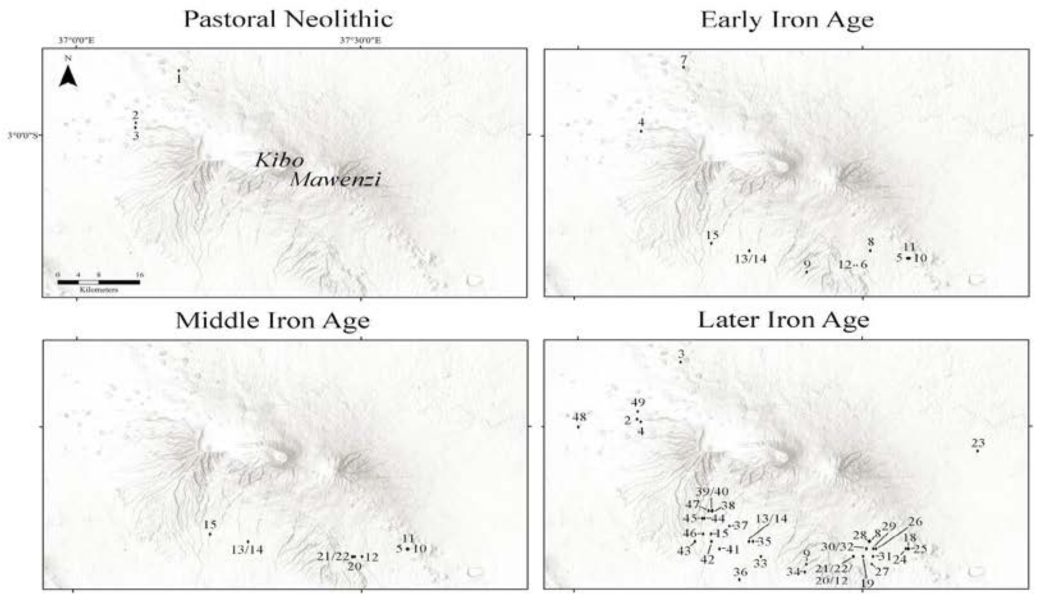

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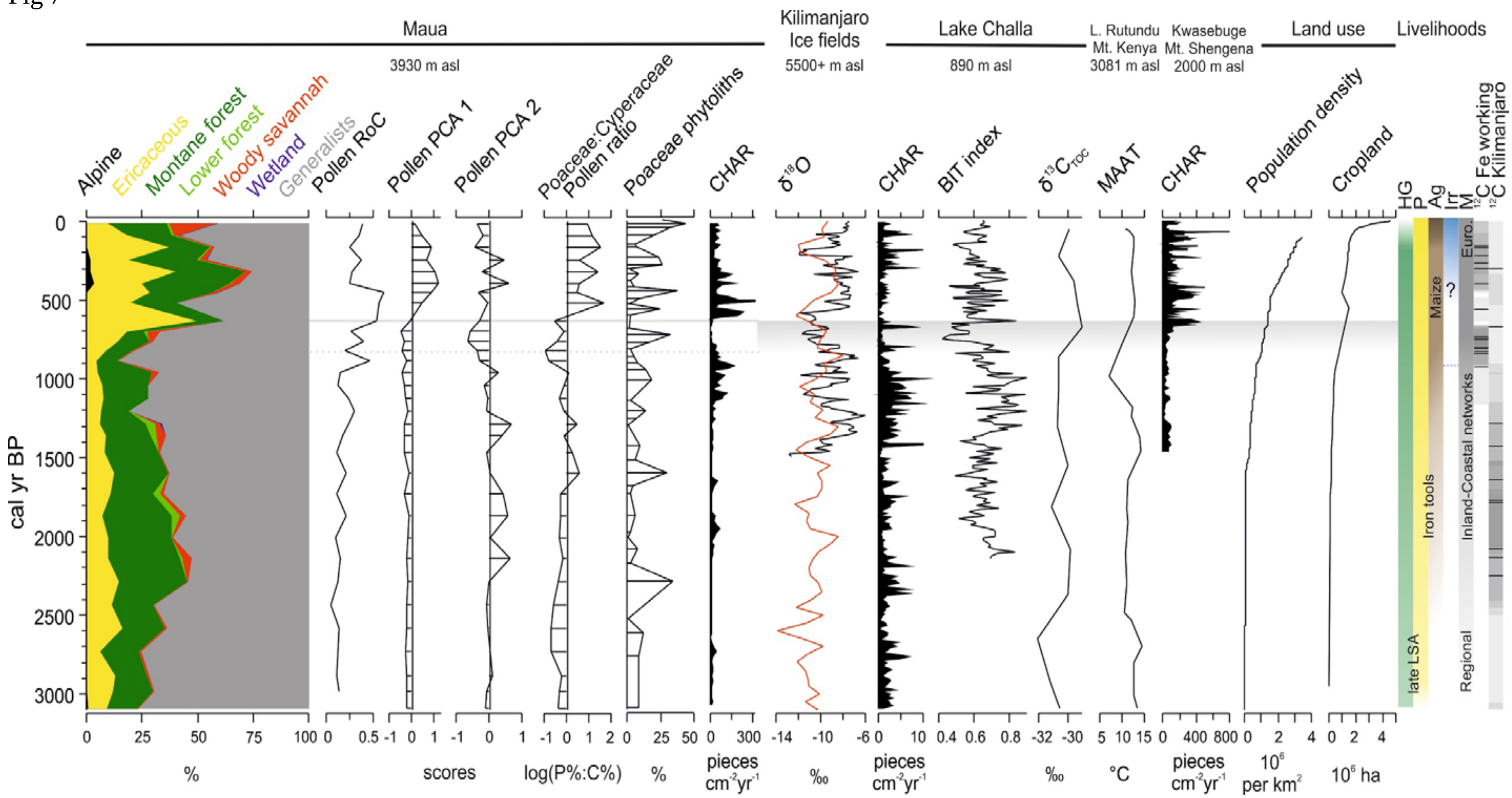
Fig 7



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Supplementary material

Supplemental Table 1: List of published archaeological finds on Kilimanjaro shown in Figure 6 (corresponding numbers in the first column). Conventional radiocarbon dates (with reported laboratory error) of charcoal found at the archaeological sites are also listed (Odner, 1971; Mturi, 1986). GX laboratory code, Geochron Laboratories, Cambridge, MA, USA; N laboratory code, Nishina Memorial, Japan. Site locations (in decimal degrees) were estimated from the publications for replotting in Figure 6 and are presented in the electronic supplemental material.

Number	Site name	Reference	Radiocarbon age (^{14}C years BP, 1σ error)	Laboratory code
1	Maua farm	Mturi, 1986	1545±140	GX-3348
			2160±190	GX-3347
			4140±200	GX-3346
2	Wasendo Madukani	Mturi, 1986	1420±135	GX-3916
			1885±120	GX-3910
			1895±120	GX-3915
			2170±165	GX-3913
			3145±160	GX-3912
			3200±180	GX-3914
			3225±140	GX-3911
3	Lemigushira	Mturi, 1986		
4	Simba 1	Mturi, 1986	4930±180	GX-3917
			5020±165	GX-3918
5	Mwika III	Odner, 1971		
6	Lombeta III	Odner, 1971		
7	Farm No.8. 01 Molog	Odner, 1971		
8	Arisi II	Odner, 1971		

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9	Old Moshi I	Odner, 1971		
10	Mwika I	Odner, 1971		
11	Mwika IV	Odner, 1971	1700±330	N-883
12	Lombeta II	Odner, 1971		
13	Kirima Lower Primary School	Odner, 1971		
14	Kirima II	Odner, 1971		
15	Machame Kisiki	Odner, 1971		
16	Marangu Market I	Odner, 1971		
17	Lombeta VI	Odner, 1971		
18	Mwika VI	Odner, 1971		
19	Hamurukana	Odner, 1971		
20	Lombeta I	Odner, 1971		
21	Lombeta IV	Odner, 1971		
22	Lombeta V	Odner, 1971		
23	Rombo	Kiriama, 1990; Shoemaker, 2018		
24	Mwika II	Odner, 1971		
25	Mwika V	Odner, 1971		
26	Marangu East	Odner, 1971		
27	Kirefure	Odner, 1971		
28	Arisi I	Odner, 1971		
29	Marangu Teachers' College	Odner, 1971	745±190	N-882
30	Sembetti School 3	Odner, 1971		
31	Sembetti II	Odner, 1971		
32	Sembetti III	Odner, 1971		

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33	Lombeta VII	Odner, 1971		
34	Old Moshi II	Odner, 1971	2260±430	N-884
35	Kibosho Mkorina	Odner, 1971		
36	Matunda	Odner, 1971		
37	Kombo	Odner, 1971		
38	Nkweseko II	Odner, 1971		
39	Nkweseko III	Odner, 1971		
40	Nkweseko IV	Odner, 1971		
41	Narumu Orori	Odner, 1971		
42	Kikafu Cave	Odner, 1971		
43	Sienyi	Odner, 1971		
44	Kalali I	Odner, 1971		
45	Kalali II	Odner, 1971		
46	Nshahara	Odner, 1971		
47	Kihalia	Odner, 1971		
48	Ngare Nairobi north	Odner, 1971		
49	Wasendo Glade	Odner, 1971		

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Supplemental Table 2: List of accelerator mass spectrometry (AMS) and one conventional radiocarbon dates associated with iron working archaeological material at Mwanga, North Pare Mountains, Tanzania (Iles et al., 2019), used in Figure 7. AA laboratory code, NSF-Arizona AMS Facility, USA; LTL laboratory code CEDAD - AMS Radiocarbon Dating and IBA Facility, Italy; N laboratory code, Nishina Memorial, Japan (conventional radiocarbon dating).

Site	**Reference**	**^{14}C age, 1σ error (^{14}C years)**	**Laboratory code**
Mwanga A	Iles et al., 2018	862 ± 40	LTL5138A
Mwanga C	Odner, 1971b	1020 ± 110	N-649
Mwanga C	Iles et al., 2018	560 ± 50	LTL5140A
Mwanga G	Iles et al., 2018	366 ± 45	LTL5139A
Mwanga G	Iles et al., 2018	873 ± 36	AA103978
Campi ya Simba	Iles et al., 2018	900 ± 36	AA103979
Campi ya Simba	Iles et al., 2018	927 ± 36	AA103980
Campi ya Simba	Iles et al., 2018	945 ± 36	AA103981
Campi ya Simba	Iles et al., 2018	900 ± 36	AA103982
Ngalanga	Iles et al., 2018	194 ± 45	LTL5136A
Ngalanga	Iles et al., 2018	236 ± 41	AA103983
Ngalanga	Iles et al., 2018	278 ± 42	AA103976
Ngalanga	Iles et al., 2018	261 ± 41	AA103975
Ngalanga	Iles et al., 2018	245 ± 41	AA103974

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SM2 References

Iles, L., Stump, D., Heckmann, M., Lang, C., Lane, P.J., 2018. Iron Production in North Pare, Tanzania: Archaeometallurgical and Geoarchaeological Perspectives on Landscape Change. African Archaeological Review, 35(4), 507-530.

Odner, K., 1971b. Usangi hospital and other archaeological sites in the North Pare Mountains, north-eastern Tanzania. Azania 6, 89-130.

SM Figure 1: Biplots of principal components analysis (PCA) of the relative pollen abundances (square-root transformed) and charcoal accumulation rate (CHAR, charcoal >125 m, log transformed) data from the same sampling level (co-located pollen and CHAR samples), excluding rare taxa with <1% relative abundance. Taxa in bold font are plotted as relative abundances in Figure 6.