

A palaeoecological investigation into the role of Pre and human activity in the development of montane grasslands in East Africa

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Abstract Human activity has been widely implicated in the origin and expansion of montane grasslands in East Africa, yet little palaeoecological evidence exists to test whether these grasslands are natural or secondary. Pollen and charcoal data derived from two Holocene records in the Eastern Arc mountains of Tanzania are used as a case study to investigate the supposed secondary nature of montane grasslands in Africa. Fossil pollen data are used to detect vegetation change, and charcoal analysis is used to reconstruct Pre history. The pollen data are characterised by stable proportions of local taxa suggesting permanence of grasslands throughout the past 13,000 years. Recent increases in Pre adapted taxa such as *Mosselia* point towards the development of a grassland/forest patch mosaic possibly associated with burning. However, robust evidence of human activity is absent from the records, which may be attributed to the late human occupation of the mountains. The records indicate long-term persistence of grasslands which, coupled with a lack of evidence of human activity, suggests that these grasslands are not secondary. The data support the hypothesis that grasslands are an ancient and primary component of montane vegetation in Africa, but that they experienced some expansion during the late Holocene as a result of changing Pre regime.

Keywords Eastern Arc mountains · Uluguru mountains · Secondary grassland · Pollen · Charcoal

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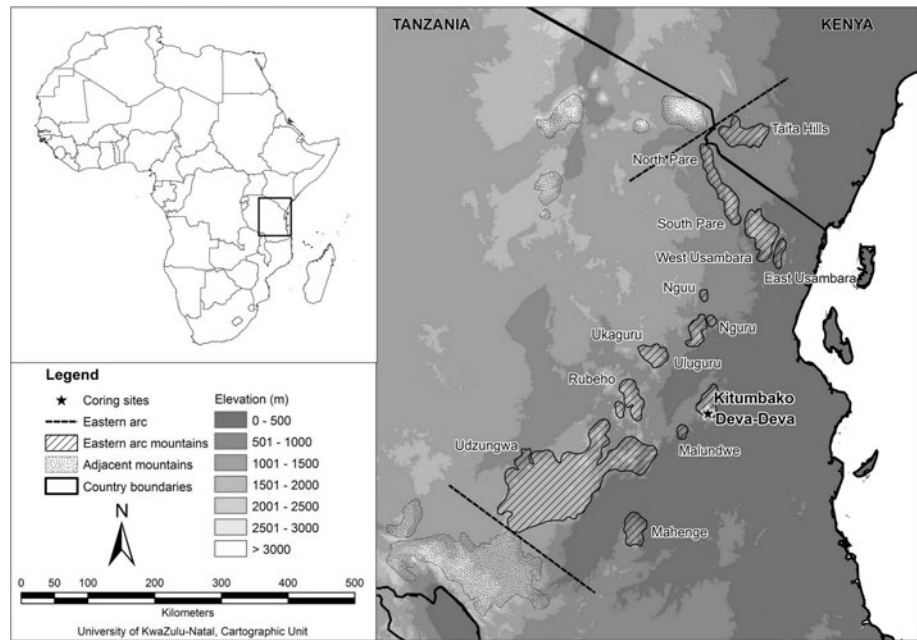
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Human activity has been widely implicated in the origin and expansion of montane grasslands in Africa (Acob 1953; Chapman and White 1970; White 1983; Meadows and Linder 1993; Bredenkamp et al. 2002; Bond et al. 2003, 2008; Willis et al. 2008). Whilst it has been argued that Afro-montane grasslands (sensu White 1983) are a recent and secondary phenomenon, mainly a result of forest clearance and burning by humans (Chapman and White 1970), little palaeoecological evidence exists to directly test their origins (Meadows and Linder 1993). The Uluguru mountains of Tanzania are host to extensive high altitude grasslands, the origin of which are also subject to uncertainty (Fig. 1). The Ulugurus form part of the Eastern Arc mountains, recognised for the exceptional levels of biodiversity and endemic nature of their forests (Myers 1988, 1990; Myers et al. 2000; Lovett et al. 2005; Mittermeier et al. 2005; Burgess et al. 2007a, b). As with grasslands in other regions with climates that can support forests (Willis et al. 2008), conservation efforts in the Eastern Arc are focussed on forest rather than grassland ecosystems. According to Bond (1976a, p. 494), "there is no doubt that the (Uluguru) grassland in its present form and extent is secondary, the result of Pre caused by man". Yet the Uluguru grasslands have a distinct flora with a number of restricted range taxa such as *Mosselia callista*, suggesting that they are unlikely to have been derived from human activities (Bond et al. 2008).

Determining whether grasslands are natural (primary) or derived as a result of human impacts (here termed "secondary") is important for conservation and management

Fig. 1 Map of the Eastern Arc Mountains within Tanzania (after Lovett 1990), indicating the position of Kitumbako and Deva-Deva swamps in the Uluguru mountain bloc



strategies in this biodiversity hotspot. For example, this information could inform the extent and frequency of controlled burning regimes or the suppression of natural forest reserves. The conservation of natural or primary ecosystems as opposed to secondary or derived systems is beneficial to biodiversity conservation, especially in the case of threatened habitats. Arguably, however, secondary grasslands which are derived from past human activity constitute cultural landscapes which should be valued in their own right (Agnoletti 2006; Willis et al. 2008). Scientists and managers alike now recognise the ecological importance of past burning regimes in informing present management of biodiversity and ecosystem function (Conedera et al. 2009).

The recent history of Afrotropical grasslands in general, and the Uluguru grasslands in particular, can only be directly tested by palaeoecological means, which are capable of tracking changing vegetation composition and regime over long timescales. Although a number of palaeoecological records exist from Tanzania (Cohen et al. 1997, 1999, 2007; Johnson et al. 1998; Alin et al. 2002; Erickson et al. 1999; Barker et al. 2002; Thompson et al. 2002; Vincens et al. 2003, 2005, 2007; Muzuka et al. 2004; Garcin et al. 2006a, b, 2007; Ryner et al. 2006, 2007; Brown et al. 2007; Felton et al. 2007; McGlue et al. 2008; Tierney et al. 2008), only two records have been published from the Eastern Arc (Mumbi et al. 2008; Finch et al. 2009).

In this paper, evidence derived from a new palaeoecological record from Kitumbako, East Africa, in conjunction with supporting evidence from the previously published record from Deva-Deva (Finch et al. 2009; Fig. 1), is used

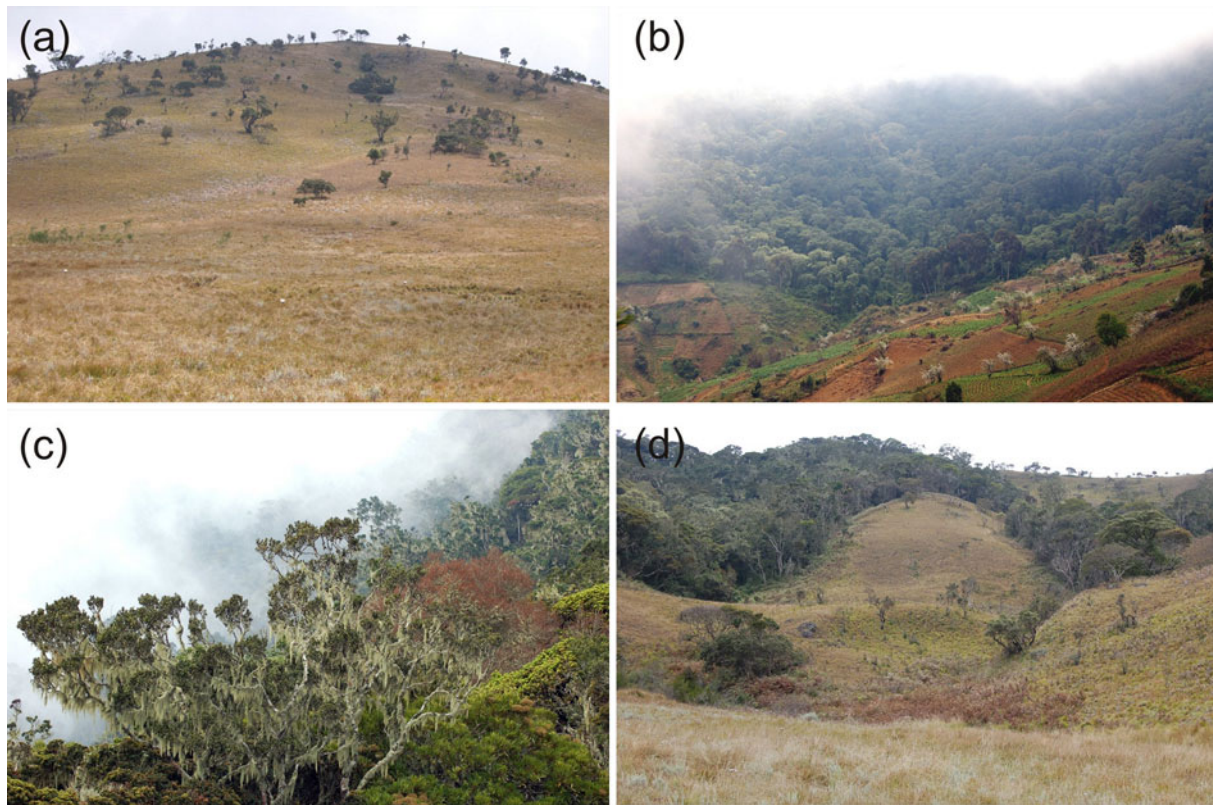


Fig. 2 Photo-montage of the Uluguru mountains depicting the grassland/forest patch mosaic which characterises the Lukwangule plateau; b cultivated areas below the treeline; c mist-affected upper montane forests are covered by epiphytic bryophytes and lichens indicating high air humidity (Peters 1976); and d Kitumbako is situated close to the upper montane treeline

palaeoecological record. It is anticipated that these mountains receive more than 100 mm of rainfall per month by humans may be identified by their simultaneous occurrence throughout the year (Peters 1976). occurrence together with other signs of human activity.

Environmental setting

Geology and climate

The Eastern Arc mountains range from the Taita hills of southern Kenya to the Makambako gap in the southern Udzungwa mountains of Tanzania (Lovett 1990, 1993). The Uluguru mountains form an outlying southeastern component of the Eastern Arc, rising to an altitude of 2,638 m a.s.l. on the Lukwangule plateau. The mountains are developed from Precambrian granulite, gneiss and migmatite rocks (Griffiths 1993; Schlüter 1997), whilst soils are characterised by acidic lithosols and ferrallitic red-yellow and brown latosols (Lovett and Peters 1993).

Temperature, rainfall, dry season length and frost occurrence are the primary bioclimatic factors influencing forest distribution in the Uluguru (Peters 1976). The eastern windward slopes receive maximum orographic rainfall estimated at 2,500–4,000 mm/year while the driest western slopes receive up to 2,000 mm/year. The Uluguru

Modern vegetation

Although there are no distinct altitudinal vegetation zones, as in many other East African montane areas, subjective divisions are used for descriptive purposes based on Lovett and Peters (1993). These zonation guidelines should be treated as guidelines rather than discrete units as there are species which overlap between zones. Eastern Arc endemics and near endemics are denoted with an asterisk.

Upper montane forest zone (>2,400 m) This zone is characterised by *Allanblackia uluguruensis*, *Bersamia abyssinica*, *Cassipourea malosana*, *Cornus volkensii*, *Cussonia spicata*, *Dombeya torrida*, *Dracaena afro-montana*, *Garcinia volkensii*, *Halleria lucida*, *Maesa lanceolata*, *Myrsine melanophloeos*, *Mystroxydon aethiopicum*, *Nuxia congesta*, *Ocotea usambarensis*, *Podocarpus latifolius*, *Polyscias stuhlmannii*, *Schefflera lukwangulensis* and *Xymalos monospora* (Lovett and Peters 1993). The upper tree line is determined by regular frosts and burning. The Lukwangule plateau (2,600 m) is characterised by open

Panicum lukwangulense grassland and pre-tolerant patches of *Adenocarpus mannii*, *Agarista salicifolia*, *Berberis* sp. and *Morella salicifolia* (Lovett and Pors 1993). Forest patches on the plateau include species such as *Aspidytes dimidiata*, *Ochna oxyphylla*, *Olea capensis*, *Pittosporum goetzii*, *Schefflera lukwangulense*, *Syzygium cordatum* and *Syzygium parvulum* (Lovett and Pors 1993). *Sphagnum* and *Pycreus* bogs are common on the plateau.

Montane forest zone (1,600–2,400 m) Dominant montane forest species include *Bridelia bridelifolia*, *Cornus volkensii*, *Cussonia spicata*, *Ficalhoa laurifolia*, *Ocotea usambarensis*, *Podocarpus latifolius*, *Syzygium guineense* and *Zenkerella cappariaceae* (Lovett and Pors 1993).

Submontane zone (<1,500 m) Submontane forests are dominated by *Albizia gummifera*, *Allanblackia stuhlmannii**, *Anthocleista grandis*, *Cephalosphaera usambarensis**, *Cyclicomorpha parvisora*, *Funtumia africana*, *Myrianthus holstii*, *Pouteria adolfi-friedericii*, *Sapium ellipticum* and *Syzygium guineense* (Lovett and Pors 1993).

Human impact

Prior to significant human impacts on the landscape, the wetter eastern slopes sustained continuous forest cover, while the drier slopes were characterised by deciduous woodland and evergreen forest (Newman 1998). Eastern Arc forests are thought to have been affected by low level burning and forest clearance by hunter-gatherers and subsistence farmers for at least the past 8,000 years (Rodgers 1993). However, the permanent settlement of the Uluguru mountains by the Luguru people was relatively recent, estimated at around 300 years ago (Young and Fosbrooke 1960). The original vegetation of the western and southwestern slopes was almost completely destroyed by pre- and cultivation when initial conservation measures were applied in 1909 (Fig. 2b; Temple 1972). Burgess et al. (2002) estimated a 60% loss in forest cover in the Uluguru mountains based on the bioclimatic potential, with major changes in forest cover found at lower altitudes (500–1,600 m). Current human activities include burning and forest clearance for agricultural purposes, with the Uluguru mountains recognised as one of the most productive agricultural areas in Tanzania (Masawa 1992). Other human impacts include the collection of medicinal plants, timber, fuel wood and building poles.

Methods

Selection of suitable sites for analysis was based on the availability of sediments for coring, and the Lukwangulense

plateau was searched for such sediments. Two coring sites, Kitumbako swamp (2,413 m a.s.l.; 8°7'2"S; 37°37'8"E) and Deva-Deva swamp (2,600 m a.s.l.; 7°33'S; 37°37'23"E), were located on the plateau. This paper will focus primarily on the results from Kitumbako, while previously published data from Deva-Deva (Finch et al. 2009) are used for supportive purposes. Analyses are restricted to data from the upper 140 cm of the Deva-Deva record to provide a comparable timescale to the Kitumbako record, rescaled to focus on taxa present at both sites.

Kitumbako is located within a small valley, relatively close to the forest margin (Fig. 2), while Deva-Deva is more central to the plateau, being situated within a longitudinal valley dominated by grassland and small forest patches. Both sites were anticipated to be responsive to changes in forest composition, being positioned within the upper montane forest zone above the forested slopes of the Uluguru mountains. The two perched wetland sites are fed by drainage off the surrounding slopes, each being topographically situated within a valley (Fig. 2). Both sites are located in close proximity to a path in frequent use by the Luguru people and could, therefore, be subject to accidental or intentional human-induced pre. Apart from this, the sites are unlikely to have been largely influenced by

human activity. A 1.3 m core and a 3.4 m core were extracted from the vertically accumulating sediments of Kitumbako and Deva-Deva respectively, using a 50 cm long, 5 cm diameter Russian corer, from parallel boreholes at each site with overlapping sections. Samples were placed within PVC guttering, packaged in aluminium foil and polythene sheeting and transported to the laboratory for cold storage, stratigraphic description (Troels-Smith 1955; Kershaw 1997), subsampling and subsequent analysis.

Subsamples for pollen analyses were extracted at 5 cm intervals. An adaptation of the Ôswirling techniqueÕ developed by Hunt (1985) was used for pollen extraction. Sediments were disaggregated by boiling in 5% Potassium hydroxide and Sodium pyrophosphate solution, followed by sieving using 140 µm nylon mesh. Samples were then swirled on a clock-glass to remove silt and sand and finally sieved and rinsed using a 60 µm mesh to remove solutes and fines.

Pollen was counted using a Leica DM4000B microscope at a magnification of ×400. A total of 26 samples were counted from Kitumbako and 28 samples from Deva-Deva, with a minimum of 600 pollen grains and spores counted per sample. Identification was achieved using a reference collection derived from fresh specimens collected in the local catchment area during fieldwork, in addition to pollen and herbarium specimens from the National Museums of

Kenya and the University of Dar es Salaam herbarium, respectively. Published works on East African pollen

morphology were used to supplement this (African Pollen smooth clay (Argilla steatodes) (Fig. 4). Consolidated and Database 2004; Association des Palynologues de Langue well humid black peat containing fine detritus (Detritus Francaise 1974; Bonne Pille 1971; Bonne Pille and Riollet 1980). granosus) dominates between 112 and 61 cm. Peat sediments become more fibrous comprising a mixture of her-

Palynomorphs were grouped into the following ecolog-baceous (Detritus herbosus) and fine rootlet (Detritus ical units to aid interpretation: upper montane herbs and granosus) material between 61 and 5 cm. The upper 5 cm shrubs, upper montane forest, montane forest, lowland consists of a fibrous moss mat (Tufta bryophytica) forest, aquatics and undetermined (Table). Interpretation Boundaries between stratigraphic units were in all cases was further aided by calculating percentages in two sums gradual.

regional and total. Pollen data were plotted against a dual Four AMS radiocarbon dates on bulk sediment samples age/depth axis using Psimpoll 4.26 (Benne 2005) in provide chronological control for Kitumbako (Table conjunction with CorelDRAW X3 (Coburn 2006). The Fig. 3). A basal age determination of 10650±50 B.P. Constrained Incremental Sum of Squares (CONISS) cluster (12680±40 cal. B.P.) places the record within the late technique within Psimpoll was used to inform pollen zones Quaternary period, covering the Pleistocene/Holocene (Grimm 1987). Stratigraphically constrained cluster analysis yielded five pollen zones for Kitumbako, K-1 is indicated around 95 cm with an age determination of (1300±122 cm), K-2 (1220±102 cm), K-3 (1020±92 cm), K-4 (720±80 cal. B.P.), K-5 (370±37 cm) and K-6 (210±30 cal. B.P.). The late Holocene is (2210±80 cal. B.P.) described according to Kitumbako-derived pollen zones. at 61 cm and 1919±30 B.P. (1880±40 cal. B.P.) at 28 cm.

Percentage charcoal content was analysed for Kitumbako using a Nitric acid digestion technique (Winkler 1985) at a resolution of 5 cm. Four samples were selected between 28 and 62 cm where it increases to 0.138 cm and four samples from Kitumbako, for accelerator mass spectrometry (AMS) radiocarbon dating at Beta Laboratory, NERC Radiocarbon Laboratory and Waikato Radiocarbon Dating Laboratory. Laboratory pre-modern, with the most recent part of the record missing. treatment included the removal of visible contaminants. However, the swamp surface vegetation and decaying sediment such as rootlets. Samples were washed in hot HCl, rinsed and treated with a series of hot NaOH washes. Finally, the NaOH insoluble fraction was treated with hot HCl, filtered, rinsed and dried.

Results were calibrated to calendar years before present (cal. B.P.) using the CALPAL radiocarbon calibration program (Weninger et al. 2009) in conjunction with the CalPal-2007_Hulu calibration dataset (Weninger and Joris 2008). For standardization purposes, all uncalibrated radiocarbon ages cited from supporting literature are calibrated to calendar years before present (cal. B.P.) using the same approach, with original radiocarbon ages provided in parentheses. A basic age model was developed using a linear interpolation between adjacent calibrated finite dates, and approximate ages of pollen zones were interpolated accordingly (Fig. 5).

Results

Stratigraphy and chronology

Stratigraphic terminology is in accordance with the Troels-Smith (1955) system in conjunction with modifications by Ericaceae, Podocarpus and Tubuliiflorae co-dominate the Kershaw (1997). Basal sediments (1300±112 cm) consist of regional pollen signal. Upper montane herbs and shrubs are

Pollen preservation was excellent throughout the Kitumbako sequence, with 67 taxa identified. Pollen data for Kitumbako are presented as regional and local diagrams (Figs. 4, 5); in addition, comparative pollen diagrams for Kitumbako and Deva-Deva are provided (Fig. 6).

K-1 (1300±122 cm; 13000±11700 cal. B.P.)

Table 1 Palynomorphs identified from Kitumbako, and associated ecological groupings

Upper montane herbs and shrubs (R, T)	Pteridophyta
Acanthaceae:Hypoestes-type	Cyathea-type
Acanthaceae:Mimulopsis-type	Rhizophoraceae:Cassipourea
Asteraceae:Carduus-type	Rubiaceae undiff.
Asteraceae:Crassocephalum-type montuosum	Sapindaceae:Allophyllus
Asteraceae: Tubulißorae undiff.	Lowland forest (R, T)
Upper montane forest (R, T)	Anacardiaceae:Ozoroa-type
Aquifoliaceae:Ilex mitis	Anacardiaceae:Baobab-type natalensis
Cornaceae:Cornus volkensii	Anacardiaceae:Rhus-type tripartita
Ericaceae undiff.	Boraginaceae:Cordia africanatype*
Loganiaceae:Nuxia-type	Boraginaceae:Heliotropum
Oleaceae:Olea	Burseraceae:Commiphora
Rosaceae:Cliffortia nitidula-type	Caryophyllaceae:Silene/Uebelintype
Rosaceae:Hagenia abyssinica	Caryophyllaceae:Stellaria mannii-type
Montane forest (R, T)	Celtidaceae:Celtis
Araliaceae undiff.	Euphorbiaceae undiff.*
Araliaceae:Cussonia	Euphorbiaceae:Croton-type
Araliaceae:Polyscias fulva-type	Euphorbiaceae:Euphorbia-type
Asteraceae:Vernonia-type	Euphorbiaceae:Phyllanthus-type*
Brassicaceae undiff.	Fabaceae (C)Berlinia-type
Celastraceae:Cassinia-type	Fabaceae (B)achystegia
Celastraceae:Maytenus	Fabaceae (C)soberlinia-type*
Combretaceae:Combretum-type	Hymenocardiaceae:Hymenocardia acidatype
Commelinaceae:Commelinatype*	Aquatics (T)
Ebenaceae:Euclea	Cyperaceae undiff.
Euphorbiaceae:Acalypha	Eriocaulaceae:Eriocaulon
Euphorbiaceae:Alchornea	Haloragaceae:Laurembergia
Euphorbiaceae:Macaranga	Liliaceae undiff.
Euphorbiaceae:Neoboutonia-type	Lycopodiaceae:Lycopodiumfoveolate-form type
Lamiaceae:Satureja	Lycopodiaceae:Lycopodium jussiaeiform type
Lauraceae:Ocotea	Nymphaeaceae:Nymphaea lotus-type*
Lobeliaceae undiff.	Poaceae < 40 µ
Loganiaceae:Anthocleista	Poaceae > 40 µ
Loranthaceae:Englerina	Pteridophyta: Monoletes undiff.
Malvaceae undiff.	Pteridophyta: Triletes undiff.
Meliaceae:Ekebergiatype capensis	Restionaceae undiff.
Moraceae:Ficus*	Undetermined (T)
Myricaceae:Morella	Indeterminable (Corroded/Broken)
Myrtaceae:Syzygium-type	Indeterminable (Obscured)
Podocarpaceae:Podocarpus	Undetermined

R regional pollen sum, T total pollen sum. Rare taxa, excluded from the diagrams, are shown with an asterisk

represented by *Cornus volkensii* Hypoestes-type, Mimulopsis-type and Tubulißorae. The upper montane forest taxa *Cliffortia nitidula*-type, Ericaceae, *Hagenia abyssinica* Nuxia-type and *Olea* are present at moderate frequencies. Montane forest comprises *Englerina*, *Neoboutonia*, *Podocarpus*, *Syzygium*-type and *Vernonia*-type. *Stellaria mannii* nitidula-type registers a steady decline after 10500 cal. dominates amongst the lowland forest taxa, whereas *P. A* 20% increase in *Tubulißorae* is observed while *Euphorbia*-type occurs at low frequencies. *Cyperaceae*, *Vernonia*-type records its highest values in the sequence. A *Poaceae* and trilete spores dominate the local pollen sum and decline in lowland forest taxa. *Stellaria mannii* is recorded

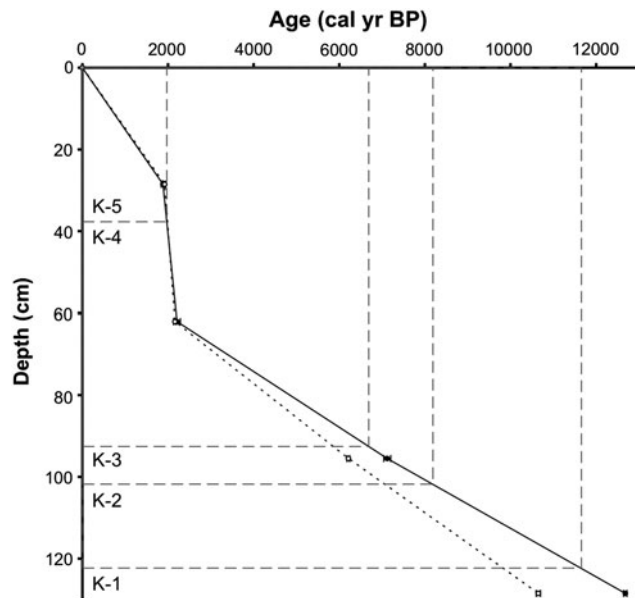


Fig. 3 Age-depth profile for Kitumbako (solid line) and Deva-Deva (dashed line), plotted using linear interpolation of calibrated ages, indicating Kitumbako pollen zone boundaries

after ≈ 10000 cal.B.P. Locally, Poaceae and trilete spores record large increases from Zone K-1.

K-3 (102–92 cm; 8300–6700 cal.B.P.)

During this zone *Podocarpus* increases by $\approx 20\%$, reaching a peak of $\approx 44\%$. *Hagenia abyssinica* and *Cliffortia nitidula*-type all but disappear from the record. *Cyathea* and *Stellaria mannii* record a similar decline. Amongst local aquatics, *Laurembergia* becomes important in the record while the proportions of other local taxa remain stable.

K-4 (92–37 cm; 6700–1970 cal.B.P.)

Ericaceae increase to 40% , while *Podocarpus* registers a decline of $\approx 15\%$. Upper montane forest components *Nuxia*-type and *Olea* recover, albeit at low frequencies, while *Ilex mitis* increases after 2200 cal.B.P. A diversity of montane forest taxa (*Brassicaceae*, *Combretum*-type, *Cussonia*, *Malvaceae*, *Morella* and *Polyscias fulva*-type) are recorded towards the end of the zone. Locally, *Poaceae* record an initial increase and remain dominant $\approx 80\%$ for the remainder of the zone.

K-5 (37–0 cm; 1970–0 cal.B.P.)

Allophylus, *Anthocleista*, *Brassicaceae*, *Ilex mitis*, *Morella*, *Ocotea* and *Polyscias fulva*-type are prominent during

most recent zone. Lowland forest is represented by *Cliffortia nitidula*-type, *Euphorbia*-type, *Ozoroa*-type and *Rhus*-type tripartita. Amongst local taxa, *Laurembergia* records a recent increase while *Poaceae* remain dominant.

Charcoal content

Percentage charcoal content remains relatively constant at $\approx 14\%$ throughout the Kitumbako profile (Fig. 6). Values decrease slightly to $\approx 11\%$ during Zone K-5. Charcoal content at Deva-Deva increases from 10 to 15% by ≈ 4500 cal.B.P. in Zone K-4. Thereafter, values decline to $\approx 7\%$ by the K-4/K-5 Zone boundary. Values during Zone K-5 increase to $\approx 20\%$ by the present day (Finch et al. 2009).

Comparison with Deva-Deva

Regional pollen data are compared for the Holocene period of the Kitumbako and Deva-Deva records to investigate regional signals of vegetation change in the Uluguru mountains (Fig. 6). Despite different catchment areas for each site, the recorded responses are similar in that the dominant taxa are the same and the timing and trends in certain individual taxa are close, for example *Cliffortia nitidula*-type declines at ≈ 9000 cal. B.P. and reappears between 3000 and 2000 cal. B.P. at both sites. Similarly, *Hagenia abyssinica* occurs in the early part and disappears during the later part of both records. Despite some changes in the overall pattern, *Ericaceae* frequencies are high after ≈ 4000 cal.B.P. in both records. *Olea* and *Nuxia*-type are present at moderate levels throughout both records. *Podocarpus* is dominant ($>20\%$) throughout both records but the short-term trends recorded at each site differ considerably; in addition, the overall frequencies appear to have been higher at Deva-Deva.

Several major discrepancies between the two records can be identified. Noticeably, Kitumbako registers a higher diversity of forest taxa while the regional pollen signal at Deva-Deva is dominated by a single taxon, *Podocarpus*. The forest taxa *Araliaceae*, *Ilex mitis* and *Vernonia*-type occur at much higher frequencies throughout the Kitumbako sequence. This reflects the positioning of the Kitumbako site close to the forest margin. Low frequencies of *Morella* recorded at Kitumbako as compared with Deva-Deva are a result of the latter site being situated within a mosaic of grassland and *Morella salicifolia* forest patches.

Analysis of percentage charcoal content from the two sites reveals entirely different trends. Kitumbako shows very little change in charcoal content with a slight recent decline. Deva-Deva shows high variability and a pronounced increase towards the recent day.

Table 2 Radiocarbon results for Kitumbako and Deva-Deva, indicating calibrated and uncalibrated ages determinations

Site	Lab code	Depth (cm)	$\delta^{13}\text{C}$ (‰)	^{14}C yearB.P.	Cal. yearB.P.
Deva-Deva	SUERC-16754	22.5–23.5	−22.9	223± 35	230± 90
Deva-Deva	Beta-249995	38.5–39.5	−20.6	1140± 40	1070± 60
Deva-Deva	Wk-22548	78–79	−21.1	3618± 30	3930± 40
Deva-Deva	SUERC-16757	122.5–123.5	−24.0	8101± 40	9050± 50
Kitumbako	Wk-23589	28–29	−21.3	1919± 30	1880± 40
Kitumbako	Wk-22550	61–63	−18.5	2161± 30	2210± 80
Kitumbako	Wk-23590	95–96	−21.3	6213± 34	7120± 80
Kitumbako	OS-60147	128–129	−23.32	10650± 50	12680± 40

Given the similarities and differences observed, especially as regards the timing of recorded changes for many taxa, it is difficult to conclude with confidence that there is a clear regional signal of vegetation change to be elicited rather than loss of the taxon from the site. What the pollen record clearly demonstrates is the reduced extent of Res- regional pattern, but that the sites are strongly driven by site-specific factors including locality and surrounding vegetation, resulting in a catchment scale response.

Discussion

Environmental reconstruction

By combining the available indicators, the following environmental reconstruction has been developed.

K-1 (* 13000–11700 cal.B.P.)

A diversity of arboreal pollen taxa including *Olea*, *Podocarpus* and *Vernonia* type are recorded, suggesting the presence of closed-canopy forest indicative of relatively moist climatic conditions. Late Pleistocene forest tree species is observed from sites across East Africa such as Kuruyanga (Jolly et al. 1994), Lake Naivasha (Maitima 1991), Lake Victoria (Beuning 1999), Mt. Elgon (Hamilton 1987), and Mt. Kenya (Rucina et al. 2009). Upper montane forest pollen taxa *Hagenia abyssinica* and *Cliffortia nitidula*-type are present at moderate frequencies during this zone. Similar vegetation composition is recognised at Deva-Deva, although this site records higher initial frequencies of *Ericaceae* pollen, reflecting its greater distance from forest margin.

Amongst local pollen elements, *Cyperaceae*, *Poaceae*, and monolete and trilete fern spores dominate throughout this period. *Restionaceae* pollen is present within this zone but is replaced by *Poaceae* thereafter. *Restionaceae* currently recorded as an extant population in the Uluguru

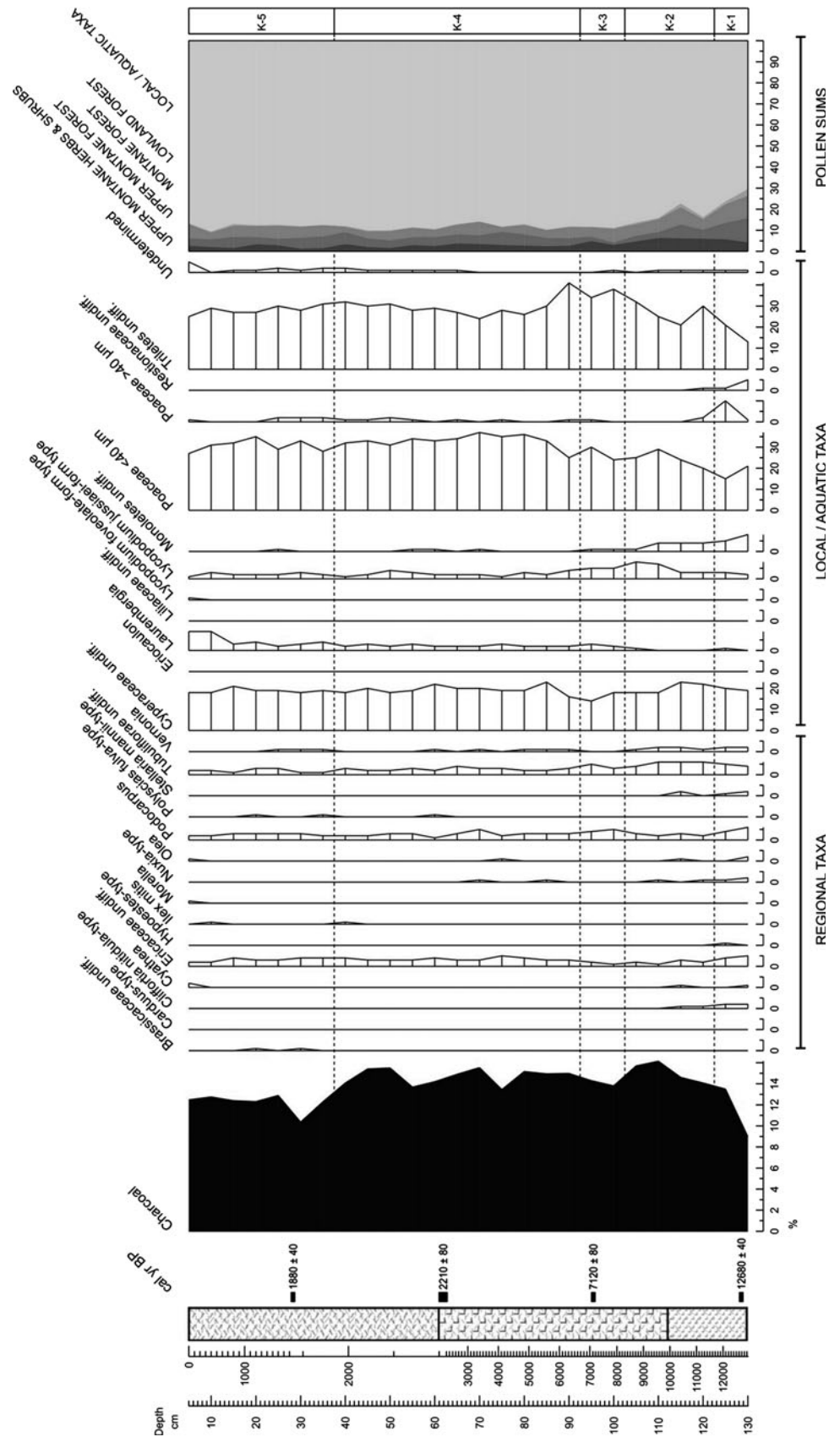
(BonnePille et al. 1990), so their disappearance from the most recent part of the pollen record may therefore reflect limited abundance or poor pollen production rather than loss of the taxon from the site. What the pollen record clearly demonstrates is the reduced extent of Res- regional pattern, but that the sites are strongly driven by site-specific factors including locality and surrounding vegetation, resulting in a catchment scale response. Deva (Finch et al. 2009) supports the hypothesis of BonnePille et al. (1990) that this family once occupied a much larger range across Africa (Hamilton 1982, BonnePille and Riollot 1988), but was reduced to extant populations towards the end of the Pleistocene.

K-2 (* 11700–8300 cal.B.P.)

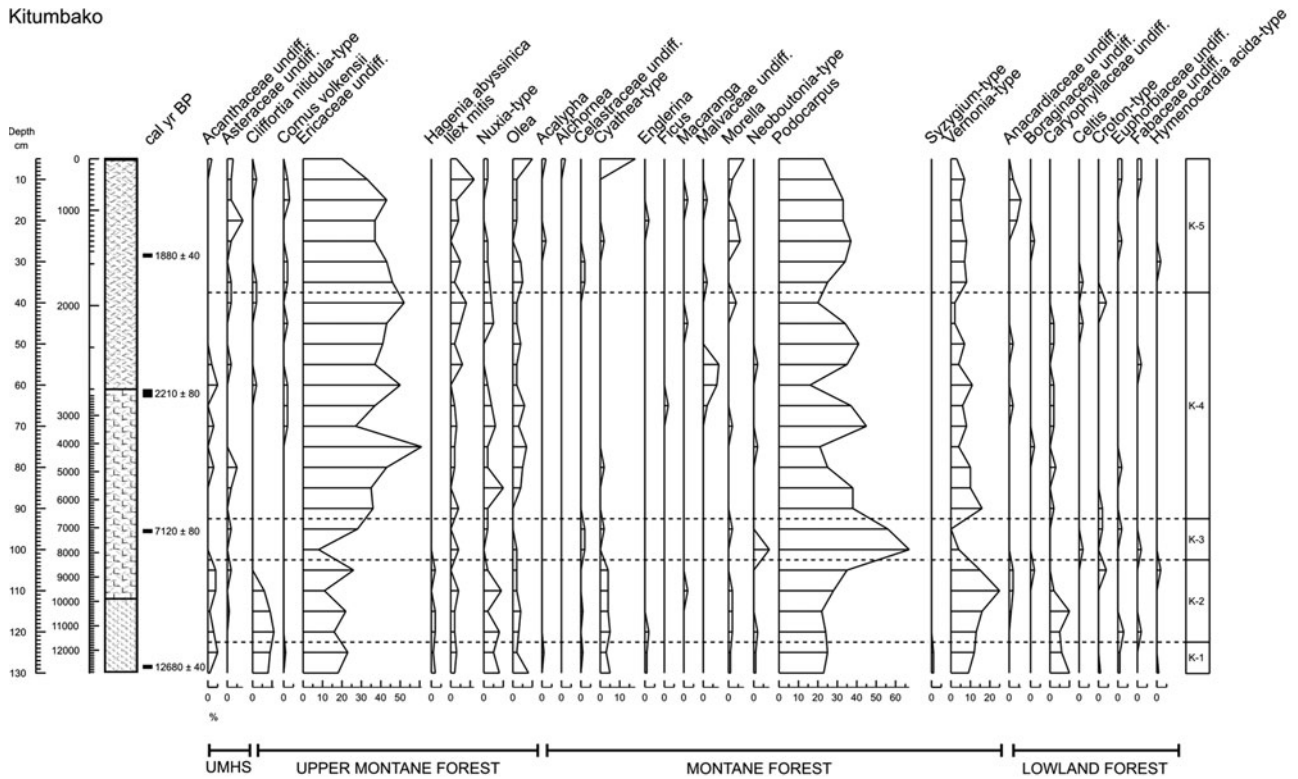
This zone represents the Pleistocene/Holocene transition and shows a continuation of the trends recorded in Zone K-1 for most pollen taxa. *Cliffortia nitidula*-type and *Hagenia abyssinica* decline towards the end of the zone and disappear from the sequence thereafter. *H. abyssinica* is often associated with moist conditions and forms monospecific stands at high altitudes (White 1983). This tree species is pre-tolerant (Lange et al. 1997) and may replace moist forest taxa after periods of burning, thereby acting as a pioneer following disturbance (Greenwood 1973, White 1983, Lovett et al. 2006). The appearance of *H. abyssinica* pollen during the Late-glacial period and Pleistocene/Holocene transition is a trend recognised from several East African pollen records as at Sacred Lake, Mt. Kenya (Coetzee 1967, Olago et al. 1999), Muchoya, Uganda (Taylor 1990), Rusaka, Burundi (BonnePille et al. 1995), Lake Emakat, Tanzania (Ryner et al. 2006), probably reflecting warmer and wetter climatic conditions at this time.

The presence of *H. abyssinica* pollen in the early parts of the Kitumbako and Deva-Deva records is unexpected since it is not currently recorded from the Uluguru South Forest Reserve. It is possible that the *H. abyssinica* pollen recorded may have originated from long distance dispersal,

Fig. 5 Total pollen profile and charcoal data for the Kitumbako record. Zonations are based on the regional pollen data; for stratigraphy see Fig. 4



Kitumbako



Deva-Deva

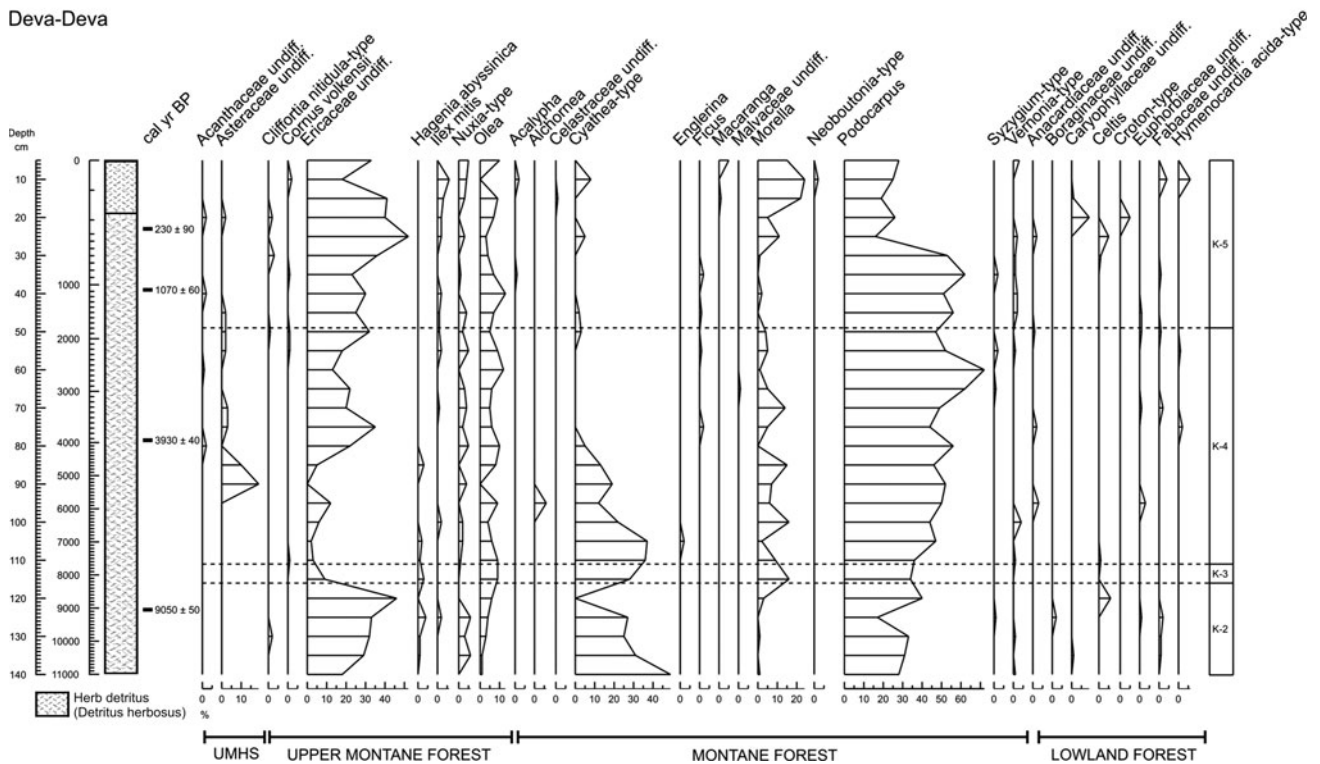


Fig. 6 Comparative regional pollen diagrams indicating taxa common to the Kitumbako and Deva-Deva records. Locally common taxa are excluded. Zonations are based on regional Kitumbako data; for stratigraphy see Fig.

as this species tends to be overrepresented in the pollen unlikely, however, owing to the geographic isolation of the signal (Hamilton 1982, Marchant and Taylor 2000) due to Uluguru mountains from other high altitude environments high pollen production (Hamilton 1972). This seems where *H. abyssinica* may have occurred.

K-3 (* 8300 ± 6700 cal.B.P.)

A large increase in Podocarpus pollen is observed, supporting the development of more closed forest and a relatively moist climate during the early Holocene. Although Podocarpus pollen is often associated with dry conditions on the plateau. High frequencies of Ericaceae pollen (Coetzee 1967), this pollen type is here interpreted as a wet indicator with the following explanation. The likely source of Podocarpus pollen in the Uluguru records is *P. latifolius*, which occurs abundantly in the upper montane and montane forest zones of the Uluguru South Forest Reserve (Lovett and Pe 1993). According to Dale and Greenway (1961) and Hamilton (1982), *P. latifolius* is more characteristic of wetter montane forest than other Podocarpus species, supporting our interpretation of increases in Podocarpus pollen as indications of moist conditions. This interpretation is compatible with warm and wet conditions observed from sites across East Africa during the early Holocene (reviewed in Kiage and Liu 2006). It is important to moderate these interpretations with the acknowledgement that Podocarpus pollen is very well dispersed (Hamilton 1972), consequently, the source taxa are over-represented within the pollen record (Marchant and Taylor 2000).

the only species of the genus *Morella* currently recorded from the Eastern Arc mountains. High frequencies, especially at Deva-Deva, may be indicative of increased frequencies, potentially as a result of drier conditions, and linked with an opening up of the vegetation. High frequencies of Ericaceae pollen corroborate this inference, as Ericaceae can act as pioneers following disturbance such as fire (Wesche et al. 2000). The development of more open vegetation coupled with increased fire frequency is concordant with a palaeoecological record from Rumuiku swamp on Mt. Kenya (Rucina et al. 2009). Similarly, evidence of grassland expansion and increased burning are observed from the Lake Masoko record in southwestern Tanzania (Vincens et al. 2005), although in this case these changes were attributed to human activity.

Pollen derived from the local aquatic *Laurembergia* (Haloragaceae), records a recent increase, perhaps supporting locally wet conditions at the site. This is also found in late Holocene sediments at Deva-Deva and Dama swamp in the Udzungwa mountains, recorded by Muriophyllum pollen, Haloragaceae, Mumbi et al. 2008

Limitations

K-4 (* 6700 ± 1970 cal.B.P.)

Covering the mid to late Holocene, this zone is characterised by a peak in Ericaceae pollen, accompanied by a steady decline in Podocarpus pollen, suggesting a transition towards drier conditions. Dry conditions at Kitumbako agree with evidence from elsewhere in East Africa, with the onset of a long drier period recorded after 4000 cal. (Kiage and Liu 2006). This aridification trend is part of a broader signal across Africa and indeed the wider tropics (Marchant and Hooghiemstra 2004). The Kilimanjaro ice core records a strong drying phase at 4490 cal.B.P. (4000 B.P.) (Thompson et al. 2002). Similarly, data from Lakes Masoko and Rukwa in southwestern Tanzania record a period of increased aridity at 3500 cal. B.P. (Vincens et al. 2003, 2005).

The pollen data from Kitumbako are characterised by stable proportions of local taxa, suggesting the long-term existence of grasslands on the plateau throughout the record. This raises the issue of timescale; as it may be argued that the past 13,000 years does not provide an adequate timeframe to test the secondary nature of the Uluguru grasslands. However, given that the mountains were only recently settled, approximately 300 years ago (Young and Fosbrooke 1960), there can only have been intensive human impacts in the very recent past. The limited temporal resolution of the record (average 500 years) may be subject to criticism. It can be argued, however, that it is the evidence of the long-term dominance of these grasslands which is of consequence. It can be concluded that the possible inadequacy of this temporal scale, both in length and resolution, can largely be ruled out.

K-5 (* 1970 ± 0 cal.B.P.)

The most recent zone is characterised by high *Morella* pollen frequencies at Kitumbako. *Morella* pollen records a similar, albeit much earlier, increase at Deva-Deva after * 8000 cal.B.P. The late appearance of *Morella* pollen in the Kitumbako record is probably due to a time lag in the expansion of this taxon across the plateau, with the Deva-Deva site being more central to its present day distribution. This pollen is likely to have been derived from the resistant taxon *M. salicifolia* (Hemp 2006a, b), which is

As the focus of this paper relates to proportional changes in the composition of grasslands and forests, further emphasis should be placed on local and regional pollen signal differentiation. Generally, locally abundant and aquatic taxa are excluded from the regional pollen sum in order to prevent their overrepresentation in relation to rarer types (Moore et al. 1991). As is the case in this paper, the local sum often includes Poaceae (grasses) as they tend to be grossly overrepresented in the pollen record due to their abundance and high pollen production. The apparently pre-counterintuitive interpretation of regional changes in grassland distribution from a local pollen type could be

considered problematic. However, grass pollen is wind-pollinated and therefore very well dispersed despite being included in the local pollen sum. Hence, the reasoning behind Poaceae pollen being designated as a local taxon is its interpretation in the regional environmental context.

Holocene grassland development

The consistent dominance of Poaceae pollen in the Kitumbako record, coupled with stable relative proportions of forest (arboreal) and grassland taxa throughout the past 13,000 years, supports the long-term existence of grasslands on the Lukwangule plateau. A minor increase in Poaceae between the late Pleistocene and mid Holocene is observed; however, this trend is likely to reflect local dynamics of Poaceae outcompeting Restionaceae at the site. Indeed, supporting evidence from the longer Deva record suggests that high altitude grasslands appear to have persisted throughout the past 50,000 years (Finch et al. 2009). These data therefore suggest that these grasslands are a natural and primary component of the Uluguru vegetation.

An opening up of the vegetation on the Lukwangule plateau is inferred primarily from increases in *Morella* interpreted as reflecting a reduction of continuous forest into patches of woodland dominated by *Morella*, potentially linked with increased burning. This is supported at both sites by a steady increase in pioneering Ericaceae, which colonises land following disturbances such as fire (Wesche et al. 2000). These changes suggest an expansion in existing montane grassland and opening up of closed canopy vegetation due to sustained or increased burning, probably due to dry regional conditions in the late Holocene.

The Kitumbako record lacks robust indicators of human activity such as exotic and agricultural taxa such as *Zea* implying that inferred changes in the vegetation structure are unrelated to human activity. This deficit may be attributed to the inaccessibility of the mountain (2,000 m) and consequently, the late human settlement there (Finch et al. 2009).

Charcoal data from Kitumbako show relatively little change in fire frequency through the past 13,000 years, but moderately high values throughout the record (4%).

No recent increases in charcoal content are observed which could be linked to human activity. Charcoal content, as determined using Winkler's chemical digestion method (Winkler 1985), provides a broad estimate of elemental carbon within the peat sample. The Winkler method has been subject to some criticism in the past. Firstly, carbon derived from the burning of fossil fuels may influence results pertaining to sediments less than 100 years old.

However, it seems unlikely that elemental carbon from fossil fuels has had any consequence to the Kitumbako record given the temporal range and resolution of the record. The second criticism levelled at the Winkler technique is that results tend to overestimate percentage charcoal content as a consequence of the loss of moisture from certain minerals following ignition (MacDonald et al. 1991; Bonnefille et al. 1995).

Despite this critique, the technique and modifications of it have been widely utilized in East African studies (Taylor et al. 1990, 1993; Taylor and Marchant 1994; Marchant et al. 1997; Marchant and Taylor 1998; Taylor et al. 1999) and the speed and efficiency of the method cannot be disputed. The limitations of the Winkler methodology are widely included to (Whitlock and Larsen 2001; Carcaillet 2007) yet there seems little evidence to justify this censure. A comparative study between microscopic charcoal, macroscopic charcoal, percentage charcoal (chemical digestion) and historical records of past fires combined with fire scar data found the Winkler technique unreliable (MacDonald et al. 1991). However, none of the methods used to reconstruct

past fire regimes produced significantly correlated results, nor were any of the indices consistently accurate in reconstructing local fires. Nonetheless, the use of size class and count data of microscopic charcoal fragments (Clark 1982) as an additional proxy in parallel with percentage charcoal content may be an advantageous addition for future studies, as this could potentially allow for differentiation between local and regional charcoal signals. Given the constant moisture supply to the Uluguru mountains (Peters 1976b), the persistence of high altitude grasslands in this ecosystem is curious. Although potential forest distribution is determined by environmental factors,

particularly climatic ones, Geldenhuys (1994) found the actual position of forest boundaries in the southern Cape in South Africa to be dictated by fire. In the case of the Uluguru mountains, it may be that natural fire regimes, together with frost, have been instrumental in maintaining the grassland system. The high altitude *Panicum lukwangulense* grasslands on the Lukwangule plateau are adapted

to frosts and regular burning which are important in their maintenance above the upper montane forest tree line (Peters 1993).

Local edaphic and topographical factors resulting in an uneven moisture balance across the mountains may be partly responsible for grassland distribution in the Uluguru. Peters (1976b, c) noted the very large number of epiphytic bryophytes and lichens covering upper montane forests in the mountains, indicating continuous high air humidity (Fig. 2c). These mossy forests occupy the eastern slopes, effectively stripping out moisture from oceanic

winds, and creating a rain-shadow on the upper slopes and plateau (Pos 1976b, c). The moisture deficit created by this topographic rain shadow may play a role in retarding forest expansion on the Lukwangule plateau and thereby maintaining grassland at an altitude otherwise suitable for forest development.

Conclusion

The pollen and charcoal data presented from Kitumbako represent a new Holocene record of vegetation dynamics from East Africa, with supporting evidence from the previously published Deva-Deva record. These data allow for the following conclusions to be drawn: (i) pollen data show moderately stable proportions of local taxa and relative proportions of arboreal and grassland pollen, suggesting the permanence of Uluguru grasslands throughout the past 13,000 years; (ii) the recent appearance of the pre-adapted taxon *Morella* suggests an opening up of the vegetation which may be related to increased frequencies; (iii) no robust evidence of human activity is observed in the record which may be attributed to the inaccessibility of the mountain and the resulting late settlement there; and (iv) the record presented supports the hypothesis that grasslands are a natural and long-standing component of Afromontane vegetation but that they underwent some expansion during the late Holocene as a result of increased burning.

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