Late Quaternary vegetation reconstruction from the Eastern Arc Mountains, Tanzania

C.T. Mumbia, R. Marchant,⁎, H. Hooghiemstra, M.J. Wooller

Abstract

Pollen, spore, macrofossil and stable isotope (C and N) analyses from a 266-cm sediment core collected from a swamp on the Eastern Arc Mountains, Tanzania, are used to reconstruct vegetation and environmental history. An estimated time scale based on five 14C ages records approximately 38,000 yr. This palaeorecord is the first from this biodiversity hotspot and importantly extends through the last glacial maximum (LGM). The altitudinal transition from montane to upper montane forest shifted from 1700 – 1800 m (38,000 14C yr BP) to 1800 – 1900 m (35,000 – 29,000 14C yr BP). From 29,000 to 10,000 14C yr BP, it shifted from 1850 – 1950 m across the LGM to 1750 – 1800 m (during 10,000 – 3500 14C yr BP), and to present-day elevations at 2000 m during the last 3500 14C yr BP. The relative ecosystem stability across the LGM may be explained by the Indian Ocean’s influence in maintaining continuous moist forest cover during a period of East African regional climate aridity. During the late Holocene, presence of abundant coprophilous fungi and algal blooms demonstrates increasing human impact. Neurospora spores indicate frequent fires, coinciding with clear signals of decline in Podocarpus and Psychotria trees that possibly represent selective logging.

Keywords: Eastern Arc Mountains; Pollen; Spores; LGM; Ecosystem stability

Introduction

Relatively few palaeoecological records have been generated from Tanzania, with those records being largely associated with the Rift Valley lakes located in the west of the country (Johnson et al., 1998 (Lake Victoria); Alin et al., 1999, 2002; Cohen et al., 1997, 1999 (Lake Tanganyika); Barker et al., 2002; Thévenon et al., 2002 (Lake Rukwa); Vincens et al., 2003; Garcin et al., 2006a,b, 2007; Vincens et al., 2007; (Lake Masoko); and Johnson et al., 2002; Barry et al., 2004; Gasse et al., 2004 (Lake Malawi)). Other records include Erickson et al. (1999) (central Tanzania), Muzuka et al. (2004), Ryner et al. (2006) (Empakaaai Crater), and Thompson et al. (2002) (Mount Kilimanjaro) in northern Tanzania (Fig. 1). No record exists from the Eastern Arc Mountains and the regional palaeoecology is uncertain.

The Eastern Arc Mountains (EAM) is one of the world’s biodiversity hotspots due to their high diversity of plant and animal species and unusually high number of endemic species (Myers et al., 2000). The high species diversity and endemism of the Afromontane forests along the EAM are in contrast to the adjacent savannas and woodlands (Lovett, 1993). Evidence on the long-term history of EAM ecosystems is lacking and hypotheses about the long-term ecological stability, as with other tropical areas, are still not substantiated and remain contentious (Fjeldså et al., 1997; Lovett et al., 2005). Despite this lack of evidence, the EAM have been proposed as one of several moist forest refugia in Africa retaining moist forest through the last glaciation (Diamond and Hamilton, 1980; Hamilton, 1982). This concept of ecological stability is presently based upon three indirect lines of evidence: (1) the large numbers of species and endemics; (2) the centers of distribution for many disjunct species; and (3) declining species diversity with increasing distance from this region (Lovett,
This study represents the first direct test of ecological stability. Pollen data are combined with spores, macrofossils, stable isotopes, and charcoal to reconstruct past environmental changes. Analysis of plant macrofossils (Birks, 2003; Birks and Birks, 2003) is a technique not commonly applied in East Africa primarily because it requires access to a reference collection of local material. Macrofossil identification is generally to the specific level for seeds, fruits, and needles; they are produced in small numbers compared to pollen, and although their dispersal varies among types, it is generally over shorter distances and, therefore, provides a good record of local vegetation change (Birks, 2001). Stable carbon isotopic composition of sediments have previously been used in East African palaeoecological studies to track changes in the proportion of plants using either the C₃ or C₄ photosynthetic pathways (Olago et al., 2001; Ficken et al., 2002; Wooller et al., 2003). Organic material produced by C₃ plants has characteristic δ¹³C values around −27‰ (O’Leary, 1981, 1988), whereas that of C₄ plants higher in δ¹³C and shows characteristic values of around −12‰ (Bender, 1971).

Changes in environmental conditions, including atmospheric pCO₂ concentration, disturbance, temperature, aridity, and seasonality, can influence the competitive balance between plants using the C₃ and C₄ photosynthetic pathways (Ehleringer, 1991; Tieszen, 1991; Wooller et al., 2001, 2003, 2005). C₄ plants have an advantage in the competition with C₃ plants when conditions are less mesic and/or low atmospheric CO₂ pressure, such as during LGM conditions. C₄ plants are favoured under higher temperatures and, therefore, are mostly
confined to lower elevations (Boom et al., 2002). The present-day vegetation in our study area is dominated by C₃ plants with C₄ plants mainly occurring in swamps (e.g., Cyperus alopecuroides, Cymbopogon sp., and Digitaria diagonalis). In the adjacent savannas, including the Maasai Steppe corridor, which stretches into the northern part of the study area, C₄ grasses predominantly occur.

The objective of this paper is to reconstruct vegetation changes from a hitherto under-researched area using several proxies to reconstruct ecosystem and environmental history. We evaluate current hypothesis on the long-term ecological functioning of forest ecosystems in the EAM, in particular the claim that present high biodiversity relates to long-term ecosystem stability.

Environmental setting

Geographical and climatic setting

The EAM are formed from heavily metamorphosed Pre-Cambrian basement rocks, periodically uplifted by faulting and weathering over millions of years. These block-faulted mountains have been ecologically isolated, probably since the Miocene (Hamilton, 1976, 1982). The mountains cover an area of 5400 km², with highest peak in South Uluguru (Kimahandu) rising to 2600 m although maximum altitudes of 2200 to 2500 m are more typical. Rainfall patterns in the EAM are associated with the passage of the Intertropical Convergence Zone (ITCZ), which migrates from approximately 10°S during January to 10°N during August (Fig. 2). The southeast trade winds are driven by annual oscillation of the ITCZ bringing monsoonal rainfall to the east of Tanzania (Trewartha, 1981; Nicholson, 1996). Wet and dry seasons are clearly defined; northern Tanzania experiences rainy seasons from March to May and from October to December, while southern areas have one long rainy season (November to May). The average rainfall is 1700 mm yr⁻¹; on the eastern sides of the mountains (facing the Indian Ocean), precipitation is up to 2000 mm yr⁻¹. The elevational gradient on the eastern slopes of the EAM is steeply sloping (Usambara, Pare, and Uluguru), while the western sides are relatively gentle sloping (Udzungwa) (Hamilton and Bensted-Smith, 1989; Lovett, 1999). The coring site is located at 7°49' S, 35°55' E, 40 km east of Iringa town, at 2100 m altitude on the southwestern edge of the main southern block of the Udzungwa Mountains (Fig. 1). The mountain area, which includes Kising’a-Rugaro Catchment Forest Reserve, covers an area of 130 km² with an altitudinal range from 1700 to 2330 m. At the nearest weather station, the average annual temperature is 18°C, with maximum monthly values of 20°C in December and minimum values at 15°C in July.

Figure 2. (a) The position of Intertropical Convergence Zone (ITCZ) during January and July–August mainly drives the climate systems in East Africa (adapted after García et al., 2006a, b). (b) Major vegetation types of Tanzania (modified after Rodgers et al., 1985; Danish International Development Agency, 1989), and the passage southeast trade winds and the northeast trade winds along the EAM and the coastal belt. EAM ranges are showed in capital letters (A=Udzungwa, B=Mahenge, C=Rubehe, D=Malundwe, E1,2=North and South Uluguru, F=Ukaguru, G=Nguru, H=Ngau, J1,2=East and West Usambara, K1,2=North and South Pare, and L=Taita).
Modern vegetation

It is estimated that forests and woodlands cover 45% of Tanzania (Fig. 2) (Burgess et al., 1997; Rodgers et al., 1985; DANIDA, 1989). The EAM forests were described on the basis of botanical surveys that found the high number of endemic species is in marked contrast to montane forests elsewhere in Africa, which are primarily composed of plants with a more cosmopolitan distribution (Lovett, 1985, 1988, 1998a,b). The widespread flora on mountain islands led to the view of a continent-wide ‘archipelago-like’ center termed Afromontane (Lind and Morrison, 1974; White, 1978, 1981; Kingdon, 1989); however, the distinct flora of the EAM suggest that they are floristically different from other African mountains (White, 1983). Firstly, the EAM is an altitudinally well-defined floristic unit. Secondly, there is reduced altitudinal separation into upper and lower Afromontane types: the biogeographic distribution patterns of plants in the upper and lower forest types are similar (Hamilton et al., 1989; Hawthorne, 1993; Lovett, 1988, 1993, 1996; Tallents et al., 2005). Furthermore, the EAM endemics tend to occupy narrow elevational ranges (Lovett et al., 2001), whereas more widespread species can have extraordinarily broad ecological tolerances. For example, trees that are often regarded as classic Afromontane species, such as Bersama abyssinica, Podocarpus milanjianus and Rapaneca melanophloeo, also occur at low elevation.

The vegetation in the Kising’a-Rugaro catchment forest has been described by Minja (1991) and revisited by Lovett and Pocs (1993). The forest types are based on the definitions given in Lovett (1993). There are relatively few endemic plant species in this catchment forest and, similar to other forests on the Udzungwa Block (Lovett and Congdon, 1989), they are floristically more akin to the montane forests of Malawi (Dowsett-Lemaire, 1989) than the typical endemic-rich EAM forests. This may be due to the Udzungwa Block having a more variable climate than the eastern escarpment, hence favouring plants with broader ecological tolerances. Alternatively, it may be due to past human disturbance as disturbed forests lose their endemic species relatively easily (Lovett, 1994, 1999).

The altitudinal distribution of forest types comprises three major vegetation categories: upper montane forest (UMF), upper montane herb and shrub (UMHS), and montane forest (MF) (Lovett, 1996). We use an altitudinal temperature gradient of 0.6°C 100 m−1 (Bonnefille et al., 1990; Rundell et al., 1994; Stute et al., 1995; Farrera et al., 1999) to infer temperature fluctuations from changes in floral composition. UMF extends from 2000 to 2330 m; average monthly temperatures range from 15 to 20°C. This forest is characterised by tree species with a canopy height from 10 to 15 m. Characteristic taxa include Clausena anisata, Dombeya torrida, Halleria lucida, Macaranga kilimandscharica, Myrica salicifolia, Myrsine africana, P. milanjianus and Ocotea usambarensis. UMHS is characterised by Aloe spp., Bidens pilosa, Erica arborea, Helichrysum sp. and Protea angolensis, often associated with ferns (Cytishe marniana and Polyodium sp.) and grasses (D. diagonalis and Pennisetum unisatum). Associated with UMF are the edaphic grasslands in open forest patches with the following characteristic trees and shrubs: Allophylus africana, Carissa edulis, Clatia abyssinica, Coffea mufindensis, Maesa lancifolia, Schrebera alata and Tecoma capensis. MF extends from 1700 to 2000 m with average monthly temperatures from 20 to 25°C. This forest is characterised by 20–30 m-tall trees including Acalypha orata, Casearia battiscombei, Cassowaria spicata, Euphorbia hirta, M. salicifolia, Syzygium sp., Vernonia pauciflora and Zanthoxylum gillettii. Swamp vegetation is largely determined by the basin hydrology. The standing biomass is composed of Blechnum sp., C. alpoeceuroides, Cymbopogon sp., Myriophyllum sp., Senecio syringofolius, Sphagnum cuspidatum, Sporobolus sp. and Typha latifolia. At the borders of the swamp, shrub vegetation was characterised by A. orata, Asteraceae, Ericaceae and M. salicifolia.

Human impact

During the Holocene, it is likely, as elsewhere in East Africa, that there was a gradual increase in human impact associated with arrival of food crops, technologies (in particular iron smelting) and population migration (Hamilton et al., 1986). More recent human impact is indicated by old secondary forest growth following past cultivation and timber abstraction. Heavy logging was illegally carried out in the 1950s and 1960s (Minja, 1991); valued timber trees that were largely affected consisted of C. battiscombei, Cassipourea gummiflua, Chrysophyllum gorungosanum, Macaranga kilimandscharica, O. usambarensis and P. milanjianus. Other human activities include extensive cutting of bamboo to make baskets for the thriving tomato trade, small game and honey hunting, removal of forest top soil for use in nurseries, cattle and sheep grazing on the grassland, fuel wood, and harvesting of medicinal plants for local use. Many streams that originate from the reserve are used locally for irrigation.

Methods

Sediment cores were collected between two small streams, one running through and the other transecting the swamp. Sediments were collected in 50-cm sections using a 75-mm-diameter Russian sampler. The studied core was 266 cm long and named Iringa-1, abbreviated IR1. Sediment cores were fixed with PVC guttering, wrapped in plastic, and transported to Amsterdam for storage in a dark room at 4°C. Lithological changes were described along the core before sampling for pollen, stable isotopes, radiocarbon dating, and macrofossils. For pollen analysis, 133 sediment samples of 1 cm3 were taken at 2-cm intervals along the profile. For pollen preparation, we used the standard pre-treatment technique, including sodium pyrophosphate, acetolysis, and heavy liquid separation with bromoform. Exotic Lycopodium spores were added to each sample before treatment to calculate the pollen concentration (Faegri and Iversen, 1989). Exotic Lycopodium spores can be easily separated from native Lycopodium foveolate-type and Lycopodium jussieui-type based on shape and structural differences in equatorial and polar views.

Chronological control is provided using Accelerator Mass Spectrometry (AMS) radiocarbon dating on five samples from
core IR1 (Table 3) and four samples from core IR2 (Table 3). The radiocarbon determinations from core IR2, abstracted in close proximity to IR1, were used to address chronological uncertainties (Fig. 3) and will be discussed in further detail.

Standard stable isotope techniques (Wooller et al., 2004) were applied to 36 samples at the Alaska Stable Isotope Facility, University of Alaska, Fairbanks, USA. Samples of core material were freeze-dried and then acid-fumed with concentrated HCl to remove carbonates. An aliquot (1.1–3.5 mg) of each sample was weighed into a tin capsule, crimped and introduced into the autosampler (type A2100) of an NA 2500-series elemental analyzer. Purified combustion gases (CO₂ and N₂) were separated in a gas chromatographic column prior to entering the Finnigan Conflo II interface and the stable isotope ratio mass spectrometer (Finnigan MAT, DeltaPlusXL). Peptone was analyzed (every ∼ 7th sample) as a check on the analytical precision throughout the analyses, which was +0.06‰ for δ¹³C (C%=+2.6) and +0.20‰ for δ¹⁵N (N%=+0.5) (n=7). Isotopic compositions are expressed in per mil (‰) relative to Vienna PeeDee belemnite (VPDB) standard.

δ¹³C(‰)=1000[(Rsample/RVPDB)−1], where R=¹³C/¹²C for carbon isotope; and δ¹⁵N(‰)=1000[(Rsample/RVPDB)−1], where R=¹⁵N/¹⁴N for nitrogen isotope.

Results

Lithology and chronology

The 266-cm-long sediment core consists mainly of organic-rich sediments (Table 2). Sand was present at the bottom of the core. The five AMS ¹⁴C dates on bulk sediment samples from IR1 (Table 3) show a complex time-depth relationship; the lowermost two ages show an inversion (Fig. 3). To support the chronology of IR1 sediments, a second core (IR2) was raised at point slightly higher (30 cm) and some 20 m from site IR1 in case its sediment archive had been influenced by cross cutting of the drainage system in the valley. Four sediment samples from core IR2 were dated, and the results are shown in Table 3. The sample at 258 cm (19,230 ± 100 ¹⁴C yr BP) is close to the interval with grey, sandy clay; therefore, the relatively young age could be explained by the vertical migration of components down the sediment sequence possibly recording contamination. The age 37,940 ± 480 ¹⁴C yr BP from IR2 core is considered as relatively reliable with regard to its position just above 258 cm and the large age difference of 18,710 ± 380 ¹⁴C yr BP. Based on...
Table 1
List of identified taxa of pollen, spores and other non-pollen palynomorphs in the sediments of core IR1

(A) Pollen
Upper montane herbs and shrubs
Acanthaceae: Justicia anelliana-type
Peristrophe bicolorulata-type*
Apiaceae: Eryngium-type
Azorella-type
Asteraceae: Bulens pilosa-type
Cardus-type*
Enciplia-type
Helichrysum-type
Senecio deltoideus-type
Lilacemae: Aloe-type

Upper montane forest
Araliaceae: Cussonia-type*
Arecaeeae: Socratea-type
Podococcus-type*
Asclepiadaceae: Asclepias curassavica-type
Aquifoliaceae: Ilex mitis
Ericaceae: Erica arborea-type
Fabaceae (P): Erythrina abyssinica-type*
Fabaceae (C): Pierocarpus-type
Lauraceae: Ocotia-type*
Loganiaceae: Naia congentsa-type*
Meliaeaceae: Trichilia-type
Myricaceae: Myrica salicifolia-type
Podocarpaceae: Podocarpus falcatus-type
Rosaceae: Alchemilla-type*
Pruma africana-type
Hagenia abyssinica-type*
Sorbaria-type*
Rubiaeae: Psychotria-type
Rubiaeae: Spermacoce-type
Rutaceae: Zanthoxylon gillettii-type*
Scrophulariaceae: Halenia-type
Sterculiaceae: Dombeya torrida-type
Ulmaceae: Celtis integrifolia-type

Montane forest
Balsaminaceae: Impatiens volkensii-type*
Capparidaceae: Caubha farinosa-type*
Cleome usambarica-type
Maerua oblongifolia-type*
Ebenaceae: Diospyros whitewater-type*
Euphorbiaceae: Acalypha diversifolia-type
Alchornea hirta-type*
Croton-type
Dalechampia-type*
Euphorhia hirta-type*
Phyllanthus fischeri-type*
Macaranga kilimanischarica-type*
Maytenus-type
Flacourtiaeae: Caesaria-type
Geraniaceae: Geranium-type
Myrtaceae: Syzygium-type
Olanaceae: Strombosa-type
Proteaeeae: Protea angolensis-type
Rutaceae: Clausena anisata-type, Citrus-type

Forest patches in edaphic grasslands and lowland forests
Anacardiaceae: Lannea-type*
Amaranthaceae: Celosia schweinfurthiana-type*
Cyathula cymindrica-type*
Apoecynaceae: Maloeta-type*
Asteraceae: Vernonia pauciflora-type*
Bombacaceae: Ceiba pentandra-type
Chorisia-type*

List of identified taxa of pollen, spores and other non-pollen palynomorphs in the sediments of core IR1

(A) Pollen
Forest patches in edaphic grasslands and lowland forests
Boraginaceae: Cordia-type*
Heliotropium somalense-type
Caryophyllaceae*
Commelinaceae: Commelina-type
Convolvulaceae: Merremia-type*
Cucurbitaceae: Coccinia milbraedii-type*
Echinopsor type*
Luffa-type*
Fabaceae (C): Combretum-type
Fabaceae (P): cf. Kotschya-type*
Labiatae: Leonitis africana-type
Malvaceae: Abutilon-type
Pavonia-type
Moraceae: Ficus-type
Myrsinaceae: Myrsine africana-type*
Polygalaceae: Polygalia virgata-type
Polygonaceae: Polyganum-type
Sapindaceae: Allophylus africana-type*
Paulinia pinnata-type*
Solanaeae: Solanum nigrum-type
Browalia-type*
Urticaceae: Arthrocarpus-type

Bog vegetation
Cyperaceae: Cyperus-type**
Haloragidaceae: Myrthophyllum-type**
Lentibulaceae: Utricularia-type
Poaceae**
Typhaceae: Typha latifolia-type**

(B) Spores
Algae
Botryococaceae: Botryococcus-type**
Hydrodictyaceae: Debarya-type**
Zygnemataceae: Gleotrichia-type**
Mongostea-type**
Spirogyra-type**
Zygmena-type**

Bryophytes (mosses)
Anthocerotaceae: Anthoceros**
Bartramiaceae: Bartramia-type**
Sphagnaceae: Sphagnum**
Cyanobacteria
Anabaena-type**

Ferns (trilette spores)
Cystaceae: Cysthea mantinniana-type**
Cysthea frigida-type**
Dennstaedtiaceae: Saccoloma-type**
Hymenophyllaceae: Hymenophyllum-type**
Lycopodiaceae: Lycopodium clavatum-type**
Lycopodium foveolate-form type**
Polypodiaceae: Polypodium pectinatum-type**
Polypodium tussarius-type**
Ophioglossaceae: Ophioglossum-type**
Selaginellaceae: Selaginella-type**

Monolete spores
Psilatate and verrucate**

Fungi (according to van Geel et al., 2003)
Type 55A: Sordaria-type**
Type 207: Glomus-type**
Type 55C: Neurospora-type**
Type 140: Valaria-type**
Type 1: Gelasinospora-type**
Type 3B: Pileospora-type**
Type 172: Conioscheta cf. lignantia**

(continued on next page)
the lithology and biostratigraphy of IR1 and 2, there is a fairly constant pollen concentration, which indicates limited evidence for hiatus, and we suggest that the record extends through most of the Holocene. Furthermore, this interpretation is supported by the date of 8345±4514 C yr BP from core IR2, located in time and depth from the middle of a possible potential hiatus. Thus, we use the age–depth relationships for the record as indicated in Figure 3 with a caveat of a floating chronology, although we acknowledge chronological difficulty and apply this caveat to our interpretation of the palaeoecological data.

Zonation and description of the pollen record

Down-core changes in pollen data are shown in Figure 4 for the regional forest taxa and Figure 5 for the local taxa. The sum of ecological groups, pollen sum values, pollen concentration values and the CONISS dendrogram are shown in Figure 6. Cluster analysis recognised five main pollen zones: IR1-1 to IR1-5. Zone IR1-2 is divided into two sub-zones (2a and 2b). Rare taxa are not shown in the pollen diagrams but listed in Table 1.

Pollen zone IR1-1 (266–240 cm, 14 samples). UMF is represented by Areceaceae, Ericaceae, Dombeya, Halleria, Myrica, Podocarpus, Prunus, and Psychotria. UMHS comprises Aloe, Bidens, Eclipta, Geranium and Helichrysum. Acalypha, Bombacaceae, Croton, Euphorbia and Phyllanthus represent MF. Local taxa comprise Cyperaceae, Senecio and Poaceae, the later dominating the pollen record.

Pollen sub-zone IR1-2a (238–200 cm, 20 samples). UMF comprises Areceae, Celtis, Ericaceae, Dombeya, Halleria, Podocarpus, Prunus and Psychotria. UMHS comprises Aloe, Apium, Bidens, Cleome, Eclipta, Eryngium, Geranium, Helichrysum and Justicia. MF comprises Acalypha, Bombacaceae, Croton, Euphorbia, Heliotropium, Phyllanthus and Solanum. Taxa of local importance are Cyperaceae and Senecio. Moss spores (Anthoceros) and algae (Zygnema) are more abundant in this zone. Poaceae are increasingly common.

Pollen sub-zone IR1-2b (198–140 cm, 30 samples). UMF comprises Areceae, Celtis, Dombeya, Ericaceae, Halleria, Podocarpus, Prunus and Psychotria. UMHS is represented by Aloe, Bidens, Eclipta, Eryngium, Geranium, Helichrysum and Spermacoce. MF is represented by Acalypha, Bombacaceae, Carphophyllaceae, Croton, Euphorbia, Heliotropium, Moraceae/Urticaceae, Phyllanthus and Solanum. Local taxa include Cyperaceae, Senecio and Poaceae. Fern spores, moss spores (Anthoceros) and algae decrease in abundance relative to the previous zone.

Pollen zone IR1-3 (138–74 cm, 33 samples). UMF comprises Areceae, Caesaria, Celtis, Dombeya, Ericaceae, Halleria, Podocarpus and Psychotria. UMHS comprises Aloe, Bidens, Eclipta, Eryngium, Geranium, Helichrysum and Spermacoce. MF comprises Acalypha, Croton, Euphorbia, Heliotropium, Moraceae/Urticaceae and Phyllanthus. Taxa of local importance are Cyperaceae, Senecio, Sphagnum and Poaceae. Ferns and algae increase in abundance and coprophilous spores appear in the upper part of this zone.

Pollen zone IR1-4 (72–40 cm, 17 samples). UMF is mainly dominated by Areceae, Celtis, Ericaceae, Halleria, Myrica, Podocarpus, Prunus and Psychotria. UMHS is dominated by Aloe, Bidens, Cleome, Eclipta, Eryngium, Helichrysum and Spermacoce. MF comprises Acalypha, Euphorbia, Heliotropium, Moraceae/Urticaceae and Phyllanthus. Taxa of local importance are Cyperaceae, Myriophyllum, Senecio, Poaceae and Ferns. Algae and coprophilous fungi are increasingly abundant relative to the previous zone.

Pollen zone IR1-5 (38–0 cm, 19 samples). UMF mainly comprises Caesaria, Dombeya, Ericaceae, Myrica, and Psychotria. UMHS is represented by Aloe, Bidens, Cleome, Eryngium, Helichrysum, Protea and Spermacoce. MF comprises Acalypha, Apocynaceae, Euphorbia, Heliotropium, Mortaceae/Urticaceae, Phyllanthus, Solanum and Sycgynia. Taxa of local importance are Cyperaceae, Myriophyllum, Senecio, Sphagnum, Poaceae and fern spores. Algae and spores of coprophilous fungi are abundant throughout.

Table 1 (continued)

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<tr>
<th>Type</th>
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<tr>
<td>368A</td>
<td>Podospora-type**</td>
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<td>124*</td>
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<td>195*</td>
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<td>Testae amoeba</td>
<td>Arcella-type**</td>
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Table 2

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<th>Stratigraphy of sediments from core IR1</th>
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<td>0–10 cm</td>
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Table 3

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<th>δ13C (%)</th>
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<td>GrA-24635</td>
<td>30</td>
<td>1480±60</td>
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<td></td>
<td>GrA-24637</td>
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<td>GrA-24597</td>
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<td>23,950±200</td>
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<td>GrA-28023</td>
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</tbody>
</table>
Apart from the upper part, the record contains poorly preserved macrofossils. The presence of seeds is expressed in numbers; all other materials are expressed as a percentage by volume. We recognised five zones by visual inspection of the diagram: zone IR1-M1 to IR1-M5 (Fig. 7). Zone IR1-M1 (260–245 cm) contains 90% of sand with low proportion of plant fragments and charred particles. Zone IR1-M2 (245–175 cm) still contains high proportion of sand, with higher proportions of plant fragments and charred particles. Zone IR1-M3 (175–65 cm) is represented by a first appearance of Sphagnum leaves; plant fragments increase together with the proportion of charred particles fluctuating between 30% and 10%; the proportion of sand decreases markedly. Zone IR1-M4 (65–15 cm) is represented by the presence of seeds of Cyperaceae, Sphagnum capsules and leaves. The proportion of plant fragments increases and the number of charred particles decreases relative to zone IR1-M3. Zone IR1-M5 (15–0 cm) is composed of Sphagnum leaves (90%) with all other components decreasing sharply. Depth intervals of macrofossil zones differ from the depth intervals of pollen zones, indicating that the vegetation development in the basin differed from the development of the regional vegetation.

Stable isotope and element analysis and its environmental significance

Results from the stable isotope and elemental analyses (C and N) of the Total Organic Matter (TOM) from core IR1 are shown in Figure 8. Based on visual inspection we recognised intervals mainly coeval with the pollen zone boundaries, numbered IR1-IS1 (266–205 cm), IR1-IS2 (205–150 cm), IR1-IS3 (150–60 cm), IR1-IS4 (60–30 cm), and IR1-IS5 (30–0 cm). With the exception of pollen zone IR1-5, the C:N values are generally above 20%, indicative of organic matter originating from terrestrial, riparian or emergent higher plants, rather than from aquatic macrophytes, algae, or phytoplankton (Meyers, 1992). N increases from 3% at the base of the core to 25% at the top, a well-known trend associated with the loss of nitrogen from decomposed organic matter. C also shows a general increase from 5% at 240 cm to 30% at the top of the core. However, there is a marked decrease in the %C from 40% to 5% at 245 cm. δ^{15}N increases markedly from ~0.5‰ at the base of
the core to 3.5‰ at ∼200 cm during pollen zones IR1-1 and IR1-2a. δ15N values range between 3‰ and 4.25‰ during pollen zone IR1-2b and then gradually decrease to 1‰ during pollen zone IR1-3. δ15N values remain relatively constant during pollen zone IR1-4 but show a slight increase (1‰) followed by a marked decrease (2.5‰) during pollen zone IR1-5. With the exception of a marked rise (3‰) at the bottom of the core and a decrease (4‰) at the top of the core, the δ13C values remain relatively constant at a mean of −21‰. A simple mass balance mixing model equation, assuming average δ13C values of −27‰ and −12‰ for C3 and C4, respectively, and a mean sediment δ13C value of −21‰ suggests that the organic material composing core IR1 was primarily derived from plants using the C3 photosynthetic pathway (60%). The C4 proportion (40%) of the organic matter composing the core could be derived from the C4 grasses that are evident in the modern swamp plant community (e.g., *D. diagonalis* and *P. unisetum*).

**Data interpretation and environmental reconstruction**

The radiocarbon ages of cores IR1 and IR2 (Tables 3; Fig. 3) leave some uncertainty about the precise age control of the sediments in the depression. In core IR1, the samples at 160 and 220 cm show similar ages of 23,950 ± 210 and 22,950 ± 570 14C yr BP, respectively. Both ages determination have no specific doubts on their integrity and therefore the average calculated age of 23,450 ± 390 14C yr BP was attributed to the average depth level of 190 cm. The age estimates at 258 cm caused an inversion of the depth-vs.-age relationship and this age was rejected. A straightforward explanation for this erroneous age is not available, but contamination of sediments with terrigenous material from elsewhere is plausible in a dynamic environment where organic-rich sediments are starting to accumulate on minerogenic substrate. In core IR2, samples at 156 and 206 cm showed similar ages of 25,580 ± 200 and 23,690 ± 120 14C yr BP, respectively. As with ages core IR1, both are not subject to specific doubts. In both cores, the paired samples with similar age show a consistent older age in the upper sample and a younger age in the lower sample.

The calculated average age in core IR2 of 24,635 14C yr BP was attributed to 181 cm, and this is remarkably close to the calculated average age in core IR1. The age of 8345 ± 45 14C yr BP at 106 cm in core IR2 shows that sediments of Holocene age have been preserved in the bog. However, at site IR1 a much
The significant difference in age between both samples around 1-m core depth suggests the presence of a hiatus in core IR1 above 97-cm core depth. This interpretation is substantiated by the understanding that site IR1 was permanently close to the drainage system (the present small stream in the bog) while site IR2 was not. The sample dated 8345±4514C yr BP is evidence that the location of site IR2 was well chosen for the purpose of assisting in understanding the complex sediment history of this site. The lowermost 14C sample in core IR2 shows an age of 37,940 ± 48014C yr BP at 256 cm, which supports well the general accumulation rate of sediments found in the upper 200 cm of both cores (Fig. 3).

In order to arrive at the most plausible chronology for core IR1, the following ages were used to feed the TILIA-based interpolation program: 1480± 6014C yr BP (30 cm); 15,110± 80 14C yr BP (97 cm) assuming a hiatus in the pollen record between both ages; the calculated average age of 23,450 14C yr BP at 190 cm; and the age of 37,940 ±48014C yr BP, taken from core IR2 and reflecting the start of organic-rich sediments on the minerogenic substrate. Ages of the periods for which environmental and climatic change has been reconstructed are given in multiples of 1000 yr to reflect the degree of uncertainty in time control. Notwithstanding the limited chronological control of the record, environmental change in this biodiversity hotspot can be evaluated from a maximum glacial to interglacial and the late Holocene climate.

Combining information from the different proxies we arrive at the following reconstruction of environmental change at Kising’a-Rugaro catchment area.

**Period 1 (pollen zone IR1-1, macrofossil zone IR1-M1, isotope zone IR1-IS1, estimated age 38,000 to 35,000 14C yr BP)**

Abundant sand and clay and almost absence of plant fragments and charred particles (Fig. 6) indicate a high-energy minerogenic depositional environment with the drainage passing close to the coring site. On the adjacent wet soils Lycopodium and palms (Arecaceae) were common. Presence of algae (Mougeotia and Spirogyra) indicates local presence of aerated water. Pollen and spores reflective elements of wet and low energy conditions (Myriophyllum, Sphagnum...
and **Typha** are almost absent further supporting the interpretation of a dynamic hydrological environment. The presence of **Celtis, Dombeya, Ericaceae, Myrica, Podocarpus, Prunus** and **Psychotria** indicate that UMF surrounded the site.

However, representatives of open herb and shrub vegetation, such as **Aloe, Bidens, Eclipta, Geranium, Helichrysum, Protea** and **Spermacoce**, were also abundant indicating regional vegetation was a mosaic of closed forest and patches with herbs and

![Macrofossil diagram of IR1 core](image1.png)

**Figure 7.** Macrofossil diagram of IR1 core. Changes in the proportions of plant fragments, sand, and charred particles are expressed in percentage by volume. The lithological column, pollen zones, and macrofossil zones (with prefix M) are shown. Also shown: \( n \) = number and vol.% = volume percentage.

![Downcore changes of stable isotopes](image2.png)

**Figure 8.** Downcore changes of stable isotopes \( \delta^{13}C \) and \( \delta^{15}N \), and elemental composition (percentage and C/N ratio) of total organic matter of core IR1. For comparison, pollen zones are also shown.
shrub. MF taxa, such as Acalypha, Croton, Euphorbia, Heliotropium, Bombaceae, Moraceae-Urticaceae, Phyllanthus and Solanum, indicate that MF was close to the site. However, MF is recorded at its lowest percentage (Figs. 4 and 5), suggesting the transition from UMF to MF was lower than today’s altitude; we estimate this altitude at around 1700–1800 m. This suggests UMF lowered by 200 to 300 m relative to today. Abundant open vegetation and high representation of grasses compared to the present (40–50% vs. 10–20%) also suggest drier climatic conditions. The $\delta^{13}$N increases during pollen zones IR1-1 and IR1-2a could be associated with drier conditions or with an increase in denitrification, leading to an increase in the $\delta^{15}$N of remaining nitrogen in the soil.

**Period 2 (pollen zones IR1-2a, macrofossil zone IR1-M2, isotope zone IR1-IS2, estimated age 35,000 to 29,000 $^{14}$C yr BP)**

Accumulation of black amorphous peat, locally with sandy and clay intercalations, indicate that the sediments were deposited in a semi-lacustrine environment. Senecio became more abundant, suggesting more stable conditions, with the presence of Sphagnum and algae (Mougeotia, Spirogyra, and Zygnema) indicative of acidic and nutrient poor stagnant water. Decreasing presence of Areceae and Myrica and increasing presence of Caesaria, Celtis, Clausena, Dombeya, Halleria and Psychotria indicate a change in the floral composition of the UMF. The proportion of UMHS vegetation did not change compared to the previous period. Azorella, Cleome and Eryngium became more abundant. The presence of MF increased by about 10%, suggesting the lowermost boundary of UMF shifted to 1800–1900 m. High C:N ratios (>20) indicate the organic matter was derived from terrestrial plants outside the swamp.

**Period 3 (pollen zones IR1-2b, macrofossil zone IR1-M2/M3, isotope zone IR1-IS2, estimated age 29,000 to 21,000 $^{14}$C yr BP)**

Black amorphous peat with decreasing sand fraction and higher proportions of plant fragments indicate a lower-energy depositional environment. Cyperaceae, Senecio, and ferns were dominant in the swamp. During the second part of this period, swamp vegetation and hydrophytic taxa, such as ferns, Typha, and algae, decreased (Fig. 4). Compared to the previous period, there is a minor change in the proportion of UMHS vegetation and UMF, reflecting an upslope shift of some 50 m. Prunus and Psychotria decreased in abundance suggesting slightly less humid conditions. MF recorded a slight change in composition: Acalypha, Bombaceae, Euphorbia, Heliotropium and Phyllanthus all decrease, suggestive of less humid conditions. This period seems slightly drier and cooler than the previous one; the UMF/MF boundary is estimated at 1850–1950 m elevation.

**Period 4 (pollen zone IR1-3, macrofossil zone IR1-M3, isotope zone IR1-IS3, estimated age 21,000 to 10,000 $^{14}$C yr BP)**

During the first part of the period, sandy and clay horizons indicate water channels occasionally passed close to the core location. During the second part, such incursions did not occur and peat formation continued. Such hydrological activity, although not recorded as significant changes in any of the other proxy studies, may have produced an erosional hiatus. Sphagnum leaves recorded during the later part of this period indicate a continuous accumulation of black amorphous peat and relatively stable swamp conditions. Increased abundance of Cyperaceae, Typha and algal species indicate locally wet conditions. During the last few thousand years of this period the amount of coprophilous fungi increased. Also, grasses reached high percentages between approximately 19,000 and 14,000 yr ago, which may indicate drier and cooler conditions. Psychotria recorded highest values during this period pointing to short-lived moist forest. The proportions and composition of UMF, UMHS, and MF vegetation hardly changed compared to the previous period (Fig. 5), indicating that the UMF/MF transition remained around 1850–1950 m.

**Period 5 (pollen zone IR1-4, macrofossil zone IR-1M3/4, isotope zone IR1-IS3/4, estimated age 10,000 to 3500 $^{14}$C yr BP)**

As explained in the chronology section and suggested by the environmental reconstruction of the previous period, this period is incompletely reflected in the record. Possibly, sediments of late glacial age and a significant part of the Holocene are missing. During this period, plant fragments are replaced by an increasing proportion of Sphagnum leaves as herbaceous peat continued to accumulate in the basin. Seeds of Cyperaceae and Sphagnum are more abundant, suggesting wet to very wet swamp conditions at the coring site. Myriophyllum became abundant for the first time and algae (Mougeotia, Spirogyra and Zygnema) are common. Coprophilous fungi (Pleospora and Sordaria) are present throughout the period, indicating the presence of grazing animals around the swamp. The proportion of UMHS increased to highest level; in particular, Ericaceae, Myrica, Podocarpus, Prunus and occasionally Psychotria reached high percentages. Taxa of UMHS dominated with Aloe, Bidens, Eclipta and Helichrysum becoming potentially common. It is likely UMF, including the patches of open herb and shrub vegetation, expanded at the expense of MF and the lowering of the transition from MF to UMF is estimated at some 150 m elevation compared to the previous period. Maxima of UMHS may point to short-lived drier climatic conditions.

**Period 6 (pollen zone IR1-5, macrofossil zone IR1-M4/5, isotope zone IR1-IS4/5, estimated age 3500 $^{14}$C yr BP to the present; 3000 cal yr BP to the present)**

Accumulation of black peat with abundant plant fragments continued (Fig. 6), initially composing high amounts of Cyperaceae seeds and leaves. The proportion of Cyperaceae, Anthoceros, Sphagnum and ferns decreased significantly during the last part of this period as Myriophyllum became abundant, reflecting the present-day conditions on the swamp. The high representation of algae (Mougeotia, Spirogyra and Zygnema) point to eutrophication of the swamp. Abundant coprophilous fungi (Pleospora and Sordaria) indicate presence of herbivores, including cattle, around the swamp that would contribute to
eutrophication. This period is also characterised by presence of *Neurospora* and *Valsaria*, reflecting more acidic and nutrient-rich waters. The record of *Neurospora* reflects the increasing occurrence of fire within the catchment, in particular during the last 2000 yr when human impact on the environment intensified. The proportion of UMF decreased, particularly the contribution of Arecaceae, *Celtis*, *Clausena*, Ericaceae, *Myrica*, *Podocarpus* and *Prunus*, whereas Dombeya showed high representation relative to the previous period. Selective logging is indicated by the decrease in the records of key timber species such as *Caesaria*, *Celtis*, *Podocarpus*, *Prunus* and *Psychotria*. Although UMHS vegetation showed general decrease, taxa such as *Eryngium*, *Helichrysum* and *Protea* increased slightly during the last millennium. *Acalypha*, *Apopynaceae*, *Moraceae*- *Urticaceae*, *Solanium* and *Syzygium* had higher proportions, reflecting an upslope shift of the MF belt by some 250 m relative to the previous period.

**Discussion and conclusions**

The pollen record shows a shift from cooler and moister conditions, prior to LGM, to generally dry and cool conditions during the last part of the glacial period (ca. 20,000 $^{14}$C yr BP to the start of the Holocene). Similar conditions have been recorded from a number of studies in East Africa (Coetzee, 1967; Hamilton, 1982; Van Zinderen Bakker and Coetzee, 1988; Marchant et al., 1997). However, unlike these other records, the IR1 record shows relatively benign environmental change with temperatures estimated to have been between 0.6 and 1.5°C cooler (periods 1 to 3) than Holocene levels (periods 5 and 6). The $\delta^{13}$C record shows there is no marked shift in the contribution of C$_3$ and C$_4$ plants in the basin. This is in contrast to marked shifts of contribution of C$_3$ and C$_4$ plants in other East African mountain areas (Street-Perrott et al., 1997; Ficken et al., 2002). Some studies from the eastern highlands of Central Africa recorded the persistence of arboreal taxa, such as *Ilex*, *Myrica*, *Olea*, *Podocarpus* and *Syzygium* during the full glacial period (Livingstone, 1980; Bonnefille and Riollet, 1988; Bonnefille et al., 1990; Taylor, 1990; Jolly et al., 1997), although these were generally much more reduced than at Kising’a-Rugaro which recorded stability in floral composition.

Fjeldså and Lovett (1997) suggest (and were later supported by Anhuf et al., 2003) that moist forests along the EAM were continually present throughout the LGM. Our pollen record shows the presence of moist forest about 21,000 $^{14}$C yr BP, and the transition between UMF and MF shifted minimally (0.6°C during periods 3 and 4) relative to today. Thus, stable altitudinal forest distribution and composition through LGM supports the hypothesis that the EAM were relatively stable through time. One mechanism that promotes localised ecological stability is the influence of the Indian Ocean Monsoon (Fig. 2). Although it is proposed the intensity of moisture bringing southeast trade winds was reduced during the last glaciation (Nagai et al., 1995), this is yet to be quantified. Moreover, as our study area is at some 400-km distance from the Indian Ocean, a reduction in monsoonal intensity or duration would have a strong impact on the vegetation within this catchment.

With respect to precipitation during the last glaciation, records in East Africa indicate a decrease of some 30% (Bonnefille et al., 1990). Although we do not provide quantitative estimates of the reduction in precipitation, such a magnitude of change seems high given the relative constancy of pollen and isotopic composition; therefore, we suggest a period of benign climatic cooling and aridification relative to other comparable pollen records located farther west. This first record from the EAM shows evidence of ecosystem and environmental stability during periods of some 10,000 yr immediately before and after the LGM. Specific characteristics of this mountain area, in combination with the stabilising impact of moisture derived from the Indian Ocean, may explain this history (Marchant et al., 2006). More records are required to substantiate the hypothesis that long-term ecological stability during the Pleistocene can explain why the EAM is so rich in species and, as a consequence, a biodiversity hotspot.

Vegetation change during the late Holocene is associated with a continued climatic warming and human impact, both on the forests and on the catchment water quality. Anthropogenic clearance of UMF and MF during the late Holocene has been related to multiple causes: agriculture, pastoralism, timber abstraction, and hunting (Kikula, 1986). Significant decrease of some taxa during the last 3000 yr, for example *Psychotria*, indicates targeted forest degradation. At present *Psychotria* is very rare in the catchment area and is endangered in other parts of the EAM forests. In central East Africa, late Holocene human-induced forest clearing in the highlands of Burundi, Rwanda, and Uganda was locally correlated with political and economic changes, such as the entry of Bantu-speaking people and the onset of the early Iron Age, some 2300 yr ago (Taylor et al., 1999). Most severe deforestation seems to be associated with the beginning of the late Iron Age, about 1500 yr ago (Marchant and Taylor, 1998). The present-day open nature of the vegetation in the Kising’a-Rugaro catchment is directly related to increased human-induced forest degradation. The presence of coprophilous fungi in the IR1 record is associated with the increased presence of grazers (Van Geel et al., 2003); whether this is a result of domesticated animals or increased use of the swamp by wild populations cannot be substantiated by this study and requires independent evidence.

It is concluded that the first palaeoenvironmental record from the EAM shows a glacial cooling of 0.6 to 1.5°C during a 20,000-yr envelope around the LGM, which reflects a remarkable stability of tropical montane ecosystems. If environmental stability is needed to develop and maintain a biodiversity hotspot, the present data reflect a first substantiation of this hypothesis. The Indian Ocean may be responsible for the low amplitude in environmental change. Additional records from other EAM sites and better estimates of the age of the changes are needed to improve the understanding of the palaeoenvironmental history of this biodiversity hotspot.

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References


Bonnefille, R., Riollet, G., 1988. The Kashiru pollen sequence (Burundi) palaeoecological implications for the last 40,000 yr B.P. in tropical Africa. Quaternary Research 30, 19–35.


