Kenya ecosystem dynamics: perspectives from high and low altitude ecosystems

Stephen Mathai Rucina

KENYA ECOSYSTEM DYNAMICS: PERSPECTIVES FROM HIGH AND LOW ALTITUDE ECOSYSTEMS

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Kenya ecosystem dynamics: perspectives from high and Low altitude ecosystems

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ABSTRACT

Palaeoecological data from sediments taken from one highland and two lowland sites are used to compare and contrast ecosystem response to late Quaternary environmental change and human interactions in Kenya. A core from Rumuiku Swamp, located on the southeast of Mount Kenya within montane forest ecosystem extends back to 26,430 cal yr BP and forms a basis of environmental and ecosystem reconstruction from a high altitude montane rainforest location. In the 14.6 m long core ninety six sediment samples were analysed for pollen and charcoal. The pollen and charcoal data reflect a lowering of high altitude vegetation by more than 1000 m under a cool and moist climate during Last Glacial Maximum (LGM). The pollen data also reflect a mixture of high and relatively low altitude vegetation. Especially common was *Juniperus* that is presently found on the relatively dry part of the Mount Kenya but at lower altitudes than Rumuiku Swamp catchment. Mixed montane forest dominated by *Hagenia* and taxa from the ericaceous belt characterised the ecosystem from 24,500 to 17, 250 cal yr BP. *Juniperus, Olea* and *Podocarpus* were less common during the Lateglacial as there was high presence of more mesic taxa during the period leading up to the Younger Dryas.

During the Holocene a reorganization of the ecosystem occurred reflecting a shift to warmer and moister climate conditions with montane vegetation dominating. The Holocene was characterized by numerous events of environmental change recorded by increased charcoal abundance and ecosystem shifts. A drier climate is recorded around 9000 cal yr BP and between 4000 and about 3500 cal yr BP with increased presence of Poaceae, *Polyscias* and *Podocarpus*. Strong human impact is not evidenced in the Rumuiku Swamp sediments though increased Asteraceae and *Podocarpus* in the upper most sediments reflects open montane forest since 500 cal yr BP.
Namelok Swamp is located some 400 km south of Mount Kenya within the savanna ecosystem. 41 samples from a 400 cm long core reflecting the last 3000 cal yr BP were analyzed for pollen and

charcoal at intervals varying from 5 to 10 cm. The record shows the dynamic nature of savanna taxa as a response to natural climate change. Strong human impact is also recorded in the Namelok Swamp sediments during the late Holocene by showing increased fire intensity linked to regional drought. *Cannabis sativa*, cereal and *Ricinus communis* pollen are recorded in the same period. A dynamic herbivore-plant interaction is also thought to have contributed to changes in vegetation composition in the Namelok Swamp ecosystem. For instance, at present-day when the elephant population decreases or is controlled a rapid recovery of woody vegetation can be observed. Climate variability is also documented by the pollen record from Namelok Swamp sediments: a relatively moist climate is recorded from 3000 to 2400 cal yr BP and drier and warmer climatic conditions from 2100 to 1675 cal yr BP. A relatively wet period is recorded from 1675 to 550 cal yr BP with another drier period after 550 cal yr BP. Impact of increased sedentary settlement is recorded during the last 150 cal yr BP by increased amounts of pollen grains from cereals and plants characteristic of disturbed ecosystems.

Lake Challa (3° 19′ S, 37° 43′ E) is a 4.2 km2 and 94 m deep crater lake situated at 880 m elevation close to the Kenya-Tanzania border. High-resolution pollen and radiocarbon analyses on late Holocene sediments document the response of lowland dry forest to regional climate variability over the last 2700 years. Century-scale periods of climatic drought are recorded by an increases in pollen abundance of Poaceae and dry savanna trees and shrubs (*Combretum, Commiphora, Salvadora* and *Rhus*) and herbs (*Corchorus* and Urticaceae), and a reduction of other common savanna trees and shrubs (*Maerua* and *Sideroxylon*). Montane forest trees (*Celtis, Juniperus, Olea* and *Podocarpus*) most likely located on the slopes of nearby Mount Kilimanjaro expanded at the same time. Increased pollen from aquatic plants and sedge swamp vegetation on exposed shallow margins reflect low lake stands indicative of dry climatic conditions. Environmental conditions were drier than today from 2700 to 2300 cal yr BP, 1800 to 1500 cal yr BP, 1300 to 800 cal yr BP, and from ~250 to 70 calendar years.. Conversely, wetter conditions than today were inferred for the periods from 2300 to 1800 cal yr BP, 1500 to 1300 cal yr BP, and from 800 to 300 cal yr BP. The Challa pollen record indicates that the wettest climatic conditions of the last 2700 cal yr BP occurred from ~600 to 300 cal yr BP, i.e. coeval with the main phase of the Little Ice Age in Europe. The low abundance of large Poaceae pollen grains as early as ~2650 cal yr BP, likely to have originated from cereal crops, is suggestive of intermittent agricultural activity within the Lake Challa catchment. This suggested the agricultural activities were not localized due to variability in climate, encouraging human migration to climatically suitable areas for farming activities. Higher cereal pollen abundance after around 150 cal yr BP is associated with an increase in herbaceous plants indicative of more widespread deforestation. This reflects intensifying farming activities in an increasingly human-impacted landscape. Marked ecosystem changes during the late Holocene are most pronounced in the savanna ecosystems around Namelok Swamp and Lake Challa documenting a long history of human impact on the savanna ecosystem of southern Kenya.

SAMENVATTING

Paleoecologische gegevens uit sedimenten van een locatie uit het hoogland en van twee locaties in het laagland van Kenya zijn met elkaar vergeleken. Hieruit is op te maken hoe ecosystemen tijdens het laat Kwartair op klimaatverandering en menselijke invloed reageren. Een sedimentkern komt uit het Rumuiku Veen dat in het bergbos ligt op de zuidoostelijke helling van Mount Kenya ligt op 2154 m hoogte. Deze kern laat de veranderingen zien tijdens de laatste 26.430 jaar en vormt de basis voor de reconstructie van het milieu en de ecosystemen van een hoog gelegen bergbos. In de 14,6 m lange kern is in 96 monsters het fossiel pollen en het houtskoolresten geanalyseerd. De resultaten laten zien dat tijdens de koudste fase van de laatste ijstijd (Last Glacial Maximum; LGM) de vegetatie meer dan 1000 m bergafwaards was gemigreerd en duidt op koude en nattere klimaatsomstandigheden. The pollen spectra laten een mix zien van hoogland en laagland vegetatie. Vooral Juniperus was algemeen, een struik die nu op de relatief droge hellingen van Mount Kenya voorkomt op lagere hoogten dan het Rumuiku Veen. Van 24.500 tot 17.250 kalenderjaar voor heden werd het bergbos gedomineerd door Hagenia en soorten uit de zone met heidevegetstie. Tijdens het Laatglaciaal waren *Juniperus, Olea en Podocarpus* minder algemeen en in de periode voorafgaand aan de Jonge Dryas tijd vertoonden soorten van meer vochtige omstandigheden een hoge presentie. Tijdens de overgang naar het Holoceen vond er een reorganisatie van ecosystemen plaats die een overgang naar warmere en nattere klimaatcondities weerspiegelt en berbos werd dominant.

Migraties van ecosystemen en veranderingen in het voorkomen van houtskool laten ziendat Het Holoceen is gekenmerkt door vele veranderingen in milieucondities. Onstreeks 9000, en van 4000 tot 3500 kalenderjaar voor heden is een droger klimaat geregistreerd en het aandeel van Poaceae, *Polyscias* en *Podocarpus* in de vegetatie was hoger. Er zijn geen aanwijzingen gevonden voor sterke menselijke invloed rond het veen. Wel laten een hogere presentie van Asteraceae en Podocarpus tijdens de laatste 500 kalenderjaar voor heden meer open bergbos zien.

Het Namelok Moeras ligt op 1146 m hoogte in de savanne ongeveer 400 km ten zuiden van Mount Kenya. In een 400 cm lange sedimentkern die de laatste 3000 kalenderjaar voor heden representeert zijn op afstanden van 5 tot 10 cm langs de kern 41 monsters geanalyseerd op pollen en houtskoolresten. Dit sedimentarchief laat het dynamische karakter van savanna zien als reactie op klimaatverandering. Het pollen diagram toont een reletief vochtig klimaat van 3000 tot 2400 kalenjaar voor heden, en drogere en warmere condities van 2100 tot 1675 kalenjaar voor heden. Een relatief nat klimaat is gedocumenteerd van 1675 tot 550 kalenjaar voor heden en weer drogere omstandigheden tijdens de laatste 550 kalenjaar. De sedimenten uit het Namelok Moeras laat tijdens het laat Holoceen een sterke menselijke invloed zien op de savanne in de vorm van een verhoogde brandintensiteit gekoppeld aan regionale droogte. Pollen van *Cannabis sativa*, cerealen, en van *Ricinus communis* zijn in dezelfde periode geregistreerd. Er wordt aangenomen dat een dynamische interactie tussen de vegetatie en herbivoren ook heeft bijgedragen aan veranderingen in de vegetatie in de regio. Dit wordt onderbouwd door recente observaties dat bij een afnemende populatie olifanten de houtige vegetatie snel regenereert. Een toename van het aandeel pollen van cerealen en planten die typisch zijn voor een beschadigd ecosysteem tijdens de laatste 150 kalendejaar wijst op een toegenomen sedentaire leefwijze.

Het Challa Meer (3°19′ ZB, 37°43′ OL) ligt op 880 m hoogte en is een kratermeer van 94 m diep en een oppervlak van 4.2 km^2. Het ligt dicht bij de grens tussen Kenya en Tanzania. Pollenanalyse met hoge resolutie en koolstof-14 datering van de laat Holocene sedimenten laten zien hoe het droge bos in het laagland gereageerd heeft op klimaatverandering tijdens de laatste 2700 kalenderjaar voor heden. Het voorkomen van een droog klimaat op een schaal van enkele eeuwen is af te leiden uit een toename van het aandeel van grassen, bomen en struiken die typisch zijn voor savanne (*Combretum, Commiphora, Salvadora* and *Rhus*), kruiden (*Corchorus* en Urticaceae), en een afname van andere algemeen voorkomende savannebomen en struiken (*Maerua* en *Sideroxylon*). Tegelijkertijd een geregistreerde toename van bomen van het bergbos (*Celtis, Juniperus, Olea* en *Podocarpus*) reflecteert waarschijnlijk een uitbreiding van het bos op de hellingen van Mount Kilimanjaro. Een toename van aquatische vegetatie en zeggenmoeras op ondiepe en drooggevallen oevers documenteren lage waterstanden in het meer en daardoor een droog klimaat. Van 2700 tot 2300 kalenderjaar voor heden, en ook van 1800-1500, 1300-800, en 250-70 kalenderjaar voor heden waren klimaatcondities droger dan nu. Tegenovergesteld was het klimaat natter gedurende de perioden van 2300-1800, 1500-1300, en van 800 tot 300 kalenderjaar voor heden. Het pollendiagram van het Challa Meer laat zien dat gururende de laatste 2700 jaar de periode van ~600 to 300 kalenderjaar voor heden het natste klimaat heeft gekend, dus in tijd samenvallend met de periode van de Kleine IJstijd in Europa. De grote pollenkorrels van cerealen zijn vanaf ~2650 kalenderjaar voor heden in lage proporties aanwezig hetgeen duidt op de verbouw van granen en de, wellicht discontinue aanwezigheid van landbouw in het bekken van het Challa Meer. Rond 150 kalenderjaar voor heden neemt de proportie van pollen van cerealen en tegelijkertijd het aandeel van kruidachtige planten toe hetgeen duidt op toenemende ontbossing. Dit reflecteert intensievere landbouwactiviteiten in een landschap dat in toenemende mate door de mens wordt beïnvloed.

Tijdens het laat Holoceen zijn in de ecosystemen van zuidelijk Kenya veranderingen het duidelijkst in de savannes bij het Namelok Moeras en het Challa Meer en deze veranderingen laten een lange geschiedenis zien van menselijke invloed op de savanne.

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CHAPTER 1

INTRODUCTION

1. Introduction to East Africa palaeoenvironments

Although there are numerous records from montane ecosystems, records from savanna ecosystems are relatively few; this scarcity is likely to be largely due to the lack of suitable sedimentary basins. High altitude lakes and bogs have been the focus of palaeoecological investigations (Coetzee 1964; 1967; Hedberg, 1954; van Zinderen Bakker, 1964; Kendall, 1969; Hamilton, 1979; Harvey, 1976; Johannessen, et al., 1985; Hamilton, et al., 1986; Maitima, 1991; Street-Perrott, et al, 1993; Johnson, et al., 1996; Beuning, 1997; Street-Perrott, et al, 1997; Karlen, et al., 1999; Barker, et al., 2001; Ficken, et al., 2002; Lamb, et al., 2003). Many high altitude records show a shift of high altitude vegetation to lower altitudes during the last glacial period reflecting cold and dry climate with temperatures estimated to be 4° C colder than the present on Mt Kenya (Coetzee, 1964). Natural fires have also shown to be important controls on ecosystem composition, for example fires were common in the areas of Sacred Lake at 2400 m and Rumuiku Swamp at 2154 m on Mount Kenya (Rucina et al., 2009; Wooller, 2000) (Figure 1). From 26,000 to 19,000 cal yr BP montane forests comprised taxa from the ericaceous belt dominated by C_3 plants reflecting a dry and cool climate throughout the last glacial period (Rucina et al., 2009). Low lake levels recorded from 25,000 to 15,000 cal yr BP throughout East Africa pointing to cool conditions and a prolonged dry period (Kendall, 1969; Beuning et al., 1997). Low abundance of Cyperaceae and Poaceae pollen from sediments recovered from Kashiru Swamp at 2104 m in Burundi suggest this period was relatively wet and warm (Bonnefille and Riollett, 1988). Sediments from Muchoya Swamp (2260 m) in Uganda record the establishment of taxa from the ericaceous belt until 19,000 cal yr BP, coeval with lowering of temperature and rainfall in the region (Taylor, 1990). Lake Victoria (1134 m) sediments record presence of gastropods in the core sediments suggesting a low stand from 13,500 cal yr BP onwards indicating a drier period with oxidation of sediments under extremely low lake levels (Stager et al., 1997). Pollen record from Sacred Lake on Mount Kenya records this period as drier around 13,500 cal yr BP (Coetzee, 1967). The transition from the glacial period to the early Holocene is a period of rapid environmental change reflecting the climate became relatively warm and wet. Montane forests shifted to higher altitudes replacing grasslands that were much more extensive during the Last Glacial Maximum (LGM) (Wooller et al., 2003; Rucina et al., 2009). This replacement of ecosystems is recorded by pollen from Kashiru Swamp (2104 m) sediments in Burundi between 11,500 and 5700 cal yr BP (Roche and Bikwemu, 1989). This transition was punctuated in many lake records from East Africa by low water stands pointing to relatively arid conditions at the Pleistocene-Holocene transition (Williamson et al., 1993). Carbon and nitrogen isotopic composition and bulk organic matter in sediment cores from Lake Bosumtwi (150 m) in Ghana, also reveal a dry phase (Talbot and Johannessen, 1992).

Pollen studies from sites throughout East Africa during the late Holocene show distinct vegetation changes that record a combination of climate change and events of human impact. During the Holocene climatic conditions became moister with forest in Central Africa continuing to expand, reaching the equivalent of its present range and density about 10,700 cal yr BP (Hamilton, 1988). In the mid Holocene, from around 5500 cal yr BP onwards, tropical African sites show a lowering of lake levels (Stager et al., 1997) and an abrupt decline in arboreal pollen percentages reflecting drier conditions all pointing to a relatively abrupt shift toward arid conditions ((Jolly et al., 1994; Ricketts and Johnson, 1996; Wooller et al., 2000). These changes culminated towards a 4000 cal yr BP drought period that was recorded across the African tropics (Marchant and Hooghiemstra, 2004). Changing lake levels during the late Holocene (Rickets and Johnson, 1996; Alin et al., 2003; Russell and Johnson, 2005) record the magnitude of a variable climate. For example, a high stand was recorded at Lake Edward (920 m) (Russel et al., 2004) and Lake Tanganyika at (773 m) from 1750 to 1450 cal yr BP (Alin and Cohen, 2003). Arid to wet climate oscillations continued through the late Holocene and intensified after 1500 cal yr BP when forests were replaced by grasslands such as recorded in Lake Tanganyika catchment (Msaky et al., 2005). In the catchment area of Lake Masoko *Ricinus communis* pollen became more abundant from 1650 to 1550 cal yr BP (Vincens et al., 2003). Lake levels of Lake Naivasha (1884 m) and Lake Tanganyika lowered by some 40 m during the last 1000 years (Alin and Cohen, 2003; Verschuren et al., 2000). Diatom and midge evidence from Lake Naivasha indicate that the period from 1000 to 740 cal yr BP was notably drier than at present (Verschuren et al., 2000) while the period from 740 to 160 cal yr BP was relatively wet. Other lakes, such as Lake Victoria, Lake Chibwera (970 m) , Lake Kanyamukali (1150 m) and Lake Baringo (1050 m) suggest the period from 460 to 160 cal yr BP was dry (Bessems et al., 2008).

The late Holocene is increasingly characterized by signals of human activity. Initially it is likely that these early inhabitants exerted low-level impacts upon the landscape. Microscopic charcoal particles and pollen from food crops in sediments show human ecosystem interactions were increasingly prevalent throughout the late Holocene (Kiage and Liu, 2009; Rucina et al., 2009; 2010; Taylor et al., 2005; Lamb, 2003).

Namelok pollen record documents presence of *Cannabis sativa,* cereal and R*icinus communis* since 2650 cal yr BP. This reflects an early settlement in the Amboseli Basin (Rucina et al., 2010). Regionally starting at 2200 cal yr BP there is pollen evidence for forest clearance at Muchoya (2260 m) and Ahakagyezi swamps (1830 m) in the Rukiga Highlands (Taylor, 1990). This conclusion is based on the replacement of forested areas by open vegetation and degraded scrubland. For example, within the Lake Tanganyika catchment there is evidence of widespread deforestation and increased erosion from the late 18th century onwards (Alin et al., 2003). At Lake Naivasha, maize (Zea mays) pollen appears in the record after 300 cal yr BP (Lamb et al., 2003).

Human-ecosystem climate interactions are inherently dynamic and complex (De Fries et al., 2004), particularly given the diversity of the Eastern African landscapes, ecosystems and cultures that interact. People and ecosystems have responded and adapted to past change in a variety of ways. During droughts a diverse range of adaptation strategies of people can reduce vulnerability to climate change by making communities better able to adjust to climate change and variability, moderating potential damages, and helping them cope with adverse consequences (Robertshaw et al., 2004). For example pastoral communities maintain wealth and their environmental ‘buffer’ in herds of cattle; during extreme periods of drought these ‘stores’ can be massively impacted on. Agricultural communities will turn to more drought-resistant crops such as millet and sorghum, crops that were grown much more extensively prior to the relatively recent import of maize (Håkansson, 2008) and banana (Neumann and Hilderbrand, 2009) which form the stable crops of today for large parts of East Africa. Due to these relatively new recent focus of agriculture, compounded with social, public and economic shifts, we can reconstruct how past communities have responded to droughts (Eriksen and Watson, 2009).

2. Aim of the study

The study aims to advance knowledge of long term ecosystem dynamics from equatorial East Africa and to provide contrasting perspective that cover low and high altitude sites in Kenya. The studied lowlands and highlands of Kenya are vulnerable to changes related to both climate and land use. These areas have undergone rapid population increases and development, yet they include some of the most fragile ecosystems being situated in the wettest and driest parts of Kenya. Combined, these three catchments (Mt Kenya, Namelok Swamp and Lake Challa) allow for a comparison of high altitude forest dynamics with savanna ecosystem and offer a contrasting response to environmental and ecosystem human interactions.

The aim of this study was also to reconstruct late Quaternary changes of ecosystems and environments of lowland and high altitude sites using a multi-proxy approach. Reconstructions of late Quaternary palaeoenvironments from Mount Kenya, Namelok Swamp and Lake Challa are presented in this thesis and form the basis of regional analysis. The research objectives to be specified as follows:

1. Palaeoecological evidence is used to determine how the vegetation composition of low and high altitudes has changed throughout the late Quaternary
2. Past anthropogenic activity have been implicated in the origin and expansion of savanna grasslands in East Africa and degradation of Afromontane forests. Palaeoecological analysis is used to determine whether grasslands are a natural andlong-standing component of savanna and Afromontane forests
3. Archaeological evidence suggests that low and high altitudes have been subject to extensive forest loss and fragmentation as a consequence of human activity in the late Holocene. Multi-proxy palaeoecological evidence is applied to explore the nature and timing of long-term human impacts of low and high altitude ecosystems.

3. Study areas

Like other tropical mountains of East Africa, Mount Kenya is characterized by high environmental and climatic sensitivity and offers particularly good sedimentary archives for palaeoecological reconstructions and to identify factors driving ecosystem change. One such site is Rumuiku Swamp at 2154 m is located in the southeast montane rainforest of Mount Kenya. Similarly, in the south of Mount Kenya Namelok Swamp (1146 m) in the Amboseli Basin and Lake Challa (880 m) southeast of Kilimanjaro are also sensitive to record ecosystem change.

Rumuiku Swamp is located on the southeast of Mount Kenya in the montane rain forest ecosystem at 00°11′8.93″S 037°55′9.65″E (Figure 1). The swamp is bordered to the southwest by a small cliff and a small river emerges from the swamp flowing to the east (Plate 1).
The site is highly disturbed with original montane forest replaced by *Croton* *macrostachyus,Macaranga kilimandscharica* and *Neoboutonia macrostachys*. The original montane rain forest included taxa such as *Ocotea usambarensis, Podocarpus spp., Polyscias spp., Schefflera spp*. and *Tabarnaemontana holstii* as common elements. *Syzygium cordatum* and *Morella* (previously named (*Myrica salicifolia)* are recorded as small trees close to the swamp margins. Vegetation on the swamp surface is dominated

Plate 1. Rumuiku Swamp and surrounding montane forest in the catchment.

by tussock species of the sedges. Sedges are the main peat forming plants. The large tussock-forming grass *Pennisteum mildbraedii* is locally abundant on the margins as are local patches of the moss *Sphagnum*. Exotic tree species (*Cupressus lusitanica, Pinus patula* and *Pinus radiate*) are cultivated towards the north and *Eucalyptus spp* to the south of the catchment under management of the Forest Department of Kenya. The swamp is situated close to communities with half of the catchment used for agriculture: tea and a wide range of crops are cultivated. Cattle and goats are kept and they graze in open areas of forest and during extreme droughts, they are driven into the dense forest.

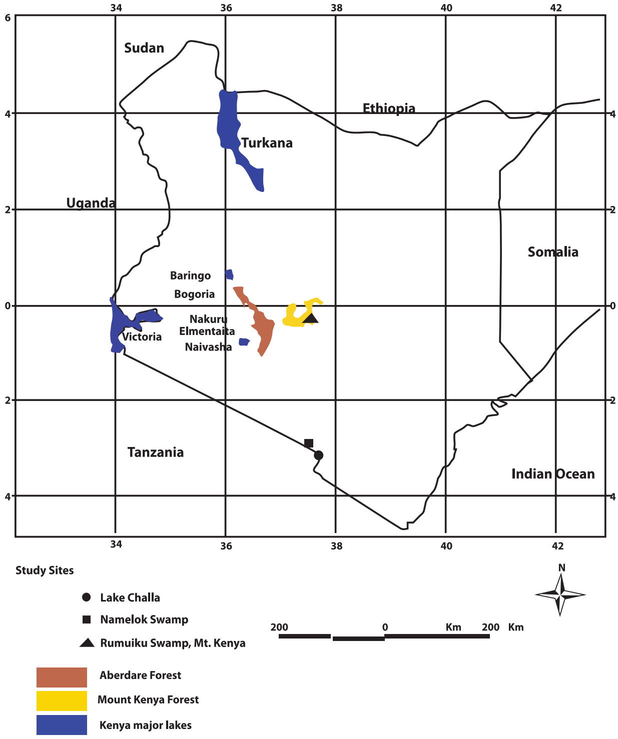

Fig. 1. Map of Kenya showing study sites, major lakes and Aberdare Forest.

Namelok Swamp (2°54′52.50″S, 37°30′23.28″ E; elevation 1146 m) lies in the Amboseli Basin, in the Kajiado District of southern Kenya (Figure 1). The area is dominated by Poaceae, and a tree and shrub layer of variable densities. Today the area is characterized by strong human impact that has converted much of the savanna into agricultural land being particularly intensive where water is available. The vegetation composition in the Amboseli Basin is determined by climate, soil type (including nutrient availability), and plant symbiotic interactions, disturbance by fire and interaction with herbivores (Gillson, 2004; Skarpe, 1992). Much of the land around Namelok Swamp has been converted to agriculture because water is available throughout the year for irrigation. Livestock is grazed on the swamp during the dry season (Plates 2A and 2B). Grasslands are dominated by *Chloris rocksburghiana, Eragrostis tennuifolia, Sporobolus homblei, S.robusta* and *S. spicatus.*

Plate 2A. Namelok Swamp dominated by Cyperus immensus, Typha sp., Pennisteum mildbraedii and Polygonum spp. On the background the trees are Acacia xanthophloea.

Plate 2B. Namelok Swamp in dry season and forms a refuge for livestock.

In the flooded areas, *Psilolemma jaegeri* and common species of *Sporobolus* occur. The woodlands and bushlands are composed of *Acacia drepanolobium, A. mellifera, A. nubica, A. tortilis, Aristida keniensis, Azima tetracantha, Commiphora spp., Eragrostis aspera, Salvadora persica* and *Solanum* species. The adjacent riverine areas are mostly dominated by *Acacia xanthophloea, Ficus thonningii, Salvadora persica* and two species of *Syzygium (S. cordatum* and *S. guineense)*. *Syzygium cordatum* is recorded as small trees close to the swamp margins. Vegetation on the swamp surface is dominated by *Cyperus immensus* (Papyrus) with tussock

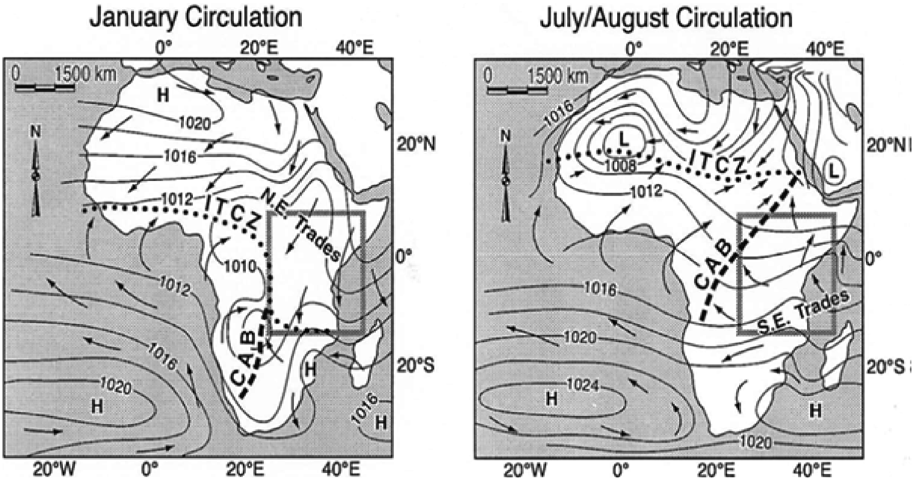

Fig. 2. Sources of African rainfall showing the annual passage of the ITCZ and direction of the main wind systems. The dotted lines indicate postion of the ITCZ, dashed lines the Congo Air Boundary (CAB). Source: Kiage and Liu 2006 and modified from Nicholson (2000)

species of the sedge *Carex, principally C. monostachya*. Locally the large tussock-forming grass *Pennisteum mildbraedii* is abundant on the swamp margins.

Lake Challa has a surface area of 4.2 km2 and water depth reach 97 m (Plate 3). The lake is situated on the lower east slopes of Mount Kilimanjaro (3° 19′ S, 37° 42′ E) close to the Kenyan-Tanzanian border (Figure 1). The lake is located within the savanna ecosystem and surrounding vegetation is dominatewd by trees such as *Acacia, Combretum, Lannea* and *Terminalia*. Due to increasing anthropogenic influence including fires, grazing and collecting of firewood, the wooded savanna is increasingly replaced by savanna grassland and agricultural fields of maize, sunflower, millet and beans.

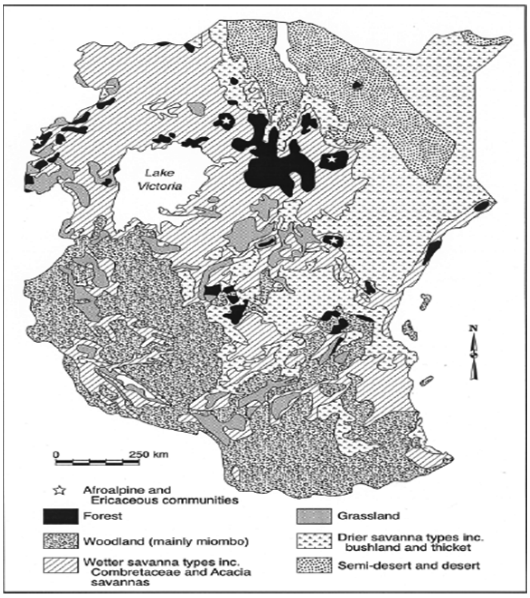

Fig. 3. Major vegetation types and distribution in East Africa modified from Lind and Morrison (1974). Source: Kiage and Liu (2006).

4. Ecosystems of East Africa

The vegetation distribution in East Africa (Figure 3) is largely controlled by rainfall and temperature (Figure 2) distribution compounded by a strong influence of topography (Lind and Morrison, 1974; White, 1983) Six major vegetation types have been identified that include Afroalpine and Ericaceous community forests, woodlands (mainly Miombo),

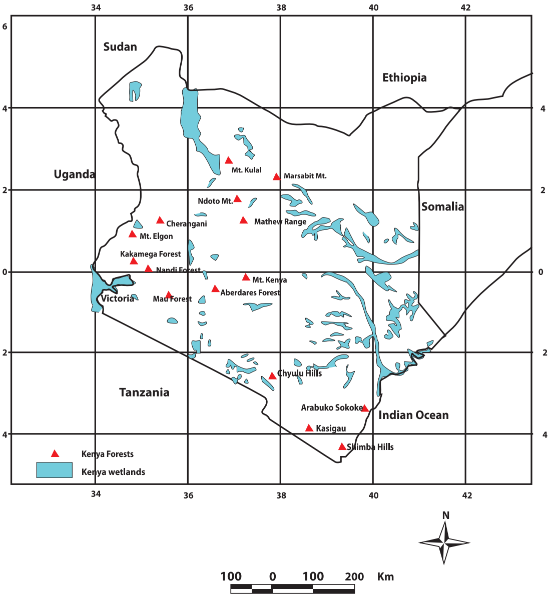

Fig. 4. The main forests and wetland areas of Kenya.

Combretaceae and *Acacia* savannas, montane and lowland coastal forests, dry savanna types including grasslands and thickets, and semi desert and desert. Forest distribution in Kenya (Figure 4) is broadly controlled by rainfall, temperature and topography. Forest cover is abundant along the coast, in the central highlands and in the highlands bordering with Uganda where rainfall is high. Other parts of the country are semi-arid and support wood lands, bushlands and open grasslands commonly referred as savanna ecosystem with scattered trees such as *Acacia, Balanites, Combretum, Commiphora* and *Terminalia* species, and herbaceous layer primarily consisting of C_4 grasses (Plate 4). Most highland forests have been extensively cleared and the remnants are mainly located on the high mountains and ranges such as Mt. Elgon, Mt. Aberdares, Mt. Cherangani and Mt. Mau (Figure 4). Forests on the higher slopes between 2200 and 3500 m are dominated by moist forest trees which include *Cassipourea, Ocotea, Polyscias*, and *Podocarpus* with *Juniperus-Olea* abundant on the drier slopes. Most lowland forests have also been extensively cleared and the remnants are contained within protected areas such as Kabarnet, Kakamega, Nandi and the Arabuko Sokoke forest (Figure 4). In the southern part of Kenya forest remnants are found on the Taita

Plate 3. Anchored platform and boat which were used during the coring In Lake Challa. The lake is shared by the two neighbouring countries of Tanzania and Kenya. On the background is Mount Kilimanjaro.

Plate 4. Savanna with Acacia trees and open spaces dominated by C_4 grasses.

Hills, Kasigau Hills, Shimba Hills and Chyulu Hills (Figure 4). This diversity of these forests biogeographically affinities with the diverse Eastern Arc Mountains of Tanzania (Sayer et al., 1992). Riverine forests concentrate along the Tana River and tributaries, Ewaso Ngiro River, Kerio River, Turkwell River and Galana River (Ahmed & Mloy, 1998). Coastal mosaic forests especially mangroves are common around Lamu Town in coastal Kenya (Plate 5) and along the Tana River Delta.

Plate 5. Mangrove forests along the Kenyan coast.

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CHAPTER 2

Stephen Rucina, Veronica M. Muiruri, Rahab N. Kinyanjui,
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Late Quaternary vegetation and fire dynamics on Mount Kenya

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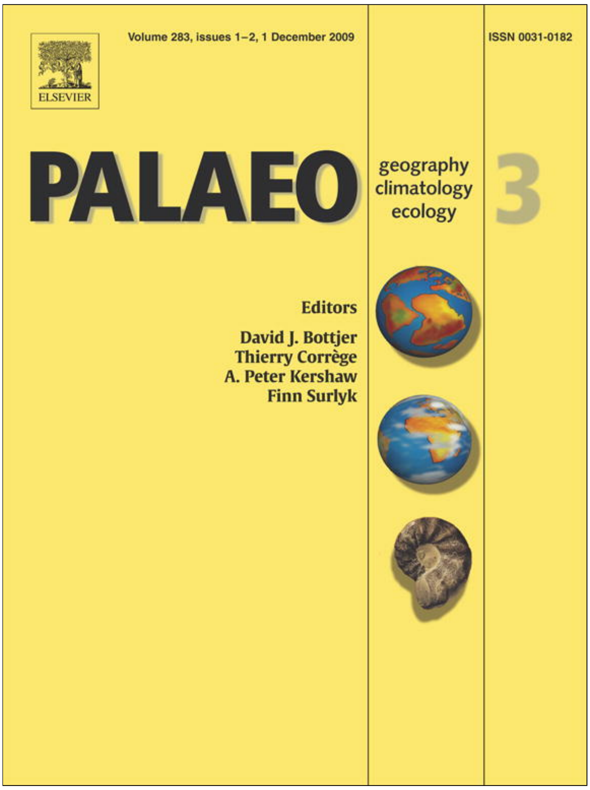
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Late Quaternary vegetation and fire dynamics on Mount Kenya

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ABSTRACT

Pollen and charcoal data generated from a 1469 cm core, radiocarbon dated to 26,430 ^{14}C yr BP, recovered from Rumuiku Swamp on the southeast of Mount Kenya, are used to document changes in the distribution and composition of montane vegetation and fire regimes over the Late Quaternary. Throughout the transition from the Last Glacial Maximum (LGM), high resolution (sub-centennial scale) analysis documents a highly dynamic ecosystem and fire regime. The pollen record shows that under a cool, but rather moist LGM climate, Ericaceae and *Stoebe* species shifted down-slope more than 1000 m relative to the present day. Rather than simple altitudinal lowering of current vegetation zonation, these taxa formed a vegetation assemblage that mixed high altitude components with relatively lowland taxa; in particular *Juniperus* that is presently found at altitudes lower than the study site, but on the drier side of Mount Kenya. There is noticeable addition and co-dominance of *Hagenia* to the ecosystem from 20,500 ^{14}C yr BP, until around 14,000 ^{14}C yr BP when a mix of Ericaceous Belt and upper montane forest taxa, such as *Artemisia*, *Polycias*, *Schefflera* and *Stoebe*, dominated the initial development of montane forest. Reduced levels of *Hagenia*, *Juniperus*, *Olea* and *Podocarpus* are recorded about the time of the Younger Dryas with highly variable presence of more mesic taxa such as *Polyscias* and *Schefflera*. This development of montane forest over the Late Pleistocene to Holocene transition reflects a significant reorganization of the ecosystem composition that was heavily influenced by a variable fire regime. Shifts in vegetation composition reflect the onset of a warmer moist climate from the beginning of Holocene, as mixed montane forest became more established. The latter part of the Holocene registers human impact and forest clearance with increased anthropogenic impact marked by a transition to open vegetation and increased fire frequency.

1. Introduction

The Intergovernment Panel on Climate Change (IPPC, 2007) recognizes Africa as one of the least studied continents in terms of ecosystem dynamics and climate variability (Hely et al., 2006). Despite the importance of knowing how ecosystems respond to climate change, only a handful of records extend back to the Last Glacial Maximum (LGM), the period dated to 21,000 calibrated radiocarbon years before present (cal yr BP). Those records that do exist are either characterised by sedimentary hiatus (Marchant et al., 1997), or only have a few samples dating to this period (Bonnefille and Riolett, 1988). Shifting snowlines and glacier extent clearly indicate the sensitive nature of Eastern Africa Mountains to register past environmental shifts (Karlen et al., 1999; Thompson et al., 2002). Through the LGM, Eastern Africa climates were colder and drier than at the present (Coetzee, 1964; 1967; Perrott and Street-Perrott, 1982; Hamilton and Perrott, 1979; Olago, 2001) and atmospheric carbon dioxide concentrations lower than today (Jolly and Haxeltine, 1997). This different environmental regime had a strong impact on ecosystem composition and distribution with taxa presently found in the Ericaceous Belt shifting to lower altitudes (Hedberg, 1954; Coetzee, 1967; Hamilton and Perrott, 1981; Bonnefille et al., 1990; Taylor, 1990). Such altitudinal shifts have been used to develop palaeoclimate reconstructions based on a modern analogue approach (Farrera et al., 1999; Peyron et al., 2001), however, these climate reconstructions must be taken in the context of relatively sparse spatial coverage and dating problems about the LGM (Marchant and Hooghiemstra, 2001). Despite these excellent records documenting ecosystem response to past environmental changes there remains considerable uncertainty regarding the spatial and temporal response of Afromontane ecosystems to climate and environment shifts about the LGM.

The Late Holocene was characterised by significant population migration into Eastern Africa, primarily Bantu immigrants, bringing new technologies and land-use strategies (Holl, 2000). A common signal from this time is pronounced vegetation clearance, particularly from around 3000 ^{14}C yr BP with farming activities intensifying across Central and Eastern Africa (Eggert, 1993). These vegetation clearances were widespread and included montane forest sites such as the Rukiga Highlands in Uganda around 2200 ^{14}C yr BP (Marchant and Taylor, 2000). Mount Kenya experienced similar anthropogenic

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activities with major impact on vegetation associated with the use of fire to increased agricultural activities (Boyes, 1911; Wimbush, 1937; Muiruri, 2008).

We present a 26,000 cal yr BP palaeoenvironmental record from Rumuiku Swamp catchment situated on the southeast of Mount Kenya (Fig. 1). This is a new pollen record from a pivotal area for understanding long term ecosystem dynamics in Eastern Africa, and indeed the wider tropics. The record will be used to unravel the long-term ecology of the area and determine the climate, anthropogenic and ecological influences on the ecosystem during the Late Quaternary.

1.1. Environmental setting of the study area

The environment of the study site will be described in terms of the climate and vegetation of the Mount Kenya region with specific links to the Rumuiku Swamp catchment provided. Mount Kenya is situated in the centre of Kenya (Fig. 1); at 5199 m, it is the second highest mountain in Africa. Much of the mountain is contained within Mount Kenya National Park of which Mount Kenya forest covers 70,520 ha. Kenya receives most of the rainfall during the months of March to May (long rains) and September to October (short rains); this bimodal rainfall is due to the Intertropical Convergence Zone (ITCZ) that migrates south and north about the equator. There is high inter-annual and seasonal variability in rainfall resulting from interaction between atmosphere, sea surface temperature, trade winds and diverse topography (Mutai and Ward, 2000; Marchant et al., 2006). The strong impact of topography is clearly reflected by the regional microclimate: the southern flank of Mount Kenya receives about >2500 mm yr^{-1} rainfall with the northern flank of the mountain being much drier receiving <1500 mm yr^{-1} (Thompson, 1966). Mount Kenya does not experience marked seasonal variations in temperature due to its location on the equator but does exhibit strong

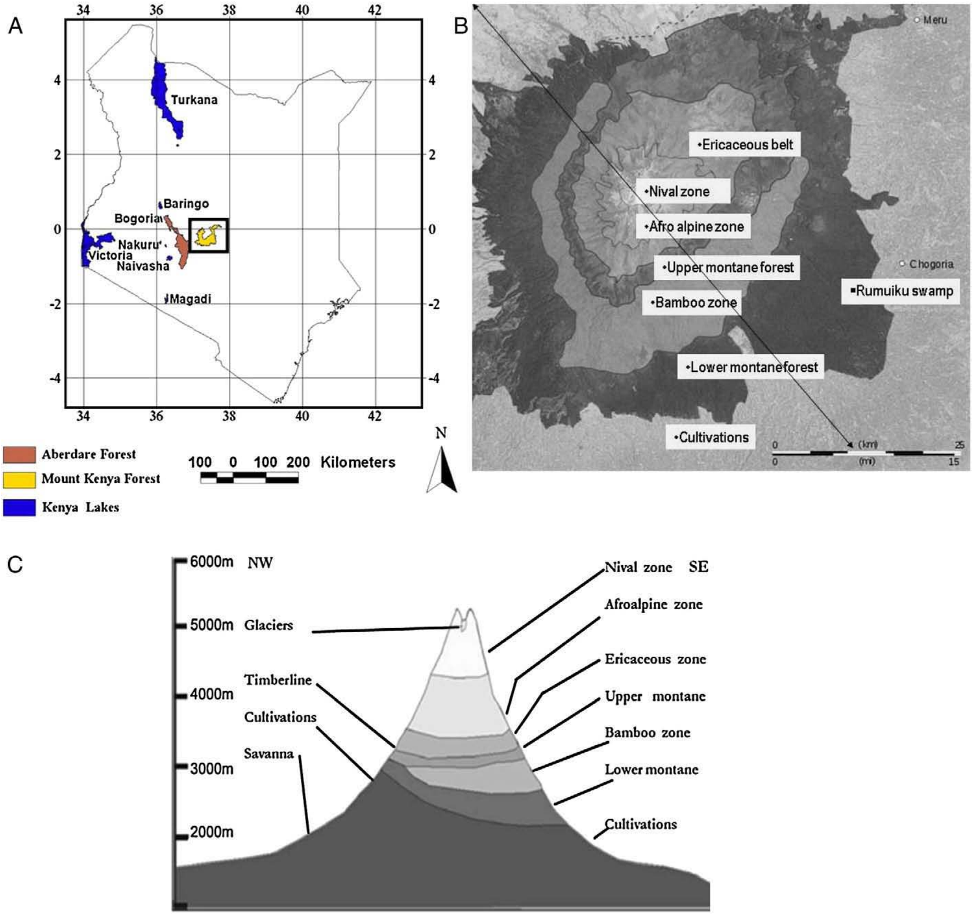

Fig. 1. Zonation and characteristics of vegetation of Mount Kenya showing the location of Rumuiku Swamp. The vegetation zones around Mount Kenya interpreted from Landsat TM satellite scenes from 1976 to 1990s are shown (after Niemela and Pellikka, 2004).

altitudinal changes. Temperature change on Mount Kenya can be summarized by the lapse rate: applying a lapse rate of 6.6 °C $1000\ \mathrm{m}^{-1}$ (Van Der Hammen and Gonzalez, 1965) the approximately 4000 m of altitudinal change from the foothills to the summit equates to a temperature change of more than 24 °C that is reflected by the vegetation composition (Fig. 1). The annual-mean maximum temperatures are 26 °C at the decreasing to 2 °C at the nival zone. Diurnal variations in temperature are pronounced with daily temperatures commonly fluctuating by around 20 °C (Survey of Kenya, 1970) and 14 °C at the tree line (Coe, 1967).

1.2. Vegetation distribution on Mount Kenya

Changes in plant distribution on Mount Kenya are dramatic and are predominately driven by the changes in moisture and temperature outlined above, the later being the most important of the two climatic variables (Beentje, 1994). Inter-gradation of the different vegetation belts, as on most Eastern Africa Mountains, can make the delimitation of the upper altitudinal limit of the vegetation belts very difficult, this is compounded by the variation imposed by the topographic and human influence (Hamilton et al, 1986). Montane forest is the most common form of vegetation cover; *Juniperus procera* and *Podocarpus milanjianus* are the dominant tree taxa on the drier parts of the lower slopes (below 2500 m) where rainfall is between 875 and $1400\ \mathrm{mm\ yr}^{-1}$. *Hagenia abyssinica* and *Hypericum revolutum* predominate in areas of maximum rainfall (up to $2400\ \mathrm{mm\ yr}^{-1}$) between 2500 and 3500 m. Higher altitudes between 2500 and 3000 m characterised by rainfall over $2000\ \mathrm{mm\ yr}^{-1}$ are dominated by *Arundinaria alpina* (bamboo) on south-eastern slopes, and a mosaic of bamboo and *Podocarpus milanjianus* at intermediate elevations (2000 to 2800 m). Towards the west and north of the mountain, bamboo becomes less dominant; on the northern slopes there is no bamboo and the montane forest is poorly developed with open gaps. Frequently occurring species in montane forest include *Neouboutonia macrocalyx* and *Syzygium cordatum* that are common on the lower slopes of valleys, while on land at mid-altitude *Chrysophyllum albidum* and *C. gorungosanum* are abundant in association with *Cassipouria ruwensoriasis*, *Drypetes albidi* and *Strombosia schefflera*; at higher altitudes taxa such as *Faurea saligna*, *Hagenia abyssinica*, and *Nuxia congesta* become common. As one moves down into drier montane forest species, composition changes and is characterised by *Celtis africana*, *J. procera*, *Olea europaea* ssp *africana* and *Teclea noblis*. Changes in the composition of the montane forest around Mount Kenya appear to be predominately driven by moisture. Tree cover declines above 3000 m with *Podocarpus* being replaced by *Hypericum* spp. The Afroalpine and Ericaceous Belts are more uniform in distribution on both sides of the mountain (Fig. 1). Rapid changes in temperature are the main characteristic of the climate in this belt causing physiological drought (Coetzee, 1967). Subsequently the vegetation is characterised by microphyllus, thorny habit and possess other xeromorphic features. Montane grassland is often extensive at this altitude, especially in the drier areas. The following genera are well represented *Alchemilla*, *Cliffortia*, *Deschampsia*, *Helichrysum*, *Hypericum*, *Phillipia* and *Protea*. The lower alpine zone (up to 3800 m) is characterised by high rainfall and low species richness with *Carex* spp. and *Festuca pilgeri* dominant. *Alchemilla cyclophylla*, *A. johnstonii* and *Geranium vegans* are also found in this zone. The upper alpine zone (3800 to 4500 m) is topographically more diverse, and contains a more varied flora, including the giant rosette plants *Carduus* spp., *Lobelia keniensis*, *L. telekii* and *Senecio keniodendron*. Continuous vegetation cover stops at about 4500 m although isolated vascular plants have been found over 5000 m (Hedberg, 1951).

Although the Mount Kenya National Park management plan implemented by Kenya Wildlife Service (KWS, 1993) aims to: 1) preserve the afro-alpine ecosystem; 2) preserve the traditions and values of a high mountain wilderness for enjoyment by visitors and 3) preserve Mount Kenya's contribution of Kenya's environmental quality, Mount Kenya has been subjected to logging for many years. In 1979 the estimate of the natural forest cover in Kenya was about 80,000 km² (Myers, 1979). Only a quarter of this forest extent remains today even including plantations of exotic species. Human interference within the National Park boundaries is low but more common within gazetted forest areas at lower altitudes (Bussmann, 1996). Fires (from humans and lightning) are common, particularly in the dry lower altitude forest. With demand for more timber forest clearance continues; key commercial species such as *Juniperus procera* and *Ocotea usambarensis* being the main targets of this activity. Much of the remaining montane forest is secondary and dominated by *Macaranga kilimandscharica* and *Neoboutonia macrocalyx*. Threats to the remaining forest are similar to other areas of indigenous forest in Kenya: illegal logging, firewood collection, poaching, charcoal burning, destructive honey collecting, settlement and encroachment (KWS, 1993; Bussmann, 1994; 1996). Other illegal activities such as growing of *Cannabis sativa* also threaten the forest as does grazing of livestock by removing herbaceous cover and preventing regeneration (Bussmann, 1994) (Plate Ic).

1.3. Study site

Rumuiku Swamp (Plate Ia) is located on the southeast of Mount Kenya in the montane rain forest at 2154 m (Fig. 1). The almost circular, approximately 150 m diameter, swamp is bordered to the southwest by a small cliff (Plate Ib). A small river emerges from the swamp flowing to the east. The site is surrounded by disturbed montane rain forest with secondary tree species (*Croton macrostachyus*, *Macaranga kilimandscharica* and *Neoboutonia macrostachys*) dominating. More primary montane rain forest taxa such as *Ocotea usambarensis*, *Podocarpus* spp., *Polyscias* spp., *Schefflera* spp. and *Tabarnaemontana holstii* are also common. *Syzygium cordatum* and *Myrica salicifolia* are recorded as small trees close to the swamp margins. Vegetation on the swamp surface is dominated by tussock species of the sedge *Carex*, principally *C. monostachya*, which is believed to be the main peat-former. The large tussock-forming grass *Pennisteum mildbraedii* is locally abundant on the margins as are local patches of the moss *Sphagnum*. Exotic tree species (*Cupressus lusitanica*, *Pinus patula* and *Pinus radiate*) are cultivated towards the north and *Eucalyptus* spp. to the south of the catchment under management of the Forest Department of Kenya. The swamp is situated close to communities with half of the catchment used for agriculture: people grow tea, a wide range of crops and keep cattle and goats that graze in open areas of forest (Plate Ic).

2. Methods

2.1. Core collection, dating and pollen analysis

A 1469 cm long core was recovered from Rumuiku Swamp using a 5 cm diameter Russian corer in 50 cm overlapping sections from two adjacent bore holes 10 cm apart. The recovered core was described in the field and transferred into 50 cm section PVC pipes and wrapped in aluminium foil and polythene for transport to Palynology and Palaeobotany Laboratory of the National Museums of Kenya (NMK) Nairobi and to the University of York for cold storage. Nine bulk sediment samples were selected for AMS radiocarbon dating. Each sample was chosen to date significant changes in the stratigraphy, or fluctuations in the pollen or charcoal data (Table 1). Eight samples were sent to NERC laboratories in the UK where they were digested in 2 M HCL (80 °C for 2 h), washed using deionized water then digested in 1M KOH (80 °C for 2 h). The digestion was repeated until no further humic acids were extracted. The residue was rinsed free of alkali, digested in 1 M HCl (80 °C for 2 h) then rinsed free of acid, dried and homogenized. The total carbon in the treated sample was recovered as CO_2 by heating in a sealed quartz tube and converted to graphite by Fe/Zn reduction. One sample was sent to the University of Waikato

Radiocarbon dating laboratory New Zealand (WK notation) where they were washed in hot 10% HCL, rinsed and treated with hot 0.5% NaOH. The NaOH insoluble fraction was treated with hot 10% HCL, filtered and dried. Results were calibrated to calendar years using the CALIB 5.1 radiocarbon calibration program (Stuiver et al., 2005). An age model was developed using a linear interpolation between adjacent calibrated dates and approximate ages of pollen zones were interpolated accordingly (Fig. 2). δ^{13}C values were calculated as part of the radiocarbon analysis and plotted against depth and the age–depth profile (Fig. 2).

Ninety six samples were sub-sampled for pollen analysis and shipped to the Palynology and Palaeobotany Laboratory, National Museums of Kenya (NMK) Nairobi for analysis. The standard palynological procedure for concentrating pollen grains (Faegri and Iversen, 1975) was followed.

Plate I.

(A). Showing the extent and local vegetation of the Rumuiku swamp catchment,

(B). The cliff that delimits the northwestern extent of Rumuiku swamp is clearly seen as is the relatively open nature of the surrounding montane forest, and

(C). Heavily impacted montane forest adjacent to the Rumuiku swamp catchment where almost pure stands of *Podocarpus* remain following forest clearance and subsequent grazing impact.

B

Plate I (*continued*).

One slide was mounted per processed sample under a 22×40 mm cover slip. Pollen counts were performed using a Leitz microscope at ×400 magnification; critical identifications were made using ×1000 magnification under oil immersion: 127 terrestrial and 8 aquatic taxa were identified. The percentages of total fossil pollen were calculated from the pollen sum with aquatic pollen and spores excluded from the pollen sum, but unknown and undifferentiated pollen grains included. CONISS was applied using the numerical clustering package within the TILIA computer programme to identify zones of similar floristic composition. Results are presented as a pollen diagram using the software TILIA and TILIAGRAPH (Grimm, 1991). The pollen taxa are grouped together in Afromontane, Ericaceous Belt, Woodland, Herbaceous, Aquatics and Spore taxa. Correspondence analysis identified five distinct pollen zones labelled Rum I to Rum V (Fig. 3).

2.2. Charcoal analysis

Two different procedures were used to determine the abundance of charcoal in sediment sub-samples extracted every 20 cm. Firstly; a size class method was applied to the slides prepared for pollen analysis where individual charcoal fragments on the pollen slides were counted and measured at 400× magnification. The process involved in preparing samples for pollen analysis could have an influence on the size distribution, particularly by fragmenting larger pieces of charcoal. Although the impact of this was not account for, the influence would be standard across the core samples. Indeed, as we are primarily interested in changes relative to adjacent samples this will not hinder our interpretation. Smaller fragments may be mistaken for pyrite, biotite or macrasite (Rhodes, 1998) and the techniques involved in the pollen to slide process, particularly acetolysis can considerably darken or blacken unburned plant pieces (Rhodes, 1998; Blackford, 2000; Carcaillet et al., 2001). Given the assumption of a homogenous distribution of charcoal particles on a pollen slide (Clark et al., 1989), counts were made on successive traverses across the pollen slide until a minimum of 500 fields of view were completed. Charcoal selection was limited to fragments that are black, opaque and of angular form (Waddington, 1969; Patterson et al. 1987; Pitkanen and Huttunen, 1999; Clark, 1982; 1988a; 1988b; Clark et al. 1989), but fragments less than 3 μm were excluded, as they cannot be reliably identified (Blackford, 2000). The charcoal counts for each size class are presented as the total number of fragments per 500 fields of view. The count-based charcoal data is divided into four classes (3 to 25 μm, 26 to 75 μm, 75 to 150 μm and >150 μm) (Fig. 4).

Chemical digestion assay of charcoal amount in the sediment provides an alternative to the counting method; the Winkler (1985) technique was used to quantify the elemental carbon content giving an absolute charcoal content (Fig. 5). The technique used is based on nitric digestion of the organic component and loss-on-ignition (LOI) to separate and quantify organic and inorganic carbon. Sediment samples (~0.5 ml) are dried and weighed, digested in concentrated

C

Plate I (*continued*).

nitric acid and weighed, and ignited at 450–500 °C for 3 h before a final weight is calculated. Replicates were made every 200 cm. The percentage of charcoal is calculated as the difference of the dry weight before and after ignition, using the following equation:

$$\frac{(NW-IW)\times 100}{DW} = \%charcoal$$

NW = the dry weight after nitric digestion
IW = the dry weight after ignition
DW = the dry weight of the sample

The charcoal data from both methodologies is plotted alongside the core stratigraphy and radiocarbon dates using TILIA and TILIAGRAPH (Grimm, 1991) (Fig. 4). The data is expressed as a percentage of charcoal dry weight, the size class data are standardized to number per 500 fields of view for each size class. Similarly to the pollen data, CONISS is applied to cluster the charcoal data into zones of similar spectra: three zones are identified and labelled Char I, Char II and Char III (Fig. 4).

3. Results

3.1. Stratigraphy

Based on direct observations and interpretation in the field, the stratigraphy from the 1469 cm core from Rumuiku Swamp can be divided into seven different sections (Figs. 3 and 4). The sediments from 1469 cm to 1050 cm comprise fine silt and decomposed organic

Table 1
Radiocarbon dates showing the publication codes with the core depth. Sample ages, calibrated dates (^{14}C yr BP) and δ^{13}C results are also included.

Publication code	Sample depth (cm)	Sample age BP	Calibrated dates (^{14}C yr BP)	δ^{13}C	Criteria for dating
SUERC-22553	100	2252±30	2260±65	−10.7	End of charcoal peak
SUERC-17195	245	7763±40	8535±49	−21.8	Range finders and decline in forest taxa
SUERC-22554	400	13,325±75	16,256±423	−23.1	Rum IV to Rum V zone boundary
SUERC-17196	545	13,953±59	17,205±209	−24.5	Peak in Poaceae
SUERC-17197	745	15,759±71	18,995±227	−29.8	Range finder dates, peak in charcoal and lake to swamp transition
SUERC-17198	945	17,296±85	20,761±292	−29.6	Rum II to Rum III zone boundary
SUERC-17199	1145	19,578±111	23,370±349	−31.5	Rum I to Rum II zone boundary
WK-18792	1400	22,016±180	26,430±405	−29.7	Stratigraphic change
SUERC-17200	1465	19,006±112	22,871±302	−30.0	Basal date

matter that change to silty grey lake mud from 1050 to 950 cm. The bottom 20 cm of the record comprises a grey basal clay that contains little organic material. From 950 to 710 cm the sediments comprise brown/grey lake mud. From 710 to 600 cm the sediments are brown grey in colour and change to a more compacted mud containing herbaceous material and plant roots. From 600 to 250 cm the sediments comprise brown peat with large amount of herbaceous material and fibrous roots. From 250 to 50 cm they comprise very dark compacted peat with herbaceous material and roots. From 50 cm to the top of the core, the sediments are a poorly humified peat composed of fibrous roots and vegetation remains.

3.2. Age depth relationship and δ^{13}C values

The age depth plot from the Rumuiku sediments (Fig. 2) shows a largely coherent age–depth profile with the chronology particularly well constrained through the LGM with seven radiocarbon dates being placed between 16,000 and 26,000 years. The sample at 1465 cm (dated 22,871 ± 302 ^{14}C yr BP) is a little younger than the sample above at 1400 cm dated to 26,430 ± 405 ^{14}C yr BP. Given the coherence of the overlying age–depth relationship, it is thought the basal date is erroneously young and could result from possible contamination of the sample with young material through vertical migration of the sediment or humic acids. Such an impact would have been exacerbated by the low level of radiocarbon in the sediment sample and the clay-rich nature of the sediment. Alternatively the date above, obtained from a different laboratory (Waikato), could have been erroneously old. However, the subsequent age–depth profile demonstrates remarkably constant sediment accumulation at approximately 1000 yr^{-1} a meter until around 400 cm when there is a marked slow down in sediment accumulation through the Holocene. The change in age–depth relationship and sediment accumulation rate, from about 4 meters, may represent a break in sediment accumulation and a sedimentary hiatus — this will be discussed further in light of other data for this period. δ^{13}C values (Fig. 2) are consistently low at around −30‰ until soon after the LGM (the radiocarbon date of 18,995 ± 227) when there is an increase to around −23‰ before a rapid increase after the radiocarbon date of 16,256 ± 23 to values about −10‰ (Fig. 2).

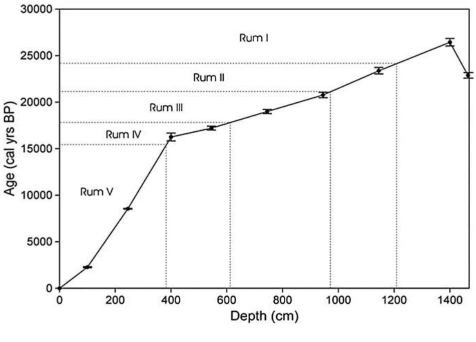

Fig. 2. Linear age–depth plot based on nine ^{14}C dates. The position of the pollen zone boundaries are also shown and labelled concordant with Fig. 4.

3.3. Pollen

Pollen results are described following the zonation identified by the CONISS analysis (Fig. 3).

Pollen zone Rum I extends from 1469 to 1210 cm and is dated from 26,430 to 24,000 ^{14}C yr BP. Afromontane pollen taxa dominate the zone, in particular *Juniperus* (20%) and *Podocarpus* (40%). *Alchornea*, *Canthium*, *Celtis*, *Hagenia*, *Ilex*, *Macaranga*, *Polycias*, *Rapanea* and *Schefflera* are present at low percentages. Herbaceous taxa such as the Asteraceae and *Stoebe* are present with *Artemisia* and Ericaceae also present throughout the zone at low pollen percentages (<10%). Poaceae dominates the zone within the herb category with about 35% at 1465 cm decreasing to around 20% throughout the upper part of the zone. *Stemodia* and Umbelliferae record very low percentages throughout the zone. The aquatic group is dominated by *Potamogeton* (<10%) while Cyperaceae is poorly represented. The zone boundary dates to 24,000 ^{14}C yr BP and is characterised by low pollen percentages of *Juniperus*, Poaceae, *Podocarpus* and *Stoebe* while there is an increase in *Allophylus*, Asteraceae, *Polyscias*, *Rapanea*, *Schefflera* and Urticaceae percentages. *Cyathea*, *Myriophyllum*, Spores and Cyperaceae are also present about the pollen zone boundary.

Pollen zone Rum II extends from 1210 to 970 cm and dates from 24,000 to 22,000 ^{14}C yr BP. *Podocarpus* initially decreases to <8% then increases to dominate the zone about 40%. Percentages of *Juniperus* also decrease at the same period that *Podocarpus* does. Other arboreal taxa present are *Celtis*, *Ilex*, *Macaranga*, *Olea*, *Polyscias* and *Rapanea*; pollen percentages are very low for all these taxa. The Ericaceous Belt taxa is dominated by *Stoebe* (<10%) with *Artemisia* and Ericaceae also present at low percentages. No woodland taxa are present in this zone. Asteraceae and *Stemodia* pollen are present in the zone with Asteraceae dominating amongst the herbaceous taxa. Poaceae is abundant throughout the zone recording around 20%. Cyperaceae is also present but poorly represented. *Myriophyllum* and *Potamogeton* are present but record low percentages. The pollen zone boundary is characterised by decreases in *Alchornea*, *Artemisia*, *Juniperus* and *Schefflera* and a prominent increase in *Hagenia*. This pollen zone boundary is coeval with the Char I–Char II zone boundary (Fig. 4).

Pollen zone Rum III extends from 970 to 610 cm and dates from 22,000 to 17,500 ^{14}C yr BP. The zone is characterised by high percentage of *Juniperus* and *Podocarpus* and increased amounts of *Hagenia* pollen throughout the zone. *Juniperus*, *Polycias* and *Schefflera* decreases towards the upper zone boundary. Asteraceae and *Stoebe* decreases as *Juniperus* increases to 20%. Other Afromontane taxa present in the zone are *Celtis*, *Hypericum*, *Ilex*, *Macaranga*, *Olea*, *Polyscias*, *Rapanea* and *Schefflera* but these taxa have very low percentages. Woodland taxa start appearing in this zone with the

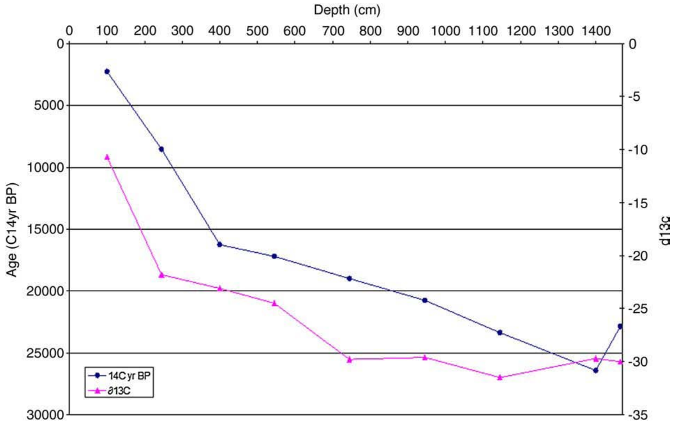

Fig. 3. Carbon isotope ($\delta^{13}C$) distribution within the Rumuiku Swamp sediments and the nine ^{14}C radiocarbon dates that are used to develop a linear age–depth plot.

presence of *Allophylus*, *Canthium*, Capparaceae, *Dombeya* and *Euphorbia*. Non arboreal taxa are characterised by *Artemisia*, Asteraceae, Brassicaceae, Ericaceae, *Justicia*, Labiatae, *Stemodia*, *Stoebe* and Umbelliferae with *Stoebe* decreasing throughout the zone. Poaceae is most abundant (>30%) when Cyperaceae is poorly represented. *Typha* appears only in one depth at 30%. The pollen zone boundary is characterised by decreases in *Cyathea*, *Hagenia*, *Juniperus* and *Podocarpus* and prominent increases in *Rapanea* and *Stoebe*.

Pollen zone Rum IV extends from 610 to 380 cm and dates from 17,500 to 15,500 ^{14}C yr BP. *Hagenia*, *Polyscias*, *Podocarpus* and *Schefflera* are present in the beginning of the zone with *Hagenia* and *Polyscias* being characterised by a large increase relative to zone Rum III. *Juniperus* percentages start to decrease in the zone while *Rapanea* increases compared to zone Rum III. Other arboreal taxa present in the zone are *Afrocrania*, *Alchornea*, *Croton*, *Hypericum*, *Ilex*, *Macaranga*, *Myrica*, *Olea* and *Schefflera*. The Ericaceous Belt taxa present (*Artemisia*, *Cliffortia*, Ericaceae, *Stoebe* and *Valeriana*) all record low percentages. Woodland taxa present at low percentages include *Allophylus*, Capparaceae, *Dombeya*, Moraceae and Rubiaceae. The herbaceous taxa in this zone are dominated by Asteraceae with *Impatiens*, *Rumex*, *Stemodia* and Urticaceae present in variable amounts, for example Urticaceae records a concentration of about 30% in only one depth. Poaceae fluctuates widely (15 to 60%) and there are slight increases in Cyperaceae relative to zone Rum III. The pollen zone boundary is characterised by large decreases in *Hagenia* and *Polyscias* and increases in Cyperaceae, *Juniperus*, Poacaeae, *Schefflera* and Uriticaceae pollen.

Pollen zone Rum V extends from 380 to 0 cm and dates from 15,500 to 0 ^{14}C yr BP. The zone could be subdivided into three subzones, however, given the length of the record and focus of this paper on the response, the vegetation about the LGM zone Rum V will be described as a single zone. Afromontane taxa dominate this zone with *Podocarpus*, *Polycias* and *Schefflera* being abundant. Other taxa include *Alchornea*, *Afrocrania*, *Celtis*, *Croton*, *Hagenia*, *Ilex*, *Juniperus*, *Macaranga*, *Myrica*, *Neoboutonia*, *Olea*, *Protea* and *Rapanea*. Most of the taxa representing the Ericaceae Belt record very low percentages throughout the zone; woodland taxa are also poorly represented. Urticaceae increases from 15,500 ^{14}C yr BP at the zone boundary with rises in Cyperaceae and Poaceae and decrease in *Hagenia*, *Polyscias* and *Schefflera*. Asteraceae and Urticaceae are abundant; particularly for the first half of the pollen zone with the former taxa increasing again in the top 50 cm. Poaceae fluctuates quite widely in the zone increasing to 40% while Cyperaceae, after an initial dominance, decreases towards the core top. *Myriophyllum* records high percentages in the middle of zone Rum V increasing to about 40% before decreasing towards the top of the core.

3.4. Charcoal

Zone *Char-I* extends from 1465 to 990 cm and dates from 26,430 to 20,000 ^{14}C yr BP. The charcoal content in this zone is generally low but more abundant in the large charcoal class sizes of 75 to 150 μm and >150 μm. Zone Char I is characterised by numerous peaks and troughs indicative of a generally low but variable fire regime with isolated large fires, for example around 1125 cm. Zone *Char-II* extends from 990 to 510 cm and dates from 20,000 to 16,500 ^{14}C yr BP. All classes decrease to the top of the zone, particularly from 700 cm when all size classes reach a peak. Zone *Char-III* extends from 510 to 0 cm and dates from 17,500 to 0 ^{14}C yr BP. This zone has very high charcoal percentages, particularly from 450 cm with some depths recording <40%. All charcoal class sizes are very variable, particularly the 26 to 75 μm class. Towards the top of the zone there is a strong reduction in the charcoal percentages, particularly from 75 cm.

4. Discussion

The palaeoenvironmental proxies from the Rumuiku Swamp sediments provide a new insight into ecosystem response to climate variability and changing fire regimes through the LGM, the late glacial transition and with much less resolution through the Holocene. The resolution of the analysis is about 200 years between sample points for period from 26,000 to 16,000 cal yr BP. Elsewhere on Mount Kenya, Rutundu and Small Hall Tarn lakes also record a high rate of sedimentation during the glacial period and early Holocene (Street-Perrott et al., 2007) making this an exceptional location in Eastern Africa, and indeed throughout the wider tropics to understand past ecosystem response to climate change, particularly about the LGM.

Most previous palaeoenviromental analyses on lacustrine and swamp sediments have suggested a downward extension of the treeline on Eastern Africa Mountains by some 900 to 1100 cm about the

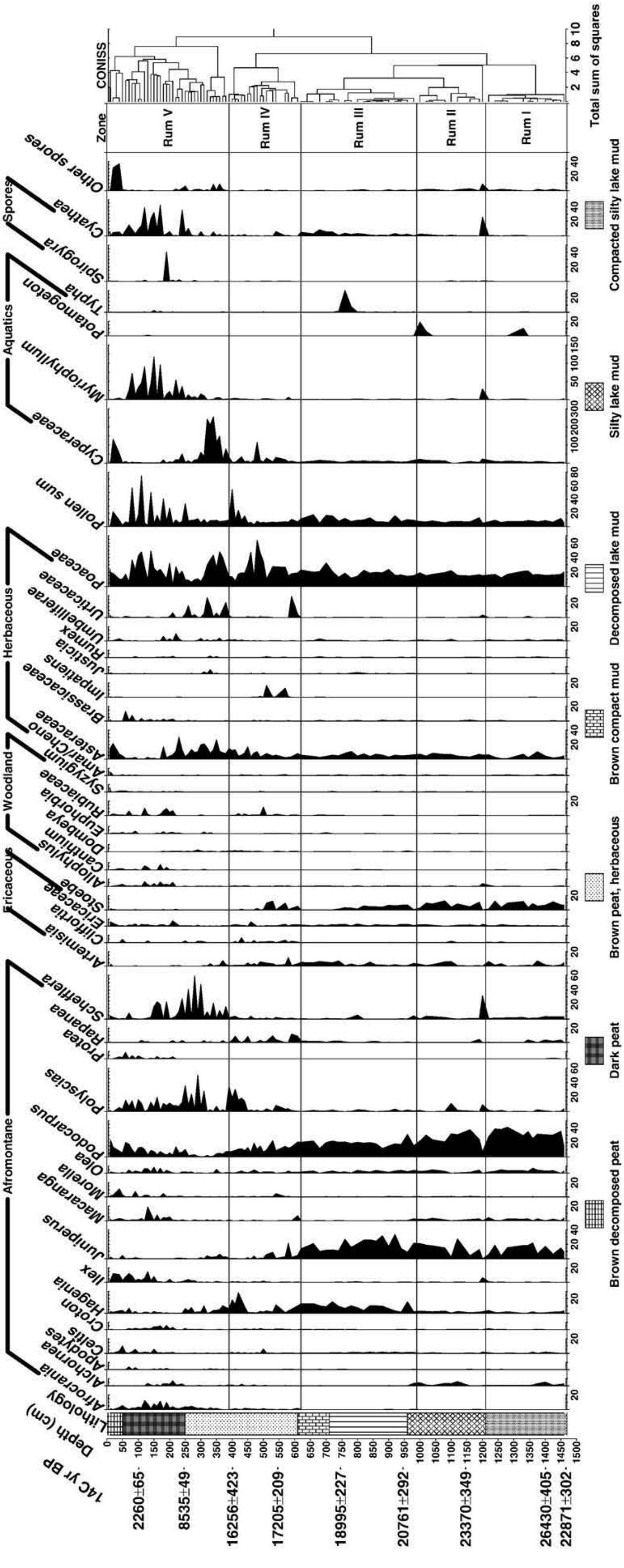

Fig. 4. Rumuiku pollen diagram showing down core percentages of selected taxa in the Afromontane, Ericaceous Belt, Woodland, Herbaceous, Aquatic and the Pteridophytes groups. The vertical scale represents the sample depth with lithology and radiocarbon dates shown. Results are presented in five major pollen zones identified by the numerical clustering program CONISS.

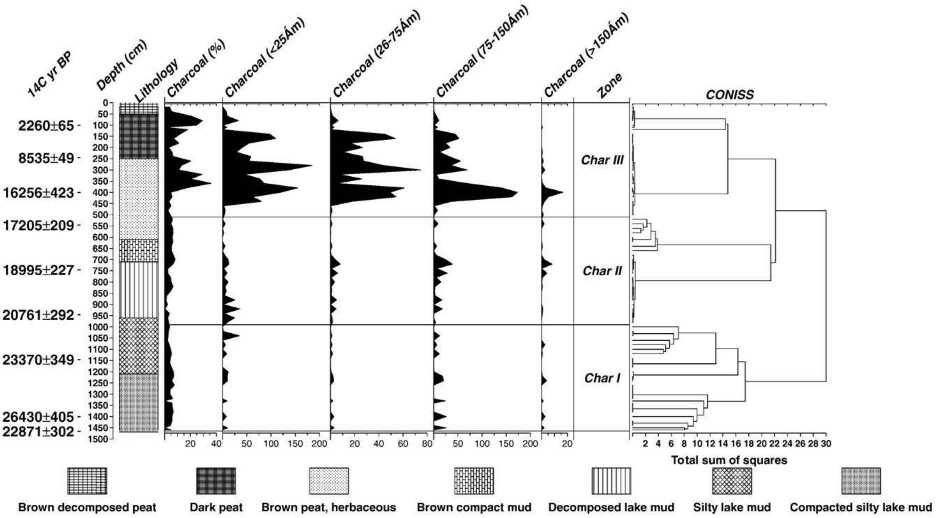

Fig. 5. Charcoal percentages determined using the Winkler method and charcoal size classes following microscopic examination. CONNIS applied to the data group the charcoal results into three zones. Core lithology and radiocarbon dates are also shown.

LGM and replacement of the montane forest taxa with higher altitude, xerophytic vegetation (Coetzee, 1967; Perrott and Street-Perrott, 1982; Bonnefille and Riolett, 1988; Bonnefille et al., 1990; Wooller et al., 2000; Olago, 2001). The pollen record from Rumuiku Swamp also provides clear evidence for the impact of past climatic conditions, with the vegetation dominated by *Artemisia*, *Stoebe* and other Ericaceous Belt taxa in the period from 26,000 to 24,000 ^{14}C yr BP. However, the pollen record shows that the ecosystem shift was not solely a situation of high altitude vegetation moving to lower altitudes, with continual presence of *Alchornea*, *Hagenia*, *Olea*, *Podocarpus*, *Rapanea* and *Schefflera* within the Rumuiku Swamp catchment — all representatives of montane forest. Interestingly, these montane forest and Ericaceous Belt taxa grow in association with *Juniperus*, a tree that is presently found at lower altitudes than Rumuiku Swamp but on the relatively dry side of Mount Kenya (Fig. 1). Such a lateral expansion of vegetation belts, contrary to the classical view of down-slope vegetation movement, has also been invoked to explain vegetation shifts at Lake Rutundu (Wooller et al., 2003). At Lake Rutundu, *Artemesia* increased from 24,000 to 14,000 yr BP at a similar time to the Rumuiku Swamp record. Such a non-uniform specific ecosystem response to late glacial environmental shifts has also been detected in Central Africa where catchment characteristics, particularly slope angle, were thought to be responsible (Jolly et al., 1997). For example, within the Muchoya Swamp catchment in southwest Uganda the vegetation was characterised by moderate presence of moist lower montane taxa such as *Schefflera*, *Polyscias*, *Ilex* and Urticaceae from 20,200 to 15,700 yr BP (Taylor, 1990). The persistence of moist forest from 24,000 to 22,000 ^{14}C yr BP farther south on the Udzungwa (Mumbi et al., 2008) and Uluguru highlands (Finch et al., 2009) of the Eastern Arc Mountains of Tanzania is further indication of locally differential ecosystem response to LGM climatic change. Thus, it is quite clear that some areas appear to have remained relatively moist throughout the LGM.

Such a change in ecosystem composition is not restricted to arboreal cover; grass cuticles, pollen and charred fragments of epidermis confirm that pooid taxa using C_4 photosynthetic pathways were common in the late glacial environment at higher altitudes on the north of Mount Kenya (Street-Perrott et al., 2007; Ficken, et al, 2002; Wooller et al., 2000). Adjacent montane areas, such as the Aberdares, had larger lakes with C_4 grasses also spreading into their catchments due to the cold environment and changed atmospheric composition (Street-Perrott et al., 1997): C_4 plants being more CO_2 and water efficient and having a competitive advantage when $_PCO_2$ is lower and climate arid (Bond et al., 2003; Ehleringer et al., 1997). Within the Rumuiku Swamp catchment C_3 grasses were dominant throughout this period with the expansion of pooid taxa using C_4 photosynthetic pathways not apparent as shown by the low (−30‰) values for δ^{13}C about the LGM. It has been suggested that such dominance of C_4 Poaceae taxa on Mount Kenya in the glacial period can be largely explained by lower $_PCO_2$ rather than aridity (Jolly and Haxeltine, 1997), however as there is little C_4 expansion at lower altitudes (2100 m) it seems reduced temperature and/or moisture are a prerequisite for the development of this flora. An additional insight into the nature of the environment comes from targeted analysis on the Lake Rutundu sediments that show the presence of the C_4 grass *Themeda triandra* within the catchment, this implying that precipitation was high during the growing season (Wooller et al., 2003). Thus, this new record from Rumuiku Swamp, and reassessment of other long records in Eastern Africa, casts further doubt on traditional interpretations of ecosystem response to the LGM and highlights the dynamic nature of the vegetation response to climate forcing, likely to be modified by local factors (topography, soil, and geology), CO_2 concentration, fire and ecological inertia. Certainly, there seems to be considerable support for the strong role of local topographic and climatic conditions in influencing vegetation response. There remains very strong evidence for pronounced aridity at the LGM, particularly manifested as a lowering of lake levels in the Rift Valley (Kendall, 1969; Harvey, 1976; Richardson and Dussinger, 1986; Gasse et al., 1989; Talbot and Livingstone, 1989; Johnson et al., 1996; Beuning, 1997; Beuning et al., 1997) with the Lake Tanganyika diatom record reflecting a lake level drop of some 300 m about the Last Glacial Maximum (Gasse et al., 1989). However, the Lake Naivasha diatom, ostracod and pollen record suggests a high lake level (Maitima, 1991) although it is the only record in the region to record the LGM as being a relatively wet period. Although it is suggested this record is unreliable, and the possibly erroneous signal is associated with dating problems (Kiage and Liu, 2006), the original interpretation is supported by the Rumuiku Swamp record, and the spatio-temporal response of catchments and lakes to environmental changes about the LGM, clearly warrants further investigation.

To explain the apparent discrepancy between high altitudinal sites being relatively moist and lower altitudinal lakes recording pronounced aridity, alternative explanations to wholesale aridity need to be sought. A drier environment has been attributed to lower tropical sea surface temperatures (SSTs) during glacial phases (Hostetler and Clark, 2000). However, Eastern Africa SSTs were not massively lower at the LGM (Farrera et al., 1999), and although global sea levels were some 100 m lower at 21,000 ^{14}C yr BP there is not an extensive continental shelf off the Eastern Africa coast. These factors would have the net effect that land–ocean coupling and associated delivery of moisture would not have been markedly different than today, with stratified clouds continuing to deliver moisture to montane areas (Marchant et al., 2006). Another explanation to account for the high-lowland decoupling could be via changed lapse rates, and/or moisture delivered to montane areas not being readily transferred to the lowlands. Such a discrepancy between the highland and lowland ecosystem response is not so surprising given that lowlands will have a more pronounced precipitation: evaporation ratio. With the significant expansion of low stature Ericaceous Belt vegetation and C_4-domiated grasslands at high altitudes on Eastern Africa Mountains, as evidenced by the numerous palaeoenvironmental records, then there would be significantly reduced ability of the vegetation to strip out moisture from incoming non-precipitating clouds. This reduction of occult precipitation would result in reduced river flows and associated lake level declines as the high altitude ‘water towers’ become less effective at collecting moisture. It is about this time that the Rumuiku Swamp site passes through the hydroseral succession; the transformation from a lake to a swamp, as denoted by the stratigraphic change from a lake mud to a herbaceous peat at about 600 cm, is dated to approximately 17,000 cal yr BP. Although such a shift may be attributed to climate change, it is difficult to assess as all lakes will ultimately infill with sediment and pass through a hydroseral succession. The strong impact of vegetation change on the montane hydrology, and connection to lowland drought, can be seen today on numerous Eastern Africa Mountains where human-induced vegetation clearance has resulted in reduced river flows and declining lake levels. For example, on Mount Kilimanjaro where there has been recent extensive clearance of the *Ocotea*-dominated forest this is thought to be accountable for more than a 90% reduction in moisture of the reduced flows and associated regional aridity (Hemp, 2006). Such a more complex vision of ecosystem response to the LGM renders current tropical palaeoclimatic reconstructions (Bonnefille et al., 1990; Peyron et al., 2001; Farrera et al., 1999) potentially erroneous, and certainly highlights that they need to be treated with caution, particularly when used as a test of the validity of output from other applications, such as a test of climate model performance (Marchant and Hooghiemstra, 2001). Developing this understanding on ecosystem response to climate change is highly relevant to predicting future climate change impacts on Afromontane ecosystems, particularly so as the LGM is a critical period for a palaeoclimate data-model comparisons (Elenga, et al., 2001; Peyron et al., 2001; Braconnot et al., 2007). This relevance is particularly trite when we consider that ecosystems have spent some 80% of the Quaternary under a glacial environment, and are most adapted to a cool, dry, low CO_2 environment.

Whatever the explanation for differential ecosystem response to the LGM, the record from Rumuiku Swamp presented here shows the ecosystem composition within the catchment was highly dynamic — a situation that continues into the late glacial period. For example, during the period from 17,500 to 16,500 ^{14}C yr BP there was increased abundance of montane taxa with *Juniperus* becoming less important providing some evidence for a slightly wetter environment than previously. From 16,500 ^{14}C yr BP there was a notable change in vegetation composition; a large increase in *Hagenia* was followed by *Polyscias* and *Schefflera* around 12,000 yr BP in the Rumuiku Swamp catchment: these shifts are concomitant with a similar expansion of montane forest at Muchoya (Taylor, 1990) and Mubwindi Swamp (Marchant et al., 1997) in the Rukiga Highlands of southwest Uganda. This increase in *Hagenia* is interesting as it coincides with a significant and sustained increase in charcoal indicative of greater fire activity. *Hagenia* is a known fire tolerant taxa (Lange et al., 1997) and was growing successfully at higher altitudes during this time (Coetzee, 1967; Swain, 1999; Wooller et al., 2003). Extensive biomass burning about this time may have encouraged the spread of woody vegetation (Kutzbach and Street-Perrott, 1985), in particular *Hagenia* until a period when climatic amelioration was significantly strong to allow colonisation of more sensitive montane taxa such as *Schefflera*. Farther south in the Lake Masoko catchment, *Olea* expanded between 16,000 and 14,100 ^{14}C yr BP (Vincens et al., 2007); with Lake Tanganyika recording similar expansions from 16,000 to 14,000 yr BP (Vincens, 1991) that indicated there was rapid climatic amelioration after the LGM and associated vegetation response.

In Eastern Africa, the period from 12,400 to 10,000 ^{14}C yr BP is characterised by marked climatic transitions (Barker et al., 2001; Olago, 2001), with rapid rise in temperature and increased moisture. For example, the diatom record from Lake Victoria shows a highly variable climate from 11,400 to 10,000 ^{14}C yr BP (Stager et al., 1997; 2002). Interpretations about this period from the Rumuiku record are difficult as this period corresponds to a marked change in sedimentation rate between the radiocarbon dates of 16,256 ± 423 cal yr BP at 400 cm and 8535 ± 49 cal yr BP at 245 cm. Although the stratigraphy does not show marked changes in this section, the majority of the pollen taxa (Fig. 3) and the charcoal data (Fig. 4) show very strong fluctuations in this upper section of the core further indicating the potential of a hiatus. With this caveat, using the existing age–depth profile the Rumuiku Swamp record shows pronounced increases in Asteraceae, Cyperaceae, Poaceae and Urticaceae as *Hagenia* decreased around the beginning of Younger Dryas. In the Empakai Crater of northern Tanzania, from 13,200 to 10,100 ^{14}C yr BP *Hagenia* similarly decreased as *Nuxia* and Poaceae increased (Ryner et al., 2006). This coeval reduction of *Hagenia* at Empakai Crater and Rumuiku may be indicative of a regional climate shift and associated ecosystem response. The Younger Dryas has been recorded in many areas of Africa (Johnson et al., 2002; Maley and Brenac, 1998; Bonnefille et al., 1995) although the wider signature is often controversial as the transition from the late glacial and early Holocene is not generally well preserved in Eastern African sedimentary records (Jolly et al., 1997). Where the Younger Dryas is recorded it is characterised by a brief episode of aridity (Bonnefille et al., 1995; Olago et al., 1999) with lake levels recording a low stand around this period. For example Lake Albert was some 46 m lower than present levels at 12,500 yr BP (Beuning et al., 1997) with Lake Victoria also lower at this time (Kendall, 1969). As documented by the stratigraphic changes at 250 cm and the increased presence of Cyperaceae, Poaceae and *Typha* the Rumuiku Swamp sediments suggest that the swamp dried out further during, or soon after, the Younger Dryas. Increased amounts of Cyperaceae and *Myriophyllum* in the late Holocene are also good indicators of low water levels and swamp development.

Following the transition into the Holocene, mixed montane forest taxa, particularly *Shefflera* and *Polycias*, replaced *Hagenia* as the ecosystem composition responded to warmer and wetter climatic conditions. Similarly, taxa characteristic of the dry Ericaceous Belt, like the shrub *Stoebe*, became less common until it was virtually absent. The Holocene in Eastern Africa was generally characterised by warmer temperatures and greater precipitation resulting in the decreased extent of higher altitudinal vegetation associations (Street-Perrott and

Perrott, 1993). Within this general environmental synopsis the Holocene was characterised by rapid environmental shifts. For example, the terminal moraine in Teleki valley Mount Kenya was 200 m lower between 6070 and 4135 ^{14}C yr BP indicative of a reduction in average temperature by 1.2 °C relative to present day (Johannessen and Holmgren, 1985). A short-lived temperature increase resulted in the expansion of C_4 grasses from 4500 to 4000 ^{14}C yr BP on Mount Kenya (Olago, 2001) with the pollen record from the Cherangani Hills (Coetzee, 1964; 1967) and Sacred Lake on Mount Kenya (Coetzee, 1967) all showing a shift to more xeric ecosystems reflecting a relatively dry climate. Mount Kilimanjaro also experienced a strong drying phase around 4000 ^{14}C yr BP with a distinctive layer of dust recorded in the ice core (Thompson et al., 2002) that agrees with lowered lake levels in numerous African countries (Stager, 1988; Talbot and Livingstone, 1989) and appears to be part of a pan-tropical environmental shift (Marchant and Hooghiemstra, 2004). Thus, during the Holocene tropical mountains have undergone quite strong phases of climate change (Thompson et al., 2002) with variations in the pollen spectra at Rumuiku Swamp suggesting that the composition of the moist montane forest within the catchment did not remain stable throughout the Holocene. Three relatively significant changes in pollen spectra are apparent; during the mid Holocene, Rumuiku swamp reflects a pronounced growth of *Hagenia* concomitant with dramatic increase in *Poaceae* and *Myriophyllum* which are not comparable with any other site in Mount Kenya. From about 6500 and 4000 ^{14}C yr BP, Rumuiku Swamp sediments record a rise in *Podocarpus*, reduced presence of *Polyscias*, *Afrocrania*, *Macaranga* and *Schefflera* with high increases in Poaceae. Charcoal in the Rumuiku Swamp sediments record dramatic increases about this time, particularly in the large size classes, that is likely to reflect a significant increase in large fires local to the swamp. Such a shift in fire regime is likely to follow a warmer climate with greater fuel availability following increased forest growth. Associated with this increased fire regime is greater abundance of fire-tolerant taxa such as *Hagenia*. This period is also marked by a dramatic and extended period of drought around 4000 ^{14}C yr BP that is observed throughout the region and indeed the wider tropics (Street-Perrott and Perrott, 1993; Thompson et al., 2002; Marchant and Hooghiemstra, 2004).

During the Late Holocene, pollen records from Eastern Africa start to register human settlement and associated ecosystem impact. In the Late Holocene humans progressed from having a relatively minor impact, to becoming a major external force on vegetation change. This impact can give rise to complications when interpreting palaeoenvironmental records, simply due to the difficulty in isolating the climatic signals from the anthropogenic (Lamb et al., 2003; 2004; Kiage and Liu, 2006). The Late Holocene at Rumuiku Swamp records a progressive degradation in the arboreal cover, most clearly seen in the response of *Polyscias* coupled with an expansion of grasses and herbaceous taxa such as *Artemisia* possibly related to forest clearance. The decline in shade-loving species, such as Urticaceae, also suggests a conversion from a canopied montane forest to a more open forest. The increased fires in the Late Holocene may also be linked to forest clearance to extend agricultural land. The high accumulation of charcoal, reduction in forest taxa in the late Holocene coincides with immigration of the Kikuyu tribe and onset of agriculture in the region (Dunda, 1908; Muriuki, 1974), an impact that has increased into the present day with the Kikuyu being held accountable for clearing large expanses of montane forest for agriculture (Lamb et al., 2003; Muiruri, 2008). It is interesting to see the steady presence of *Podocarpus* and rapid rise of this taxa in the most recent sediments; in some areas adjacent to the Rumuiku Swamp catchment this taxa forming monospecific stands with open ground between the mature trees maintained by grazing (Plate I). This situation is converse to other areas in Eastern Africa where *Podocarpus* was a particular focus of forest clearance (Marchant and Taylor, 1998).

5. Conclusions

The pollen record from Rumuiku Swamp shows that climate change about the LGM resulted in a very different ecosystem composition than is presently found within the catchment. However, the ecosystem shift was not singly high altitude vegetation moving to lower altitudes, but there was a mixing of vegetation currently found within different altitudes and environments. During this period *Stoebe* and Ericaceae shifted down into the montane forest belt and *Juniperus* established itself on the south east of Mount Kenya with *Hagenia* common from around 17,500 ^{14}C yr BP. The abundance of more mesic montane forest taxa persisted, albeit at lower levels throughout the LGM and the late glacial period.

The Younger Dryas, and the transition into the Holocene, is recorded as quite dramatic shifts in ecosystem composition; increased presence of *Myriophyllum* and Poaceae, with reduction of *Polyscias* and *Schefflera* are thought to reflect a relatively dry climate. *Myriophyllum* and Cyperaceae also increase as the former lake evolved to become a swamp. The decline of *Hagenia* and montane forest taxa, combined with increased presence of Poaceae and *Myriophyllum* and rise in charcoal accumulation, reflect increasingly frequent fires possibly linked to regional drought phases in the Holocene. Most recently the swamp sediments reflect a change in ecosystem composition that follows increasing human impact on the forest.

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Chapter 3

Holocene montane forest ecosystem dynamics from Mount Kenya

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Abstract

Abstract

Pollen, charcoal and radiocarbon data from a sediment core abstracted from Rumuiku Swamp (Mount Kenya) records ecosystem response to Holocene environmental changes. Early Holocene vegetation was characterized by mixed montane forest comprising *Polyscias* and *Schefflera*, with lower levels of *Afrocrania, Hagenia, Ilex* and *Podocarpus* from 10,000 to 8500 cal yr BP. There was a rapid increase in charcoal occurrence around 9000 cal yr BP indicative of a short-lived phase characterized by more flammable conditions. Increases in *Cyathea, Cyperaceae* and *Myriophyllum* signify a warm and moist period around 8200 cal yr BP, reduced charcoal concentrations also suggest less frequent burning about this time. The mid Holocene period is marked by an increase in the diversity of the montane forest, possibly in response to increased disturbance in the catchment. From between 4000 to 3500 cal yr BP there is a marked change in the composition of the forest as Poaceae, *Polyscias* and *Podocarpus* became co-dominant in the Rumuiku catchment indicative of a more open forest. There was also a pronounced vegetation shift around 2200 cal yr BP as *Ilex, Morella* and *Polyscias* dominated the montane forest composition. The timing of this vegetation shift follows a short-lived period of very high charcoal concentration followed by a sustained reduction in charcoal. This suggests the onset of a relatively moist environment following a brief, but intense, dry phase. The uppermost samples, covering the past 500 years, do not register strong evidence of human impact although there was an increase in Asteraceae and a dominance of *Podocarpus* that mark a transition to more open montane forest from approximately 500 cal yr BP.

Keywords: Charcoal, Ecosystem change, East Africa, Human impact, Pollen

1. Introduction

As ecosystems respond to current environmental change there is a pressing need to understand how these ecosystems have responded to environmental changes in the past. Although the broad patterns of Holocene vegetation dynamics across East Africa are reasonably well documented (Kiage and Lui 2006), the more local response of ecosystems and specific detail about the timing and character of these patterns remains poorly constrained. This uncertainty results mainly from relatively poor dating (few dates and wrong interpolations) and / or local response of the environmental change (Karlén et al. 1999).

One area that is relatively well understood is Mount Kenya due to the relatively long history of palaeoecological research (Coetzee 1967; Swain et al. 1999; Barker et al. 2001; Olago 2001; Wooller et al. 2000; Rucina et al. 2009). The early Holocene was characterized by more mesic environmental conditions on Mount Kenya that resulted in the expansion of moist montane forest types to lower altitudes (Coetzee 1967, Olago 2001; Rucina et al. 2009; Swain et al. 1999). This warm environment is confirmed by an oxygen isotope record from two alpine lakes on Mount Kenya that record two major negative shifts from 12,900 to 9550 cal yr BP and from 7580 to 6370 cal yr BP (Barker et al. 2001). During the middle through to the late Holocene there was rapid ecosystem changes reflected by pollen and charcoal records that mark the onset of a more arid phase which is commonly recorded across tropical Africa (Marchant and Hooghiemstra 2004). The ice core from Mount Kilimanjaro recording a dust layer around 5175 cal yr BP thought to reflect marked regional drought (Thompson et al. 2002). Superimposed on this generally more arid late Holocene were a series of rapid shifts in moisture availability. For example, Lake Naivasha at 1184 m altitude experienced low stands from 874 to 664 cal yr BP with a high stand from 664 to 150 cal yr BP (Verschuren et al. 2000).

In addition to being characterised by pronounced environmental changes, the late Holocene in East Africa is marked by increasing anthropogenic activities as Bantu agricultural and Cushitic and Nilolitic pastoral populations migrated into East Africa bringing a combination of agricultural, pastoral and iron technology that resulted in a significant landscape modification (Holl 2000). Herbaceous taxa became more abundant with increasing agricultural activities and associated management practices such as increased use of fire (Lejju et al. 2005). These anthropogenic activities are also detected within the pollen records; for example the presence of *Elaeis guineensis* (oil palm) from the Lake Masoko pollen record is accompanied by increased soil erosion following forest clearance (Vincens 2003). These anthropogenic influences were widespread and included a range of impacts from complete forest clearance to undetectable and silent signals of human presence, either resulting from the lack of people or the selective preservation of forest areas due to political or cultural beliefs (Marchant and Taylor 2000).

We present a new record of Holocene vegetation dynamics from Mount Kenya, which expands on a longer secondary record that documents ecosystem and environmental change dating back 26,430 cal yr BP. The previously published results from the site (Rucina et al. 2009) concentrated on the full sediment core that largely focused on the last 47 glacial maximum and late glacial–Holocene transition resulting in the Holocene section being very poorly constrained. This focus was largely due to the sedimentary character of the core and the sampling regime employed: the 1469 cm core was sampled every 20 cm for pollen analysis resulting in the top 270 cm, that comprised the Holocene, having a low temporal resolution and being constrained within a single pollen zone. To improve our interpretation on the Holocene section of the core we present here new pollen and charcoal results, new radiocarbon data combined with a re-analysis of the data.

2. Setting of the study site

Mount Kenya, situated in the centre of Kenya (Fig. 1A and 1B),is the second highest mountain in Africa with a maximum altitude of 5199 m. Much of the mountain is contained within the Mount Kenya National Park, which contains a wide variety of ecosystems along steep altitudinal and rainfall gradients (Fig. 1). Rumuiku Swamp is situated on the southeast of Mount Kenya at 2154 m in the montane rain forest belt. Rumuiku Swamp is bordered to the

Plate 1. Rumuiku Swamp bordered to the southwest by a small cliff with a small river emerging from the swamp flowing to the east..

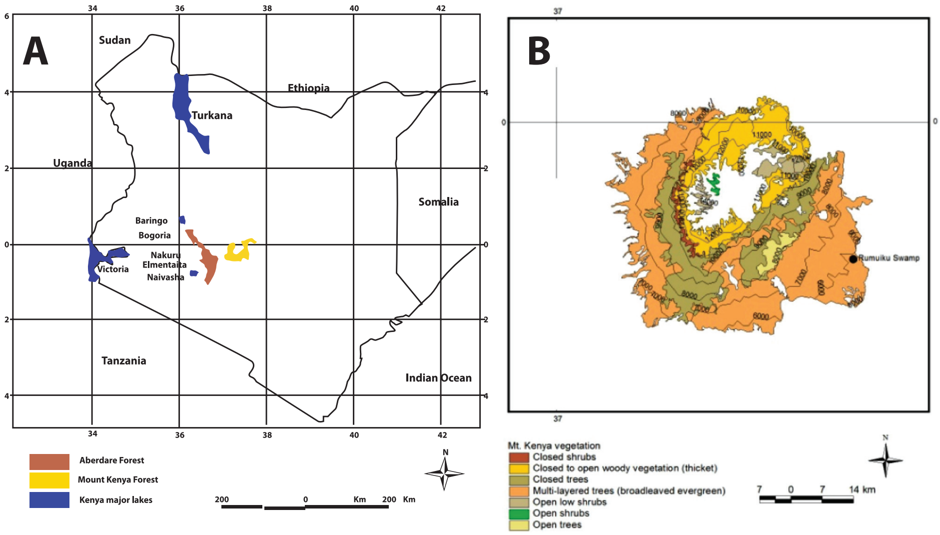

Figure 1. Location map of Rumuiku Swamp catchment area on Mount Kenya (A) and the altitudinal vegetation distribution with the major vegetation zones (B).

southwest by a small cliff with a small river emerging from the swamp flowing to the east (Plate 1). The vegetation in the Rumuiku Swamp catchment is highly disturbed with the original montane forest dominated by *Croton macrostachys, Macaranga kilimandscharica* and *Neoboutonia macrostachys*. Many of the original montane rain forest taxa such as *Ocotea usambarensis, Polyscias spp., Schefflera spp*. and *Tabarnaemontana holstii* are present in reduced numbers. *Morella salicifolia* and *Syzygium cordatum* are recorded as small trees close to the swamp margins.

Vegetation on the swamp surface is dominated by sedges that form the peat. The large tussock forming grass *Pennisteum mildbraedii* is locally abundant on the margins as are local patches of *Sphagnum* moss. Exotic tree species (*Cupressus lusitanica, Pinus patula* and *Pinus radiata)* are cultivated towards the north, and *Eucalyptus spp*. to the south of the catchment under management of the Forest Department of Kenya. The southeastern and eastern slopes are characterised by intensive smallholdings producing both subsistence and cash crops. Approximately half of the catchment is used for agriculture with a wide variety of crops being cultivated. Cattle and goats are an integral part of the mixed agricultural system and graze in open areas of forest characterised by almost pure stands of *Podocarpus* (Plate 2).

Plate 2. Open area of forest characterized by almost pure stand of Podocarpus

Mount Kenya receives most of the rainfall during the months of March to May (long rains) and September to October (short rains); this bimodal rainfall resulting from passage of the Intertropical Convergence Zone (ITCZ) that migrates south and about the equator. There is high inter-annual and seasonal variability in rainfall resulting from interaction between atmosphere, sea surface temperature, trade winds and diverse topography (Mutai et al. 2000; Marchant et al. 2006). The strong impact of topography is clearly reflected by the regional microclimate: the southern flank of Mount Kenya receiving >2500 mm yr-1 rainfall with the northern flank of the mountain being much drier receiving <1500 mm yr-1 (Thompson 1966). Mount Kenya does not experience marked seasonal variations in temperature due to its location on the equator but does exhibit strong altitudinal changes and associated temperature gradients. Temperature change on Mount Kenya lapses at a rate of 6.6°C 1000 m-1; the approximately 4000 m of altitudinal difference from the foothills to the summit equates to a temperature range of more than 24°C that is reflected by the vegetation composition. The mean annual maximum temperatures are 26°C at the foothills (1982 m) to 2°C in the nival zone. Diurnal variations in temperature are much more pronounced than mean annual temperature with daily temperatures commonly fluctuating by around 20°C (Survey of Kenya 1966) and 14ºC at the forest line (Coe 1967).

3. Methods

3.1 Coring, chronology and pollen analysis

The pollen and charcoal data presented here are from a 270 cm uppermost section of a 1469 cm sediment core recovered from Rumuiku Swamp using a 5 cm diameter Russian corer in 50 cm overlapping sections from two adjacent bore holes situated 10 cm apart. After core recovery the sediments were described at the coring site before being transferred into 50 cm long longitudinally split PVC pipes and wrapped in aluminium foil and polythene for transport to Palynology and Palaeobotany Laboratory of the National Museums of Kenya (NMK) in Nairobi and later to the University of York for cold storage. Five bulk sediment samples composed of charcoal and wood fragments were selected for accelerator mass spectrometry (AMS) radiocarbon dating; each sample was chosen to date significant changes in the stratigraphy, or fluctuations in the charcoal,isotope or pollen records. Three samples were sent to NERC and two to the Waikato radiocarbon laboratories in the UK and New Zealand respectively where they were digested in 2M HCl (80°C for 2 hours), washed using deionized water then digested in 1M KOH (80°C for 2 hours). The digestion was repeated until no further humic acids were extracted. The residue was rinsed free of alkali, digested in 1M HCl (80°C for 2 hours) then rinsed free of acid, dried and homogenized. The total carbon in the treated sample was recovered as CO_2 by heating in a sealed quartz tube and converted to graphite by Fe/Zn reduction. The NaOH insoluble fraction was treated with hot 10% HCL, filtered and dried. Results were calibrated to calendar years using the CALIB 5.1 radiocarbon calibration program (Stuiver et al. 2005). An age model was developed using a combination of linear and polynomial interpolation between adjacent calibrated dates and the ages of pollen zones approximated.

Twenty seven samples were sub-sampled for pollen analysis at the Palynology and Palaeobotany Laboratory of the NMK in Nairobi. The standard laboratory procedure of acetolysis and removal of silica by HF was used to concentrate the pollen grains (Faegri and Iversen 1975). One slide was mounted per processed sample under a 22x40 mm cover slip. Pollen counts were performed using a Leitz microscope at x400 magnification; critical identifications were made using x1000 magnification under oil immersion. The percentages of total fossil pollen were calculated from the pollen sum (minimum 500 pollen grains) with aquatic pollen and spores excluded from the pollen sum counted in each of the levels analyzed, but unknown and undifferentiated pollen grains included.

3.2 Charcoal analysis

Charcoal fragments were counted from pollen slides to determine size class distribution. Given the assumption of a homogenous distribution of charcoal particles on a pollen slide (Clark et al. 1989), counts were made on successive traverses across the pollen slide until a minimum of 500 fields under x400 magnification of view were completed. Charcoal particle selection was limited to fragments that are black, opaque and angular in form (Waddington 1969; Patterson et al. 1987; Pitkänen and Huttunen 1999; Clark 1982, 1988a, 1988b; Clark et al. 1989). When processing for pollen analysis, acetolysis mixture darkens or blackens plant fragments (Rhodes 1998; Blackford 2000; Carcaillet et al. 2001). Hence only angular fragments were enumerated and any fragments less than 3µm were excluded as they cannot be reliably identified (Blackford 2000). Samples prepared for pollen analysis probably do influence charcoal size distribution by fragmenting larger pieces although this was not taken into consideration but the influence is considered standard across the core sample. In some cases smaller charcoal fragments may reflect biotite, pyrite or macrasite (Rhodes 1998). The charcoal counts for each size class are presented as the total number of fragments per 500 fields of view. The count-based charcoal data is divided into four classes (3 to 25 µm, 26 to 75 µm, 70 to 150 µm and >150 µm). The charcoal data is plotted alongside the core stratigraphy and radiocarbon dates using TILIA and TILIAGRAPH (Grimm 1991). To aid comparison with the pollen data the location of the pollen zones is also shown.

4. RESULTS

4.1 Chronology

Chronological control of the sediments is provided by five AMS radiocarbon samples that were chosen on the basis of changes in the stratigraphy or proxy data (Table 1). Based on observation and interpretation in the field the stratigraphy divides into three different sections. The sediments from 270 to 200 cm core depth comprise brown peat and herbaceous material, and from 200 to 50 cm dark compacted peat with herbaceous material and roots. From 50 cm to the top of the core sediments are characterized by poorly humified peat comprised of fibrous roots herbaceous remains (Table 1).

Laboratory code	Sample depth (cm)	Sample Age ^{14}C yr BP	Age (cal yr BP)	δ^{13}C	Dated material
WK-24681	57	1565±30	1653 ±30	-11.4	Very high charcoal concentration, charcoal fragment dated
SUERC-22553	100	2252 ±30	2260±65	-10.7	End of charcoal peak Charcoal fragment used for dating
WK-24680	145	7607±30	7569±30	-14.4	Decreasing in charcoal concentration, Peat dated
SUERC-17195	245	7763±40	8535±49	-21.8	Range finders and decline in forest taxa, wood fragment dated
WK-18791	270	8535±30	9519±22	-20.4	Low presence of fire and open forest, wood fragment dated

Table 1. Radiocarbon dates showing laboratory code, sample depths, ^{14}C age, calibrated age, ^{13}C value and the type of material dated.

The age-depth relationship was established with a combination of linear and polynomial regression (Fig. 2) that shows two periods with relatively linear sediment accumulation rate: from 10,000 cal yr BP to approximately 8000 cal yr BP, and from approximately 2500 cal yr BP to the top (present day). The sedimentation rate is approximately 1cm per 20 years. For these sections of the core pollen and charcoal analysis is carried out at 10 cm intervals giving a temporal resolution of approximately 200 years between sampling points. Between the dates of 7569±30 cal yr BP at 145 cm and 2260±65 cal yr BP at 105 cm the sedimentation rate is much slower and the temporal resolution of the analysis reduces dramatically to approximately 1000

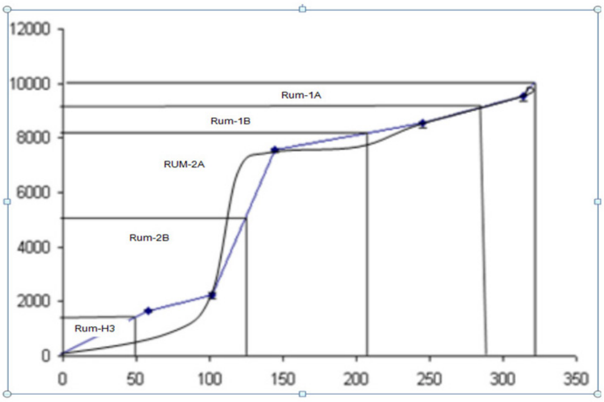

Figure 2. Polynomial and linear age vs. depth curve based on five ^{14}C dates. The position of the pollen zone boundaries is shown.

years between each 10 cm sampling point. We acknowledge there may be a break in sediment accumulation during this period. However, there is no evidence from the stratigraphy neither from the sediment analysis, such as a change in sediment type or rapid change in any of the palaeoenvironmental consistent across the proxies to indicate the presence of such a break in sediment accumulation.

4.2 Pollen record

The cluster analysis of the data identifies three pollen zones labelled Rum-H1, Rum-H2 and Rum-H3 with zones Rum-H1 and Rum-H2 divided into subzones Rum-H1A, Rum- H1B and Rum-H2A and Rum-H2B respectively. Results are presented as pollen diagram (Fig.3).

The pollen taxa are grouped together in Afromontane, Ericaceous, Herbaceous, Woodland, Aquatic and Spores ecological groups as shown in (Fig. 3). Pollen analysis in Rumuiku Swamp sediments yielded 135 identifiable taxa of terrestrial plants and 8 aquatic taxa (Table 2). These taxa are show in the appendix.

Consistent with the swamp location in the montane zone, 31 pollen taxa in the pollen diagram are associated with Afromontane ecosystem and three taxa from the Ericaceous belt ecosystem. Among the three common taxa that belong in the Ericaceous belt include *Artemisia, Cliffortia* and Ericaceae. Of the common pollen taxa represented in the pollen diagram five are herbaceous (including Poaceae), three belong to the Woodland ecosystem and the remaining four pollen taxa are classified as aquatics and assumed to be from the local populations of the aquatics. Cyperaceae and *Myriophyllum* are common in all zones while *Hydrocotyle, Nymphaea, Typha* and the algal colonies of *Spirogyra* are rare in the pollen diagram.

Zone Rum H-1 extends from 10,000 to 8200 cal yr and we recognized two subzones with a transition at 8900 cal yr BP. *Polyscias* records high percentages (35%) about 10,000 cal yr BP decreasing from 9500 cal yr BP towards the subzone boundary where it reaches a constant level (15%). *Schefflera* increases to 40% at 9500 cal yr BP and decreases towards the subzone boundary. *Allophylus, Croton, Macaranga, Morella, Neoboutonia, Olea* and *Rapanea* all increase in subzone Rum H-1B. Other montane taxa, include *Afrocrania, Alchornea* and *Olea* record low percentages (<2%) although become more common in pollen subzone Rum H-1B relative to Rum H-1A. *Apodytes, Croton, Ilex, Hagenia, Lasianthus* and

Rapanea are sporadically present, particularly in pollen subzone Rum H-1B. Asteraceae

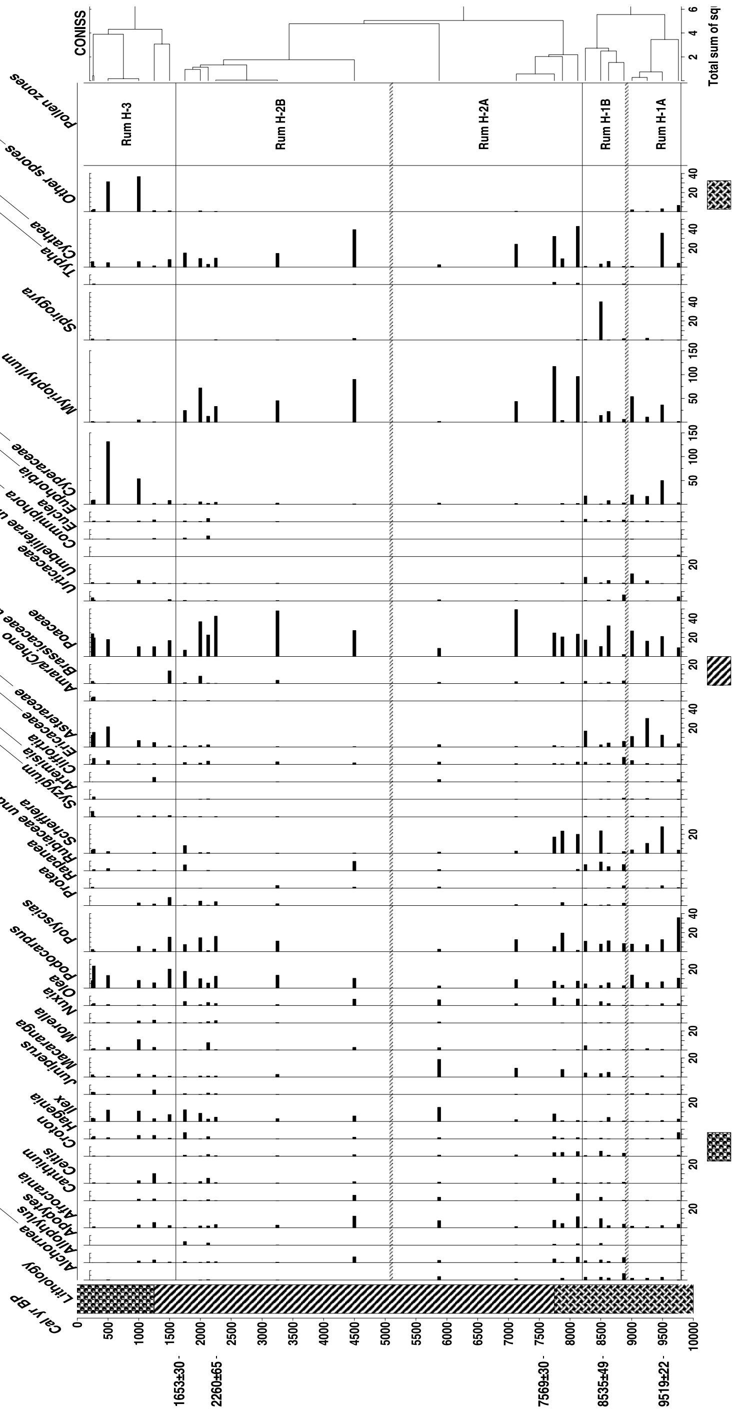

Figure 3. Pollen percentage diagram showing changes in proportions of selected taxa plotted against a linear age scale (cal yr BP). Taxa are grouped in the ecological categories Afromontane vegetation, Ericaceous vegetation, Woodlands, Herbaceous vegetation and Aquatics.

increases to 30% in subzone Rum H-1B before decreasing to 10% towards the subzone boundary. Poaceae are present throughout the zone reaching 30% towards the subzone boundary. Cyperaceae and *Myriophyllum* attain their highest percentages about 9500 cal yr BP before decreasing towards the subzone boundary.

Zone Rum H-2 extends from 8200 to 1600 cal yr BP and is divided into two subzones at 5100 cal yr BP. The pollen zone is dominated by montane forest taxa (*Afrocrania Alchornea, Apodytes, Canthium, Celtis, Hagenia, Ilex, Lasianthus, Macaranga, Protea, Morella* and *Olea*) that are present throughout the pollen zone but are less common in pollen subzone Rum H-2B. *Ilex, Macaranga* and *Polyscias* are present at about 10% with many of the montane forest taxa reaching highest percentages about 6000 cal yr BP before recording low percentages throughout the rest of the zone. Brassicaceae, Urticaceae and Umbelliferae are sporadically present when Poaceae is abundant and fluctuating between 10 and 45%. *Myriophyllum* and *Cyathea* are abundant, especially in the first half of subzone Rum 2-A.

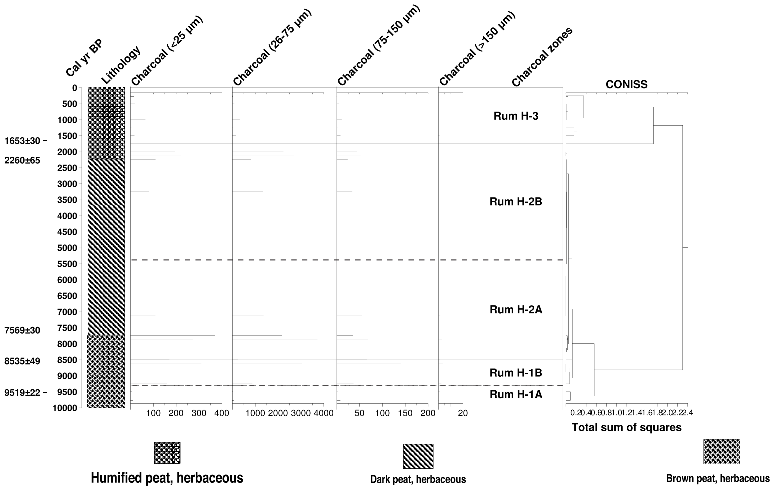

Figure 4: Diagram showing charcoal counts counted as the number of charcoal fragments within four size classes enumerated during microscopic examination of samples prepared for pollen analysis.

Zone Rum-H3 extends from 1600 cal yr BP to recent. Mixed montane forest taxa (*Afrocrania, Alchornea, Allophylus, Apodytes, Celtis, Croton, Hagenia, Lasianthus, Macaranga, Neoboutonia, Nuxia, Olea,* and *Polyscias)* are all present at low percentages <10%. Ilex and Morella record high percentages (>10%) relative to the previous zone with Ilex especially abundant from 1000 to 500 cal yr BP. *Podocarpus* dominates the zone increasing to >40% about 100 cal yr BP. Similarly from 1000 cal yr BP Asteraceae increases to 25% with Brassicaceae, *Protea, Rapanea, Typha, Schefflera*, Umbelliferae, Urticaceae and algal colonies of *Spirogyra* being sporadically present within some levels. Poaceae is constantly present at about 20%. Cyperaceae shows a large increase from 1000 to 500 cal yr BP. *Myriophyllum* records low percentages throughout the pollen zone. *Cyathea* is present at consistently low levels (15%) from 1500 cal yr BP towards the core top.

4.3 Charcoal record

The pollen zone boundaries are plotted to highlight the stratigraphical relationship between the pollen and charcoal data which show coeval shifts. The charcoal content in pollen zone Rum H-1 is variable: from 10,000 to 9250 cal yr BP values are very low before a subsequent increase to high counts in all size classes. The large charcoal classes (75-150 µm and > 150 µm) reach a maximum around 8800 cal yr BP before a secondary peak in the small fragments around 8000 cal yr BP (Fig. 4). The charcoal in pollen zone Rum H-2, although starting at very high concentrations is generally characterised by decreasing levels to a minima about 4500 cal yr BP before increasing. There is a peak in the small class size about 2400 to 2000 cal yr BP. The charcoal in pollen zone Rum H-3 is characterized by low concentrations towards the core top (Fig. 4).

5. Environmental reconstruction and discussion

The pollen data from Rumuiku Swamp records a highly dynamic ecosystem within the catchment that has undergone notable changes in composition and abundance over the Holocene. Pollen and charcoal data from Rumuiku Swamp sediment records a mixture of Afromontane taxa from 10,000 to 8900 cal yr BP. The montane forest taxa were dominated by *Podocarpus, Polyscias* and *Schefflera* with *Allophylus, Celtis, Cyathea, Croton, Lasianthus* and *Nuxia* reflecting a relatively moist environment with low presence of fire. The forest appeared to have been relatively open as demonstrated by the high presence of Asteraceae and Poaceae. The wider East Africa palaeoecological evidence indicates the early Holocene was warm and moist (Kiage and Lui 2006). From 8900 cal yr BP Afromontane forest became more diverse in the Rumuiku Swamp catchment, possibly, as recorded by the massive increase in charcoal concentration, likely to be related to fire. Palaeoecological research on Mount Kenya (Wooller et al. 2000), as elsewhere in the tropics (Haberle et al. 2001), has clearly shown strong variability in fire events throughout the late Quaternary. Most notable about 9000 cal yr BP is and intensity within the Rumuiku Swamp catchment. Fire can be central to disturbance regimes that, by promoting intermediate and small-scale environmental instability, promote species diversity (Connell 1978; Laurance and Williamson 2001). Once burnt, the forest may become more open and fragmented and thus even more susceptible to drought and fire. This phenomenon also has been reported for the Amazon (Laurance and Williamson 2001). Such large infrequent disturbances like wildfires are experienced by many ecosystems: particularly common in lowland dry forests where these events can shape ecosystem composition and structure for decades to hundreds of years, for example through their effects on tree recruitment and mortality (Gillson 2006). Certainly the periods of increased charcoal recorded at Rumuiku Swamp last for a significant duration and clearly reflect either a phase of environmental change and impact on the forest composition.

A period of pronounced ecological change within the Rumuiku Swamp catchment about 8200 cal yr BP is characterized by large increases in *Cyathea* and *Myriophyllum* and reduced Poaceae with a broad decrease in Afromontane vegetation. There are taxa normally indicative of relatively moist conditions; such an interpretation is also supported by a decrease in charcoal indicative of a less flammable environment. Although, the resolution of most palaeoecological sites in the early Holocene is quite poor (Marchant et al. 1997). most, sites that do have a sedimentary sequence record forest pollen types continue to dominate (Coetzee 1967; Bakker and Coetzee 1972; Maitima 1991; Beuning et al. 1997; Olago 2001). It has been suggested that an ‘8.2 event’ was characterized by dry conditions across East Africa (Alley and Ágústsdóttir 2005; Rohling and Pälike, 2005). One site with good resolution is the ^{18}O and aerosol icecore record from Kilimanjaro that indicates a warm early Holocene with a variable and much wetter climate apart from about 8200 cal yr BP when two contiguous samples show an increase in wind-blown fluoride from dry lake surfaces (Thompson et al. 2002). The increase in *Cyathia* and *Myriophyllum* at Rumuiku Swamp may reflect local colonization of the swamp surface and hence also record a relatively dry environment, the nature of this event clearly warrants further investigation.

East African palaeoecological records show that the mid Holocene is recorded as relatively dry with a transition from wet to dry conditions in the mid Holocene being recorded by changes in the water balance in many African lakes (Maitima 1991; Gasse 2001). From 7850 to 6840 cal yr BP the pollen record from Lake Victoria shows a transition from evergreen to deciduous forest type (Kendall 1969). Such proposed regional aridity is a little at odds to some of records on Mount Kenya that recorded negative shift in ^{18}O diatom between 7580 and 6370 cal yr BP, corresponding with enhanced graminoids, shrubs and forest taxa reflective of wetter and warmer conditions (Barker et al. 2001). However, Coetzee (1967), recording a pollen assemblage from a lake situated a little higher than Rumuiku Swamp at 2400 m, shows evidence of a cooler and drier climate between 7100 to 6100 cal yr BP. The Kilimanjaro ice core ^{18}O record indicates that cooler and drier conditions dominated in East Africa from 6200 to 5200 cal yr BP (Thompson et al. 2002). A relatively short lived wet phase recorded at Lake Challa from 6800 to 5500 cal yr BP (Verschuren et al. 2009) broadly corresponds with the timing of neoglacial glacier advance on Mount Kenya (Karlén et al. 1999). This period is not reflected by the sediments at the Rumuiku Swamp catchment as interpretation is hampered by very slow sediment accumulation and / or a probable hiatus centered around 6000 cal yr BP.

Afromontane forest taxa in the Rumuiku Swamp catchment became more open between 5800 and 4500 cal yr BP marked by an increase in Poaceae. Regionally, drought has been recorded from 5000 to 2500 cal yr BP across tropical Africa (Msaky et al. 2005; Maitima 1991; Thompson et al. 2002; Richard and Dussinger 1986; Elenga et al. 1994; Barker et al. 2001). For example, the Lake Bogoria pollen sequence shows an abrupt disappearance of high altitude forest pollen such as Ericaceae, *Hagenia, Hypericum* and *Stoebe*, and increases in more drought-adapted taxa such as *Acacia, Dodonaea, Juniperus* and *Podocarpus* after 5170 cal yr BP (Vincens 1986). It is now clear that major drought occurred in most parts of Eastern Africa centred about 4000 cal yr BP (Marchant and Hooghiemstra 2004). Termination of this extensive and pervasive period of aridity appears to have ended relatively abruptly (within decades to a century) (Thompson et al. 2006). If these high magnitude / high frequency environmental changes were abrupt responses to gradual changes in incoming solar radiation, then it would require additional forcing by nonlinear processes, possibly through vegetation and/or ocean temperature feedbacks (deMenocal et al. 2000). Such strong feedbacks between ecosystem composition and generation of local moisture availability have been clearly shown from Mount Kenya (Rucina et al., 2009).

Considerable climate variability and associated ecosystem response was experienced across East Africa in the last two millennia with lakes experiencing low and high stands (Verschuren et al. 2009). Increased soil erosion, ice advances and forest expansion on Mount Kenya have been interpretated as reflecting increased convective rainfall from 2900 to 1900 cal yr BP (Barker et al. 2001). Closer to the Rumuiku Swamp catchment a biogenic silica record from Hausberg Tarn on Mount Kenya indicates a warm period from 2300 to 1500 cal yr BP (Rietti-Shati et al. 1998). From 2000 to 1500 cal yr BP the Rumuiku Swamp catchment reflects more open Afromontane forest and increased grassland indicative of a mosaic of open and closed canopy forest. The period is also characterized by an increase in charcoal suggesting the Rumuiku Swamp catchment also experienced irregular fire events. This period is followed by another period of strong drought as recorded from 2050 to 1850 cal yr BP from Lake Edward (Russell and Johnson 2005). Other sites from East Africa show lake levels rising rapidly after extremely low levels about 2000 cal yr BP (Barker et al. 2001; Verschuren 2001; Russell and Johnson 2005). The continued low presence of Afromontane forest in the catchment, including taxa such as *Afrocrania, Alchornea, Celtis, Hagenia, Ilex, Macaranga, Morella* and *Olea*, suggests more open vegetation around the catchment. *Ilex* and *Morella* increased from 1000 to 500 cal yr BP with *Podocarpus* becoming the most important taxon in the forest. Fire resistant *Morella* became important in the catchment: this taxa often reflects a more open Afromontane woodland grassland mosaic due to burning and/or anthropogenic clearance (Finch et al. 2009). An increased abundance in Poaceae at Namelok Swamp, located in the savanna environment to the south of Mount Kenya, from 2000 to 1675 cal yr BP also is likely to respond to a drier climate at this time (Rucina et al. 2010). Sediments from Crescent Island Crater Lake and Lake Turkana located to the north of Mount Kenya also record this desiccation phase (Halfman et al. 1994; Rickets and Johnson 1996). Similarly, the low levels of Lake Tanganyika experienced before 1750 and after 1450 cal yr BP recorded a period of drought (Alin and Cohen,2003). Three most prominent dry episodes within the last two millennia are recorded at Lake Challa from 2000 to 1600 cal yr BP, from 800 to 600 cal yr BP and from 200 to 150 cal yr BP (Verschuren et al. 2009). Although these droughts are known to have had broad regional impact, particularly in the drier lowlands (Rucina et al. 2010), montane vegetation in East Africa appear to be relatively buffered from these impacts. Such a buffering is at odds to significant expansion of glaciers on Mount Kenya occurred around 1200 cal yr BP and 300 cal yr BP (Karlén et al. 1999) indicative of both responsive nature of mountain environments and the lagged ecosystem response. The timing of the maximum dry period from 1200 to 1000 cal yr BP recorded in the Rumuiku Swamp fossil pollen correlates well with higher tropical Atlantic sea surface temperatures coeval with the 'Mediaeval Warm Period' (Keigwin 1996; deMenocal et al. 2000; Brncic et al. 2009).

During the last 250 cal yr BP there were increased amounts of Asteraceae, Cyperaceae, Poaceae, *Podocarpus* and ferns within the Rumuiku Swamp catchment. The conversion to a more open forest suggests anthropogenic disturbance although the nature of this was quite different to that of extensive clearance and conversion of forest to agriculture. It is always difficult to differentiate a climate signal from the impact of anthropogenic activities, particularly when there is lack of direct archaeological evidence to constrain the interpretation (Robertshaw et al. 2003). This is particularly the case in this study due to limited archaeological research on Mount Kenya. Within wider East Africa there is an abundance of archaeological sites that document a transition through Iron Age development with associated movement of Bantu migrants from areas to the west, bringing with them a distinctive language, ceramic culture and possibly greater range of agricultural crops and increased food production to support a growing population (Holl 2000; Taylor et al. 2000; Marshall 2000; Robertshaw 1990; Sutton 1993, 1998). More generally the African archaeological evidence indicates that, outside of Egypt, agriculture was a late phenomenon compared to other continents, developing from about 2500 cal yr BP (Neumann 2005). It is apparent from the palaeoecological record that the Holocene in East Africa has been characterized by alternating phases of regional drought and flood that may have induced people to seek areas of greater or more reliable precipitation away from lowland areas towards higher elevations. The reasons why certain areas have not experienced extensive forest clearance whereas other areas have can stem from a number of possible causes for the persistence of the Afromontane forest on Mount Kenya when other areas have been a focus of extensive clearance. These include: (a) the ground is more dissected and potentially less favorable to agriculture, (b) the area presently covered by the forest was furthest from the main influx of agriculturists and simply therefore the last area to be reached, or (c) there has been some degree of protection by the resident indigenous population. Situations a and b seem unlikely as there is extensive agriculture on much more mountainous terrain such as Mount Elgon to the West and Kilimanjaro to the South. As suggested for elsewhere in East Africa (Taylor et al. 2000), the forests on Mount Kenya may well have corresponded to some form of disputed border between territories and had some protected afforded by the resident Kikuyu for which Mount Kenya is a sacred location; associated value beliefs with the mountain would have placed severe limitations on the development of sedentary agriculture. Interestingly, within the Rumuiku Swamp catchment the focus of this clearance appears to have been quite different to other areas in East Africa where selective logging has been recorded and where *Podocarpus* was a particular focus of forest clearance (Marchant and Taylor 1998).

Within the Rumuiku Swamp catchment *Podocarpus* appears to have been preserved and now forms almost mono-specific stands. An explanation for such a situation may be found in the Kikuyu belief system and associated agricultural practice. Kikuyu believe in trees possessing spirits that can interfere in human affairs: by leaving a series of large conspicuous trees at regular intervals they can absorb spirits from those trees cut down (Castro 1991). Alternatively, a more mundane reason such as leaving these trees to hang bee hives off or to provide a convenient supply of forest products, however, *Podocarpus* is not a preferred tree for such a use (Castro 1991).

6. Conclusions

The observed changes in forest species over time reveals that the composition of the vegetation within the Rumuiku Swamp catchment responds to both climate change and more recently human interaction. Pollen and charcoal data from Rumuiku Swamp show that the early Holocene (from 10,000 to 8000 cal yr BP) forest was characterized by a mixture of afromontane taxa and ericaceous vegetation, in particular the families Asteraceae and Ericacaeae. It has been suggested that an '8.2 event' was characterized by dry conditions across East Africa although within the Rumuiku Swamp catchment afromontane vegetation reflect relatively warm and moist climate with a rise in charcoal concentration reflecting increasingly frequent fires. This 'contradiction' of a more mesic forest type with evidence of increased fires may be reflecting different signals: with fires within the catchment and climate aridity allowing plants to colonize the swamp surface. The mid Holocene was characterized by a relatively warm and moist environment with more open vegetation and decrease in charcoal indicative of a less flammable environment. However, the middle Holocene section of the Rumuiku Swamp core is poorly resolved, either due to very low sediment accumulation or a sedimentary hiatus. The last 3000 to 2000 years records relatively minor changes in forest composition with the vegetation increasingly dominated by *Podocarpus* and Asteraceae that is reflective of the present day open and disturbed afromontane forest within the Rumuiku Swamp catchment. Thus, the new palaeoecological record from Mount Kenya shows the vegetation is responsive to climate change and more recently human interaction. Such an understanding is important to contextualize how current environmental change will impact on Mount Kenya vegetation, and the associated goods and services that people who live on the mountain are reliant on.

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APPENDIX

Table 2: Pollen taxa identified in the Rumuiku Swamp sediments.

Pollen taxa identified in Rumuiku Swamp sediments, Mount Kenya	Family	Life form	Ecological zones associated with each of the pollen taxa identified
Abutilon	Malvaceae	H	Common in secondary forest
Acacia	Mimosaceae	T	Common in wooded grassland, bushlands in dry environments
Acalypha	Euphorbiaceae	S / H	Common in moist forest, woodlands, grasslands and riverine vegetation
Acanthaceae	Undifferentiated	H	Common in most dry land habitats
Afrocrania	Cornaceae	T	Locally common in wet upland (e.g. *Ocotea*) forest or in bamboo zone
Albizia	Mimosaceae	T	Locally common in dry or wet, lowland or upland forest edges. Also along riverine forest
Alchornea	Euphorbiaceae	T	Found on moist forest forests
Allophylus	Sapindaceae	T	Dry or moist forest (remnants) and riverine forest
Amar./Cheno.	Undifferentiated	H	Widely distributed and common as a weed of cultivated land in hotter climates
Anthocleista	Loganiaceae	T	Common along rivers in forest areas, in swamps edges (cabbage tree)
Anthospermum	Rubiaceae	T	Heath zone or moorland or mountains; also on rocky hills in grassland or bush land; rarely in forest margins.
Antidesma	Euphorbiaceae	T	Wooded grasslandnand secondary bushland at forest edge, riverine and moist forest.
Apodytes	Icacinaceae	T	Upland dry forest (also in edges or remnants) less often in wet upland forest may also be locally dominant in dry forest.
Artemisia	Asteraceae	H /S	Colonizing burnt areas; locally common in heath zone; grassland, upland bushland (edges), forest edges.
Asteraceae	Undifferentiated	H	variable weeds, annual in disturbed places, grasslands / forests
Bosquea	Moraceae	T	Common in moist forests.
Brassicaceae	Undifferentiated	H	Escape, occasionally introduced
Canthium	Rubiaceae	T	Common in moist *Ocotea* forests

Capparaceae	Undifferentiated	S / T	Dry bushland or bushed grassland
Caryophyllaceae	Undifferentiated		Wooded grasslands
Cassipourea	Rhizophoraceae	S /T	Moist evergreen (*Ocotea)* forest. S Mt Kenya
Celtis	Ulmaceae	T	Dry moist evergreen forest; also in riverine forest.
Chlorophytum	Liliiflorae (Hyacinthaceae)	H	Shady wet places in forest
Cissampelos	Menispermaceae	C	Common in swamps
Clausena	Rutaceae	T / S	Moist or dry forest margins or secondary bushland
Clematis	Ranunculaceae	C	Forest margins, bamboo / *Hagenia* / heath zone, secondary bushland
Cleome	Capparaceae	H	Local in upland rain forest margins, sometimes a weed in cultivated land
Clerodendron	Verbenaceae	S / C	Wooded grassland, forest clearings
Cliffortia	Rosaceae	S	Bamboo glades, moorland; may for pure stand
Cocculus	Menispermaceae	H	Uncommon in riverine vegetation
Combretum	Combretaceae	T	Riverine forest
Commelina	Commelinaceae	H	Seasonally swampy grassland
Commiphora	Burseraceae	T	Dry semi-deciduous dense bushland or low dry forest on rocky slopes
Corchorus	Tiliaceae	S	Seasonally in wet shallow soils and roadsides
Cordia	Boraginaceae	T	Common in wooded grassland, forest, riverine,
Croton	Euphorbiaceae	T	Moist or dry evergreen upland forest (remnants, edges; also riverine forest
Cucurbitaceae	Undifferentiated	C	Common in dry bush land especially where disturbed.
Cuscuta	Convolvulaceae	C	Common in forest areasparasite
Cyathea	Cyatheaceae	T	Moist evergreen forest along streams and in valleys;
Cyperaceae	Undifferentiated	?	Aquatic and terrestrial in some cases after rain
Dombeya	Sterculiaceae	T	Forest, often in *Podocarpus* or *Hagenia* forest
Dracaena	Dracaenaceae	T	Moist forest or bamboo
Drypetes	Euphorbiaceae	T	Dry (or less often moist) upland forest or riverine forest.
Ekebergia	Meliaceae	T	Common in dry forest (*Podo/Olea* types), less often in moist often at forest edge or in forest remnants; also in riverine forest.
Ericaceae	Undifferentiated	S	In rocky high-altitude bushland;

			co-dominant in a zone above *Hagenia* belt on high mountains.
Euclea	Ebenaceae	S / T	Dry forest (margins), riverine in bushland or forest bushed grassland or pasture.
Euphorbia	Euphorbiaceae	T / S	Dry or moist upland forest; also in bamboo zone
Faurea	Proteaceae	T / S	An Afromontane form in forest margins and secondary (wooded) grassland derived from forest at (1800-) 2200-3100m.
Ficus	Moraceae	T/ S/ L	Riverine forest
Galium	Rubiaceae	C	Swamps and moist woodland
Gnidia	Thymeleaceae	S	Dry forest (margins) or evergreen bushland.
Gunnera	Haloragaceae	H	Uncommon in riverside marshes and low vegetation in the upper forest levels.
Gynodropsis	Capparidaceae	H	Common as a weed of cultivation and disturbed roadside, and in dry bush land.
Hagenia	Rosaceae	T	Dominant in the woodland zone just above bamboo; also in moist forest below the bamboo.
Heliotropium	Boraginaceae	S / H	Locally common in dry bushland
Hydrocotyle	Umbelliferae	C	Quite common on the forest floor in and below the bamboo zone
Hygrophila	Acanthaceae	H	Woodland, thicket, forest and damp grassland.
Hypericum	Guttiferae	T	Dry forest margins, *Hagenia*/bamboo zone, *Hypericum* zone.
Hypoestes	Acanthaceae	H	Forest undergrowth or on forest edges, 1600-3300m.
Hyptis	Labiatea	H	Swamp grassland.
Ilex	Aquifoliaceae	T	Moist (or dry) upland forest, also river forest.
Impatiens	Balsaminaceae	H / S	Common in wet places in the lower highland forest.
Indigofera	Papilionaceae	H	Moist grasslands / especially in rocky places
Ipomoea	Convolvulaceae	H	Frequent in riverine forest edges.
Juniperus	Cupressaceae	T	Drier upland forests, associated with *Podocarpus, Olea* or *Croton*.
Justicia	Acanthaceae	H	Locally common in dry disturbed places
Kedrostis	Cucurbitaceae	C	Deciduous (Acacia-Commiphora) bushland.

Kohautia	Rubiaceae	H	Uncommon in dry country
Labiatae	Undifferentiated	H	Common in woodlands and forest edges
Lannea	Anacardiaceae	T / S	Wooded grassland, usually in rocky sites.
Lasianthus	Rubiaceae	T / S	Moist (Ocotea) forest
Legume	Undifferentiated		Widely distributed in most ecosystems
Leucas	Labiatae	H	Locally common in disturbed bushland
Liliaceae	Undifferentiated		Woodlands and flood plains
Loranthaceae	Undifferentiated		Parasite
Ludwigia	Onagraceae	H	In rivers, ditches, pools or on moist sites
Macaranga	Euphorbiaceae	T	Moist forests, especially near streams.
Maesa	Myrsinaceae	T	Widespread, often in secondary forest. A pioneer in forest margins.
Malvaceae	Undifferentiated		Woodlands, bushlands and grasslands
Merremia	Convolvulaceae	H	Widespread in rocky grassland and bush land.
Moraceae	Undifferentiated		Woodlands and riverine
Myrica	Myricaceae	S / T	(*Protea*) bush land
Myriophyllum	Callitrichaceae	H	Uncommon in riverside marshes and low vegetation in the upper forest levels,
Neoboutonia	Euphorbiaceae	T	Upland forest, mostly on edges and in clearings.
Newtonia	Mimosaceae	T	Riverine, swamp or moist forest, locally common.
Nuxia	Loganiaceae	T	In light upland or montane forest, and often very common
Nymphaea	Nymphaeaceae	H	Common in swamps and lakes
Oenostachys	Pontederiaceae	H	Uncommon in montane grassland.
Olea	Oleaceae	T	Wet and dry upland evergreen forest.
Pavetta	Rubiaceae	S	Forest; less often in secondary bush land derived from forest
Phyllanathus	Ephorbiaceae	S	Dry upland forest margins and clearing, also in riverine forest or woodland
Pittosporum	Pittosporaceae	T	Drier evergreen forest, often in isolated forest clumps.
Plectranthus	Labiatae	H	Moist forest undergrowth, locally common
Poaceae	Undifferentiated	H	Commonly common.
Podocarpus	Podocarpaceae	T	Upland forest, drier and wetter zones

Polygonum	Polygonaceae	H	Common in disturbed ground, often secondary
Polyscias	Araliaceae	T	Wet upland forest or riverine forest
Potamogeton	Potamogetonaceae	H	Locally common in slow-moving water as well as in lakes
Protea	Pittosporaceae	S / T	On rocy slopes in *Hagenia*, moorland or heath zone of Mt.Kenya or Cherangani, Elgon.
Prunus	Rosaceae	T	Moist evergreen forest, riverine, often in remnants or on margins.
Raninculus	Ranunculaceae	H	Uncommon in marshy places near streams
Rapanea	Myrsinaceae	T	Widespread, particularly in upland dry forest and rocky hillsides.
Rhus	Anacardiaceae	S / T	Riverine forest; less often in wooded grassland or forest margins.
Ricinus	Euphorbiaceae	H	In a wide variety of habitats, from bushed grassland to rainforest; often ruderal.
Rubiaceae	Undifferentiated		Common in most habitats in our area
Rubus	Rosaceae	S	Riverine, disturbed forest, forest margins, secondary bush land.
Ruelia	Acanthaceae	H	Dry (rocky) bush land; also in woodland or dry wooded grassland.
Rumex	Polygonaceae	S	Bushed grassland, rocky bush land, often in damp sites a weed in pasture.
Rutaceae	Undifferentiated		Woodlands/bushalnds
Sapindaceae	Undifferentiated		Wet forests, woodlands
Sapotaceae	Undifferentiated		Moist forest and dry woodlands
Schefflera	Araliaceae	T	Wet or dry upland forest, sometimes in *Hagenia* woodland or bamboo zone
Solanum	Solanaceae	S	*Podocarpus* forest margins or bamboo zone;
Stemodia	Scrophulariaceae	H	Rare in rock crevices in dry country
Stephania	Menispermaceae	L	Forest margins, riverine, bamboo and *Hagenia* zone
Stoebe	Asteraceae	S	Heathzone and moorland, also in bamboo-and *Hagenia-Hypericum* zones. Locally dominant.

Striga	Scrophulariaceae	C	Locally common in dry grassland
Syzygium	Myrtaceae	T	Riverine
Tapinanthus	Loranthaceae	S	Lakeside, riverine and mid-altitude western forests.
Tarenna	Rubiaceae	S	Bush land on rocky hills, drier forest (margins), thickets (often riverine), bushed grassland
Teclea	Rutaceae	T / S	Evergreen forest, thickets on rocky hills, riverine, Wooded grassland. Common in dry forests
Terminalia	Combretaceae	S / T	Deciduous bush land or woodland, often on rocky outcrops, or riverine
Tiliaceae	Undifferentiated		Woodlands, grasslands/bushlands
Trema	Ulmaceae	T / S	Forest margins, riverine (secondary) Bushland, a pioneer where forest has been disturbed.
Typha	Typhaceae	H	In swamps and fresh still permanent water.
Umbelliferae	Undifferentiated		Woodlands, grasslands and moist forests
Urticaceae	Undifferentiated		Moist forests and in rocky areas
Valeriana	Valerianaceae	H	Among tussock grassland in the alpine region
Vernonia	Asteraceae	H	Forest edges, cleared lands, woodland and grassland derived from forests, riverine or along lakeshores.
Vicia	Papilionaceae	H	Locally common in highland grassland and possibly indigenous although it has been cultivated
Ziziphus	Rhamnaceae	S	Dry bushland, woodland, wooded grassland.

CHAPTER 4

Late-Holocene savanna dynamics in the Amboseli Basin, Kenya

Stephen Rucina, Veronica M. Muiruri, Laura Dowton
and Rob Marchant

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Research paper

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Late-Holocene savanna dynamics in the Amboseli Basin, Kenya

Stephen M. Rucina,[1] Veronica M. Muiruri,[1] Laura Downton[2] and Rob Marchant[2]

Abstract

Pollen, microscopic charcoal and radiocarbon data are used to document changes in vegetation dynamics during the late Holocene from Namelok Swamp in the Amboseli Basin (Kenya). The data reveal changes in savanna vegetation composition driven by an interaction of climate change, anthropogenic and herbivore activities. The abundance of *Celtis*, *Podocarpus* and *Syzygium* reflects a relatively moist climate from around 3000 to 2400 cal. yr BP. Increased abundance of *Acacia*, Amaranthaceae/Chenopodiaceae and Poaceae suggest a drier and/or warmer climate from 2150 to around 1675 cal. yr BP. The expansion of *Syzygium* within the catchment and decrease in Amaranthaceae/Chenopodiaceae reflect a relatively wet phase from around 1675 to about 550 cal. yr BP – superimposed on this is a large increase in Poaceae from 1400 to 800 cal. yr BP indicative of a drier environment. The dominance of Amaranthaceae/Chenopodiaceae and Poaceae with an associated decrease in *Syzygium* from 550 cal. yr BP is thought to correspond to a drier climate. The uppermost samples, dating to the last 150 years, record a large increase in *Acacia*, Amaranthaceae/Chenopodiaceae and Poaceae with decrease in *Syzygium* and are attributed to recent land-use changes associated with increased sedentary settlement. The increased presence of *Cannabis sativa*, Cereal and *Ricinus communis* pollen, combined with charcoal in the sediment record, particularly from 2500 but more constantly from 1600 cal. yr BP, indicate a long history of human–ecosystem interaction in the Amboseli Basin that has implications for future management of the area.

Keywords

Amboseli, charcoal, human impact, Kenya, pollen, savanna

Introduction

As ecosystems respond rapidly to present and predicted future environmental shifts there is a pressing need to understand how these ecosystems have responded to past environmental changes. Information on past ecosystem dynamics can be retrieved from sediment archives analysed for their pollen context to quantify ecological change that has been driven by episodes of climate change, anthropogenic and herbivore activities. Unfortunately, palaeoecological records from savanna ecosystems are scarce because of lack of suitable sedimentary basins and, until relatively recently, much palaeoecological work in the tropics was traditionally focused in montane areas or on large lakes. Records that have been produced from savanna areas demonstrate a highly changeable ecosystem responding rapidly to climate change (Gillson, 2004; Taylor *et al*., 2005; Vincens *et al*., 2003) with a long history of human–ecosystem interactions. The late-Holocene environment of Kenya experienced marked climate variability, particularly rainfall shifts with wide-ranging impacts on ecosystems (Lamb *et al*., 2003). For example, a continent-wide shift to more arid climatic conditions around 4000 cal. yr BP (Marchant and Hooghiemstra, 2004) resulted in the savanna biome becoming much more open than previously, with lakes in East Africa experiencing very low levels (Bonnefille and Umer, 1994; Cohen *et al*., 1997). Over the past 2000 years water levels in Lake Naivasha and Lake Tanganyika fluctuated dramatically with a well-defined warmer/drier period recorded between 950 and 650 cal. yr BP, and further short periods of drought registered from 560 to 530, 490 to 325 and 190 to 150 cal. yr BP (Alin and Cohen, 2003; Verschuren *et al*., 2000).

Climatic shifts make the composition and distribution of savanna vegetation adjust quite dramatically (Higgins *et al*., 2000; Knoop and Walker, 1985; Scholes and Archer, 1997). Combined with fire, high rainfall variability will limit tree recruitment and create a patchy distribution of trees in space and time (Higgins *et al*., 2000; Gillson, 2004). Transitions from woodland to grassland-dominated savanna is generally attributed to more xeric environmental conditions with disturbance induced by fire, humans and/or large herbivores also being a strong control on savanna competition (Gillson, 2004; Western and Maitumo, 2004). Grassland to woodland transitions are also limited by recruitment events, but can be quite rapid possibly because of reduced disturbance or an abrupt shift to more favourable growth conditions (Bond and Midgley, 2000; Bond *et al*., 2002, 2005). For example, recent postindustrial increases of atmospheric CO_2 have been shown to aid the transition from grass- to tree-dominated savanna (Bond *et al*., 2005). This process is not due to direct CO_2 fertilization but

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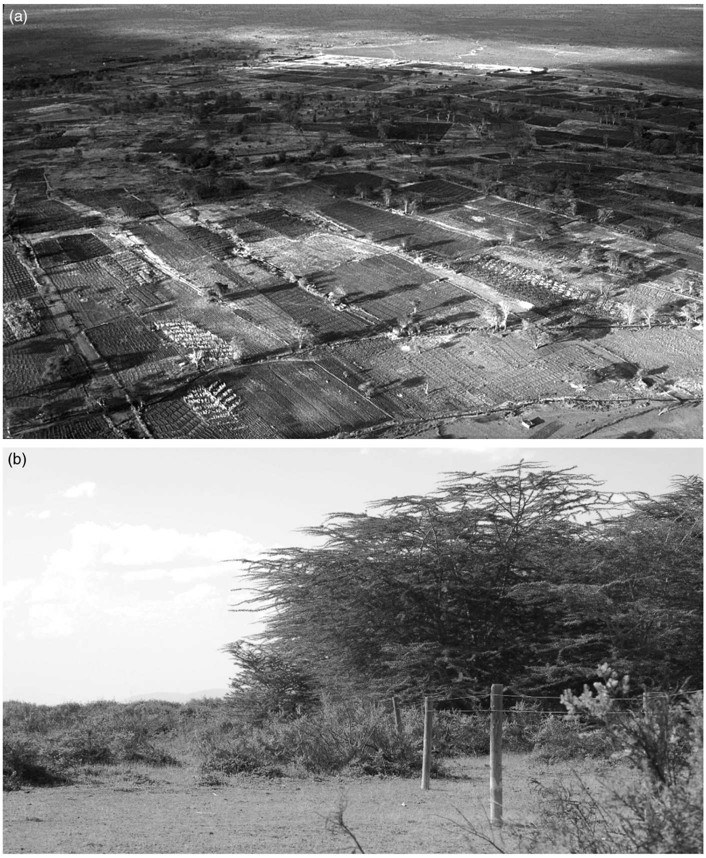

Figure 1. (a) Agriculture encroachment within the Namelok catchment and (b) the impact of elephant enclosures on the growth and extent of tree cover, the fence has been in existence for about seven years

to greater water-use efficiency of plants and increased growth rates of trees and shrubs so they grow above a height where fire regimes are able to maintain an open savanna patchwork (Bond *et al*., 2002). Grassland to woodland transitions may also be facilitated by a dramatic reduction in herbivore populations brought on by hunting (Dublin, 1995) or diseases such as rinderpest. When elephant populations decrease, or are controlled (Figure 1a), there is a rapid recovery of woody vegetation (Brockington, 2002; Dublin, 1991; Hakansson, 2004; Western and Maitumo, 2004).

Against this backdrop of continuous environmental shifts and savanna ecosystem response, East African ecosystems also experienced major human interactions during the late Holocene (Leiju *et al*., 2005; Marchant and Taylor, 1998; Taylor *et al*., 1999; Muiruri *et al*., unpublished data, 2008). One common signal from this increased interaction is of vegetation clearance to support a growing population with a combination of new crops and technologies as hunter-gatherer populations adopted, and/or were replaced by, a stock-herding pastoral subsistence economy that created open pasture (Marean, 1992). The landscape transformation process in East Africa was widespread, being recorded from montane to lowland savanna ecosystems – as increasing need for resources fuelled migration of pastoralists to the central Rift Valley between 1850 and 1100 cal. yr BP that led to land clearance for pasture (Bower, 1991). Accompanying these population migrations was the development of iron smelting technology from around 2000 cal. yr BP as evidenced by finds from the surrounding Eastern highlands, the coastal hinterland of Kenya and the Usambara and Pare Mountains of Tanzania (Phillipson, 1993). Herbaceous taxa became more abundant with the increase in large-scale food producing activities and associated management practices such as the use of fire. Such an impact is recorded on the Laikipia Plateau of central Kenya where burning of the savanna intensified from 1620 to 670 cal. yr BP (Taylor *et al*., 2005). Evidence from archaeological sites along the Galana River in Tsavo, Kenya suggests that mobility in some Pastoral Neolithic communities was restricted as they relied heavily on riverine resources (Wright, 2005, 2007). Archaeological evidence, including

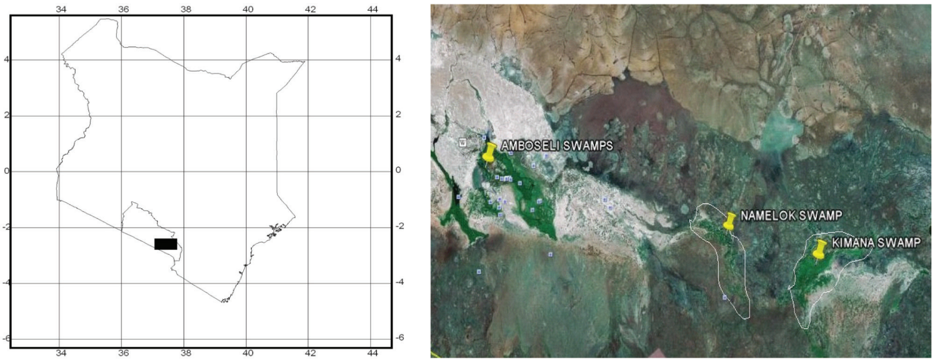

Figure 2. Map of Kenya (a) showing the study area region within the Amboseli Basin (b) and more details of the Namelok Swamp and environs (Source: Google, 2009)

pots and faunal remains, suggest that some populations continued to rely on hunting and gathering as their mode of subsistence (Childs and Killick, 1993). An increasing focus of research on the environmental history of East African ecosystems is to assess the timing and magnitude of human and large herbivore impact in relation to climate-driven changes in terrestrial ecosystems. Human impacts might have started sometime in the middle Holocene but large-scale vegetation disturbance is generally considered much more recent. The Amboseli Basin is a savanna ecosystem located northeast of Mount Kilimanjaro, famous for supporting high density and diversity of wildlife, especially the big herbivores, with the backdrop of Mount Kilimanjaro. Indeed, the hydrology of the Amboseli Basin is closely linked to precipitation and subsequent groundwater channelling to lowland springs and their associated swamps. The Amboseli Basin has recently been losing tree and shrub cover with expansion of open water and the spread of halophytic plants (Altmann *et al*., 2002; Western and van Praet, 1973; Young and Lindsey, 1988). These recent changes need to be placed within a long-term context to provide the temporal foundation for understanding the behaviour of this important location. We present a 3000 cal. yr BP palaeoenvironmental record from Namelok Swamp in the Amboseli Basin ecosystem, Kenya (Figure 2). This record is used to unravel the long-term ecology of the area and determine the climatic, anthropogenic and ecological influences on the ecosystem during the late Holocene.

Environmental setting, land use and climate

The Amboseli Basin, extending from the northern slopes of Mount Kilimanjaro on the Tanzania border to the savanna rangelands of Amboseli National Park, is characterized by strong ecological gradients. The surrounding area is described by undulating plains and volcanic hills that vary in altitude from about 500 m around Lake Magadi to 2500 m in the Ngong Hills; altitudes around 1200 m are most common. The climate of the area is dominated by a combination of the migrating Intertropical Convergence Zone (ITCZ) that seasonally moves north and south about the equator, and trade winds originating from the Indian Ocean. The diverse topography and locally high mountains break up classical circulation patterns (Griffiths, 1972; Trewartha, 1961) with moisture-bearing winds from the Indian Ocean also strongly influenced by the local topography that result in a highly variable local climate, particularly rainfall distribution. Temperatures vary both with altitude and season; monthly mean temperatures range from 34°C in February–March to as low as 12ºC in July (Altmann *et al*., 2002). The highest temperatures are recorded around Lake Magadi while the lowest minimum of 10°C is experienced at Loitokitok on the northeastern slopes of Mt Kilimanjaro. The district has a bimodal rainfall pattern; short rains fall between October and December while the long rains fall between March and May. Loitokitok, which has a higher elevation than the study site, records average rainfall around 1250 mm/yr while Magadi and Lake Amboseli (with slightly lower elevations than the study site) have an annual average rainfall of about 500 mm/yr. The rainfall pattern on the slopes of Mt Kilimanjaro (Loitokitok region) differs in that the rainfall from October to December is greater than the period from March to May. Heavy rains are largely convective and occur on the Ngong Hills, Chyulu Hills and the Nguruman escarpment.

Namelok Swamp

Namelok Swamp (2º54′52.50″S, 37º30′23.28″E; elevation 1146 m) lies in the Amboseli Basin, in the Kajiado District of southern Kenya (Figure 2). The area is dominated by Poaceae, and a tree/shrub layer of variable densities. Today the area is characterized by strong human impact that has converted much of the savanna into agricultural land (Figure 1a), being particularly intensive where water is available. The vegetation composition in the Amboseli Basin is determined by climate, soil type (including nutrient availability), plant symbiotic interactions, and disturbance by fire and interaction with herbivores (Gillson, 2004; Skarpe, 1992; Touber, 1993). The grasslands are dominated by *Chloris rocksburghiana*, *Eragrostis tennuifolia*, *Sporobolus homblei*, *S. robusta* and *S. spicatus*. In the flooded areas, *Psilolemma jaegeri* and common species of *Sporobolus* occur. The woodland and bushlands are composed of *Acacia drepanolobium*, *A. mellifera*, *A. nubica*, *A. tortilis*, *Aristida keniensis*, *Azima tetracantha*, *Commiphora* spp., *Eragrostis aspera*, *Salvadora persica* and *Solanum* species. The adjacent riverine areas are mostly dominated by *Acacia xanthophloea*, *Ficus thonningii*, *Salvadora persica* and two species of *Syzygium* (*S. cordatum* and *S. guineense*). *Syzygium cordatum* are recorded as small trees close to the swamp margins. Vegetation on the swamp surface is dominated by *Cyperus immensus* (Papyrus) with tussock species of the sedge *Carex*, principally *C. monostachya*, also present. The large tussock-forming grass *Pennisteum mildbraedii* is locally abundant on the swamp margins.

Local communities and land use

Amboseli National Park, initially called Maasai Amboseli Game Reserve and known locally as *Empusel* (meaning ‘salty, dusty place’ in Maa), covers a total of 390 km² just north of the Kenya–Tanzania border (Figure 2). The Park contains five swamps that are remnants of a previously more extensive but dried-up lake. In 1883, Joseph Thomson, one of the first Europeans to cross through the area, was astonished by the beauty of the region and extensive wildlife population focused around a lake. The contrast of arid land, dry lake beds and swamps astonished him, as it continues to astound visitors today. Amboseli was set aside as the ‘Southern Reserve’ for Maasai in 1906 but returned to government control as a Game Reserve in 1948. Gazetted a National Park in 1974 to protect the core of this unique ecosystem, it was declared a UNESCO Man and the Biosphere Reserve in 1991. The National Park which is famous for the free-ranging elephants; with open views towards Mount Kilimanjaro and is one of the cornerstones of the Kenyan tourism industry.

The Maasai, considered as the local community, traditionally practice semi-nomadic pastoralism on communally owned land. However, this lifestyle has undergone rapid recent change because of ongoing land tenure changes and subdivision of group ranches leading to individual land ownership. These changes have encouraged farming communities from other parts of Kenya to migrate to the areas of relatively high agricultural potential. Land sold is mainly of high and medium potential, thus pushing the local pastoralists to drier, more marginal parts of the district. Owing to these recent changes in lifestyle, particularly restrictions imposed on migration, the Maasai are increasingly turning to subsistence farming. Following this shift, many swamps have been exploited for irrigation of crops, particularly maize and beans (Figure 1a), furthermore, during the dry seasons, livestock are moved around the swampy areas for grazing and watering that can lead to local hydrological shortages and local tensions over resource use. The Kenya Wildlife Services (KWS) have used electric fences to preserve some of the swamps (Figure 1b) and adopted policies to reduce human–wildlife conflicts. These policies extend to areas adjacent to Amboseli National Park.

Methods and analysis

A 400 cm sediment core was raised from Namelok Swamp in 50 cm overlapping sections, using a 5 cm diameter Russian corer. The recovered sediments were described in the field and transferred into 50 cm PVC pipes sectioned in half, wrapped in aluminium foil and transported to the Palynology Laboratory of the National Museums of Kenya and later to the University of York for cold storage. The 400 cm core comprises organic sediment composed mainly of herbaceous plant material with occasional pieces of wood; variable amount of inorganic material is present with occasional charcoal fragments. The sediments below 291 cm comprise a dark peat with decomposed plant material. Radiocarbon dating was performed on four depth intervals of the core (78, 170, 270 and 370 cm). Bulk peat sediment samples from these depths were dried and packed in aluminium foil and sent to the University of Waikato Radiocarbon dating laboratory (New Zealand) where they were washed in hot 10% HCl, rinsed and treated with hot 0.5% NaOH. The NaOH-insoluble fraction was treated with hot 10% HCl, filtered and dried. The results were calibrated to calendar ages using CALIB 3.0 (Stuiver and Reimer, 1993) (Table 1). The dates were used to construct an age–depth profile (Figure 3).

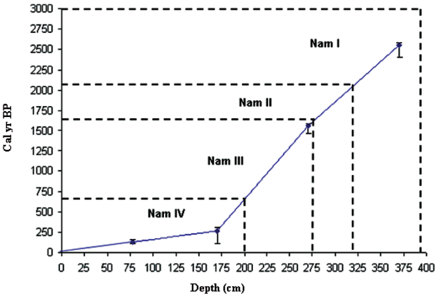

Figure 3. Calibrated age–depth plot showing the pollen zones from the pollen diagram (Figure 4)

A total of 41 samples were subsampled at 10 cm intervals and shipped back to the Palynology and Palaeobotany Laboratory, National Museums of Kenya (NMK) Nairobi for pollen analysis using the standard pollen concentration method (Faegri and Iversen, 1975). At least two slides were mounted per processed sample, with pollen counts done using a Leitz microscope at ×400 magnification; critical identifications were made using ×1000 magnification under oil immersion. A total of 78 terrestrial and 5 aquatic plant taxa were identified, with spores, unknown and undifferentiated taxa also recorded. To assist in identification, modern pollen reference slides from the Palynology Laboratory of the National Museums of Kenya were used. The percentages of total fossil pollen were calculated from the pollen sum with aquatic pollen, spores and Poaceae excluded from the pollen sum, but unknown and undifferentiated pollen grains included. Poaceae was considered as local taxa because of a combination of it dominating the pollen flora and numerous grasses growing on Namelok Swamp. The trees and shrubs were grouped together as arboreal taxa (AT) while herbaceous taxa were grouped as non-arboreal (NAT). Cyperaceae, *Hydrocotyle*, *Nymphaea* and *Typha* were grouped together as aquatics. Spores were grouped separately as undifferentiated spores. Percentages of the local taxa are calculated as a percentage of the non-local pollen sum and presented using the TILIA program 2.04 (Grimm, 1991) and plotted on an age scale using the calibrated age–depth relationship (Figure 4). Apart from *Cannabis sativa*, other pollen types that did not exceed 2% were excluded from the pollen diagram. CONISS was applied using numerical clustering package within the TILIA computer programme that identified four stratigraphic clusters of samples with similar floristic composition (Figure 4).

Table 1. Radiocarbon results showing the sample depth, sample age and the calibrated age

Publication code	Sample depth (cm)	Sample age (^{14}C yr BP)	Calibrated age (cal. yr BP)	AD	δ^{13}C
WT-18788	78	132±37	140±101	1811±101	−18.5
WT-22555	170	273±30	361±57	1589±57	−21.5
WT-22556	270	1558±30	1461±44	489±44	−19.1
WT-18789	370	2550±30	2650±85	700±85 BC	−22.6

Charcoal and loss-on-ignition analysis

Charcoal concentrations for each depth where there was pollen data were calculated using the Winkler (1985) method. Dried and weighed sediment samples (1 g) were digested in concentrated nitric acid then dried and re-weighed. A final weight is calculated after igniting at 450–500°C for 3 h. The percentage of charcoal is calculated as the difference of the dry weight before and after ignition, using Equation (1):

$$\frac{(NW - IW)}{DW} \times 100 = \%\ \text{charcoal} \qquad (1)$$

where, NW is the dry weight after nitric acid digestion, IW is the dry weight after ignition, DW is the dry weight of the sample.

The charcoal results are presented as a curve in the pollen diagram (Figure 4) using the TILIA and TILIAGRAPH software. The charcoal data are expressed as a percentage of charcoal dry weight and are plotted alongside the core stratigraphy and radiocarbon dates.

Results

Zone Nam I: 3000–2140 cal. yr BP

Acacia is abundant throughout the zone ranging from 10 to 20% with a decrease towards the zone boundary around 2140 cal. yr BP. *Acalypha*, *Anthocleista*, Capparaceae, *Celtis*, *Euphorbia*, *Maerua*, *Phyllathus*, *Podocarpus* and *Rhus* are sporadically present at percentages of <5%. *Salvadora* is common throughout the zone fluctuating about 5%. *Syzygium* is also common increasing to 15% around 2900 and 2700 cal. yr BP decreasing to <5% around 2800 to 2450 cal. yr BP, with low representation towards the pollen zone boundary. *Tarchonanthus*, *Tapinanthus*, *Tarenna* and *Terminalia* are occasionally present in the zone. The non arboreal taxa are dominated by Amaranthaceae/Chenopodiaceae which is common in zone Nam I; increasing to 25% from 3000 to 2800 cal. yr BP, further increasing to 30% around 2650 cal. yr BP before decreasing to 15% around 2400 cal. yr BP and increasing again to 25% at the zone boundary. Asteraceae is also common in the zone; it increases to 30% around 2900 and 2400 cal. yr BP later decreasing to <10% from 2700 cal. yr BP. This fluctuation corresponds in an antiphase manner with changes in Amaranthaceae/Chenopodiaceae percentages. The zone contains low cereal percentages around 2650 cal. yr BP. *Cissampelos, Commelina*, Cucurbitaceae and *Rumex* record very low percentages. *Impatiens* is commonly presently throughout the pollen zone, fluctuating from 5 to 10%. Other non-arboreal taxa present include *Indigofera*, *Justicia*, *Solanum* and *Tribulus*. Poaceae is present at constant percentages throughout the zone. Cyperaceae and Typha are present in low percentages. *Ficus* is present from 2300 cal. yr BP to the zone boundary. The charcoal content of sediment in Zone Nam I is generally low (<5%) increasing to 10% around 2600 cal. yr BP before decreasing back to <5% at the zone boundary.

Zone Nam II: 2140–1675 cal. yr BP

Acacia is present throughout the zone reaching a maximum of 15%, decreasing to about 5% around 1950 cal. yr BP before increasing again to 10% towards the zone boundary. Other arboreal taxa present in low percentages include *Acalypha*, *Anthocleista*, Capparaceae, *Celtis*, *Euphorbia*, *Pimpinella*, *Podocarpus*, *Tapinanthus*, *Tarenna* and *Terminalia*. *Salvadora* and *Ficus* records a low percentage from 2140 to 2050 cal. yr BP and increases to 15% about 1950 cal. yr BP before being almost unrepresented in the rest of the zone. *Tarchonanthus* was present from 2140 to 1950 cal. yr BP, but represented by two peaks of about 10% at 2100 and 1800 cal. yr BP. The non-arboreal taxa are dominated by Amaranthaceae/Chenopodiaceae that increase to 50% about 1800 cal. yr BP before decreasing rapidly towards the pollen zone boundary. Asteraceae is constantly present from the zone boundary at 2140 to 1800 cal. yr BP with a peak at 1700 towards the zone boundary. From 2140 to 1675 cal. yr BP Poaceae records increased percentages, with relatively low values at 1950 and 1700 cal. yr BP. Cyperaceae, *Hydrocotyle* and *Typha* are represented by low constant percentages throughout the pollen zone. Charcoal fluctuates between 5 and 10% throughout the pollen zone.

Zone Nam III: 1675–680 cal. yr BP

Acacia is present throughout this zone increasing from 5 to 10% with a peak at 1250 and 1000 cal. yr BP before decreasing around 1150 cal. yr BP and remaining <10% towards the zone boundary. Other arboreal taxa represented in sporadic percentages include *Acalypha*, *Anthocleista*, Capparaceae, *Celtis*, *Commiphora*, *Pimpinella*, *Podocarpus*, *Rhus*, *Salvadora*, *Tarchonanthus*, *Tarenna* and *Terminalia* with *Salvadora* attaining up to 10%. *Syzygium* dominates the zone increasing to 50% from 1675 to 1150 cal. yr BP, decreasing to 25% from 1150 to 950 cal. yr BP before increasing again to 55% at the zone boundary. In the non-arboreal taxa, Amaranthaceae/Chenopodiaceae decreases to 15% coincident with the increase in *Syzygium*. Asteraceae is present throughout the zone fluctuating about 15%. Non-arboreal taxa that are sporadically present include *Commelina*, Cucurbitaceae, *Hypoestes*, *Indigofera*, *Justicia*, *Ricinus*, *Rumex*, *Solanum* and *Tribulus*, with *Ricinus* becoming common from 1500 cal. yr BP. Poaceae although initially low increases to a peak centred around 1000 cal. yr BP. Cyperaceae is present throughout the zone with *Hydrocotyle* and *Typha* also represented. Charcoal fluctuates between 5 and 10% throughout the zone, becoming less common towards the pollen zone boundary.

Zone Nam IV: 680–0 cal. yr BP

Acacia is present throughout the zone; from 680 to 370 cal. yr BP it is almost constant at 10%, increasing to 20% about 300 cal. yr BP, decreasing to 10% before increasing to 40% from 50 cal. yr BP to present. Low percentages of *Acalypha*, *Anthocleista*,

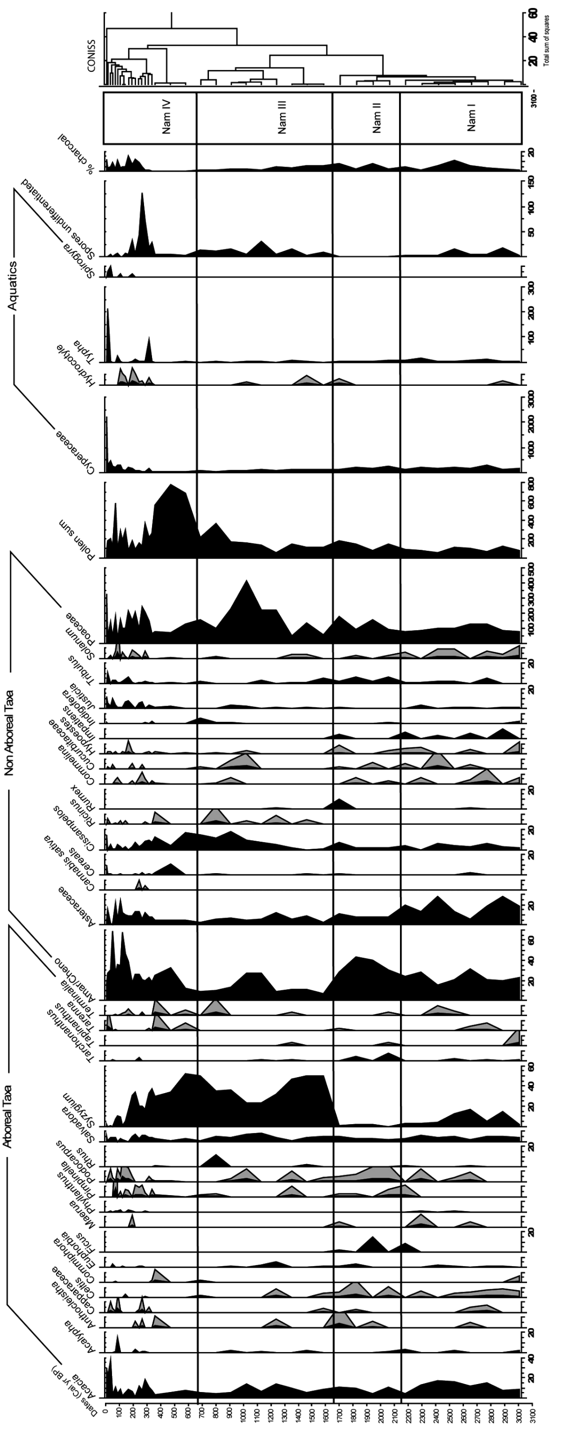

Figure 4. Namelok pollen diagram including charcoal percentages showing down-core changes in selected taxa of arboreal and non arboreal pollen types

Capparaceae, *Celtis*, *Commiphora*, *Euphorbia*, *Maerua*, *Phyllanthus*, *Pimpinella*, *Podocarpus*, *Salvadora*, *Tarchonanthus* and *Terminalia* are present from 400 to 100 cal. yr BP. From about 680 cal. yr BP *Syzygium* dominates the pollen flora at about 55%, the highest percentage attained by the taxon in the last 3000 cal. yr BP, before decreasing to 10% around 50 cal. yr BP and becoming almost absent at the end of the zone. Amaranthaceae/Chenopodiaceae, Asteraceae and Poaceae increase from 680 to 500 cal. yr BP. From 500 cal. yr BP to the end of the zone Amaranthaceae/Cheopodiaceae, Asteraceae and Poaceae are highly variable. *Cannabis sativa* is present from 300 to 250 cal. yr BP with 10% cereals from 580 to 400 cal. yr BP becoming common in low percentages towards the core top. The non-arboreal taxa of *Commelina*, *Cucurbitaceae*, *Hypoestes*, *Indigofera*, *Justicia*, *Ricinus*, *Solanum* and *Tribulus* are sporadically present throughout the zone. Cyperaceae, *Hydrocotyle* and *Typha* are present in variable amounts from 350 cal. yr BP to the end of the zone. Charcoal is particularly abundant from 350 cal. yr BP to present, increasing from <2 to about 10%.

Discussion

The vegetation composition of the Namelok swamp catchment is shown to vary over the past 3000 cal. yr BP with the savanna mosaic dominated by different amounts of *Acacia*, Amarathaceae/Chenopodiaceae, Asteraceae, *Cissampelos*, Poaceae and *Salvadora*. The late-Holocene period was characterised across Equatorial Africa by pronounced ecosystem shifts in response to a variable climate (Ngomanda *et al*., 2007). Changes in the composition of the ecosystem reflect a combination of changes in climate, human impacts and herbivory. The first major signal recorded by the sediments is an increased abundance of *Syzygium* from 2800 to 2400 cal. yr BP followed by *Podocarpus*; these changes are thought to be related to increased plant available moisture around the swamp. *Syzygium* is likely to have occupied a niche fringing the swamp/riverine habitat; a study on the representivity of the pollen from this taxon in surface sediments found percentages of the taxon in sediment samples to reflect the concentration in surrounding vegetation, in spite of the local source of the parent taxon (Hamilton and Perrot 1980; Marchant and Taylor, 2000). Such increase in local hydrology could be attributed to increased convectional rainfall on Mount Kilimanjaro that encouraged montane forest tree growth; indeed the montane forest taxa *Celtis* and *Podocarpus* are commonly present during this period. A rise in these montane trees could also be attributed to an increase in temperature that made the environmental conditions more suitable for the establishment of montane taxa. Such a drier period was observed around 2500 cal. yr BP in Kashiru area (Roche and Bikwemu, 1989). Closer to the Namelok site, increased soil erosion, ice advances and forest expansion on Mount Kenya have been interpretated as reflecting increased convective rainfall from 2900 to 1900 cal. yr BP (Barker *et al*., 2001). A subsequently drier climate in the Namelok record, somewhat earlier than on Mount Kenya at around 2400 cal. yr BP, is apparent from the low percentages of *Syzygium* (that become almost absent) as the abundance of *Acacia*, Poaceae, Amaranthaceae/Chenopodiaceae and *Salvadora* increased suggesting that the vegetation around Namelok was more open during the proposed desiccation phase. Drier conditions are recorded in the Lake Edward catchment centred around 2050 cal. yr BP, with the most pervasive drought being detected between 2050 and 1850 cal. yr BP (Russell, 2004; Russell and Johnson, 2005). This is a period when there is almost no *Syzygium* around the Namelok catchment with decreased presence of *Ficus.* Conversely Amarathaceae/Chenopodiaceae dominates the flora combined with an increased abundance in Poaceae from 2000 to 1675 cal. yr BP that is also likely to result from a drier climate. Sediments from Crescent Island Crater Lake and Lake Turkana located to the north of Kenya also record this desiccation phase (Halfman *et al*., 1994; Rickets and Johnson, 1996) as does the low levels of Lake Tanganyika before it experienced high levels from 1750 to 1450 cal. yr BP followed by drought (Alin and Cohen, 2003). Low abundance of wetland taxa such as *Typha* and Cyperaceae suggested that Namelok swamp was also less extensive as similarly recorded in Loboi Swamp (Ashley, 2004). Strong changes in ecosystem composition were experienced beginning 1675 cal. yr BP surrounding Namelok Swamp characterized by a high rise in *Syzygium* with a relative decrease in the presence of *Acacia*, Amaranthaceae/Chenpodiaceae, *Salvadora*, *Tribulus* and Poaceae. This ecosystem shift suggests the environment within Namelok catchment became wetter, similar to that reported from Lake Edward (Russel, 2004). Dramatic reduction in tree abundance over the last 1425 cal. yr BP in nearby Tsavo has been recorded with a grass phase dominating around 1380 cal. yr BP (Gillson, 2004). This change from a tree- to grass-dominated ecosystem is not recorded within Namelok ecosystem.

During the period from 1150 to 950 cal. yr BP *Syzygium* decreased with increases in *Acacia*, Amaranthaceae/Chenopodiaceae, *Euphorbia* and particularly Poaceae. This change is slightly earlier than the previously documented timing of the 'Mediaeval Warm Period' (MWP) dated to occur between 950 and 880 cal. yr BP at other sites in East Africa (Verschuren *et al*., 2000). This new record may suggest that the MWP stretched much earlier (Brncic *et al*., 2009). However, a climatic interpretation of the changes in the Namelok sediments is complicated as this is a period when there was a marked expansion of human activity as evidenced by increased overseas trade from 950 to 450 cal. yr BP (AD 1000 and 1500), increasing amount of ivory, iron and other commodities exported to the oriental and European countries (Alpers, 1992; Horton, 1987). Survey and excavations conducted in Tsavo East south of Galana River in Kenya reveals trade in Ivory between coast and Tsavo hunters in exchange of glass and beads by 750 cal. yr BP (Thorbahn, 1979). The vegetation within the Namelok Swamp catchment became more open – this could be attributed to the climate becoming drier and/or a decline in human impact (de Vere, 1993; Barber, 1968; Berntsen, 1976). Evidence from Lake Naivasha (Verschuren *et al*., 2000) and Lake Tanganyika (Alin and Cohen, 2003), to the northwest and southwest of Namelok Swamp respectively, both record significant low stands about this time. *Syzygium* increases again from 750 to 500 cal. yr BP; this ecosystem shift may reflect increased moisture availability registered as increased dominance of *Syzygium* swamp forest. Asteraceae, *Cissampelos* and *Syzygium* decreased with increases in *Acacia*, Amaranthaceae/Chenopodiaceae, Cyperaceae and particularly Poaceae from 500 to 250 cal. yr BP that are thought to reflect a drier climate. A similarly dry climatic period, coeval with the 'Little Ice Age', has been identified from western Equatorial Africa (Ngomanda *et al*., 2007). Ostracod assemblages from Lake Tanganyika record this period as a lake level fall (Russell, 2004). Results from Lake Naivasha also indicate low stands around 560 to 530 and 390 to 325 cal. yr BP (Verschuren *et al*., 2000). Further decreases of *Syzygium* around Namelok Swamp, concomitant with increases in *Acacia*, Amaranthaceae/Chenopodiaceae, Asteraceae, *Justicia* and Poaceae with increased charcoal abundance, are also thought to be indicative of a drier climate. This vegetation change in the Namelok Swamp catchment is centred from 200 to 150 cal. yr BP at a time of regional drought with potential cultural impacts (Webster, 1979, 1980). Further changes in vegetation were experienced from 150 cal. yr BP when *Acacia*, *Acalypha*, Amaranthaceae/Chenopodiaceae, *Pimpinella* and particularly Poaceae increased. Historical sources albeit from Malawi indicate a very arid period from 150 to 110 cal. yr BP (Nicholson, 1995; Verschuren, 2001) although the resolution of the record from Namelok Swamp is not fine enough to detect these changes.

It is always difficult to differentiate a climate signal from the impact of anthropogenic activities, particularly when there is lack of direct archaeological evidence to constrain the interpretation (Robertshaw *et al*., 2003). This is particularly the case in the study owing to the limited archaeological research in the Amboseli Basin. Within the wider area of the Rift Valley there are an abundance of archaeological sites that date from 2500 cal. yr BP and document a transition through Iron Age development with associated movement of migrants and increases in food production to support a growing population (Marshall, 2000; Robertshaw, 1990; Sutton, 1993, 1998). The abundance of pasture within the Amboseli Basin would have encouraged movement of pastoralists into the area and with ensuing exploitation of the swamps, especially during dry periods when the permanent swamps acted as drought refuges. The presence of *Cannabis sativa*, cereal and *Ricinus communis* pollen grains in the Namelok sediments as early as 2650 cal. yr BP is thought to reflect early settlement around the swamp. The cultural transformation is thought to be part of a regional development stage: ceramic wares and other material culture found in the Rift Valley being associated with the so called Savanna Pastoral Neolithic (SPN) (Marshall, 2000; Robertshaw, 1988; Sutton, 1998). During this time, the pastoralists with cattle moved into Rift Valley grasslands practicing transhumance, moving through many areas from Laikipia to northern Tanzania (Sutton, 1998). Evidence of SPN culture is present within the study area: the Rombo Iron Age site (H. Kiriama, unpublished data, 1992) is situated close to the Amboseli Basin. Farther north, remains of cattle and evidence of cereals at Deloraine Farm site in the central Rift Valley indicate how pastoralism and agriculture had expanded (Sutton, 1998). Associated with the SPN is a significant impact on surrounding ecosystems; forest clearance, mainly by burning of forests, to create room for new pasture and agriculture would have been widespread in East Africa. Interestingly, the pollen record shows that *Ricinus communis* (Castor oil plant), a native plant to East Africa, is most common from 1600 cal. yr BP with cereals becoming dominant after 600 cal. yr BP. This transition is likely to be indicative of a recent change in subsistence with the growth in cereal production focused within the last 500 years, however with intercropping of *Ricinus communis*. Cereal and *Ricinus communis* pollen grains are also recorded in Lake Masoko sediments in southern Tanzania from 1550 cal. yr BP onwards with increased Asteraceae indicative of human disturbance of vegetation for agriculture and pastoralism (Vincens *et al*., 2003). Further evidence for the presence of humans are the remains of Ceramic smoking pipes at some sites in the Rift Valley used to smoke *Cannabis sativa*, a custom derived from the coast (Sutton, 1998); it is thus likely that agriculturalists in the Amboseli Basin were involved in the cultivation of the weed and were trading with coastal habitats. A remarkable increase in *Asteraceae* and Amararanthaceae/Chenopodiaceae in the last 130 years is coincident with greater charcoal percentages that are thought to mark a period of increased agricultural activity in the Namelok catchment with more permanent settlements leading to a localized and profound impact on the vegetation.

Although changes in the savanna ecosystem composition are likely to be climatic and more locally human-induced, it should be stressed that changes in herbivore densities would have played an important role in controlling vegetation change (Figure 1b). The outbreak of cattle diseases in the twentieth century had a devastating impact on the region when a massive decrease in the cattle population encouraged the increase of herbaceous taxa and displacement of pastoralists encouraging trade between the Kamba and Kikuyu cultures (Jackson, 1976; Turner *et al*., 1998). Elephants, as all large herbivores, play a major role in vegetation transformation in East Africa (Hakansson, 2004). This impact can be specifically seen within Amboseli National Park recently as the elephant population has increased over the past 40 years following a ban on ivory export, reduced poaching and intensified regional agriculture and sedentarisation (Western and Maitumo, 2004). Various studies on the relationship between elephant populations and vegetation densities in East Africa show that vegetation is open when the population of elephants is high; when the elephant population reduces there can be rapid recovery of woody species (Brockington, 2002). There have been massive recent historical changes in elephant population size, particularly relating to the ivory trade. Trade in ivory was widespread in Kenya, especially between the coastal ivory traders, exporters and interior communities such as the Kamba from the end of the 1700s (Lamphear, 1970, Soper, 1976), where the Kamba people became the dominant ivory traders. The movement of the Kamba people from Kilimanjaro to the Chyulu Hills between 510 and 420 cal. yr BP (Soper, 1976) might have significantly contributed to hunting of elephants with consequent impact on the vegetation. The Maa speaking people also became fully involved in trade e.g. beads, clothes from the coast in exchange for ivory (Krapf, 1968). At the height of the ivory trade in the mid-nineteenth century some 12 000 animals were removed per year from East Africa (Sheriff, 1987). The impact of such massive numbers on the ecosystem are unknown but it must have been significant, particularly when considered that the present population in Amboseli is around 1600 individuals and these are known to have a key role in controlling ecosystem composition and structure (Figure 1a).

In the last 150 years *Acacia* expanded with increase in Amaranthaceae/Chenopodiaceae, Cyperaceae, Poaceae and *Typha*. Charcoal also became abundant with increased anthropogenic activities. In addition to climatic and herbivory influences already discussed this ecosystem response may also relate to a rise in CO_2 that has been shown to favour growth rates of plant species, particularly drought-tolerant trees such as *Acacia*, as a result of greater water use efficiency and subsequent growth rate (Bond and Midgley, 2000; Bond *et al*., 2005; Kimball *et al.*, 1993; Laurence *et al*., 2004; Orchard and Maslin, 2003; Polley, 1997). Conversely, these ecosystem changes may result from changes in elephant and cattle population; the impact is presently unknown but research, particularly focusing on the dung fungi such as *Sporormiellai* spores, is ongoing and could be used to reconstruct past changes in herbivore densities, When used in conjunction with pollen analysis we should be able to unravel the interaction with the ecosystem composition within the Amboseli Basin. Ecosystem impacts of climate change have to be placed in a broader context: tropical forests worldwide are threatened by many factors associated with human population pressure and climate change (Wright and Muller-Landau, 2006). Major threats to ecosystems include changes in land use and fire (Bayliss *et al*., 2007; Hemp, 2006); selective harvesting, and climate change (Lewis *et al*., 2004). Because of the high human population densities and close association with primary resources from ecosystems (fuel, non-timber forest products, game) the long-term future of African savanna ecosystems depends on the development of policies which promote research capacity and the ability for communities to contribute to, and benefit from their conservation.

Conclusions

Analysis of the Namelok Swamp sediments have shown the dynamic nature of the surrounding savanna ecosystem during the late Holocene. The changing nature of the savanna ecosystem for the past 3000 years demonstrates interaction between climate variability, human activity and animal–plant interactions. Vegetation transformations resulted from climate variability, particularly following hydrological changes with episodes of droughts and increased precipitation. Changes in the density of herbivore populations and a growing human population are likely to have played a role, especially recently, but climate remained a major driver behind savanna dynamics. Anthropogenic activities contributed to changes in vegetation composition following resource exploitation and usage of the savanna ecosystem, initially for pastoralism and more recently for mixed agriculture, particularly from around 500 cal. yr BP. More recently the impact of ecosystem management and environmental change, such as increased atmospheric CO_2, are potentially recorded by recent ecosystem shifts in the Namelok Swamp catchment.

The long-term ecological information from the Namelok swamp is useful for future management of the surrounding savanna under a period of predicted climate change, increasing human impacts, human–wildlife conflicts and rising levels of atmospheric CO_2. Because of the high human population densities and close association between people and the primary resources from African savanna ecosystems we need to promote the ability for communities to contribute to, and reap maximum benefit from their conservation. For example, community-based approach for the future management of natural resources with balanced equitable distribution of power and economic benefits that reduces conflicts, increased consideration of traditional values and modern environmental knowledge offers the best potential to protect biological diversity and the sustainable utilization of the resource. The successful implementation requires a legal and policy framework that will empower local communities and grant them responsibility and authority to control natural resources in their area. However, such a framework also must incorporate knowledge on how these ecosystems have interacted with changing climates, human and animal populations over an ecologically meaningful time frame – results presented here can form part of that knowledge base.

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CHAPTER 5

High-resolution late-Holocene vegetation dynamics of lowland savannah near Mt. Kilimanjaro in equatorial East Africa

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Abstract

High-resolution pollen analysis (~ 40-yr interval) on late-Holocene sediments recovered from Lake Challa in southeastern Kenya, and supported by a well-constrained 210Pb- and ^{14}C-based chronology, show changes in adjacent lowland savannah and dry forest as well as more distant montane forest ecosystems reflecting the vegetation response to regional climate variability over the last 2700 years. Century-scale episodes of climatic drought are recorded by local increases in the pollen percentages of Poaceae and certain dry savannah trees and shrubs (*Combretum, Commiphora, Salvadora* and *Rhus)* and herbs (*Corchorus* and Urticaceae), and reductions in other common savannah trees and shrubs such as *Maerua* and *Sideroxylon*. The increased presence in Lake Challa sediments of montane forest pollen (*Celtis, Juniperus, Olea* and *Podocarpus*) during these inferred dry-climate periods suggests a greater distribution in lowland of trees from Mount Kilimanjaro slopes. Also indicative of dry climatic conditions is increased pollen from Cyperaceae and *Typha* spreading on the exposed margins of nearby shallow lake basins experiencing lowstands; the steep-sided Lake Challa itself is unlikely to have been the source of this aquatic-plant and sedge-swamp component. The combined pollen evidence indicates that regional environmental conditions were drier than today from 2700 to 2300 cal yr BP, from ~1800 to 1500 cal yr BP, from ~1300 to 800 cal yr BP (broadly encompassing the Medieval Climate Anomaly), and from ~250 to 70 cal yr BP. Conversely, wetter conditions than today are inferred for the periods from ~2300 to 1800 cal yr BP, from ~1500 to 1300 cal yr BP, and from ~800 to 300 cal yr BP (broadly encompassing the Little Ice Age). The Challa pollen record indicates that the wettest regional climate of the last 2700 years occurred from ~600 to 300 cal yr BP, when lowest Poaceae percentages combine with peak percentages of *Euphorbia,* the succulent trees which also today characterize vegetation on the steep inner slopes of the Challa basin. Significant presence of cereal pollen from ~150 to 50 cal yr BP, accompanied with increases in herbaceous plants indicative of ecosystem disturbance, reflect an increasingly human impacted landscape surrounding Challa crater from shortly before the colonial period.

Key words: Kenya, Mt. Kilimanjaro, Little Ice Age, pollen, savannah

1. Introduction

An increasing number of high-resolution pollen studies in equatorial East Africa (Lamb et al. 2003; Ashley et al. 2004; Immaculate et al., 2005; Leiju et al., 2005; Rucina et al., 2009; 2010) document the broad patterns of vegetation change during the late Holocene. For example, the pollen record from Namelok Swamp in Amboseli Basin north of Mt. Kilimanjaro (Figure 1) records high abundances of *Celtis, Podocarpus* and *Syzygium* from 2700 to 2400 cal yr BP, followed by an environmentally drier period from 2150 to 1675 cal yr BP characterized by increases in *Acacia*, Amaranthaceae-Chenopodiaceae and Poaceae (Rucina et al., 2010). Although the principal patterns of reconstructed vegetation change in equatorial East Africa are broadly coherent across space, there is considerable uncertainty on the exact timing of events, often due to a combination of limited sampling resolution and relatively poorly constrained chronology. Further, the signatures of climatic and human impacts on East African vegetation remain difficult to disentangle (Marchant and Taylor, 1998; Taylor et al., 1999; Lamb et al., 2003; Ssemmanda et al., 2005). As a result, data on the last few thousand years, when humans are thought to have increasingly affected the landscape, are not sufficiently resolved or robust to constrain our understanding on often complex and subtle signals of environmental change (Darbyshire et al., 2003; Lamb et al., 2003; Verschuren, 2004; Cohen et al., 2005). In this context, we present here the results of high-resolution pollen analysis on the uppermost, 2700-year-long section of a continuous and well-dated sediment record from Lake Challa, a crater lake straddling the Kenya-Tanzania border in the eastern foothills of Mt. Kilimanjaro (Figure 1). Lake Challa is the focus of multi-proxy paleoclimatological and paleoecological studies at multiple time scales (e.g., Verschuren et al., 2009; Moernaut et al., 2010; van Geel et al., 2011; Wolff et al., 2011). The record of late-Holocene vegetation change in the Lake Challa region presented here provides a benchmark to constrain the timing and relative magnitude of climatic and historical human impacts on the dry tropical lowland savannah ecosystem of eastern equatorial Africa.

2. Study site and regional climate

Lake Challa (3° 19S, 37° 42E) is a 4.2 km^2 and 94 m deep crater lake, filling a steep-sided volcanic caldera at 840 m elevation immediately northeast of Mt. Kilimanjaro (Figure 1). The study area is part of the East African plateau with elevations between 500 and 1500 m, dotted with mountain ranges associated with the Eastern Rift Valley and Eastern Arc Mountains (Figure 1b). Natural vegetation in the wider savannah landscape of the study area is a mixture of open deciduous woodland and open bush- and grasslands (Figure 1c) adapted to high temperatures and pronounced seasonal drought.

Lake Challa is located in the equatorial zone where twice-yearly passage of the Intertropical Convergence Zone (ITCZ) over the adjacent western Indian Ocean creates a bimodal rainfall pattern, with southeasterly monsoon winds bringing 'long rains' from March to mid-May and northeasterly monsoon winds bringing 'short rains' from late October through December. The local climate is tropical semi-arid, with monthly mean daytime temperatures ranging from 26 °C in July–August to 30 °C in February–March. Total annual rainfall is ca. 565 mm year−1 and surface evaporation ca. 1735 mm year−1, resulting in a negative water balance for Lake Challa (Payne, 1990). The lake is maintained by shallow groundwater originating from rainfall falling higher up the slope of Mt. Kilimanjaro. Rainfall in East Africa is spatially modified by the dissected topography of the plateau, and inter-annually by cyclic fluctuations in sea surface temperature linked to the Indian Ocean Dipole and the El Niño Southern Oscillation (Marchant et al ., 2006). Today Challa crater is surrounded by mostly open bush and grass savannah with scattered woodland trees and shrubs, and strips of moist riverine forest in (seasonally dry) stream gullies (White, 1983); the northern and western outer slopes of the caldera are

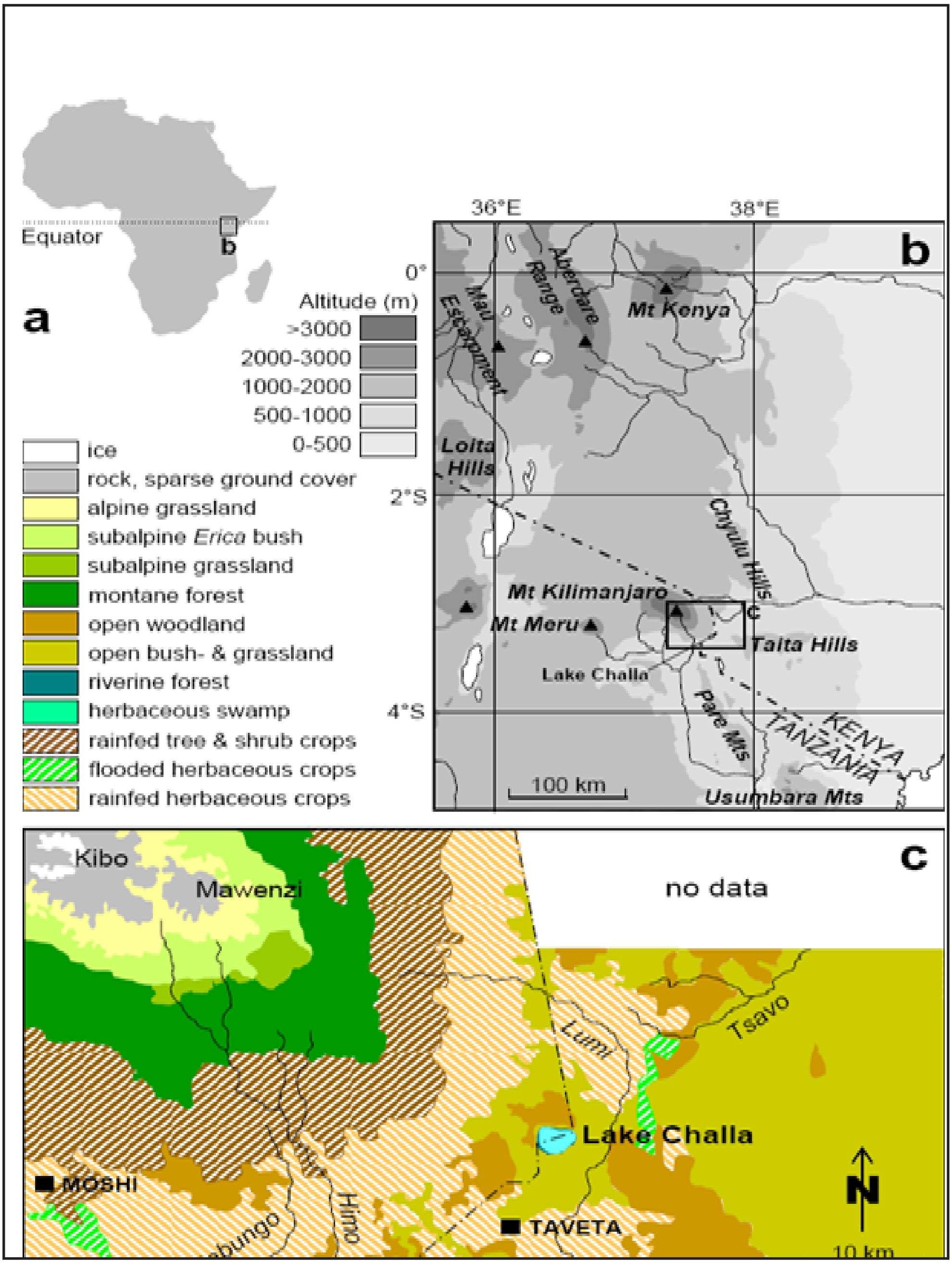

Figure 1: Location map of Lake Challa in equatorial East Africa showing regional topography and vegetation. Most of the larger study area is part of the East African plateau characterized by elevations between 500 and 1500 m, and with mountain ranges associated with the Eastern Rift Valley (and Eastern Arc (lower right B) (Source: van Geel et al., 2011).

covered with dry colline forest composed of *Acalypha fruticosa* and *Acacia species* (Hemp, 2006; Figure 1c). The inner crater slopes are covered by a narrow strip of evergreen forest growing on rock-fall along the shoreline; a dense 'succulent' forest dominated by *Commiphora baluensis* and *Euphorbia bussei* on steep middle slopes; and dry grassland with *Acacia* scrub on the gentler slopes below the crater rim. Increasing human activity across the region is rapidly replacing the woodland with agricultural fields of rain-fed herbaceous crops such as maize, sunflower, millet and beans, and managed grasslands supporting pastoralists herding cattle. Open bush and grassland with patches of woodland in the immediate vicinity of Challa crater is however still relatively undisturbed, as is natural vegetation inside the crater.

3. Material and methods

Between 1999 and 2005, increasingly longer sediment profiles were recovered from a midlake location (3° 19.05′ S, 37° 41.88′ E) in Lake Challa. Descriptions of the sediments profiles are shown in Table 1.

Coring method	Coring number	Depth (cm)	Material
Hammer driven	CH05-1G	0-12	Core section and excision that consists largely of re-deposited crater slope material
(UWITEC) Piston core	CH05-3P	12-25	Core section and excision that consists largely of re-deposited crater slope material
Kullenberg	CHO3-2K	25-250	Core section and excision that consists largely of re-deposited crater slope material. An overlap of re-deposited crater slope material and constituted a continous long composite sequence of mostly finely laminated organic mud rich in diatom silica
Kullenberg	CHO3-2K	42-250	Core section and excision that consists largely of re-deposited crater slope material. An overlap of re-deposited crater slope material and constituted a continous long composite sequence of mostly finely laminated organic mud rich in diatom silica

Table 1: Stratigraphy and lithological description of sediment cores collected in Lake Challa, Kenya.

Contiguous sections of gravity core CH05-1G (0-12 cm), hammer-driven piston core CH05-3P (12-25 cm) and Kullenberg core CH03-2K (25-250 cm) together form a composite sequence of perfectly undisturbed and finely laminated organic deep-water sediments easily cross-correlated using the visual markers of individual sediment laminae. This uppermost portion of the longer Lake Challa sediment record currently recovered (Verschuren et al., 2009) was dated using 57 accelerator mass spectroscopy (AMS) ^{14}C dates on bulk organic carbon, corrected for an evolving lake-carbon reservoir age through combination with 210Pb-dating of recent sediments and wiggle-match dating of two prominent Δ^{14}C anomalies in the radiocarbon calibration curve (Blaauw et al., 2011; Figure 2).

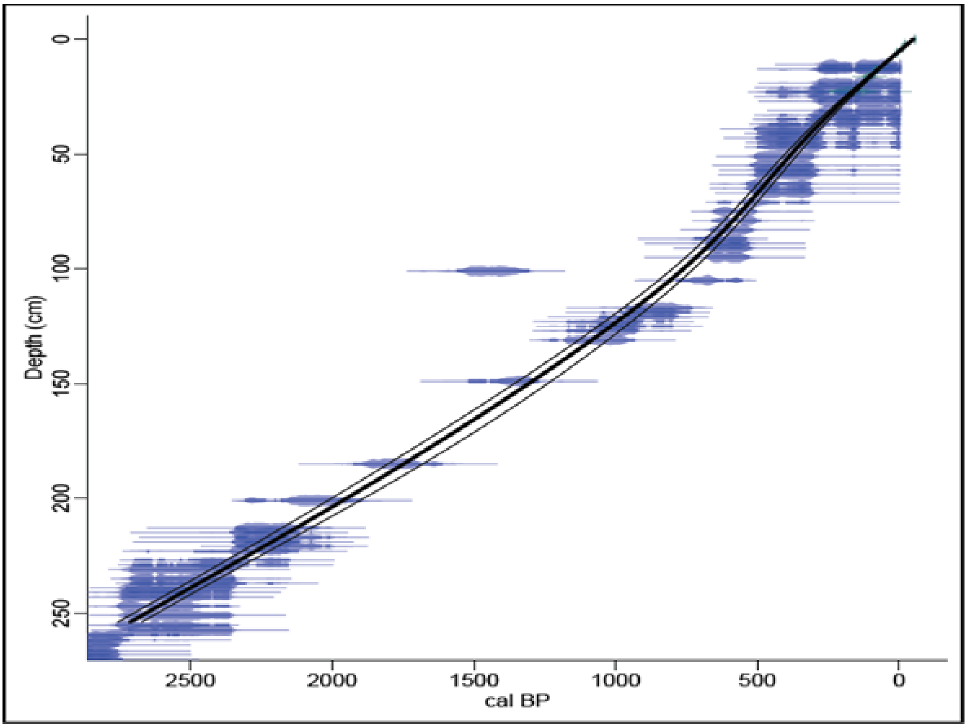

Figure 2: Age versus depth curve for the last 2700 years of the Lake Challa sediment record showing the location of the calibrated dates. The thin lines indicate 95% confidence intervals.

Taking into account all analytical, ^{14}C-calibration and age-model related uncertainty, the maximum 2-sigma (99%) error on calendar ages reported in this paper is ~45 years, except the period of laminations of this ~2700-year portion of the Challa sequence have been identified as varves (Wolff et al., 2011), with a cumulative counting uncertainty of the same order of magnitude as the ^{14}C-based chronology.

For pollen analysis, sixty-four sediment samples of 1 ml were extracted at 4 cm intervals throughout the sequence, i.e. equivalent to a time resolution of ~40 years between samples. Pollen processing was carried at the University of Amsterdam following the standard technique of Faegri and Iversen (1989), including pre-treatment with sodium pyrophosphate, acetolysis, and heavy liquid separation with Bromoform. Exotic *Lycopodium* spores were added to each sample before treatment with the intent to calculate pollen concentration and pollen influx values; however excessive variability in the resulting values for adjacent samples in a lithologically identical sediment matrix prevented us from interpreting the pollen data in terms of absolute abundances and fluxes. At least two pollen slides were mounted per processed sample, and pollen counting was done with a Leitz microscope at 400x magnification; critical identifications were made at 1000x magnification under oil immersion. Modern pollen reference slides at the Palynology Laboratory of the National Museums of Kenya, prepared using plant specimens at the museum's herbarium, were used to assist and confirm identifications. Percent abundances of fossil pollen taxa were calculated with aquatic pollen (here mostly Cyperaceae and *Typha*) and Poaceae excluded from the pollen sum. We excluded Poaceae to reduce dependency in the abundance trends of other plant taxa on prominent trends in the grass pollen.

More than 300 pollen grains were counted per sample; the non-local pollen sum (pollen from non-aquatic higher plant taxa, here including Poaceae) averaged 928 grains with a range between 302 and 2181. The identified pollen taxa were classified into five ecological groups, which partly correspond with the altitudinal zonation of African vegetation as controlled by temperature and rainfall: Ericaceous belt, montane forest trees and shrubs, woodland trees and shrubs, herbaceous taxa, and aquatic plants including Cyperaceae. The pollen assemblage zones were defined using stratigraphically-constrained cluster analysis (CONISS; Grimm, 1991), applied to all non-local pollen taxa excluding (PAZ-I) and including (PAZ-II) Poaceae, and results were graphed using TILIA 2.04 (Grimm, 1991).

4. Results

Our analysis of fossil pollen in the 64 samples of Lake Challa sediments yielded 223 identifiable taxa of higher terrestrial plants, and six aquatic taxa recovered from the top 2700 cal yr BP. The taxa are in the table in the appendix. Consistent with the lake's location in a savannah landscape, Poaceae represent a very high proportion of the non-local pollen sum, its percentage ranging 47-83% with an average of 68%. Consequently, its abundance, when excluded from the non-local pollen sum, amounts to between 88 and 494% (mean: 247%). Among the 34 other common non-local pollen taxa (each >2% of the combined sub-total across all samples), 12 taxa belong to the Woodland and 14 to the Herbaceous categories; together accounting for 2-40% (mean 19%) of the non-local pollen sum. The Woodland group is dominated by *Euphorbia* pollen, the most prominent tree in the 'succulent forest' occupying the rocky middle slopes of the crater basin. The most common taxa belonging in the Ericaceous category (Ericaceae) represent about 0.2% of the non-local pollen sum but excluded in the pollen diagram. This is not unexpected since this pollen originates from the subalpine Ericaceous bush- and grassland on Mt. Kilimanjaro, over 40 km from Lake Challa. The remaining six pollen taxa are classified as montane forest trees. Since none of these trees occur in the riparian forest fringe encircling Lake Challa at present, their pollen likely derives from populations in the montane forest on Mt. Kilimanjaro, which (at least prior to agricultural conversion of its lower slopes) occurred to within ~12 km of Lake Challa.

Classification of the *Acalypha* pollen recovered from Lake Challa is problematic, because within its probable pollen source area *A. neptunic*a and *A. ornata* are known to occur in the sub-montane forest on Mt. Kilimanjaro (Hemp, 2006), whereas *A. fruticosa* is common in the dry forest occupying the crater's outer slopes. Given the relatively short time frame of this study, we assume most *Acalypha* pollen is derived from the latter species, and hence classify it in the woodland category.

Of the six identifiable pollen taxa classified as aquatic, only *Typha* and sedges (Cyperaceae) are commonly found throughout the record (Figure 3); *Hydrocotyle, Myriophyllum, Potamogeton* and *Nymphaea* grains were rare. The Cyperaceae alone amount to between 10% and 50%. This is a strikingly high contribution because the steep and rocky shoreline of Lake Challa can support only a trivial population of riparian sedges. Although some Cyperaceae pollen may derive from the terrestrial sedge species which occupy suitable microhabitat within regional woodland and forest, by far its largest component most likely derives from sedge swamp growing in the large shallow basin of Lake Jipe (~20 km south of Lake Challa), and perhaps also Ziwani Springs in Tsavo East National Park (~40 km to the northeast).

CONISS applied to the Challa pollen stratigraphy identified five pollen zones (Figure 3): Challa I (258 to 200 cm), Challa II (200 to 160 cm), Challa III (160 to 108 cm), Challa IV (108 to 40 cm) and Challa V (40 to 0 cm), with Challa I divided into two distinct sub-zones Ia (258 to 224 cm) and Ib (224 to 200 cm).

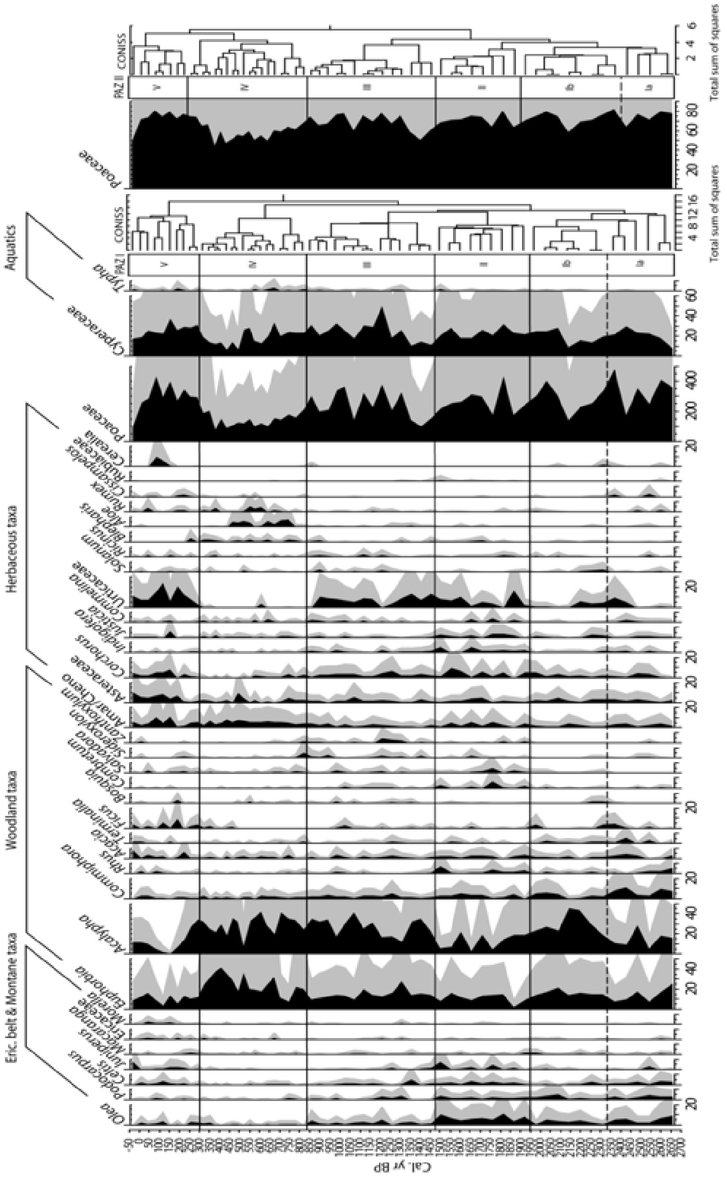

Figure 3: Pollen diagram of Lake Challa, equatorial East Africa, showing down core percentage changes of selected taxa plotted against age in cal yr BP (Verschuren et al. 2009). Of all pollen taxa identified in Lake Challa sediments only pollen taxa with a representation >2% were included in the pollen diagram.

Sub-zone Challa Ia (258 to 224 cm) spans the period from (before) 2700 to 2325 cal yr BP. The Ericaceous Belt taxa in this sub-zone include Ericaceae, which are only sporadically present. *Acalypha* is present at 30% and

Euphorbia at 25%; these taxa decrease to 10% from 235 cm onwards but increase again near the upper zone boundary. Common montane taxa include *Celtis* (5%), *Juniperus* (5%), *Macaranga* (<5%), *Myrica* (<2%), *Olea* (>5%) and *Podocarpus* (<5%). The woodland taxa present include *Acacia* (5%), *Bosquia* (<5%), *Combretum* (<5%), *Commiphora* (15%), *Ficus* (5%), *Rhus* (5%), *Sideroxylon* (<5%), *Terminalia* (<2%) and *Zanthoxylum* (<2%). This sub-zone is characterized by the low frequencies of non-grass herbaceous taxa with Amaranthaceae / Chenopodiaceae present at 5% and Asteraceae <5%. Urticaceae increase in the upper part of the zone reaching up to 10% near the sub-zone boundary. Other herbaceous taxa commonly present are *Aloe, Blepharis, Cissampelos, Commelina, Corchorus, Indigofera, Justicia, Rumex* and *Solanum*. Pollen grains attributable to domesticated grasses (cereals) occur in very low percentages from 249 to 238 cm but are commonly absent. The diameter of these grains measured more than 60µm. Poaceae is abundant from 235 cm onwards. Cyperaceae increases to 30% before decreasing again towards the zone boundary.

Sub-zone Challa Ib (224-200 cm), which covers the period 2325 to 1950 cal yr BP, is characterized by low percentages of Ericaceae and montane taxa, such as *Olea, Podocarpus* and *Juniperus*. Among the woodland taxa, percentages of *Acalypha* increase to 45% from the base of the sub-zone to 216 cm, and then stagnate to approximately 20% towards the top of this interval. *Euphorbia* is also consistently present throughout this sub-zone, reaching values near 15-20%, whereas *Acacia, Rhus* and T*erminalia* generally remain below 5%. *Commiphora* reaches its minimum values near 216 cm, followed by a slight increase exceding 5% in the uppermost part of the sub-zone. The most common herbaceous taxa besides Poaceae are the Urticaceae, which are markedly decreasing towards the end of the sub-zone, and the Amaranthaceae/Chenopodiaceae, Asteraceae and *Corchorus*, which are more stably present at 5-7%. *Indigofera, Commelina* and *Ricinus* are recorded only sporadically. Cyperaceae pollen mostly reaches values of 15-25%, except for a minimum dated to ~2100 cal yr BP.

Zone Challa II (200 to 160 cm), which corresponds with the period from 1950 to 1425 cal yr BP, shows peak abundances (>10%) of *Olea*. Broadly simultaneously, also *Celtis* and *Juniperus* increase from less to more than 5%. Poaceae, *Euphorbia* and *Acalypha* are consistently present, but strongly fluctuating. *Commiphora, Rhus, Acacia* and *Combretum* persist in low abundances. Other taxa sporadically present in this zone include

Ficus, Salvadora, Sideroxylon, Terminalia and *Zanthoxylum*. Further Amaranthaceae / Chenopodiaceae, Asteraceae, Urticaceae, *Corchorus* and *Indigofera* are present at relatively low percentages. Among the aquatics, Cyperaceae is commonly recorded throughout the zone, displaying values of ca. 20%.

Zone Challa III (160 to 108 cm) is dated 1425 to 825 cal yr BP and is characterized by low percentages of Ericaceae. *Acalypha* remains as abundant as at the Zone II-III transition, with percentage values ranging between 20 and 40% throughout Zone III. Conversely, *Celtis, Juniperus* and *Ole*a show decreasing representation compared to Zone II. Among the other montane tree taxa, percentages of *Podocarpus* vary strongly between absence and 6%, whereas *Macaranga* and *Morella* remain scarce but rather stable. *Acacia, Bosqueia, Combretum* and *Commiphora* are present at <5% throughout the zone. *Euphorbia* increases to 30% around 149 cm further increasing to 35%. Other taxa present in low percentages include *Ficus, Rhus, Salvadora, Sideroxylon, Terminalia* and *Zanthoxylum*. Amaranthaceae/Chenopodiaceae, Asteraceae, *Blepharis, Cissampelos, Commelina, Corchorus, Indogofera, Justicia,* Rubiaceae, *Rumex* and *Solanum* are also recorded sporadically throughout the zone. Urticaceae is abundant increasing to 10% and absent after 105 cm. Poaceae and Cyperaceae are abundantly present with *Typha* poorly represented.

Zone Challa IV (108 to 40 cm) is dated 825 to 300 cal yr BP. Ericaceous Belt taxa record low percentages with montane forest taxa being abundant throughout the pollen zone. *Acalypha* increases to 40%, *Euphorbia* 40% while *Ficus, Rhus, Salvadora, Sideroxylon, Terminalia* and *Zanthoxylum* record very low percentages. Aloe is present from 108 to 64 cm. Amaranthaceae / Chenopodiaceae is abundant throughout the zone increasing to <10%. Asteraceae becomes more common increasing to 10% with *Rumex* 5%. Other taxa presented in low percentages include *Blepharis, Cissampelos, Commelina, Corchorus, Indigofera, Justicia, Ricinus, Solanum* and Urticaceae. Poaceae records relatively low percentages with increases in Cyperaceae. *Typha* is present throughout the zone.

Zone Challa V (40 to 0 cm) is dated from 300 cal yr BP to present. Ericaceae record low pollen percentages. *Acalypha* increases upto 35% before decreasing to 20%. *Celtis, Juniperus, Macaranga, Morella*,(new name for *Myrica*) *Olea* and *Podocarpus* are present but not common (<5%). *Acacia* increases to 5% with *Bosqueia, Combretum* and *Commiphora* recording low percentages. *Euphorbia* is present throughout the pollen zone at about 10%. *Ficus, Rhus, Salvadora, Sideroxylon, Terminalia* and *Zanthoxylum* record very low percentages. Herbaceous taxa are occasionally common especially Amarantahaceae/Chenopodiaceae (10%), *Corchorus* (5%) and Urticaceae (30%). Cereals are recorded from about 15 cm increasing to 10% and absent from 11 cm to the top of the zone. *Blepharis, Cissampelos, Commelina, Indigofera, Justicia,* Rubiaceae, *Ricinus, Rumex* and *Solanum* are present but recording low percentages. Poaceae is abundant throughout the zone with Cyperaceae increasing to 40%. *Typha* is present at low levels (<2%).

5. Palaeoenvironmental reconstruction and discussion

The late-Holocene sequence of Lake Challa sediments available for this study consists entirely of finely laminated (actually varved, i.e. resulting from rhythmical annual deposition; Wolff et al., 2011) organic carbonate muds, deposited in a stable deep water environment. Consequently pollen taphonomy and preservation can be considered stable through time, and recorded trends in percentages of pollen taxa can be regarded as a truthful reflection of changes in local and regional vegetation through time. Secondly the chronology of the Challa sediment sequence is exceptionally well-constrained (Blaauw et al., 2011), so that also the rates of vegetation change inferred from recorded pollen trends versus time can be expected to approximate reality. The principal challenge of our paleo-environmental reconstruction, therefore, is to distinguish between pollen signatures of vegetation change inside Challa crater versus vegetation change in the wider surrounding landscape, including higher elevation portions of Mt. Kilimanjaro.

Notwithstanding prominent fluctuations in the percent abundances of Poaceae and many other taxa, overall the changes in pollen assemblage composition which define CONISS separation of the Challa sequence in five stratigraphic pollen zones are relatively modest. This result emphasizes that during the past 2700 years the Lake Challa region has always been occupied by a dynamic vegetation mosaic of savannah grassland and woodland. At the same time, the systematic nature of the recorded pollen trends, with periodic increases of Poaceae, shrubs (*Combretum, Commiphora, Salvadora* and *Rhus*) and herbs (*Corchorus* and Urticaceae) characterising dry savannah at the expense of other common savannah trees and shrubs such as *Maerua* and *Sideroxylon*, suggests real and significant shifts in vegetation ecotones through time resulting from century-scale variation in regional climatic conditions affecting seasonal or annual moisture balance.

We here summarize these changes by comparing the moisture-balance variation inferred from the Challa pollen data with those documented at two other Kenyan sites spanning the last few millennia with above-average chronological control, namely Lake Naivasha in the Central Rift Valley (Verschuren et al., 2000) and Namelok Swamp in the Amboseli Basin north of Mt. Kilimanjaro (Rucina et al., 2010), against a generalized chronology (Figure 4). Lake Naivasha is a shallow fluctuating lake with a sediment record of similar continuity and resolution, whereas Namelok is a sedge-dominated peat swamp. All three sites are situated in broadly similar dry savannah ecosystems.

Lake Challa pollen data record a high presence of Poaceae, forest and non-forest taxa such as *Acalypha* growing amongst *Commiphora* and *Euphorbia* from 2700 to 2300 cal yr BP, together suggesting a relatively dry period during deposition of pollen sub-zone Ia. However, Cyperaceae mostly record relatively high values of >20% of the non-local pollen sum in this sub-zone, which appears contradictory to the inference of a regionally dry climate. We surmise, following van Geel et al. (2011), that the positive correlation between Poaceae and Cyperaceae percentages results because sedge swamp expands across the large shallow basin of Lake Jipe 20 km to the south (only its northern limit is visible in Fig. 1c) during prolonged lowstands caused by climatic drought. In Namelok Swamp, increased moisture is recorded from 2800 to 2400 cal yr BP (Rucina et al., 2010). In the broader region of equatorial East Africa, Lake Tanganyika also recorded a lowstand with expanding grassland at decreasing arboreal taxa in the lake catchment from 2600 cal yr BP onward (Cohen et al., 2005). Similar changes are also observed at Lakes Nabugabo, Edward and Masoko from 2660 to 1980 cal yr BP (Russell and Johnson, 2005; Russell, 2004; Russell, 2003; Vincens et al., 2003).

The continued significant presence at Lake Challa of *Olea* and *Podocarpus* from 2300 to 1400 cal yr BP suggests that the regional climate continued to be dry throughout most of the period represented by pollen zones Ib and II. These trees inhabit the lower montane forest on Mt. Kilimanjaro, and thus their increasing abundance is expected to reflect wetter rather than drier conditions. We tentatively explain the observed trends by surmising that the altitudinal distribution of this forest (and thus its relative proximity to Lake Challa) did not shift much in the last 2700 years, but that drier episodes caused greater pollen production in forest trees such as *Olea* and *Podocarpus,* and/or improved its dispersion by wind. The increase in *Celtis, Juniperus, Olea* and *Podocarpus* in pollen zone II would then reflect more severely dry conditions prevailing from 1900 to 1500 cal yr BP. At Lake Challa, this most dry period is locally recorded by high Poaceae percentages, decreases in *Acalypha* and *Euphorbia,* and increases in woodland and herbaceous taxa such as Amaranthaceae/Chenopodiaceae, Asteraceae, *Corchorus, Indigofera* and *Justicia*. Regionally, persistent drought during this period is also recorded at Namelok Swamp (Rucina et al., 2010), Lake Naivasha (Verschuren et al., 2000), Lake Tanganyika (Alin and Cohen, 2003), Lake Edward (Russell et al., 2004) and Lake Turkana (Rickets and Johnson, 1996). Namelok Swamp pollen data, in particular, recorded low percentages of *Syzygium* with increased *Acacia*, Poaceae, Amaranthaceae/Chenopodiaceae and *Salvadora* reflecting a drier environment from 2000 to 1675 cal yr BP (Rucina et al., 2010) (Figure 4). Towards the end of this period from 1650 to 1450 cal yr BP, more open woodlands were also recorded in the Lake Masoko catchment thought to be indicative of a relatively weakened monsoon and the consequent dry climate (Vincens et al., 2003).

At the transition between zones II and III, increases in *Acalypha, Euphorbia* and Urticaceae pollen with decreases of Poaceae and Cyperaceae dated to between 1400 and 1350 cal yr BP suggest interruption of drought by a relatively wet period. Increased presence of *Syzygium* in the Lake Tanganyika catchment and reduced *Acacia, Salvadora* and herbaceous taxa also suggest the onset of a shift towards a wetter environment (Alin and Cohen, 2003); similarly this was experienced within the Lake Edward catchment (Russell et al., 2004).

Although the timing and regional expression of the Medieval Climate anomaly in tropical Africa is complex (Ryves et al., 2010), the Lake Challa pollen record indicates that the entire period from 1300 to 800 cal yr BP was characterized by climate variability locally expressed in low presence of *Acalypha* and *Euphorbia* and high abundances of Cyperaceae and Poaceae throughout much of pollen zone III. Aridity was also recorded in Lake Naivasha and Namelok Swamp (Figure 4).

Cal yr BP	Lake Challa	Namelok Swamp	Lake Naivasha
0	Dry punctuated by wet intervals	Warm/dry	Warm / Dry
100		Drier	Wetter
200			Drier
300	Wetter		Wetter
400		Wetter	
500			Warm and increasingly dry punctuated by wet episodes
600			
700			
800			
900	Drier		
1000		Drier	Dry
1100			
1200		Wetter	Dry punctuated by wet episodes
1300			
1400	Wetter		
1500			
1600	Drier		
1700		Drier	
1800			
1900			
2000			
2100			
2200			
2300	Drier		
2400		Variable wetter climate with drier intervals	
2500			
2600			
2700			
2800			
2900			
3000			

Figure 4: Comparison of inferred palaeoenvironmental changes during the last 2700 cal yr BP for three sites in lowland Kenya; Lake Challa, Namelok Swamp and Lake Naivasha.

Lake Victoria sediments record a similar phase of climate aridity from 1130 to 900 cal yr BP (Stager et al., 2002). This also includes the period from 1200 to 1060 cal yr BP when glaciers on Mt. Kenya in central Kenya re-advanced, thought to be due to lower temperatures and increased convective rainfall (Karlen et al., 1999).

In pollen zone IV, encompassing the Little Ice Age period from about 750 to 320 cal yr BP, Lake Challa records low presence of non-arboreal taxa such as Amaranthaceae / Chenopodiaceae, Asteraceae, Aloe, Corchorus and Urticaceae. Expansion of *Acalypha* and *Euphorbia* in the Lake Challa catchment with decreased Cyperaceae and Poaceae suggest wetter conditions similarly experienced in Lake Naivasha (Verschuren et al., 2000) and Lake Tanganyika (Cohen et al., 2005).

A high abundance of *Acalypha* and *Euphorbia* in Lake Challa catchment from 400 to 200 cal yr BP in pollen zones Challa IV and V is thought to represent a transitional phase towards a drier environmental period. From 380 to 230 cal yr BP Lake Baringo records this dry period leading to desiccation of the lake (Kiage and Liu, 2009). From 200 to 100 cal yr BP within pollen zone Challa V, decreased *Euphorbia* and *Acalypha* are recorded concomitant with increases in Cyperaceae, Poaceae and Urticaceae pollen indicating a drier climate. Expansion of *Acacia* in the Lake Challa sediments is recorded in the last 100 years; the reason for this vegetation change is unknown but such a rise is also recorded at Namelok Swamp (Rucina et al., 2010) and on the Laikipia Plateau (Taylor et al., 2005). It is suggested that elevated concentrations of atmospheric CO_2 favours growth rate of species such as *Acacia* as a result of greater water-use efficiency (Bond et al., 2005; Orchard and Maslin, 2003; Kimball et al.,1993).

The pollen data from Lake Challa sediment records the presence of cultivated food crops that have a diameter of over 60µm (cereal) from 2650 cal yr BP. Similarly, nearby Namelok Swamp sediment records *Cannabis sativa,* cereal pollen grains, *Ricinus communis* and increased charcoal abundance as early as 2650 cal yr BP interpreted as a reflection of early settlement around the northern Mt. Kilimanjaro region (Kusimba, et al., 2005; Rucina et al., 2010). On the Loitigan Laikipia Plateau in northern Kenya, archaeological evidence dated to about 2570 cal yr BP suggests that by this time the site recorded food production involving domesticated animals (Taylor et al., 2005). The area also recorded presence of *Ricinus communis* during this period, presence of disturbed soils, settlements and cultivated land (Taylor et al., 2005). From 700 to 670 cal yr BP Lake Challa ecosystems included increased presence of *Rumex* and *Ricinus communis,* that naturally occurring but promoted by human populations, thus will be recorded in greater percentage. A sustained increase in the presence of cereals in the Lake Challa sediments is recorded around 150 cal yr

BP combined with the presence of *Ricinus communis* and *Rumex* with increased grassland all indicate significant landscape changes associated with human impacts and probably increasing abundance of herbivores that were commonly associated with the savannah ecosystems. Towards the end of 19th century pastoralists were heavily impacted on by drought, Rinderpest, small pox and clan warfare: all these events would have had a major impact on the savannah ecosystem (Jackson, 1976) although these historically documented significant events are not reflected by the Lake Challa pollen record.

6. Conclusions

High-resolution pollen analysis of well-dated Lake Challa sediments demonstrates that regional vegetation was characterized by a dynamic savannah ecosystem during the last 2700 cal yr BP, mostly reflecting regional climate change. More local human impacts on the terrestrial ecosystem are less clear, at least prior to the mid-19th century. Grass pollen grains attributable to domesticated cereals are recorded from 2650 to 2100 cal yr BP, which, if confirmed, would indicate early but temporary human settlement in a relatively arid environment. From 2100 to 1350 cal yr BP Poaceae became more common with decreases in *Acalypha* and *Euphorbia* indicative of a drier climate. Increased *Acalypha* and *Euphorbia* with low levels of Poaceae from 1400 to 1300 cal yr BP are thought to reflect a more mesic climate. A relatively wetter climate is also recorded from around 780 to 300 cal yr BP, indicated by increases of *Euphorbia* and *Acalypha,* and decreases in Cyperaceae and Poaceae. The last 150 cal yr BP records a slight increase in *Acacia* in the Lake Challa catchment probably as a result of recent human-ecosystem interaction. It is interesting that although the high-resolution analysis provides remarkable insight into the relatively subtle changes in the savannah ecosystem - broader ecosystem shifts are not recorded to the similar magnitude as some other sites in East Africa such as Lake Naivasha and Namelok Swamp. The Lake Challa site, being located firmly within the lowland savannah ecosystem, is not so responsive to registering Late-Holocene ecosystem changes as those sites located in more ecotonal settings.

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APPENDIX

Pollen and spore taxa identified in Lake Challa sediments and their life form,family assignment, and ecological characterization.

Pollen taxa identified in the Lake Challa sediments	Life form	Family	Ecological preferences
Abutilon	Herbs / shrubs	Malvaceae	Dry grassland / bushland / forest edges
Acacia	Trees	Mimosaceae	Dry woodlands / grasslands / bushlands
Acalypha	Herbs / shrubs	Euphorbiaceae	Forest margins / woodlands / riverine forest / moist or dry forest
Acanthaceae undiff.	Herbs / shrubs	Acanthaceae	Dry woodlands / Forest margin grasslands / bushlands
Adenium	Shrubs	Apocynaceae	Dry bushland / Woodlands
Aechynomene	Shrubs	Papilionaceae	Riverine / swampy grasslands
Aizoaceae undiff.	Herbs	Aizoaceae	Dry grasslands / woodlands
Albizia	Trees	Mimosaceae	Wooded grasslands / riverine / lowland or upland wet forests
Alchornea	Trees	Euphorbiaceae	Moist or dry forests
Allophylus	Shrubs	Sapindaceae	Moist or dry forests
Aloe	Shrubs / herbs	Liliaceae	Dry grasslands / woodlands
Alysicarpus	Herbs	Papilionaceae	Dry grasslands / woodlands
Amaranthaceae / Chenopodiaceae undiff.	Herbs	Amaranthaceae / Chenopodiaeae	Dry bushlands / waste places / wet forests / grasslands
Ammania	Herbs	Lythraceae	Marshy places / weed of irrigated land
Anemone	Herbs	Ranunculaceae	Moist or boggy grasslands
Aningeria	Trees	Sapotaceae	Moist forests
Anthocleista	Trees	Loganiaceae	Along rivers in forest areas / swampy edges
Apodytes	Trees	Icacinaceae	Upland dry forests
Araliaceae undiff.	Trees	Araliaceae	Woodland / grasslands / wet upland mist forests / riparian forests
Artemisia afra	Shrubs / herbs	Asteraceae	Heath zone / Upland bushlands / forest edges
Asteraceae undiff.	Trees / shrubs / herbs	Asteraceae	Common in most ecological zones
Balanites	Trees / shrubs	Balanitaceae	Dry bushland / grassland / woodlands
Basilicum	Herbs	Labiatae	Grasslands
Becium	Herbs	Labiatae	Wooded grasslands
Berberis	Shrubs	Berberidaceae	Upland bushland associated with giant heath
Bergia	Herb / shrubs	Elatinaceae	Swamps in hot country
Blepharis	Herbs	Acanthaceae	Grasslands and bushlands
Borreria	Herbs	Rubiaceae	Wooded grasslands
Boscia	Tree / Shrubs	Acanthaceae	Dry bushland / woodlands
Trilepisium	Trees	Moraceae	Moist forest
Brassicaceae unddiff.	Herbs	Brassicaceae	Moist forests, woodlands / bushlands
Bridelia	Trees	Euphorbiaceae	Moist forests and forest margins
Cadaba	Trees / shrubs	Capparidaceae	Deciduous, bushed wooded

			grasslands
Cajanus	Shrubs	Papilionaceae	Cultivated
Capitanya	Herbs	Labiatae	Dry *Acacia-Commiphora* bushland
Capparidaceae undiff.	Trees / shrubs	Capparidaceae	Woodland / bushland
Capparis	Climber / shrubs	Capparidaceae	Woodland / bushland / bushed grassland
Cardiospermum	Herbaceous climbers	Sapindaceae	Upland forest edges / grassy woodlands and *Acacia* forest
Caryophyllaceae undiff.	Herbs	Caryophyllaceae	Grasslands / woodlands
Senna	Shrubs / trees	Caesalpinaceae	Grassland / forest edges / riverine / dry bushland
Casuarina	Trees / shrubs	Casuarinaceae	Beach on sand near high water / bushland
Celtis	Trees	Ulmaceae	Dry moist evergreen forest
Cereal	Herbs / shrubs	Poaceae	Cultivated as food crop
Cissampelos	Herbs / climbers	Menispermaceae	Forest and woodland areas
Cissus	Herbs / climbers	Vitaceae	Bushland / woodland
Clausena	Shrubs / Trees	Rutaceae	Moist or dry forest margine
Clematis	Herbs	Ranunculaceae	Forest edges and wooded grassland
Cleome	Herbs	Capparidaceae	Dry bushland / woodlands and grassland
Clerodendrum	Herbs / shrubs	Verbenaceae	Forest / wooded grassland
Cliffortia	Shrub	Rosaceae	Bamboo glades, moorland
Combretum	Trees / shrubs	Combretaceae	Riverine forest / , wooded grassland / bushland
Commelina	Herbs	Commelinaceae	Grasslands and cultivated land
Commicarpus	Herbs	Nyctaginaceae	Dry grassland / woodlands
Commiphora	Trees	Burseraceae	Dry woodlands / bushalnds
Convolvulus	Herbs	Convolvulaceae	Dry grasslands / bushlands
Corchorus	Herbs	Tiliaceae	Woodlands / bushlands
Cordia	Trees	Boraginaceae	Woodlands / bushlands / wet forests
Crateva	Trees	Capparidaceae	Riverine forests / woodlands
Crotalaria	Herbs, shrubs	Papilionaceae	Moist forest, Bamboo / grassland, woodland / bushlands
Croton	Trees / Shrubs	Euphorbiaceae	Moist evergreen upland forest / dry upland forest / dry woodlands
Cucurbitaceae undiff.	Prostrate herbs / climbers	Cucurbitaceae	Dry woodlands / bushlands / forest margins
Diospyros	Trees / shrubs	Ebenaceae	Dry or moist forest / bushland / wooded bushed grassland
Dobera	Trees	Salvadoraceae	Dry bushland / woodland
Dodonaea	Shrubs	Sapindaceae	Evergreen bushland / woodland / forest margins
Dolichos	Herbs	Papilionaceae	Grassland / montane forest / woodlands
Dombeya	Shrubs / trees	Sterculiaceae	Montane forest / bushland / woodland
Drypetes	Trees	Euphorbiaceae	Dry or moist upland forest
Ecbolium	Herbs	Acanthaceae	Dry sandy bushland / riverine

Ekebergia	Trees	Meliaceae	Dry / Moist forest associated with *Olea / Podocarpus* type
Elatine	Herbs	Elatinaceae	Aquatic / wet mud
Ericaceae undiff.	Shrubs / trees	Ericaceae	Alpine zone, rocky places of lower altitude
Eucalyptus	Trees	Myrtaceae	Cultivated / exotics
Euclea	Trees / shrubs	Ebenaceae	Bushland / woodland / grassland
Euphorbia	Herbs / shrubs / trees	Euphorbiaceae	Forest margine / grassland woodland / bushland
Fagaropsis	Trees	Rutaceae	Dry (less often in moist forest)
Ficus	Trees	Moraceae	Forest edge / riverine forest / moist forest / wet forest edge
Gisekis	Herbs	Aizoaceae	Dry grassland often after the rains
Gnidia		Thymelaceae	Forest margin to bamboo zone / woodland / bushland / evergreen bushland
Gomphrena	Herbs	Amaranthaceae	Path sides and waste places
Grewia	Trees / shrubs	Tiliaceae	Woodland / bushland / grassland / moist forests / riverine forests
Hagenia	Trees	Rosaceae	Woodland zone above bamboo
Haplocoelum	Trees	Sapindaceae	Evergreen / bushland / forest margins / grassland
Heeria	Trees	Anacardiaceae	Woodland / bushland / grassland
Heliotropium	Herbs	Boraginaceae	Woodland / bushland / grassland and forest margin
Hibiscus	Shrubs / herbs	Malvaceae	Grassland / bushland / woodland and forest margin
Hypericum	Shrubs / trees	Hypericaceae	Heath zone / riverine thickets
Hypoestes	Herbs	Acanthaceae	Forest, thicket and margin of relict forest / forest edges
Hyptis	Herbs	Labiatate	Swamp grassland / dry grassland
Ilex	Trees / shrubs	Aquifoliaceae	Moist or dry upland forest and also riverine
Impatiens	Herbs	Balsaminaceae	Wetter areas / upper forest levels / lowland forest areas
Indigifera	Herbs / shrubs	Papilionaceae	Grasslands / woodlands / bushlands / disturbed areas
Ipomoea	Herbs / climbers	Convolvulaceae	Bushlands / grasslands and forest margin
Iridaceae undiff.	Herbs	Iridaceae	Upland grassland / subalpine stony soils / wet areas / thickets and riverine
Jasminum	Shrubs / climbers	Oleaceae	Forest edges / wooded grassland / wet evergreen evergreen forest
Jatropha	Shrubs / herbs	Euphorbiaceae	Dry bushland / bushed grassland / woodland
Juniperus	Treess	Cupressaceae	Montane forest
Justicia	Herbs	Acanthaceae	Woodland / bushland / grassland
Kedrostis	Herbs / climbers	Cucurbitaceae	Grassland / bushland
Kohautia	Herbs	Rubiaceae	Grassland / woodland forest margins
Labiatae undiff.	Herbs / shrubs	Labiatae	Grassland / bushland / woodland /

			forest margin
Lannea	Trees	Anacardiaceae	Woodland / bushland
Lasianthus	Shrubs	Rubiaceae	Forest margin / montane forest
Lawsonia	Shrubs	Lythraceae	Woodland / bushland / riverine
Leonotis	Herbs / shrubs	Labiatae	Disturbed / cultivated soils
Leucas	Herbs	Labiatae	Bushland / grassland / disturbed land
Lippia	Herbs	Verbenaceae	Bushland / grassland / woodland
Loranthaceae undiff.	Herbs / shrubs	Loranthaceae	Parasitic plants, common in dry woodlands / bushlands
Luffa	Climbers	Cucurbitaceae	Warm areas under cultivation
Macaranga	Trees	Euphorbiaceae	Montane forest
Maerua	Trees	Capparaceae	Bushland / woodland / grassland
Malpighiaceae type	Shrubs	Malpighiaceae	Woodland / Bushland
Malvaceae undiff.	Herbs / shrubs	Malvaceae	Forest margin / woodland / bushland
Manihot	Shrubs	Euphorbiaceae	Cultivated
Merremia	Herbs / prostrate	Convolvulaceae	Grassland / bushland / dry bushland
Milletia	Trees	Papilionaceae	Semi deciduous forest
Mimosa	Herbs / shrubs	Mimosaceae	Alluvial flats / along rivers and lakes
Momordica	Shrubs / climbers	Cucurbitaceae	Bushland / Forest margins / grassland / upland forest edges
Moraceae undiff.	Shrubs / trees	Moraceae	Forest edge / riverine forest / moist / forest / wooded grassland
Moringa	Trees / shrubs	Moringaceae	Bushland / riverine
Morella (previously named *Myrica*)	Trees	Myricaceae	Montane forest
Neoboutonia	Trees	Euphorbiaceae	Montane forest
Newtonia	Trees	Mimosaceae	Montane forest
Nuxia	Trees	Loganiaceae	Montane forest
Olea	Trees	Oleaceae	Montane forest
Ormocarpum	Trees / shrubs	Papilionaceae	Dry bushland / forest margin / evergreenbushland / wooded grassland
Ozoroa	Trees	Anacardiaceae	Bushland / woodland
Paederia	Climber	Rubiaceae	Dry bushland
Pavonia	Herb	Malvaceae	Bushland / woodland / grassland
Peristrophe	Herbs	Acanthaceae	Open bushland and in dry rocky soils
Phaseolus	Herbs	Papilionaceae	Cultivated
Phyla	Herbs	Verbenaceae	Watersides in hot lowlands
Phyllanthus	Herbs / shrubs	Euphorbiaceae	Grasslands / bushland / forest edges
Pinus	Trees	Pinaceae	Cultivated / exotic
Pittosporum	Trees	Pittosporaceae	Drier evergreen forest / moist forests
Plicosepalus	Herbs	Loranthaceae	Parasite in wooded grassland / bushland
Poaceae	Herbss	Poaceae	Common in all types of environment

Podocarpus	Trees	Podocarpaceae	Montane forest / riverine
Polyscias	Trees	Araliaceae	Wet upland forest / riverine
Portulaca	Herbs	Portulacaceae	Dry grassland / woodland
Premna	Trees / shrub	Verbenaceae	Moist forest / bushland / wooded grassland
Quisqualis	Lianas	Combretaceae	Forest margin / secondary bushland
Ranunculus	Herbs	Ranunculaceae	Upland forest / grasslands / wet alpine
Rapanea	Trees	Myrsinaceae	Upland forest to edge of moorland
Rhus	Trees / shrubs	Anacardiaceae	Bushland / woodland / riverine forest
Rhynchosia	Herbs	Papilionaceae	Grassland / montane forest edge / wooded grassland / forest edges
Ricinus	Herbs	Euphorbiaceae	Cultivated / dry woodland edges
Rubiaceae undiffe.	Trees / shrubs / herbs	Rubiaceae	Widely distributed in most ecological zones
Rubus	Shrubs / herbs	Rosaceae	Montane forest / woodlands / upland bushland
Ruellia	Herbs / shrubs	Acanthaceae	Open bushland / grassland / forest
Rumex	Herbs / shrubs	Polygonaceae	Secondary shrubland / waste places in upper forest
Rutaceae undiff	Trees / shrubs	Rutaceae	Dry upland forest / moist forest bushland / riverine / moist forest
Salvadora	Trees / shrubs	Salvadoraceae	Along rivers / dry bushland / woodland
Sansevieria	Herbs	Dracaenaceae	Dry woodland / bushed grassland
Sapindaceae type	Trees / Shrubs	Sapindaceae	Dry / moist forest / riverine / woodland / bushland
Schefflera	Trees	Araliaceae	Wet upland forests or riparian forest / dry upland forest
Securinega	Shrubs	Euphorbiaceae	Riparian / bushland / bushed grassland in wooded grassland
Sedum	Herbs	Crassulaceae	Alpine zone / upland heath zone
Sesbania	Shrubs	Papilionaceae	Riverine and marshy areas / swamps / shores of alkaline lakes
Sideroxylon	Shrubs / trees	Sapotaceae	High water mark, edge of evergreen bushland
Solanum	Shrubs / Herbs	Solanaceae	Forest margins / dry bushland / grassland / bamboo zone / dry grassland
Stoebe	Shrub	Asteraceae	Heath zone / moorland and bamboo zone
Syzygium	Trees	Myrtaceae	Riverine / wooded grassland / mist forest
Tapinanthus	Shrubs	Loranthaceae	Wooded grassland / riverine and mid altitude bushland
Tapura	Shrubs / trees	Dichapetalaceae	Dry evergreen forest / riverine forest
Tarchonanthus	Shrubs / trees	Asteraceae	Dominant in evergreen or semi deciduous bushland / bushed grassland
Tarenna	Shrubs / trees	Rubiaceae	Moist forest / bushed grassland /

			riverine forest / dry bushland
Teclea	Shrubs / trees	Rutaceae	Riverine / wooded grassland / dry forest / evergreen forest
Tephrosia	Herbs / shrubs	Papilionaceae	Woodland / bushland / grassland / moist grassland
Terminalia	Trees / shrubs	Combretaceae	Evergreen bushland / deciduous bushland or woodland / grassland
Thylachium	Shrubs / trees	Capparidaceae	Deciduous bushland or bushed grassland or woodland
Toddalia	Climbing shrubs / liana	Rutaceae	Riverine / Forest margin / grassland
Trema	Shrubs / trees	Ulmaceae	Forest margin / Riverine / woodland / wooded grassland / disturbed forests
Tribulus	Herbs	Zygophyllaceae	Dry woodland / grassland
Trichilia	Trees	Meliaceae	Riverine / sites with high ground water
Triumfetta	Herbs / shrubs	Tiliaceae	Bushland / bushed grassland / forest margins / old fields
Umbelliferae undiffe.	Herbs / shrubs	Umbelliferae	Marshes / montane grassland / Bamboo and forest zones / bushland /
Urticaceae undiff.	Herbs / trees / shrubs	Urticaceae	Bushland / moist upland / montane forests / disturbed areas
Utricularia	Herbs	Lentibulariaceae	Montane grassland / fresh water lakes
Valeriana	Herbs	Valerianaceae	Alpine region / bamboo zone
Vigna	Herbs	Papilionaceae	Woodland / grassland / bushland / forest margin
Vitex	Trees	Verbenaceae	Wooded grassland / moist evergreen forest / forest margins
Wahlenbergia	Herbs	Campanulaceae	Montane grassland / lower alpine / wooded grassland
Ximenia	Trees / shrubs	Olacaceae	Wooded grassland / dry woodland
Zanthoxylum	Shrub / trees	Rutaceae	Semi evergreen or dry bushland / moist forest / dry forest
Zygophyllum	Herbs / shrubs	Zygophyllaceae	Dry woodland / bushland / grassland / disturbed ground
Hydrocotyle	Herbs	Umbelliferae	Aquatics in upper forest / below bamboo
Cyperaceae	Herb	Cyperaceae	Wetlands / woodland / bushland
Myriophyllum	Herbs	Myriophyllaceae	Aquatics
Polygonum	Herbs	Polygonaceae	Aquatics
Typha	Herbs	Typhaceae	Aquatics
Trilete undiff.	Ferns	Undifferentiated	Terrestrial
Cyathea	Ferns / Tree ferns	Cyatheaceae	Moist in evergreen forest along streams and valleys
Spores undiff.	Ferns	Undifferentiated	Terrestrial

CHAPTER 6

Synthesis

The four research papers in this thesis present new palaeoecological records from from three sites: Rumuiku Swamp on Mount Kenya, Namelok Swamp in the Amboseli Basin and Lake Challa on the border of Kenya and Tanzania (Figure 1). The three sites chosen have sediment accumulation rates varying from 50 to 1000 years per meter sediment accumulation and the vegetation dynamics reflected by the pollen in the sediment records sensitive to climate change and anthropogenic impacts on the landscape. The results serve to (i) provide a critique of palaeoecological methodologies applied in this study; (ii) to reconstruct past environmental changes for the Mount Kenya, the Amboseli Basin and Lake Challa catchment area in Kenya; (iii) asses the forcing factors (environmental, ecological and human impacts) that are likely to account for signals recorded by the palaeoecological records; and (iv) using the research results suggest future directions for palaeoecological research aiming at a more constrained understanding ecosystem dynamics in Kenya, East Africa and broader tropical realm.

Research approach

Sediments from Lake Challa were collected using combination of gravity core CH05-1G (0-12 cm), a short section of hammer-driven (UWITEC) piston core CH05-3P (12-25 cm), and Kullenberg core CH03-2K (25-250 cm). Sediments from Namelok and Rumuiku Swamps were recovered using a Russian corer. The sediments recovered were directly described in the field while those from Lake Challa were described by visual point to point tracing of individual sediment laminae, occasionally aided by high resolution magnetic susceptibility measurements. Pollen preparation followed the method of Faegri and Iversen (1975).Charcoal counts were done from slides prepared for pollen and we used the Winkler gravimentric method (1985). All pollen and charcoal counts were carried at the National Museums of Kenya, Palynology and Palaeobotany Section.Given the paucity of palaeoecological data from the three sites, a multiproxy approach was adopted for this research project, so as to explore a range of potential proxies within a relatively unstudied environment. A multiproxy approach is advantageous in that it allows for the identification of proxy-specific weaknesses, with the objective of building on consistencies and explaining discrepancies between proxy evidence (Lotter, 2005). The three sites provided excellent sediment sequences to investigate environmental change, in terms of structure and biogeographical position in location that are presently ecotonal and hence sensitive to registering past ecosystem changes. On Mount Kenya we visited Rumuiku, Rumwe, and Rurie swamps and two (Rumuiku and Rumwe) were suitable for coring. In the Amboseli Basin, we visited Namelok and Kimana swamps and both were suitable for coring. We further explored other sites on the Taita Hills, which are part of the East African Arc Mountains. Only Ngulu Swamp on the foothill of the Taita Hills was suitable for coring. The core from Lake Challa was provided by a team working for the CHALLACEA project and ideally provide a contrasting lowland savanna site with which to compare the Namelok palaeoecological record.

Chronological and stratigraphic issues - radiocarbon analysis

Since the publication of the principles of radiocarbon dating (Libby et al., 1949), this method has developed into the most widely applied and accepted means of establishing chronological control for late Quaternary sediments (Williams et al., 1998; Walker, 2006). The disadvantages of this technique for Quaternary scientists relate to the limited age that can be dated (~ 50 ky), the problem of calibration associated with the method as the production of ^{14}C is not constant, and the danger of contamination of sediment samples. As peat has a carbon content of 50% and is entirely autogenic, it provides one of the best materials for radiocarbon dating (Barber and Charman, 2005). The risk of contamination can be minimized through careful sample selection and handling during laboratory procedures (Williams et al., 1998). Radiocarbon dating remains the most widely utilized means of providing chronological control to late Quaternary sediments and was therefore applied to all cores analyzed within this study.

Following the recovery of undisturbed sediment cores in the field, cores were lithologically and stratigraphically described. Samples were picked for radiocarbon age determinations on the basis of result from pollen analysis and zonation. Radiocarbon samples were placed at either side of biostratigraphic boundaries to constrain core chronology, with basal dates placed as range finders. Radiocarbon results for all three cores are presented as calibrated radiocarbon years before present (cal yr BP).

Fossil pollen and spore analysis

Pollen analysis is a method for reconstructing former vegetation by means of pollen grains produced and preserved within a sediment archive (Faegri and Iversen, 1989), and constitutes one of the most widely applied Quaternary research tools (Edwards, 1983). The technique assumes that the number of pollen grains deposited per unit time, at a given point, is directly related to the abundance of the associated species in the surrounding vegetation (Davis, 1963). Although pollen analysis is based on sound principles, there are a number of limitations associated with the technique, as discussed below.

Pollen data are presented as proportions of a pollen sum, rather than as discrete numbers (Davis, 1963), resulting in uneven representivity both between and within pollen types (Birks and Birks, 2005). A judicious approach is therefore required when interpreting pollen spectra, as representivity is influenced by differences in pollen productivity, dispersal and preservation (Faegri and Iverson, 1989). The limited taxonomic resolution of pollen identifications, particularly with regard to certain common families such as 115 Poaceae and Cyperaceae (Scott, 1984; Sëppa and Bennett, 2003), is a hindrance to interpretation in wetland and grassland systems. Nevertheless, progress in pollen analytical precision is consistently being made (Vincens et al., 2007) and pollen identification guides with keys are available (e.g. Association des Palynologues de Langue Francaise, 1974; Bonnefille, 1971; Bonnefille and Riollet, 1980) and pollen reference collections such as that found at the National Museums of Kenya in Nairobi. The advent of digital photography has facilitated the creation of extensive pollen database resources (e.g. African Pollen Database, 2004), which provide easy access to reference images from collections around the world (Sëppa and Bennett, 2003).

Charcoal analysis

Past fire regimes can be reconstructed through analysis of particulate charcoal and other fire proxies preserved in lake and wetland sediments (Whitlock and Anderson, 2003). Charcoal analysis is typically performed on the same cores as pollen analysis, allowing for the co-investigation of past climate, vegetation, fire and human interactions (Whitlock and Larsen, 2001). In this study, a chemical assay procedure was applied to measure percentage charcoal content (Winkler, 1985), which provides a broad estimate of elemental carbon within the peat sample. The principle limitation of this technique is that it does not allow for distinction between local and regional sources of sedimentary charcoal, hence limiting its interpretive value. Another disadvantage of the method is that carbon derived from the burning of fossil fuels may influence results pertaining to sediments less than 100 years old (Winkler, 1985; MacDonald et al., 1991). An additional criticism leveled at the Winkler technique is that results tend to overestimate percentage charcoal content due to moisture loss from some minerals following ignition (MacDonald et al., 1991; Bonnefille et al., 1995). A comparative study between various charcoal proxies (microscopic charcoal, macroscopic charcoal, percentage charcoal (chemical digestion), historical records and fire scar data) in Canadian boreal forest found the results of the Winkler technique to be unreliable (MacDonald et al., 1991). However, none of the proxies applied produced significantly correlated results, nor were any of the indices consistently accurate in reconstructing local fires.

Notwithstanding the limitations described, the Winkler (1985) technique and modifications thereof have been widely utilized in East African studies (e.g. Taylor, 1990; Taylor, 1993; Taylor and Marchant, 1994; Marchant et al., 1997; Marchant and Taylor, 1998; Taylor et al., 1999; Rucina et al., 2009).

Palaeoenvironmental reconstruction

Here the results of the four records presented in the thesis are combined to reconstruct the late Quaternary palaeoenvironments of high and low altitudinal ecosystems of Kenya. We focus on a series of key intervals of time. In this section radiocarbon dates are taken from the literature and many values have not been calibrated. Therefore, to avoid a combination of uncalibrated and calibrated ages hampering comparisons all dates are presented as cal yr BP.

Last glacial period

Mount Kenya is sensitive to environmental and climatic change due to its proximity to the equator and the steep environmental gradients. Mount Kenya has sites with excellent natural sediment archives and a long history of palaeoenvironmental research (Rucina, et al., 2009; Barker et al., 2004; Olago, 2001; Street-Perrott and Perrott, 1990; Coetzee, 1967) and has been an important place for pollen based studies of vegetation change. Results show an apparent discrepancy between high altitudinal sites being relatively moist and lower altitudinal sites recording pronounced aridity during the last glacial maximum (LGM). Possibly this relates to the net effect that land-ocean coupling and associated delivery of moisture to the East African interior would have been more important than today at the LGM with stratified clouds delivering moisture more effectively to montane areas (Rucina et al., 2009). With the expansion of low stature Ericaceous Belt vegetation, and C_4 grasslands at high altitudes on Mount Kenya (Wooller et al., 2003; 2000), there would be a significantly reduced ability of the vegetation to strip out moisture from incoming non-precipitating clouds. Such reduction of plant available moisture would result in reduced river flows and associated lake level declines as the high altitude 'water towers' become less effective at collecting moisture. The strong impact of vegetation change on the montane hydrology, and connection to lowland drought, can be seen today on numerous East African mountains. For example, on Mount Kilimanjaro *Ocotea*-dominated forest has been recently cleared in large areas and is thought to account for more than a 90% reduction in moisture of the reduced flows and associated regional aridity (Hemp, 2006). Developing this understanding on ecosystem response to climate change is highly relevant to predict impacts of future climate change on African ecosystems, in particular because the LGM is a critical period in climate model comparisons (Peyron et al., 2001; Braconnot et al., 2007).

At Rumuiku Swamp 2154 m on Mount Kenya, the pollen record indicates an arid period from 26,000 to 24,000 cal yr BP with vegetation dominated by *Artemisia, Stoebe* and other taxa from the Ericaceous Belt. However, there was not only high altitude taxa shifting to lower altitudes but there appears to have been a mixture of taxa currently found at low and high altitudes also growing with other Afromontane taxa. Such changes in vegetation associations are also observed at Lake Rutundu with increases of *Artemisia* from 24,000 to 14,000 cal yr BP (Wooller et al., 2003). LGM vegetation reconstructions from several East African mountains indicate open grassland and ericaceous scrubland, with a reduction of forest concentrated into isolated patches (Bonnefille and Riollet, 1988; Jolly et al., 1997; Street-Perrott et al., 1997; Wooller et al., 2000; Ficken et al., 2002). These environmental changes have been attributed to the combined effects of reduced rainfall and lower atmospheric $pC0_2$ during the LGM, conditions which would have favoured C_4 grasses and sedges competitively (Cerling et al., 1997; 1998; Ehleringer et al., 1997; Jolly and Haxeltine, 1997; Street-Perrott et al., 1997). Many low altitude sites show similar trends. For example, results from Lake Rukwa 800 m in southwest Tanzania record a distinct reduction in Afromontane forest after the LGM

(Vincens et al., 2005) while results from Lake Naivasha at 1884 m in Kenya indicate an open grassland environment (Maitima, 1991).

In spite of generally warm and wet conditions towards the Pleistocene/ Holocene transition, some higher resolution records detect an abrupt arid episode probably coeval with the northern hemisphere Younger Dryas episode (12,500-11,500 cal yr BP) (Coetzee, 1967; Hamilton, 1982; Gasse et al., 1989; Beuning et al., 1997; Johnson et al., 2000; Olago, 2001; Kiage and Liu, 2006; Ryner et al., 2006; Talbot et al., 2007). In the case of Lake Masoko in southwestern Tanzania, wetter conditions are indicated for the Younger Dryas event (Garcin et al., 2006a; 2006b; 2007).

The Rumuiku Swamp catchment record reflects a notable change in the vegetation from 10,000 to 8900 cal yr BP with respect to composition and abundance of a mixture of dry and moist montane forest taxa dominated by *Podocarpus, Polyscias* and *Schefflera*. *Afrocrania,* associated with moist climate, was present throughout this period. The ^{13}C results also suggest presence of C_3 aquatic vegetation and lower ^{13}C due to dry conditions probably interrupted by a humid period lasting for years. The abundance of Cyperaceae and *Myriophyllum* in the shallow swamp indicates the C_3 plants recorded are from theses taxa. Charcoal records in the same period indicate a low frequency to absence of fires in the region and/ or in the catchment. The period also saw absence of *Allophylus, Celtis, Croton, Lasianthus, Nuxia* and increased Cyperaceae, *Cyathea* (tree fern), *Myriophyllum*, Poaceae and *Podocarpus* in the catchment reflecting a period of aridity.

Early Holocene

The early Holocene in the Rumuiku Swamp records Afromontane taxa expanding as the ecosystem composition responded to warmer and wetter climatic conditions. Dry Ericaceous taxa became less common until they were virtually absent (Street-Perrott and Perrott, 1993). Within this general environmental synopsis the Holocene was characterized by rapid environmental shifts. The terminal moraine on Teleki Valley in Mount Kenya was 200 m lower between 6070 and 4135 cal yr BP indicative of a lowering in mean annual temperature of 1.2°C relative to present day (Johannessen and Holmgren, 1985). Indications for a wet early-mid Holocene are supported by data from Kashiru (Roche and Bikwemu, 1989), Lake Albert (Ssemmanda and Vincens, 1993), Lake Rukwa (Vincens et al., 2005), Lake Victoria (Stager et al., 2003) and Mt. Elgon (Hamilton, 1987; Barker et al., 2001), Mt. Kenya (Ficken et al., 2002; Rucina et al., 2009) and Mt. Kilimanjaro (Thompson et al., 2002).

Temperature increase resulted in the expansion of C4 grasses from 4500 to 4000 cal yr BP on Mount Kenya (Olago, 2001) with the pollen records (Coetzee, 1967; 1964) showing a shift to more xeric ecosystems under dry climatic conditions. Mount Kilimanjaro also experienced a strong drying phase around 4000 cal yr BP with a distinctive layer of dust recorded in the ice core (Thompson et al., 2002). This marked and extended period of drought around 4000 cal yr BP (Street-Perrott and Perrott, 1993; Thompson et al. 2002; Marchant and Hooghiemstra, 2004), this is concordant with evidence from elsewhere in East Africa (Kiage and Liu, 2006). Variations in the pollen spectra at Rumuiku Swamp suggest that the composition of moist Afromontane forest throughout the Holocene suggests the ecosystem composition responded to warmer and wetter climatic conditions.

Rumuiku swamp reflects a pronounced growth of *Hagenia* concomitant with significant increase in Poaceae and *Myriophyllum* a change which is not comparable with any other site in Mount Kenya. However, the charcoal record showed a dramatic increase particularly in the large size classes reflecting fires local to the swamp. Associated with this increased fire regime the greater abundance of fire-tolerant taxa such as *Hagenia* may explain the observed increase in *Hagenia*.

Late Holocene

Reconstruction of late Holocene vegetation is complicated by increasing numbers of human settlements. The associated impact on ecosystems progressed from a relatively minor impact to becoming a major external force on ecosystem composition and change. The Lake Challa record documents the response of lowland dry forest ecosystems to regional climate variability over the last 2700 cal yr BP. Century-scale periods of climatic droughts are recorded by local increases in pollen abundances of Poaceae and certain dry savanna trees. Low presence of cereals is recorded since ~2650 cal yr BP in Lake Challa catchment. *Cannabis sativa,* cereals, increased charcoal content and *Ricinus communis* in the the nearby Namelok sediment record, also strongly suggest presence of late Holocene human settlement and disturbance in the lowland savanna ecosystem. Thus, Lake Challa and Namelok Swamp in the savanna reveal ecosystem change driven by climate change, anthropogenic and herbivore activities over the last 3000 cal yr BP. Assessing potential

evidence for natural- and/or human-induced changes in the pollen signal may be controversial (Hamilton et al., 1986; Perrott, 1987; Taylor et al., 2000; Marchant and Hooghiemstra, 2004), particularly given the lack of unambiguous indicators that occur in East African records (Vincens et al., 2003). It is therefore advisable to be cautious when interpreting recent records and only unequivocal evidence should be used where possible.
During the late Holocene period Rumuiku Swamp sediments record a progressive degradation in the arboreal cover, most clearly seen in the response of *Polyscias* coupled with an expansion of grasses and herbaceous taxa such as *Artemisia* possibly related to forest clearance. Increased fires in the late Holocene may also be linked to forest clearance that coincides with immigration of the Kikuyu tribe and the onset of agriculture in the region (Dunda, 1908; Muriuki, 1974). It is interesting to see the steady presence of *Podocarpus* adjacent to the Rumuiku Swamp catchment forming mono-specific stands. This situation differs from other areas in East Africa where *Podocarpus* was a particular focus of forest clearance (Marchant and Taylor, 1998).

Namelok Swamp and Lake Challa sediment records environmental conditions drier than today from 2700 to 2300 cal yr BP, from 1800 to 1500 cal yr BP, from 1300 to 800 cal yr BP and from ~250 to 70 cal yr BP. The wettest period was recorded from ~600 to 300 cal yr BP in Lake Challa. Namelok Swamp records a wet period from 680 to 500 cal yr BP. These ecosystem shifts could be linked to changes in solar activity influencing climate variability on decadal to centennial time scales as suggested as an explanation of changes observed in Lake Naivasha and Baringo (Kiage et al. 2009; Verschuren et al. 2000). Lake Challa records higher proportions of cereal pollen from ~150 cal yr BP, which is associated with an increase in herbaceous plants indicative of more widespread anthropogenic ecosystem disturbance. Uppermost samples of the Lake Challa and Namelok Swamp records show a large increase in *Acacia* and herbaceous taxa including Poaceae.

Review of aims and objectives

The aim of this study was to reconstruct late Quaternary environmental changes of lowland and high altitude sites using a multi-proxy and multi-site approach.

Four palaeoecological records were analysed to reconstruct late Quaternary palaeoenvironments for the Mount Kenya, Namelok Swamp and Lake Challa and results were published in two papers (Rucina et al., 2009, 2010) with two manuscripts in the process of being published.

Specific research objectives

Environmental change of high and low altitudes has been proposed as a mechanism for the accumulation and persistence of species during glacial and post-glacial periods resulting in the diverse vegetation observed today.

This hypothesis has been investigated using a single pollen record from Rumuiku Swamp on Mount Kenya (Rucina et al., 2009) which showed long-term environmental change. Changes in forest composition through the last glacial period were demonstrated with the results indicating that some individual taxa such as *Artemisia,* Ericaceae and *Stoebe* shifted to lower altitudes forming a mixture of both ericaceous and Afromontane taxa during dry glacial conditions, which does not exist today. Changes included presence of *Juniperus* at relatively high altitude during this cold and dry period. Today *Juniperus* is found at lower altitudes than Rumuiku Swamp and on the drier side of Mount Kenya.Thus, the Afromontane forest taxa recorded in the Rumuiku Swamp sediment during the last glacial maximum record a very different climate regime to that of the present day.

Past anthropogenic impacts on landscape have been widely implicated in the origin and expansion of grasslands in East Africa and degradation of Afromontane forests. Palaeoecological analysis is used to investigate the contributions of long-term natural grassland dynamics associated with late Pleistocene human activity at low and high altitudes in order to determine whether grasslands are a natural and long-standing component of savanna and Afromontane forests.

A 3000 year long pollen record from Namelok Swamp and Lake Challa were used to assess late Holocene vegetation dynamics in the savanna ecosystem. Results indicated changes in pollen composition and abundance suggesting the taxa record climate change driven variability throughout the past 3000 years. The recent appearance of cereals in Lake Challa and Namelok Swamp sediment records and other taxa (Amaranthaceae / Chenopodiaceae, *Commelina, Corchorus, Cissampelos, Justicia, Ricinus, Rumex,* Urticaceae) associated with land cover changes and burning (increased charcoal) all are indicators of anthropogenic activities. These records therefore support the hypothesis that grasslands are a natural and long-standing component of savanna vegetation with the proportions of grass and arboreal cover being highly dynamic . However, during the late Holocene some expansion of grasslands may have occurred both at low and high altitudes as a result of elevated human presence within the catchments. Notable changes in these records are the increase of *Acacia* during the last two centuries. The records demonstrate the importance of fire regimes, as opposed to human impact, as the key driver of grassland dynamics in East Africa.

Archaeological evidence suggests that the low and high altitudes have been subject to extensive forest loss and fragmentation as a consequence of human activity in the recent past. Multi-proxy palaeoecological evidence is applied to explore the nature and timing of long-term human impacts in low and high altitudes of Mount Kenya and savanna ecosystem.

There is no strong evidence to show that the Rumuiku Swamp sediments record strong past human activity on Mount Kenya. Nevertheless, evidence of human activity, including agriculture, during the late Holocene suggests that selective logging in high altitude forests occurred frequently during the last ~300 cal yr BP.

Conclusions

In this study three new palaeoecological records were presented from an under-studied tropical ecosystems in Kenya. The records were derived from three isolated sites, Rumuiku Swamp at 2154 m in the Afromontane forest of Mount Kenya, Namelok Swamp at 1146 m in savanna ecosystem and a record from Lake Challa located in the savanna at 880 m. Comparison between sites was in some cases limited by the varying temporal resolution and the different periods reflected by the records. This explains the need for further studies to fill in the substantial data gaps which exist both spatially and temporally. The three studied sites have provided insights into the long-term development of low and high altitude ecosystems with wider implications across East Africa. The results have improved our understanding of driving mechanisms that change ecosystems, such as climate change, changing fire regimes, varying herbivore populations, and changing intensities of human impact. Such information is vital for developing appropriate measurements for future conservation and management in a world of climatic uncertainties and anthropogenic impacts on the landscape. Traditionally, palaeoecological studies in East Africa have been characterised by a highly site-specific approach to past vegetation change, driven by the limitations of site intercomparability, especially with regard to chronological control, pollen identification and site characteristics (Jolly et al., 1997). In light of these challenges, a number of stratigraphically consistent palaeoecological records from the same region are required to develop a useful data synthesis – this study being a vital step towards such an integrated study. The lacustrine deposits of Central Africa form one area where such a synthesis has been achieved (Jolly et al., 1997). This has facilitated the discernment of regional and site-specific trends in the various records analysed. Incorporation of additional records and high-resolution records into future palaeoenvironmental syntheses may provide insight in distinguishing regional and site-specific trends in the records. High resolution records deserve particular attention, not only are such records less problematic chronologically, they could also provide the key to differentiating climate and anthropogenic induced changes in the past.

Recommendations for the future research

Ecosystem response to climate change is a global issue that needs a clear understanding of how ecosystems respond to climate change and human interaction. The most important factors such as changes in precipitation and temperature determine vegetation composition and distribution. These changes need long-term observations to fuel understanding how and why impacts related to climate change will occur in the future. The understanding of how climate change affects ecosystems can be achieved by understanding and identifying thresholds likely to lead abrupt changes in the climate systems. Multidisciplinary research that addresses combined scenarios of future climate change, population growth and pathways of economic development needs to be encouraged. A global network for the researchers involved is important so that they share data and develop dialogue to explore adaptation as part of long term sustainable development.

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CURRICULUM VITAE

Stephen Mathai RUCINA

Stephen M. Rucina was employed in 1982 at the National Museums of Kenya as a Herbarium Assistant after completion of high school education. He was involved in many expeditions where he gained wide experience on vegetation ecology and taxonomy. Publications have been prepared on some of the expenditions he was involved in, which includes the 'Ecological Inventory of the Kora National Researve, Kenya'. This Kora Research Project 1982-1985 was a joint venture between the National Museums of Kenya and the Royal Geographical Society.. The report was edited by Malcolm Coe and N. Mark Collins. and published by the Royal Geographical Society London UK.

His experience in Herbarium and vegetation ecology and taxonomy integrated well with pollen work and usage in understanding of vegetation dynamics. Later Stephen was transferred to the Palynology and Palaeobotany Section after showing keen interests on climate change research. In 1990 he went for further studies to Kenya Polytechnic University College. He studied Earth Sciences and majored in Metamporphic and Igneous rocks, Mineralogy and Hydrogeology, Physical and structural Geology, Soil Science, Sedimentary rocks and Palaeontology, Field Geology; Survey and Photogrammetry. He graduated in 1992 with a diploma.

He went back to his station at the National Museums of Kenya and took a position as a laboratory technician in the Palynology and Palaeobotany Section. His duties included developing a pollen and spore collection, general laboratory management including curatorial duties. From 1992 to1999 Stephen was involved in climate change research projects in various parts of Kenya and learned coring techniques to recover lake and swamp sediments. Some of the materials recovered have been used for publications of which he is a co-author.

In 1999 Stephen got funding from Dr. Henry Lamb and registered for M.Phil at the University of Wales, Aberystywth under his supervision. He graduated in 2001 with a Master of Philosophy degree majoring in modern pollen vegetation relationships. His project for the masters' degree was in the Aberdare Mountains of Kenya where he compared along an altitudinal transect the vegetation zonation with the modern pollen rain. After his master's degree, Stephen was appointed as Research Scientist II and Head of Palynology and Palaeobotany Section. He has been carrying research, training and administrative duties. He has co-authored some publications in international journals. Stephen has helped local and international researchers and students involved in palaeoecology, guiding them on requirements and needs to carry research in Kenya.

In 2005 Stephen registered for a PhD to carry out research on palaeoecology of high and low altitudes of Kenya under the direct supervision of Dr Robert Marchant of the University of York England, and Prof. Dr. Henry Hooghiemstra of the University of Amsterdam, The Netherlands as promotor. Two chapters of the current PhD thesis were published in international peer-reviewed journals with Stephen as the lead author. A third paper is in review, while a fourth paper is close to be submitted to a journal. Stephen has attended many conferences and workshops and at some of them he has presented oral presentations and posters. He has participated for field research outside Kenya in Tanzania and Ethiopia. Some of the conferences and workshops attended for the last five years include: 2006- Out of Africa Conference: Towards understanding Palaeoenvironments during the first out of Africa.

2006- National Museums of Kenya Conference: A presentation on Late Holocene vegetation dynamics, climate, fire and human activities.

2006- East Africa Quaternary Science Conference in Uganda.

2006- Workshop on Late Holocene climate variability and ecosystem dynamics from laminated Lake Challa sediments.

2006- Science for Heritage Conservation: Our Heritage Our Wealth. National Museums of Kenya Annual Scientific Conference: 15-16th November.

2008- Scientific Drilling for Human Origins: Exploring the Application of Drill Core Records to understand Homid Evolution. 2009- EAQUA Conference, Ethiopia, with a presentation on Late Quaternary vegetation and fire dynamics on Mount Kenya. 2010- Paleochronology Workshop, August 17th to 21th in Mexico.

2010- International Conference on Biodiversity, Land Use and Climate Change, Nairobi, Kenya, 15-17th September.

2011 (planned)- Continental Drilling in the East African Rift Lakes: A strategic Planning Workshop, USA.

Stephen is interested in understanding vegetation dynamics in the Holocene, pollen vegetation relationships, land use and land cover changes, and fire history and archaeology

LIST OF PEER REVIEWED PUBLICATIONS IN INTERNATIONAL JOURNALS:

in prep / in review

Rucina, S.M., McGuiness, K. & Marchant, R., in review. Holocene montane forest ecosystem dynamics from Mount Kenya. Vegetation History and Archaeobotany.

Rucina, S.M., Verschuren, D., Gelorini, V. & Marchant, R., in prep. High resolution late Holocene ecosystem dynamics in the Lake Challa catchment and wider Kilimanjaro region. To be submitted to Journal of Quaternary Science.

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List of other publications:

Maitima, J., Reid, R.S., Gachimbi, L.N., Majule, A., Lyaruu, H., Pomery, D., Mugatha, S., Rucina, S.M., Mugisha, S., 2004. Regional synthesis paper: The Linkage between landuse change, land degradation and biodiversity across East Africa. LUCID Working Paper Series 42.

Sawada, Y, Sakai, T., Sampei, Y., Ohiro, Yogolelo, H.M., Seto, K., Tanaka, S., Saneyoshi, M., Itaya, T., Hyodo, M., Nakaya, H., Nakatsukasa, M., Kunimatsu, Y., Nakano, Y., Tsujikawa, H., Shimizu, D., Takano, S., Ogiwara, N., Rucina, S.M., Mathu, E.M., Opiyo Akech, N., Olago, D.O., Kabeto, K., Pickford, M., Senut, B. & Ishida, H., 2003.Deciphering the history of environmental change related to human evolution in the Kenya Rift. Geoscince Rept. Shimane Univ. 22, p.1-14.

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