Palaeoenvironmental perspectives for sustainable development in East Africa

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Abstract

East African ecosystems are shaped by long-term interaction with changing climate, human population, fire and wildlife. There remains today a strong connection between people and ecosystems, a relationship that is being strained by the rapidly developing and growing East African population, and their associated resource needs. Predicted climatic and atmospheric change will further impact on ecosystems culminating in a host of challenges for their management and sustainable development, further compounded by a backdrop of political, land tenure and economic constraints. Given the many direct and indirect benefits that ecosystems provide to surrounding human populations, understanding how they have changed over time and space deserves a special place on the ecosystem management agenda. Such a perspective can only be derived from a palaeoecology, particularly where there is high resolution, both through time and across space. The East African palaeoecological archive is reviewed, in particular to assess how it can meet this need. Although there remain crucial gaps, the number of palaeoecological archives from East Africa growing rapidly, some employing new and novel techniques to trace past ecosystem response to climate change. When compared to the archaeological record it is possible to disentangle human from climate change impacts, and how the former interacts with major environmental changes such as increased use of fire, changing herbivore densities and increased atmospheric CO₂ concentration. With this multi-dimensional perspective of environmental change impacts it is imperative that our understanding of past human-ecosystem interactions are considered to impart effective long-term management strategies; such an approach will enhance possibilities for a sustainable future for East African ecosystems and maximise the livelihoods of the populations that rely on them.
1 Introduction

The future character of East African ecosystems, given their dynamic ecology, complexity of human-ecosystem interactions and response to atmospheric, climate and land use change is uncertain. Many debates concerning ecosystem conservation in Africa have focused not on the present or future – as one might expect – but on the past (Stump, 2010). Such a focus has been aided by a growing awareness, both within scientific and public arenas, about environmental change processes and how these impact on ecosystems as the constituent plants and animals respond by adaptation, migration or extinction. Our understanding on the impacts of increasing global temperatures, rising levels of atmospheric CO$_2$ concentration, and the impacts these may have on our planet via a series of feedback interactions between solar activity, atmospheric composition, precipitation, land surface conditions and ocean currents are being untangled. The world’s environment is changing more rapidly than at any time through human history; in the relatively short time the human species has been present (~200,000 years) on the earth they have never experienced a change in climate from a warm (dry) to warmer (drier) state concomitant with higher concentrations of atmospheric CO$_2$. There is no doubt that drought and flood episodes over the Holocene (the past 10,000 years) in East Africa have been much more dramatic, and persistent, than recorded by the instrumental record – this not representing the full range of climatic variability of the current interglacial period (Gasse, 2000). Sedimentary records of ecosystem response to past environmental variability have proven invaluable for studying the past impacts of climate change on natural systems (Willis and Birks, 2006). As more records on past environmental variability become available from East Africa, it is apparent that certain areas are more resilient to climate change than others. The relative lack of past changes in climate has been used to explain the exceptional biodiversity of the Eastern Arc Mountains of Africa (Hamilton, 1982; Mumbi et al., 2008; Finch et al., 2009). In addition to providing “observations” about past environments and ecosystems the palaeo perspective provides a benchmark against which to
compare present change, and test and constrain future predictions (Braconnot et al., 2007). However, it is vital to treat palaeoecological data carefully when reconstructing past climatic and environmental parameters; reconstructions are quickly taken on board by other disciplines that do not have, and should not be expected to develop, a comprehensive understanding of the various deficiencies associated with the primary data, how it has been analysed and ultimately interpreted (Marchant and Hooghiemstra, 2001).

Numerous studies on fluctuating past lake levels (Beuning et al., 1997; Ryner et al., 2006, 2008; Garcin et al., 2007; Vershuren et al., 2009) and vegetation change (Jolly et al., 1997; Swain, 1999; Gillson, 2004; Taylor et al., 2005) demonstrate the sensitive nature of the East African environment to register change, particularly in response to changes in the moisture regime (Vershuren et al., 2009), fire-ecosystem (Hemp, 2006a), herbivore-ecosystem (Rucina et al., 2010) and atmospheric CO$_2$-ecosystem (Jolly and Haxeltine, 1997) interactions. An understanding of past human-ecosystem-environmental interactions, and how these have evolved, is crucial for understanding present-day relationships between people and their environments (Robertshaw et al., 2004). For example, recently increased fire occurrence and forest clearance have had a dramatic impact on the area surrounding Kilimanjaro, lowering forest extent and possibly reducing regional water budgets (Hemp, 2006a). A similar situation of historical forest clearance across the Eastern Arc Mountains (Hall et al., 2009) would also have impacted on water budgets, particularly close to the coast where forest clearance on highland areas reduces the ability to trap orographic moisture and generate occult precipitation (Pocs, 1976). In addition to the long term and wide spatial perspectives on environmental change issues that palaeoecology can provide, there is little doubt that the physical, biological and climatic environment has influenced the nature and development of human civilizations in East Africa, as throughout the world (Webster, 1979; Dalfes et al., 1994; Lane, 2009; Stump, 2010). By applying methodologies suitable for disentangling human-environment-ecosystem interactions there is increasingly well-constrained evidence of complex spatial and temporal connections between...
archaeological and palaeoecological data in East Africa (Leiju et al., 2005). This interaction is particularly pertinent in East Africa as the environmental and cultural gradients are steep and hence very sensitive to climate change. East Africa is rapidly revealing its environmental and archaeological past; such knowledge can be useful in answering crucial questions facing ecosystem management in an area of rapid population and economic growth against a backdrop of rapid environmental and land use change.

2 The East African environment

East Africa consists of the countries of Burundi, Kenya, Rwanda, Tanzania and Uganda and is characterised by highly diverse topography dominated by the extensive East and West Rift valleys and the large inter-rift lakes (Fig. 1). East Africa is dominated by highland areas that fall into three broad categories distinguished by their age and geological origin. The most dominant highland areas are the Eastern and Western Rift valleys that have their origin in the late Miocene (Grove, 1986). The western Rift extends in an arc from southern Malawi to northeastern Peoples Democratic Republic of Congo where conjoins with the Ruwenzori mountain range. The Ruwenzori consists of Precambrian crystalline rock uplifted about 3 million years ago by the rifting process. Similarly ancient Precambrian crystalline geology comprise the Eastern Arc Mountains, however these are at least c. 30 million year old, but their progenitors possibly originated more than 100 million years ago from the uplift of the basement rock (Schulter, 1997). The other highland areas to dominate East Africa are the geologically recent (∼6 to 2 million year old) stratovolcanoes such as the Aberdares, Mt. Elgon, Mt. Kenya, Mt. Kilimanjaro, Mt. Meru and the Virunga Volcanoes. Most of these areas form classic cone-shaped volcanoes although the Aberdare Range, being slight older in origin, form a 160 km long mountain range (Fig. 1).

The most important climate variables for determining ecosystem distribution (Fig. 2) are annual rainfall and dry season length, with temperature, being particularly important at higher altitudes. Rainfall distribution in East Africa is complex, with pronounced
changes recorded over short distances (Fig. 3). The biannual migration of the Inter-
Tropical Convergence Zone (ITCZ) results in bimodal rainfall in the northern parts of
the region where rainfall is concentrated between October and December and from
March to May, becoming more restricted farther north (Hastenrath, 2001). Southern
parts of East Africa experience a single rainy season between November and May,
with a prolonged but variable dry season from June to September (Hastenrath, 2001).
Annual rainfall patterns on East African mountains vary according to elevation, as-
pect and distance from the sea (Newmark, 2002). Due to the proximity of the Indian
Ocean, their high elevation and prevailing easterly winds the “ecological islands” of the
East African mountains experience relatively high rainfall compared to the surrounding
“sea” of savanna (Fig. 3). Most highland areas receive on average between 1200 and
2000 mm yr\(^{-1}\) of precipitation, with the wettest areas, e.g. the eastern slopes of the
Uluguru Mountains, exceeding 3000 mm yr\(^{-1}\) (Pócs, 1976). Non-precipitating mist and
cloud are an important source of moisture at high altitudes, where forest-clad slopes
strewn with epiphytic bryophytes and lichens extract moisture via occult precipitation
(Pócs, 1976; Hemp, 2006b). Rainfall patterns are strongly influenced by sea surface
temperature gradients in the Indian Ocean, which deliver moisture-laden winds to the
eastern windward slopes of East African mountains (Nicholson, 1998). The El Niño-
Southern Oscillation and the Indian Ocean Dipole are other important controls of inter-
decadal rainfall variability in East Africa (Marchant et al., 2006; Russell et al., 2007).
Comparable to any mountainous environment there are strong altitude-temperature
gradients; lapse rates of \(\sim 0.68 \degree C/100 m\) recorded on the eastern slopes of the Usam-
bara Mountains (Newmark, 2002) are common across the East African highlands.

The steep topographic and climatic variability is mirrored by diverse ecosystems that
range from montane rainforest through to dry savannas, from mangroves to high altitu-
dinal grasslands (Fig. 2, Plate 1). East Africa contains four of the 34 global biodiversity
hotspots, thirteen world heritage sites and numerous world famous national parks such as
Serengeti and Ngorogoro. In addition to being internationally recognised as one of
the world’s most important areas for its’ biological diversity, East African ecosystems
are increasingly recognised to be highly valuable for the services they provide (Mittermeier et al., 2005; Burgess et al., 2009) such as food, materials and energy, and less tangible commodities such as pollinators, carbon storage, regulation of nutrient cycles and moderation of flows of energy and water. Many of the mountain areas support montane rain forest that has historically been the focus of forest clearance for valuable timber, originally driven by demand in European markets and increasingly those in China and India (Milledge and Kaale, 2003). For example, the Eastern Arc Mountains are one of the most threatened regions of global biodiversity, having already lost more than 80% of their original forested area with some 25% of the historical forest extent being lost in the past half century (Hall et al., 2009). Much of the remaining forests are protected within an extensive network of National Parks and forest reserves under a variety of management regimes (Blomley et al., 2007). The lowland areas (<1000 m), apart from the relatively moist areas along the coast, are dominated by dry forest associations (Fig. 2). The composition, extent, structure and function of these dry forests arise from complex interactions with wildlife, livestock, humans, fires, climatic conditions and atmospheric CO₂ concentrations (Bassett and Crumme, 2003; House et al., 2003; Scholes, 2004). Dry forests often develop where edaphic conditions and/or disturbance prevents the establishment of extensive tree cover. For example, the grass savanna of the Serengeti forms on free-draining substrates that inhibits the growth of hydrophilous trees - even under increased precipitation the area would remain moisture-stressed. Another major control on East African ecosystems, particularly dry forests, are large mammals, that maintain open woodlands by debarking and pushing over trees allowing grass to establish that subsequently attracts a variety of grazing animals (Plate 1). It is perhaps the complexity of East African ecosystems, or the spatially extensive nature of some of these, that has resulted in the ecosystem response to climatic and anthropogenic impacts to be relatively neglected while other regions, such as Amazonia or Antarctica, have attracted much public interest. Such neglect has to stop! This paper focuses on a number of thematic areas core to understanding East African ecosystem dynamics. We discuss priorities for the conservation
and sustainable development of African ecosystems, building on our palaeoecological understanding of human, animal, environmental and ecosystem interactions – emphasising how palaeoecological perspectives can be incorporated to enhance the potential for sustainable use of East African ecosystems.

3 Understanding East Africa’s past to manage the future

East Africa has long been of interest to palaeoecologists (Hedberg, 1954; Livingstone, 1962; van Zinderen Bakker, 1964; Coetzee, 1967); the development and rapid expansion of palaeoecological research in East Africa has been possible due to the wealth of sedimentary deposits that range from ice caps to swamps, from estuaries to lakes, the latter extending from small craters to the large Rift Valley lakes such as Lake Victoria. The palaeoenvironmental history of East Africa has been reviewed in detail by van Zinderen Bakker and Coetzee (1972), Hamilton (1982), Street-Perrott and Perrott (1993), Olago (1999), Marchant and Hooghiemstra (2004) and Kiage and Liu (2006). Despite this long history and abundance of sites suitable for palaeoecological research the records are spatially quite skewed; for example, there are only a couple of records derived from the Eastern Arc Mountain range (Mumbi et al., 2008; Finch et al., 2009), while a mass of information exists from Mount Kenya (Coetzee, 1967; Karlen et al., 1999; Barker et al., 2001; Olago, 2001; Ficken, 2001; Ficken et al., 2002; Wooller et al., 2000, 2003; Street Perrot et al., 2007; Rucina et al., 2009). Another review of East African palaeoenvironmental history is not the focus of this paper, but we do highlight a number of key events as examples of how the palaeo record can be useful for future perspectives. We will focus on the Holocene as, although humans have been interacting with ecosystems from much longer than the last 10 000 years, these millennia correspond to a significant increase in ecosystem impacts, providing context for present-day anthropogenic ecosystems (Foley et al., 2005; Ellis and Ramankutty, 2008).
3.1 Holocene environmental variability

Following transition from the glacial period most common Earth system state of the Quaternary period, the relatively warm and wet conditions characteristic of the early Holocene resulted in many montane areas experiencing forest expansion to higher altitudes (Fig. 4) at the expense of grasslands that were more extensive during the last glacial period (Wooller et al., 2003). For example, at Kashiru Swamp in Burundi, pollen data show widespread forest expansion between 11,500 and 5700 cal yr BP (Bonnefille and Riolett, 1988). Similarly, maximum moist forest extent was reached between ~8500 and 7600 cal yr BP within the Lake Albert catchment (Beuning et al., 1997). However, for the glacial period there is continuing discrepancy between some high altitudinal sites being relatively moist and all lower altitudinal lakes recording pronounced aridity – this was likely due to the reduced ability of vegetation (Ericaceous and C₄-dominated grasslands vs. multi-layered forests) to strip out moisture from non-precipitating clouds (Rucina et al., 2009). The importance of the vegetation in generating moisture in the montane areas can be clearly see along the Eastern Arc mountains of Tanzanian where the “high” altitudinal grassland plateaus that form around 2000 are at much lower altitudes than the upper tree line on other East African mountains (around 3800 m). These anomalously low grasslands are thought to be largely due to interaction between flat topography, low stature vegetation resulting in a rapid decline in plant available moisture – hence a clear feedback between topography, vegetation and microclimate that results in the formation of edaphic high altitudinal grasslands. Similarly during the last glacial period this reduced generation in occult precipitation would have resulted in reduced river flows and associated lake level declines as the high altitude ‘water towers’ became 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 the recent extensive clearance of the Ocotea-dominated forest is thought to be accountable for a significantly reduced hydrological budget, reduced flows and
associated regional aridity (Hemp, 2006a). In addition to providing important insight such visions of past ecosystem response and linked environmental feedbacks render current tropical palaeoclimatic reconstructions potentially erroneous, and certainly highlights that they need to be treated with caution. Using this more wholesome understanding of ecosystem response to climate change is highly relevant to predicting future impacts on African ecosystems, particularly because the LGM is a critical period for climate model comparisons (Elenga, et al., 2001; Braconnot et al., 2007).

The mid-Holocene in East Africa is characterised by relatively abrupt environmental shifts toward more arid conditions from around 5500 cal yr BP (Jolly et al., 1994; de Menocal, 2000) when lake levels fell sharply (Gasse et al., 1989; Stager et al., 1997; Johnson et al., 2000; Vincens et al., 2007), and arboreal pollen percentages declined abruptly (Fig. 4) reflecting expanding dry ecosystems (Ricketts and Johnson, 1996; Wooller et al., 2000). These changes form part of a wider signal observed about 4000 cal yr BP across the African tropics, with numerous sites recording a shift towards drier environmental conditions that could have precipitated, and certainly influenced, one of the greatest changes in population distribution in Africa, and one that is key to understanding present population – that of Bantu migration. The interlacustrine region has long been a locus of cultural and socio-economic changes and a major contact zone between diverse agricultural practices. The transformation to an agro-pastoral lifestyle in the interlacustrine area is thought to be associated with the arrival of the Bantu (Fig. 5), rather than independent domestication (Schoenbrun, 1993). Bantu agriculturalists, originally from Western Africa, migrated across the African continent taking with them crops and iron working that would transform the subsistence framework of the East African landscape (Bower and Lubell, 1988; Schwartz, 1992; Pearl and Dick-son, 2004). Agricultural transformation would have been accompanied by a range of technologies that would have made the pioneers highly effective at modifying land, in particular clearing forest for agricultural production and supporting a developing iron industry. The East Africa Iron Age is first recorded in the Lake Victoria area around 2500 yr BP where it is thought to have been introduced by Bantu speakers (Pearl and
Dickson, 2004). Although the regional pattern of spread of iron and agricultural practice is controversial, the last few thousand years has seen extensive modification of the forested landscape to support an increasingly settled population practicing mixed agriculture. The extent of this interaction has been so great that few places, if any, in East African can be thought of as “pristine” and not a product of past interaction with human populations.

The late Holocene was also characterised by a highly variable climate evident from rapidly changing levels of large Rift valley lakes (Ricketts and Johnson, 1996; Russell and Johnson, 2005). The magnitude of these shifts is quite phenomenal, with Lake Naivasha fluctuating by some 40 m in the last 1000 years (Vershuren et al., 2000). Similarly, there were major changes in ecosystem composition (Fig. 4) as increasingly arid conditions during the late Holocene, marked by intensifying droughts after ~1500 cal yr BP, resulted in the replacement of forest by open grasslands within the Lake Tanganyika catchment (Msaky et al., 2005). Similar grassland expansion, coupled with increased burning and the appearance of Ricinus communis pollen, occurred from 1650–1550 cal yr BP within the Lake Masoko catchment (Vincens et al., 2003). Namelok Swamp, located just north of Kilimanjaro, also records an increased abundance in grassland from 2000 to 1675 cal yr BP again suggestive of a period of aridity (Rucina et al., 2010). However, this is part of a broader signal of rapid climate fluctuations through the late Holocene: beginning about 1675 cal yr BP the ecosystem surrounding Namelok Swamp experienced a rise in Syzygium coupled with a relative decrease in Acacia, suggesting that the catchment became wetter (Rucina et al., 2010). Similar environmental shift have been recorded from 1750 to 1450 cal yr BP by high stands at Lake Edward (Russell et al., 2004) and Lake Tanganyika (Alin and Cohen, 2003). Diatom and midge evidence from Lake Naivasha indicate that the subsequent period from ~1000 to 740 cal yr BP was drier than the present day, while the period from ~740 to 160 cal yr BP (coeval with the Little Ice Age of Europe) was characterised by relatively wet conditions (Verschuren et al., 2000) whereas indications from Lake Victoria, Lake Chibwera, Lake Kanyamukali and Lake Baringo (Bessems et al., 2008)
suggest the period from ∼460 to 160 cal yr BP was dry. Such discrepancies, as under the LGM, are thought to result from local climatic regime and feedbacks to the hydrological system, in particular changes in ecosystem composition and distribution (that are increasingly likely to be more anthropogenic in origin) within the late Holocene and how these impact on the catchment scale hydrology.

Thus, rapid climate change with stark ecosystem responses seen today are not a new phenomenon (Fig. 4); the only constant about climate is that it changes, and local responses to such change differ according to feedbacks from topography, substrate and ecoclimatic regime. Past climate variability is much greater than recorded by the instrumental record, and indeed much greater than currently considered by policies on land-use options and livelihoods under climate change scenarios. As more palaeoenvironmental data are produced from East Africa a coherent perspective on the spatial and temporal character of climate shifts, and how these impact on ecosystems, emerges. Understanding the range of natural variability, and ecosystem response to this, has a key (and hitherto largely ignored) role for the future management of East African ecosystems. The responsive nature of East African ecosystems to a variable climate, and the dramatic impact on livelihoods, was emphasised by the 2009 drought that extended across the Horn of Africa decimating herbivore (both domestic and natural) populations and the livelihoods of people living within dry forest ecosystems, especially those on land more marginal for pastoral or agricultural production. The impact was much broader that “just” on pastoral and agricultural communities – a common manifestation was widespread rationing of electricity and water supply to urban areas, leading to reliance on generators and increased food prices that has had an economic impact on all.

3.2 Agricultural transitions: changing human-ecosystem interactions

An appreciation of the inter-linkages between societal and ecological processes underpinning livelihoods is essential to understanding the nature of human population vulnerability and ecosystem resilience under increasing habitat transformation, fragmentation
and human/animal conflicts (Eriksen and Watson, 2009). Such an appreciation must be so much more than simple deterministic relationships between environmental stress and social change (Hassan, 2000; Costanza et al., 2007). Humans have long distinguished themselves by using tools and technologies to shape ecosystems (Burgess et al., 2007; Sereno et al., 2008); a range of archaeological findings indicate a growing tendency to settle, modifying surrounding ecosystems. Counter to this is the strong impact that climate change can have on populations (Webster, 1979), whole empires rose and fell during the late Holocene as agricultural productivity and subsistence levels changed and populations migrated and adapted to new environments (Dalfes, 1994). Understanding interactions between past ecosystem dynamics, human migration and changing land use strategies has gone beyond the comparison of local records, towards integrative research that could shed light on the dynamic relationship between human societies and climate change (Stump, 2010). To rise to the challenges of managing ecosystems in an increasingly populous world we need to fully understand the history of these relationships, particularly as the very nature of long-term human-ecosystem interaction is rooted in sustainability – resilient ecosystems meeting the needs of past and present generations. Understanding where these interactions have been successful changes the narrative from one characterised by degradation, disturbance and impacts, to one characterised by abundance with societies interwoven within the ecological fabric of the ecosystem (Marchant, 2010).

Placing the archaeological record within the context of detailed and well-dated Holocene palaeoenvironmental records allows us to examine how societies responded to environmental changes. In common with palaeoenvironmental data derived from accumulated sediments, a range of techniques combine to construct how human population composition and distribution has changed, and how the interaction with the environment has evolved. This evidence varies from direct analysis of past occupation layers revealed by archaeological investigations to linguistics, from molecular markers to documentary evidence. As with the palaeoenvironmental data, the amount and quality of information is skewed towards certain locations and time periods. This also
raises several problems, mainly as the sites with archaeological and palaeoenvironmental data are often not in the same place – even with sites “close” to each other they might be recording very different signals (Robertshaw et al., 2004). Although evidence for human population change is riddled with gaps between the proxy traces, the overlap between the response of archaeological and palaeoecological sites can be close as human populations often concentrate within sedimentary basins because of the associated natural resources, in particular water and fertile land for agriculture (Lieju et al., 2005). It is often assumed that the onset of agriculture is, in the absence of direct indicators such as pollen from domesticated plants, marked by evidence of forest clearance and burning. This assumption may hold for some activities, but cultivators often make use of natural forest gaps and “forest” can be promoted by certain forms of cultivation beneath the canopy, for example the Chagga home-gardens around Kilimanjaro (Fernandes et al., 1984; Hemp, 2006c). Although signals may be strong when population levels are relatively high, traces of human activity are not always commuted to the sedimentary record – an absence of human indicators does not mean absence in the landscape and there are a number of possible reasons for weak signals of human activity. Some prehistoric societies may have trodden lightly on the landscape, particularly where population densities were low. Subsistence and mobility patterns of pastoralists leave few traces on land surfaces: pastoralists are normally nomadic, curate their tools, and reside in areas for only short periods – all leading to low archaeological visibility (Arroyo-Kalin, 2010). The late Holocene is increasingly characterised by signals of human activity that allowed their impacts upon the landscape to become visible. A good example of a “typical model of agricultural transition” can be seen within south-western Uganda where some forty years of palaeoecological research in the Rukiga Highlands (Morrison, 1968; Hamilton, 1982; Taylor, 1990; Marchant, 2007) has provided an excellent understanding of regional ecosystem transformation. To explain the changing regional vegetation composition and distribution a series of forcing mechanisms (ecological, climatic and human) need to be invoked. It must be stressed that such a “typical model” is not applicable elsewhere but it does contain common
elements of incoming agriculturalists with associated iron technology and crops, resident hunter-gatherer populations, extensive forest clearance, development of densely settled rural populations, with resultant present-day forest remnants restricted to protected areas with sharply defined boundaries (Plate 2). Pollen evidence records quite clearly the replacement of forested areas by open vegetation and degraded scrub from \( \sim 2200 \) cal yr BP (Taylor, 1990). For areas that maintained forest cover, a transition to a more open, and possibly drier, form of forest is apparent from approximately 700 yr BP; this significant spread in forest clearance to lower altitudes was possible in response to a rapidly growing agricultural population needing to cultivate new land although increased aridity or seasonality will also have impacted on forest composition (Marchant, 2007). Despite these major changes in regional land use, a large remnant of extensive montane forest has been maintained that forms the present day Bwindi-Impenetrable Forest National Park (Plate 2) that is today valued as a habitat for a third of the global mountain gorilla population and has been designated a World Heritage site. Why this particular patch of forest “survived” is unknown although it is likely there has been some degree of protection afforded by the (until recently) resident indigenous BaTwa population against the colonising agriculturists (Kingdon, 1990). For example, one possibility is that a precursor of Bwindi-Impenetrable Forest corresponded to some form of disputed border between territories; the associated economic and political instability would have placed severe limitations on the development of sedentary agriculture. Such a border may relate to the highly centralised societies in the interlacustrine region that commenced during the early part of the present millennium: forests which were intact at the time of state formation and located towards the outer-limits of the kingdoms’ spheres of influence, were “protected” as a natural deterrent to potential invaders (Taylor et al., 2000). Whatever the result of the cultural contacts between different groups in the Rukiga Highlands we can only suggest what may have occurred as modern analogues are unknown. What is quite obvious from the palaeoecological records is that agricultural land-use had rapidly spread since approximately 2000 yr BP with some protection being afforded to Bwindi-Impenetrable Forest, this protection has
continued to present day, now under the guise of National Park legislation, national and international conservation organisations.

At many sites human activity is not recorded until quite late. For example, within the Lake Tanganyika catchment there is evidence of widespread deforestation and increased erosion from the late 18th century onwards (Cohen et al., 1999). At Lake Naivasha, maize (Zea mays) pollen appears in the record after ∼300 cal yr BP (Lamb et al., 2003), at a similar time to South Pare, Tanzania, which is coupled with a reduction of lower montane forest (Fig. 4) probably as a result of anthropogenic activity (Finch et al., 2010). Thus, human-ecosystem interactions are inherently dynamic and complex (De Fries et al., 2004), particularly given the diversity of the Eastern African landscapes, ecosystems and cultures that are intertwined. People and ecosystems have responded and adapted to past change in a variety of different ways. Knowledge of the history behind human-ecosystem interactions is vital to understand how these combine to form the productive ecosystems of today (Lane, 2009). A diverse range of adaptation strategies have been employed by communities to reduce their vulnerability to climate change and variability, allowing them to adapt to and moderate potential shifts, and helping them cope with adverse consequences (Robertshaw et al., 2004). For example, pastoral communities maintain wealth and environmental “buffers” in herds of cattle; during extreme periods of drought or disease these “stores” can be massively impacted on. Agricultural communities would traditionally 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 across East Africa today. Although there has been rapid adoption of maize and banana by East Africans there is surprisingly little known about the effects these crops have had on the East African cultural landscape and ecosystems. We can see from how past communities have responded to droughts that coping mechanisms, combined with an over reliance on more exotic faunal and floral resources, rather than enabling long-term security, can be quite fragile safety nets (Eriksen and Watson, 2009). Indeed, the nature
of human-ecosystem interactions is increasingly becoming decoupled from the past; ecosystems experience a multitude of new challenges which are social, political and economic in origin and alter the boundaries and framework of the human-ecosystem interaction.

4 The future of ecosystem services

There is “consensus” on the need to limit Greenhouse gas emissions so that Global warming does not exceed 2°C (Stern, 2008). This focus on temperature is very much a temperate-world perspective; in East Africa the main focus regarding climate change concerns the frequency and variability of rainfall. Impacts of increasing water stress are predicted to become acute, even in East Africa, where most climate change models predict increased rainfall, recent research suggests that local circulation effects will result in decreased precipitation (Funk et al., 2008). Given the marked threats that anticipated climate change pose to water and associated food security there is an urgent need to assess the impacts of this on natural resources into the future. A variety of dynamic vegetation and niche-based models are available, and in development, to investigate species responses to climatic gradients (Sitch et al., 2003; Platts et al., 2008, 2010). With such tools showing that species will move into, and out of, protected areas as climates change (Hannah, 2010), it is quite alarming that much of the high ecosystem diversity in East African ecosystems is found within a network of static protected areas and game reserves surrounded by a “sea” of agriculture. The robustness of the protected area network is not just a matter of conserving wildlife for there is great economic wealth generated by the protected areas. For example, across the Tanzanian and Kenya Borderlands region some 14 protected areas, including the world famous national parks like Amboseli, Ngorogoro and Serengeti (Fig. 6), generate billions of US$ in associated tourist revenue vital to national economies. Climate change is, and increasingly will, impact on this: for example, within the Amboseli National Park in southern Kenya, the extensive 2009 drought resulted in 90% drop in
the Wildebeest population with large coeval reductions in other ungulate populations (David Western, personal communication, 2010). Although the carnivore populations flourished during the drought, the present-day lack of prey species is leading to increased human-wildlife conflicts as the carnivores turn to domesticated stock. To deal with this situation the Kenyan Wildlife Service recently trans-located 150 zebra from a private game reserve in central Kenya at a cost of US$ 1 000 000. With such ecosystem distributional changes expected to increase under predicted future environmental change there comes a great uncertainty about the future ability of parks and protected areas to meet their conservation mandates (Burns et al., 2003). As in the past (Fig. 4), the geographic ranges and/or coincidence of species that currently interact will progressively change, while species that do not presently coexist may do so in the future (Araujo et al., 2004; Thuiller et al., 2006).

Predicting and clarifying impacts of global change on biodiversity, ecosystem services, human livelihoods, and land use change (degradation, fragmentation, biotic invasion and over-use) presents considerable challenges. To meet these challenges we need to apply skills, analytical methods, data and intellect from a diverse range of actors that develop a strategic blend of disciplines, tools and understanding. One crucial area is the development of more realistic coupled ecosystem-climate change modelling approaches that can be used to assess the efficiency of current tools, such as the protected area network, under future socio-economic and climate scenarios. Future climate predictions available from the IPCC Data Distribution Centre (IPCC AR4) are spatially coarse (300 km$^2$ grid cells), that even with downscaling using present-day environmental conditions (Tabor and Williams, 2010), such surfaces are not appropriate (and potentially misleading) for understanding impacts on regional scale livelihoods and policy development. An urgent need is to estimate potential ecosystem response to future climate change using regional climate models (e.g. PRECIS and REMO) that allow reconstructions down to 25 km$^2$ resolution (Fig. 7) that can be further down-scaled using present-day climate and altitude data and can become very useful tools to assess the threats of climate change, particularly drought and changes
in seasonality, to the native biota and ecosystem services critical to human populations. This is methodologically and computational challenging, particularly in mountainous areas where the environmental gradients are at their steepest, populations often at their densest, and associated demand on ecosystem services at their highest. The potential error behind these products should be incorporated into the output by using a range of IPCC global warming and emission scenarios (e.g. A1, B1, A2, B2) combined with a range of climate models (e.g. HadCM3, ECHAM 5, CSIRO) – this range of products can be used to provide error estimates on future environmental shifts.

Comparable to the lack of attention paid to “Global drying”, there is relatively little attention played to the direct impacts that changes in atmospheric CO$_2$ concentration will have on ecosystem composition despite the well-constrained effect of this evident from the palaeo record (Street-Perrot et al., 1997; Boom et al., 2002; Wooller et al., 2002), palaeo-informed modelling studies (Jolly and Haxeltine, 1997), growth chamber experiments (Kgope et al., 2009) and historical archives (Foden et al., 2007) (Plate 3). Atmospheric CO$_2$ concentration particularly influences plants in dry forest ecosystems that are extensive across East Africa (Fig. 3) by altering water use efficiency, photosynthetic rates and light- and nutrient-use efficiency (Bond and Midgley, 2000; Bond et al., 2003, 2005; Bowman, 2005). Increased tree growth and woody thickening allows trees to grow much more quickly, reaching a size where they can survive the fire events that at lower CO$_2$ concentrations (and reduced growth) would maintain an open structure in dry forest ecosystems. The resulting more densely forested landscape, while beneficial for biomass and carbon storage, is deleterious to wildlife and tourism, preventing the open savanna structure ideal for grazing herbivores and associated game viewing. Future predicted rises in atmospheric CO$_2$ concentration will continue to modify ecosystem composition and structure such that the benefits that can be obtained will be dramatically different. The nature and rate of these interactions, and how local changes link to global environmental processes, makes it paramount to identify what conditions, and interventions, could ensure that the impacts of global environmental change can be beneficial. There is an excellent understanding of the impacts of CO$_2$
changes on tropical forests (Jolly and Haxeltine, 1997; Wooller et al., 2000; Boom et al., 2002; Ficken et al., 2002), which can be extrapolated to inform/predict ecosystem response to future concentrations. Consideration of this known ecological response within a socio-economic framework is necessary to impart effective long-term management strategies that promote the livelihoods of user communities under changing environmental conditions (Marchant, 2010).

Sensitive mountain environments, like Mt. Kilimanjaro, Mt. Kenya and the Ruwenzori mountains are locations where our coeval understanding of past impacts of environmental change are best constrained and the complex interactions between vegetation changes, climate and human populations have been demonstrated through time. It is these mountain areas where the potential for an integrated and holistic approach to understanding the processes and impacts of climate change is greatest, these maximising the potential for the application of the palaeo archive – the added value of which will only be fully realised with use. However, there are also areas where our understanding of past climates and environments is limited in both time and space, requiring targeted palaeoecological studies to fill in the gaps, particularly in vulnerable areas. These areas of deficient resolution are exacerbated in East Africa where highly diverse ecosystems and environmental diversity correlate with great cultural diversity. Such application needs a range of skilled researchers from palaeoecologists and botanists to social scientists who are able to communicate their findings across disciplines and work within a modelling context that connects people and ecosystems. For tangible progress to be made, natural and social scientists must overcome language barriers (Ewers and Rodrigues, 2006); but this is much more than just semantics there must be closer interaction between researchers, conservationists, NGOs, and Government agencies (Smith et al., 2009) that actually develop, implement and enforce policy surrounding ecosystem response to climate change (Ostom, 2005). In order to help human societies face growing environmental challenges ecology will have to deliver relevant scientific knowledge on ecosystem function and change, how these processes are linked to human well-being and how humankind has transformed them in a sustainable
way (Loreau, 2010). Countering the threats posed by climate change necessitates regional-scale conservation planning, linked by a network of communities using flexible and resilient coping strategies to maximize the potential use of ecosystem services and build on “good practice” from the past. These benefits are particularly important in East Africa where there remains a strong connection between people, landscapes and ecosystems. This reliance on ecosystem services is exemplified by a strong tourist industry, the importance of agriculture in national economies, the relatively high percentage of electricity generation based on hydroelectricity and the importance of wood fuel for cooking. The degradation of ecosystem services could grow significantly worse during the first half of this century with the possible degradation of human well-being (Dietz et al., 2009). Understanding how changes in the biophysical environment impacted on the flow of these goods and services in the past, and the social processes with which they interact (Burgess et al., 2009), must form a key focus of any ecosystem management policy. However, this is not trivial and for such an approach to be meaningful understandable metrics are required to demonstrate in unequivocal terms the societal consequences of further degradation of ecosystem services (Mooney, 2010). The histories of specific economies or environments might therefore be used as potential sources of positive precedent – that if sustainability can be demonstrated in the past, then this at least suggests the possibility of future sustainability (Stump, 2010).

East African ecosystems, and the vital services they provide, are a product of a long term climate-human interaction and a locally excellent understanding of this interaction is available for use. Sustainable ecosystem management must therefore be directed toward developing and maintaining beneficial interactions between managed and natural systems – avoiding these interactions is not a practical option (Foley et al., 2005). Humans cannot predict the future. But, if we can adequately understand the past, we can use that understanding to influence our decisions and to create a better, more sustainable and desirable future (Costanza et al., 2007). If the three pillars of sustainability (environment, society and economy) are to be reinforced, the temporal element, which is at the core of palaeoecology, should have a role to play (Fig. 8). Such
huge global problems as climate change, loss of biodiversity and pressure on ecosystem services demand solutions where nations cooperate in equitable proportions (May, 2010). The Earth System Science Partnership (www.essp.org/), through the International Geosphere-Biosphere Programme (IGBP), has embarked on a Cross-Cutting theme called IHOPE (Integrated History of People on Earth) that will reconstruct socio-ecological interactions through time, with the prime purpose of understanding better how society interacts with environmental change (Dearing et al., 2007). Such initiatives should be embedded within post-Copenhagen offset mechanisms such as REDD and REDD+ that can be used to encourage sustainable management of East African ecosystems. However, such a targeted approach should not be at the expense of other ecosystem functions, but rather build on solid ecological science and maintain ecosystem function for the benefit of society – locally, regionally and globally. For such benefits to be truly maximised there is a need for further targeted research as history, both environmental and cultural, is not sufficiently well understood and too diverse spatially and temporally to enable the formulation of simple lessons from the past (Stump, 2010) that can be used to managed the future. Although there are areas within East Africa where the history, both cultural and environmental, is very well understood and a landscape historical ecology approach allows an understanding of the interplay between multiple processes within both the natural and cultural spheres (Lane, 2009), it is vital that knowledge gaps in natural resource partitioning and ecosystem response to environmental change are filled. This will require truly inter- and intra-disciplinary perspectives, within which palaeoecology must be an integral part.
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References


Fig. 2. The major climatic gradients of temperature and precipitation across East Africa: (a) mean annual precipitation (Tropical Radar Measuring Mission (years 1997–2006) (Mulligan, 2006) and (b) mean annual temperature after WorldClim interpolated surfaces based on records from the period 1950–2000 (Hijmans et al., 2005). Although we only depict annual moisture and temperature marked seasonality, in particular moisture distribution, is important in controlling species distribution.
Fig. 3. Map showing the distribution vegetation classes across the East African environment, adapted from GLC2000 landcover data (Bartholomé and Belward, 2005).
Fig. 4. Responses of three palaeoecological sites referred to in the text. The simple plots of pollen percentages against time focus on four important taxa from each site with percentages calculated as a percentage of the pollen sum of the four pollen types. The site chosen cover a range of time periods and environments: extending to the last glacial maximum from a moist montane rain forest site (Rumiku Swamp, Mount Kenya; Rucina et al., 2009), the late Holocene from a dry forest site (Namelok Swamp, Amboseli Basin; Rucina et al., 2010) and the late Holocene from a moist montane rain forest (Mount Shengena, South Pare Mountains; Finch et al., 2010).
Fig. 5. Bantu Migration routes from the homeland in north-western Africa. Routes are likely to have passed along the Atlantic coastal margins and around and through the Congo basin. On the northern limit this would have traversed the southern limit of the expanding Sahara, then south down the Nile Valley towards the interlacustrine highlands of East Africa.
Fig. 6. The Tanzanian-Kenya Borderlands region highlighting the distribution of national parks and protected areas. Some of the more commonly known ones are labelled (A) Serengeti, (B) Ngorogoro, (C) Kilimanjaro, (D) Amboseli, (E) Tsavo West, (F) Tsavo East, (G) Tarangire, (H) Arusha National Park and (I) Masai Mara.
Fig. 7. Regional climate model forecast for 2025 showing predicted precipitation changes across the East African region as a % change relative to the present day. Model is PRECIS run with an A1 warming scenario using HadCM3 boundary conditions.
Fig. 8. The three pillars of environment, economy and society and how these interact to lead to sustainable development if taking into account the temporal perspectives possible from palaeoecology.
Plate 1. (A) Goats are very important in maintaining an open savanna structure and preventing the herb layer and tree seedlings from developing. (B) Mangroves form a fringing belt along much of the East African coast and can be locally very extensive. (C) Elephants are particularly important in maintaining open dry forest, in this case from Amboseli National Park where the importance of excluding wildlife can be seen by these exclosure plots set up by the African Conservation Centre. (D) Collecting sediment cores from Cyperaceae-dominated swamp, in this case Rumuiku Swamp, Mount Kenya. (E) Savannas are a product of a long-term interaction with human inhabitation, in this case Massai of the Kenya-Tanzania Borderland region. (F) Commonly above ~3800 m grassland ecosystem dominate with locally extensive stands of Scenecio, the plate also shows a newly cored swamp just above the treeline on Mount Kilimanjaro (G) In contrast the flat plateaux that forms around 2000 m along the East Arc mountains of Tanzania and Kenya also support extensive grasslands – once thought to be anthropogenic in origin recent palaeoecological investigation shows these to be natural and thought to form in response to interactive feedback between local climate, topography and vegetation. (H) The density of trees, shrubs and herbs vary massively in space and is particularly influenced by fire in this case Mount Kilimanjaro where a recent fire is marked by a low stature re-growth of Erica arborea. The highlands of east African are vital in generating hydrological budget that feed groundwater-fed swamps and lakes in the lowlands – these in turn are vital drought refuges for animals and people alike, increasingly these areas are the focus of agricultural encroachment as pressure for land continues compounded by a reduced ability of the upland areas to generate precipitation following forest clearance. All photographs taken by Rob Marchant.
Plate 2. The extensively deforested Rukiga Highlands Uganda following successive and organised expansion of agriculture over the past 2000 years. Formally extensive montane rainforest is now restricted to isolated remnants that are often the focus for protected area status with resulting very sharp boundaries such as Bwindi-Impenetrable Forest National Park.
Plate 3. Matching photographs from the Lolldaiga Hills, Laikipia Plateau Kenya (Robert Wells) showing increased woody thickening in Savanna over the past 70 years. The top plate was taken in 1935 with bottom plate from the same location in 2005 – the tree in the foreground used as a reference point. Although there are many causal factors responsible for such changes in landscape, including pastoral intensity, land use changes, climatic shifts etc., the impact of the increased atmospheric CO$_2$ is thought to be a key environmental factor driving this change.