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Climate, herbivory, and fire controls on tropical African forest for the last 60ka

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ABSTRACT

The Last Glacial Maximum (LGM) in Africa was drier than today and was followed by rapid step-wise climate changes during the last deglacial period. In much of Africa, these changes led to a drastic reduction of lowland forest area during the LGM, followed by recolonization of the lowlands by forest and woodland in concert with regional warming and wetting. However, the history of southeastern African vegetation contrasts with that observed further north. In particular, forest expansion appears to have occurred in southeastern Africa during episodes of high-latitude northern hemisphere cooling. Although vegetation history in Africa is generally assumed to relate purely to climate, previous studies have not addressed potential feedbacks between climate, vegetation, and disturbance regimes (fire, herbivory) that may create tipping points in ecosystems. This climate-vegetation history has profound implications for our understanding of the modern architecture of lowland and highland forests, both thought to be at risk from future climate change. Here we present analyses of fossil pollen, charcoal, and *Sporormiella* (dung fungus) on a continuous 60 kyr record from central Lake Tanganyika, Southeast Africa, that illustrates the interplay of climate and disturbance regimes in shaping vegetation composition and structure. We observe that extensive forests dominated the region during the last glacial period despite evidence of decreased rainfall. At the end of the LGM, forest opening at ~17.5 ka followed warming temperatures but preceded rising precipitation, suggesting that temperature-induced water stress and disturbance from fire and herbivory affected initial landscape transformation. Our *Sporormiella* record indicates that mega-herbivore populations increased at the early Holocene. This higher animal density increased plant species richness and encouraged landscape heterogeneity until the mid-Holocene. At this time, regional drying followed by the onset of the Iron Age in the late Holocene resulted in expansion of thicket, more open woodland, and disturbance taxa that still characterize the landscape today. This climate-vegetation history has important implications for our understanding of the modern and future distribution of lowland and highland forests, which are at risk from future climate change.

1. Introduction

Tropical semi-arid woodlands are thought to play an important role in global carbon cycling and are at great risk from changing climate in the future (Stocker et al., 2013). The Zambezian Miombo Woodland region of Eastern Africa is currently the largest contiguous region of tropical semi-arid woodland in the world (2.7 million km^2) and provides essential resources to millions of people (Campbell, 1996). Although considered a natural ecosystem, miombo is a sub-climax community, meaning that rainfall throughout East Africa is high enough to sustain forests of larger stature and higher density (Lawton, 1978). Furthermore, although miombo woodland is comprised of just a few lowland tree taxa, East African vegetation is very heterogeneous and displays a remarkably complex mosaic of ecosystems that fall across a spectrum from closed canopy gallery forests to very disturbed bushlands/thickets over just a few kilometers (White, 1983). Despite the floristic poverty of much the lowlands, the highlands contain highly biodiverse closed canopy forests that once occupied much greater spatial extents (Dupont et al., 2011). Although much of the spatial complexity in the modern vegetation is thought to be explained by climatic gradients, and in particular to the relationships of temperature and rainfall to topography, disturbance by animals and

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humans is also fundamental to the maintenance of the structure and composition of both lowland and highland vegetation (Campbell, 1996). However, the link between these climatic and ecological mechanisms and their history is largely unknown.

Vegetation change in Africa during the Quaternary is thought to have closely followed the changes in rainfall over the last glacial-interglacial transition (Hamilton, 1981; Gasse, 2000). Paleoclimate records have suggested that rainfall generally followed northern hemisphere temperature change during the Last Glacial Maximum (LGM) and last deglaciation (Gasse, 2000), with pervasive aridity during the LGM and Heinrich Event 1 (H1). Although it has widely been observed that highland forest grew at lower elevation during the LGM than at present, most paleoecological records suggest that LGM aridity resulted in the large-scale replacement of lowland forest with grassland (Hamilton, 1981; Stager et al., 2011). Following the LGM, paleoclimate records indicate a step-wise warming and wetting in most of Africa, which appears to have resulted in forest expansion (Gasse, 2000; Tierney et al., 2010). This is particularly pronounced at the Pleistocene/Holocene transition, when the North African monsoon strengthened marking the beginning of the African Humid Period (AHP; Tierney et al., 2008).

Most paleoecological and paleoclimate work to date has focused on northern and equatorial eastern Africa; however, recent studies from southern and southeastern Africa show a different pattern of climate and vegetation change (DeBusk, 1998; Vincens et al., 2007a; Ivory et al., 2012; Bouimetarhan et al., 2015). For instance, records from the Lake Malawi basin show that aridity during the LGM in southeastern Africa was much less pronounced than regions to the north (Finney et al., 1996; DeBusk, 1998; Gasse, 2000; Garcin et al., 2006). Pollen records from Lakes Masoko and Malawi further illustrate this difference and, in particular, suggest forest expansions may have occurred during periods of northern high-latitude cooling, such as the Younger Dryas during the last deglaciation. This could be due to a southerly displacement of the Intertropical Convergence Zone (ITCZ), which may have resulted in a longer rainy season despite reduced mean annual precipitation (Vincens et al., 2007a; Ivory et al., 2012). Thus far, this phenomenon is only observed in the Lake Malawi basin (10–15° S), while sites to the north of Malawi, such as Lake Tanganyika, are thought to more closely track northern hemisphere climate changes. Although paleoclimatic evidence thus suggests that a “climatic hinge” separates the Lake Malawi basin from points to the north (e.g. Barker et al., 2002), a lack of long vegetation records from southeastern tropical Africa precludes analysis of whether the vegetation transition zone could deviate from the climate one, perhaps due to changes in precipitation seasonality, or if a vegetation hinge zone also exists to separate SE and E Africa despite similar modern vegetation.

Lakes Malawi and Tanganyika are both surrounded by Zambezian Miombo Woodland, where disturbance by humans, animals, and fire is thought to play an important role in ecosystem structure. The role of changing disturbance regimes, and in particular, herbivory and fire, has gained a lot of attention in North America (Davis and Shafer, 2006; Gill et al., 2013); however, their past impact on East African vegetation has been almost completely overlooked in favor of climatic explanations (Campbell, 1996). Thus, paleoecological records which incorporate information about disturbance over the last 60ka, a period of large climatic transitions including rapid climatic changes, can help to understand how these processes relate to ecosystem change in Africa, as well as help us better disentangle how disturbance and climate processes interact to shape modern landscapes. This includes the long history of land-use by people in the East African lowlands, from which even studies of modern landscapes do not allow for determination of the baseline of climatic impacts. Thus long records beyond the Iron Age are needed.

To construct a framework for understanding feedbacks between climate, vegetation, and disturbance on long-time scales, we conducted pollen analysis on a long (>60 kyr) record from central Lake Tanganyika and paired it with paleoclimatic and paleolimnological indicators. This lake, which is the largest freshwater body in Africa, is located in southeast Africa at the junction of semi-arid and tropical forest biomes (White, 1983), and north of Lake Malawi which has been shown to be decoupled from climate change in northern and equatorial Africa (Otto-Bliesner et al., 2014). Therefore, this is a promising location for generating a regional picture of changes in southeast African vegetation structure and composition. Previous studies at this site employed hydrogen and carbon isotopic analysis of terrestrial plant leaf waxes that indicate changes in rainfall (δD_{wax}) and C3/C4 vegetation ($\delta^{13}C_{wax}$), respectively. These studies have suggested that Lake Tanganyika experienced a drier climate during much of the last glacial period, and that its catchment was dominated by C4 plants during that time (Tierney et al., 2008). Organic geochemical analyses of Archaeal biomarkers (TEX_{86} index) in the same cores suggested a cooler LGM, with a step-wise warming between ~20 and 10 ka. Here we develop a high-resolution reconstruction of vegetation changes from the longest record yet recovered from this basin to evaluate the influences of climate and disturbance regimes on vegetation composition and change. Furthermore, charcoal and *Sporormiella* records produced as part of this study are first in this region and allow us to investigate vegetation structural and compositional change due to disturbance mechanisms known today to be vital.

2. Modern setting

Lake Tanganyika is the largest rift lake in the Western Arc of the East African Rift System, extending from ~5 to 9° S (Fig. 1). It is the second largest lake in the world by depth (1470 m) and volume, and thus has an extremely large watershed (238,700 km^2). The lake is permanently stratified and remains anoxic below 150 m (Hecky and Degens, 1973). The only outlet is via the Lukuga River which drains to the west into the Congo Basin; however, the modern sill depth is quite shallow (15 m), thus minor hydrological changes can lead to basin closure. Furthermore, hydrological sensitivity is evidenced by the majority of its water loss by evaporation (Craig, 1974; Dettman et al., 2005). Rainfall around the basin varies greatly in amount and timing. Although average mean annual precipitation is 1100 mm/yr, there is a strong N-S gradient in rainfall and seasonality (Hijmans et al., 2005). The southern basin of the lake receives strongly seasonal rainfall of up to 870 mm/yr with the majority falling from November to March, while the mountains north of the lake receive more than 1600 mm/yr in two rainy seasons from March–May and September–December. Temperature varies little at low elevations (22.8–24.8 °C at 900 m asl; 15.8–20.4 °C at 1500 m asl), however, lower temperatures in the highlands can result in freezing conditions in alpine regions.

Broad-scale patterns of vegetation in southeast Africa are largely constrained by rainfall and rainfall seasonality (e.g. Ivory et al., 2012). In the low to mid-altitudes (<1500 m asl), low-diversity miombo woodlands grow in areas of highly seasonal rainfall and are dominated by deciduous trees such as *Brachystegia*, *Berlinia*, and *Isoberlinia* (Fig. 2). These woodlands can be subdivided into a drier and wetter type found in areas of more or less than 1000 mm/yr, respectively (White, 1983). The wetter miombo has a higher, denser canopy cover and is frequently associated with other trees such as *Uapaca* (White, 1983). The drier miombo displays a more open canopy and higher proportion of grasses and Combretaceae (White, 1983). In areas where rainfall is the lowest and vegetation most disturbed, miombo woodland grades into deciduous, inpenetrable thickets and bushlands. In the south, these are Itigi thickets which