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## Late Quaternary vegetation development and disturbance dynamics from a peatland on Mount Gorongosa, central Mozambique



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### ARTICLE INFO

#### Article history:

Received 14 October 2015

Received in revised form

11 January 2016

Accepted 7 February 2016

Available online xxx

#### Keywords:

Vegetation change

Southern Africa

East Africa

Mozambique

Fire history

Miombo

Podocarp forest

Grassland expansion

ITCZ

### ABSTRACT

Few long-term climate and environmental records are available for southeast Africa where millennial scale shifts in the north-south position of the Intertropical Convergence Zone (ITCZ) and changes in Indian Ocean sea surface temperatures interact with local controls (e.g., fire, hydrology) to influence vegetation and ecosystem dynamics. Reconstruction of late-Pleistocene – Holocene environmental change from peat sediments obtained from Mount Gorongosa, central Mozambique, provides insight into vegetation, climate and disturbance interactions over the past c. 27 kyr. During the late Pleistocene, cool and wet climatic conditions supported *Podocarpus* forest and Ericaceae-heathland until drier conditions led to grassland expansion and a hiatus in peat deposition between c. 22.5 and 7.2 cal kBP. Increased temperatures and fire activity since c. 7.2 cal kBP led to further expansion of grasslands. Continued warming helped maintain grasslands and fostered a diverse mix of *Podocarpus* forest with a large number of subtropical trees and miombo woodland taxa (especially *Brachystegia* spp.) until regional land-use associated with the rise of Iron Age activity promoted an increase of disturbance related taxa over the last 1–2 millennia. Recent migration of people onto the Mount Gorongosa massif in the last fifty years are linked to an increase in fire activity that is unprecedented in the 27 kyr record, resulting in shifts in vegetation composition and structure. This long-term record of environmental change from central Mozambique highlights complex interaction between overlapping climatic influences and documents important vegetation transitions linked to millennial scale climatic controls, disturbance processes and more recent land-use change from a region where few records exist.

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### 1. Introduction

Montane ecosystems in southern and southeastern Africa sustain unique mosaics of arboreal/grassland vegetation and are of particular interest because they host diverse and endemic plant and animal assemblages, are often the source of critical freshwater resources, and are culturally significant to the communities that surround them. Vegetation dynamics are poorly documented for mid latitudes of southern Africa (15–20°S), especially montane sites where *Podocarpus* forests persist within a diverse mix of

miombo woodlands, subtropical forest taxa and grassland species. The records that exist for southern and eastern Africa offer few clues into the biogeography and expansion/contraction of podocarp, heathland, grassland and miombo woodland taxa for montane sites within this latitudinal zone. While previous research by Meadows and Linder (1993) and Tomlinson (1974) showed that montane grasslands were present for millennia at sites throughout southern and East Africa, attributing their development to cooler and drier conditions in the late-glacial and, more recently to land-use; the biogeography of high-elevation grasslands in Mozambique is still poorly understood. After decades of evaluating present-day ecosystem dynamics on Mount Gorongosa, Tinley (1977b) hypothesized that the genesis of Mount Gorongosa grasslands was a recent phenomena, likely a result of contemporary anthropogenic

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disturbances and hydrologic controls. The lack of information on long-term climate-vegetation and land-use interactions for this region highlight the need to augment well researched sites in South Africa and East Africa with records from Mozambique.

Previous research from southern and eastern Africa shows that climatic variability, human activity, disturbance and local edaphic conditions mediate the distribution of forest and savanna biomes and characteristics of the ecotonal boundaries that separate them (Bond, 2008; Chevalier and Chase, 2015; Meadows and Linder, 1993). Quaternary records from the Burundi Highlands and Lake Malawi show orbital induced shifts in the ITCZ and strengthening (weakening) of SE trade winds acted as strong controls on the spatial distribution of precipitation and associated vegetation (Beuning et al., 2011; Bonnefille and Chalié, 2000; Ivory et al., 2012; Powers et al., 2005), whereas palynological records from afro-montane sites in the Drakensberg Mountains, South Africa (Neumann et al., 2014; Norström et al., 2014), emphasize the role of Indian Ocean sea surface temperature (SST) variability as the primary control on environmental change. Quaternary palynological records from the northeast coast of South Africa: Lake Sibaya (Neumann et al., 2008), Mfabeni peatland (Finch and Hill, 2008) and Lake Eteza (Neumann et al., 2010; Scott and Steenkamp, 1996) highlight climate, land-use and disturbance interactions as important drivers of long-term vegetation change as do records from savanna ecosystems including Wonderkrater, Tswaing and Tate Vondo in South Africa (Metwally et al., 2014; Scott, 1982a, b; Scott, 1999a, b; Scott et al., 2012). Quaternary paleoecological studies from Mozambique are restricted to the coastal plains of southern Mozambique (Ekblom, 2008; Ekblom et al., 2014; Ekblom and Stabell, 2008; Holmgren et al., 2012). Among these records, the longest record is available from Lake Nhaucati within the southern coastal plain and shows detailed changes for the last 1.6 kyr within miombo woodlands where the primary drivers of vegetation change are attributed to climatic variability and Iron Age land-use activities concentrated during the last 1 kBP (Ekblom et al., 2014).

### 1.1. Late-Pleistocene-Holocene climate variability

Previous research suggests important controls influencing millennial-scale late-Pleistocene-Holocene climate variability include Northern Hemisphere (NH) ice sheet extent and teleconnections between NH SSTs and Indian Ocean SSTs, direct insolation forcing and related shifts in the north-south position of the ITCZ and more local convective activity and temperate-tropical trough development (Castañeda et al., 2007; Chevalier and Chase, 2015; Tierney et al., 2008). It is clear that these controls interacted to influence both temperatures and precipitation yet the relative importance of each driver at subregional to local scales in southern and eastern Africa is still not well resolved.

Changes in late-Pleistocene-Holocene temperatures followed similar trends throughout southern and eastern Africa with the Indian Ocean moderating the magnitude of change from coast to interior. In southern Africa, cool LGM temperatures cooled further during the Pleistocene-Holocene transition, steadily increased several degrees during the early Holocene, then cooled during the last several millennia (Chevalier and Chase, 2015). In eastern Africa, temperatures were also cool during and after the LGM but increased earlier than at sites in southern Africa (Powers et al., 2005; Tierney et al., 2008; Woltering et al., 2011). Spatiotemporal variability in regional temperatures increased during the Holocene and most locations experienced thermal maximums during the early to mid Holocene.

Inter-hemispheric teleconnections between NH ice sheet extent, SSTs, and Indian Ocean SSTs (Tierney et al., 2008) and also insolation and the amplitude and seasonal north-south position of the

ITCZ (Castañeda et al., 2007; Schefuss et al., 2011) all mediate the delivery of precipitation associated with moisture availability, storm track position and convective activity across southern and eastern Africa. Tierney et al. (2008) maintain that Indian Ocean sea surface temperatures and changes in the strength of SE trade winds were the primary driver of late Pleistocene – Holocene precipitation in eastern Africa. Millennial scale variability in precipitation for regions further south, including Mount Gorongosa, was likely influenced by an interplay between Northern Hemisphere boundary conditions, Indian Ocean SST and shifts in the ITCZ and Inter-Oceanic Confluence (IOC) and subregional storm genesis (Castañeda et al., 2007; Chevalier and Chase, 2015; Schefuss et al., 2011; Tierney et al., 2008; Wang et al., 2013). According to Scott et al. (2012) and Truc et al. (2013) southeastern Africa received more rainfall during the late Pleistocene-Holocene due to the warming of the Indian Ocean. In contrast, records from Lake Malawi indicate dry seasons were longer as a result of a northward shift in the ITCZ, and increase in SE tradewinds (Ivory et al., 2012). Reconstructions of precipitation derived from hydrogen isotope values ( $\delta D$ ) of sedimentary terrestrial leaf wax from marine cores close to the Zambezi River delta (Schefuss et al., 2011; Wang et al., 2013) also highlight displacement (southward) of the ITCZ via high northern latitude forcing as primary controls on precipitation, especially increased precipitation during Heinrich Stadial 1 and the Younger Dryas.

We present the first paleoecological record from central Mozambique (18.4°S) which documents c. 27 kyrs (interrupted by a long hiatus bridging the Pleistocene-Holocene transition) of vegetation, climate and disturbance dynamics from a wetland on Mount Gorongosa and compare millennial-scale environmental change on the Mount Gorongosa massif with records from southern and eastern Africa. Here we set out to better understand long-term vegetation change in montane ecosystems during the late Pleistocene-Holocene. Key questions are: 1) How did plant communities respond to long-term changes in climate, fire and land-use? 2) When did grasslands and miombo woodland taxa develop on Mount Gorongosa and, 3) How does millennial-scale environmental change from Mount Gorongosa inform spatiotemporal dynamics of climatic variability of this region? We address these questions through analysis of pollen, charcoal, and geochemistry from a peat core obtained from a montane wetland and through comparisons with existing climate proxies specific to southeastern Africa (Ekblom and Stabell, 2008; Holmgren et al., 2012; Neumann et al., 2014; Norström et al., 2014; Powers et al., 2005; Schefuss et al., 2011; Tyson et al., 2000; Wang et al., 2013). This record from Mount Gorongosa provides important information on millennial-scale vegetation and climate interactions from a region where these are poorly understood and compliments recent work aimed at better resolving late-Quaternary climate variability in southeastern Africa (Chevalier and Chase, 2015). Investigating these interactions in the diverse plant communities of Mount Gorongosa will also provide historical context for land managers tasked with supporting an important ecological and cultural resource undergoing rapid land-use change.

## 2. Study site

Mount Gorongosa is a massive gabbroic-granitic inselberg of 30 km in length and 20 km in width (c. 700 km<sup>2</sup>) of the Gorongosa Fracture Complex in the East African Rift System, located in the Gorongosa district of the Sofala Province 100 km from the Indian Ocean (Fig. 1) (Müller et al., 2012). Mount Gogogo is the highest peak of the massif (1863 masl). Mount Gorongosa rises 1400 m above the surrounding landscape and is one of the few southern African mountains above 1700 masl apart from the Drakensberg

Mountains of South Africa. Soils are generally shallow, composed of sand (granitic) and sandy loam (gabbro component) (Müller et al., 2012). The upper elevations of Mount Gorongosa receive over 2000 mm rainfall per year – some of the highest rainfall amounts in the region, most of which occurs during a rainy season between November and March. Precipitation is largely derived from the southern African monsoon but also from orographic rainfall of locally recycled water vapor from the Rift valley floodplains and mist on the Mountain (Steinbruch and Weise, 2014). The mountain serves as the headwaters of the Vunduzi, Muera and Nhandare river catchments, providing a perennial source of water for agriculturalists as well as plant and animal communities located in the rift valley floodplains (Müller et al., 2012; Tinley, 1977b). For centuries to millennia, people have relied on Mount Gorongosa for food, medicine, safety and ceremonial purposes. It is regarded as a sacred mountain and is culturally significant to several cultures surrounding the mountain (Lynam et al., 2004). Historically, agricultural activity was focused on the more fertile foothills and valleys surrounding Mount Gorongosa below 1100 masl. Today people are increasingly moving higher seeking unoccupied land to cultivate crops, and to take advantage of the wetter and cooler climate at higher elevations to support cultivation (Jacobs, 2010). Forests on the mountain provide a vital source of fuel-wood, construction materials, food and medicine and their rapid regeneration after clearance makes shifting cultivation possible in the region.

Mount Gorongosa currently supports diverse assemblages of vegetation with evergreen forests and montane grassland above 1600 masl, mixed sub-montane forests and grasslands from 1300 to 1600 masl, afro-montane forests and grasslands above 900 and below 1300 masl, and ericoid and wooded grasslands with *Widdringtonia* forest on rock outcrops above 1700 masl (Fig. 2) (Müller et al., 2012; Tinley, 1977a). Small patches of deciduous miombo woodlands with *Brachystegia* and *Julbernardia* occur between 900 and 1100 masl. Mount Gorongosa hosts a number of endemic and near endemic plant species (Müller et al., 2012). Recognized for its unique flora, high diversity and hydrologic significance to Gorongosa National Park, the Government of Mozambique incorporated Mount Gorongosa above 700 masl into Gorongosa National Park in 2010, expanding the park from 3770 km<sup>2</sup> to 4067 km<sup>2</sup>. The government also included a 3300 km<sup>2</sup> buffer around the Mountain where management programs are being developed to reduce agricultural activity immediately surrounding intact miombo and rainforest plant assemblages at higher elevations (Rosa et al., 2010).

### 2.1. Mount Gorongosa wetlands

At the top of the Mount Gorongosa emplacement, flat pediments surrounding small granitic summit outcrops support a mosaic of montane forest, grasslands and highland peat. Tinley (1977b) described summit wetland sediments as “organic hydro-morphic peats underlain by brown to yellow compact sandy clay and weathered parent material” and hypothesized that wetlands and grasslands were expanding due to annual anthropogenic burning (Tinley, 1977b pg 38). The peat core obtained for this study was collected from a gently sloping wetland at the southeastern quadrant of a mosaic of wetlands and small patches of *Podocarpus* forest covering approximately 200 ha of the summit plateau.

## 3. Materials and methods

### 3.1. Peat core

One peat core (MGA-A) 85 cm in length was obtained using a 7.5 cm diameter polycarbonate tube (Klien corer) from a large montane wetland (−18.4396° 34.0480°; 1703 masl) approximately

1000 m to the southeast of the summit of Mount Gorongosa (Gogogo Peak, 1863 masl) in September 2010. The polycarbonate core was split at University of Minnesota's LacCore facility for imaging and high-resolution magnetic susceptibility. The split core was then sectioned continuously at 1.0 cm intervals for charcoal and pollen analysis.

### 3.2. Age-depth chronology

We derived chronology models for each sediment core from radiocarbon dates (7) obtained from bulk sediment (Supplementary Material Table A1). The chronologies are based on a stratigraphic series of accelerator mass spectrometry (AMS) <sup>14</sup>C dates obtained from the University of California Irvine KCCAMS lab and DirectAMS, Bothel Washington, from bulk sediment. All radiocarbon ages were calibrated to 1950 CE using the Southern Hemisphere SHCal13 dataset (Hogg et al., 2013) and the core chronology was estimated using age-depth modeling program Bacon v2.2, an approach utilizing Bayesian statistics to derive accumulation rates for core deposits (Blaauw and Christen, 2011) in R-Statistical program (R Development Core Team, 2015). Further information on parameters used for the age-depth chronology are provided in Supplementary Materials (Supplementary Table A1 and Fig. A1). High-resolution magnetic susceptibility was measured to provide an indicator of mineral inputs.

### 3.3. Pollen and macroscopic charcoal analysis

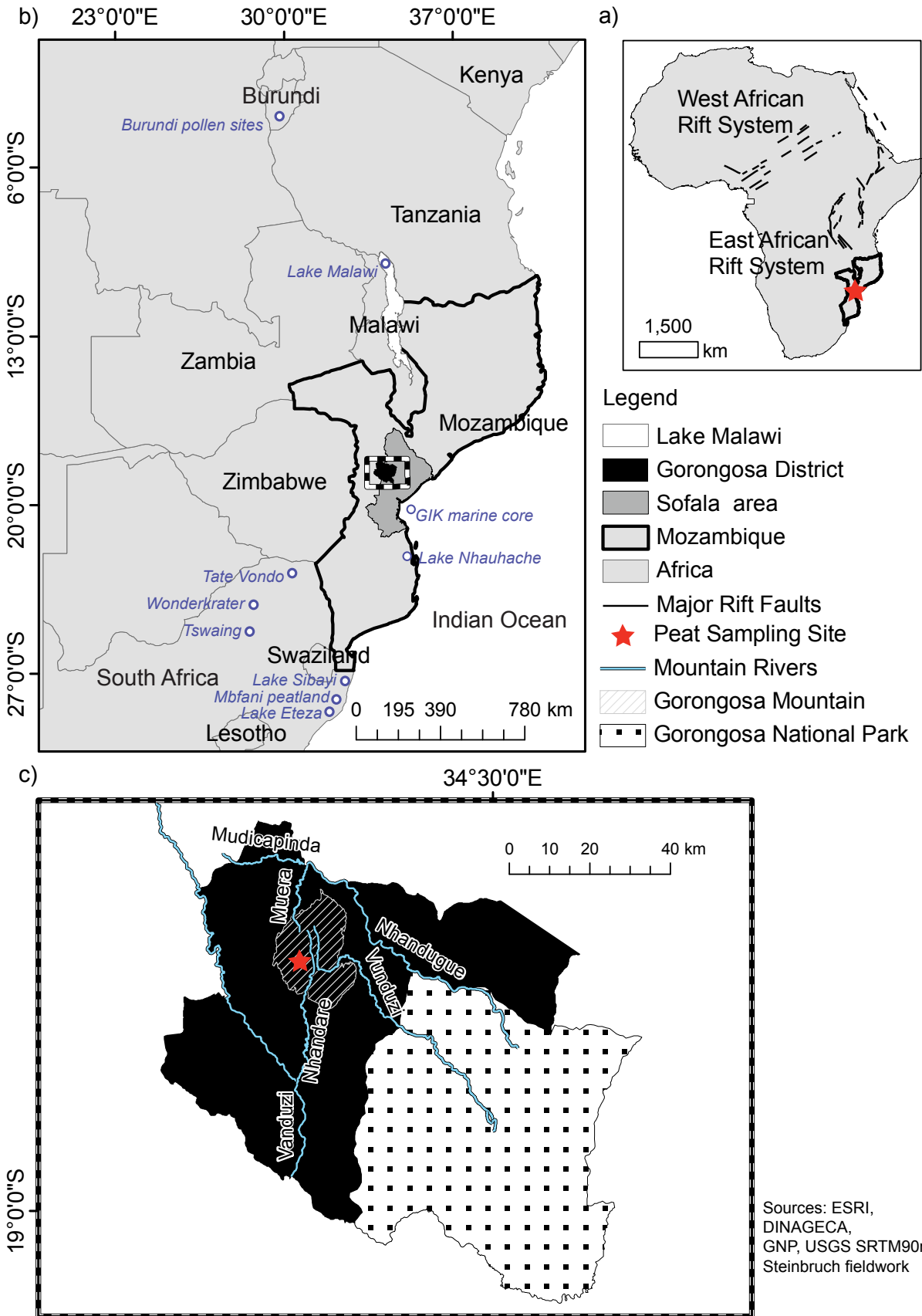
Pollen samples were prepared using HCl, KOH, (NaPO<sub>3</sub>)<sub>6</sub> (Franke, 2014; Riding and JE, 2006; Riding and Kyffin-Hughes, 2011) and sodium polytungstate for heavy liquid separation. Pollen identification was conducted with the help of a regional pollen reference collection and literature (e.g., Beug, 2004; Bonnefille and Riollet, 1980; Scott, 1982a). Terrestrial pollen sums were >300 for each sample. Pollen diagrams were constructed with TILIA 1.7.16, using the terrestrial taxa as the pollen sum.

Macroscopic charcoal analysis focuses on reconstructing local fire history through: (1) quantification of charcoal content in contiguous samples, (2) determination of an appropriate age model, (3) conversion of data to charcoal accumulation rates (particles cm<sup>-2</sup> yr<sup>-1</sup>), and (4) extraction of fire signal from noise (Whitlock and Larsen, 2001). High-resolution charcoal analysis followed methods of Whitlock and Larsen (2001). Charcoal particles >125 μm in diameter were quantified from 5 cm<sup>3</sup> samples taken from 1 cm continuous intervals to reconstruct local fire events based on charcoal accumulation rates (CHAR; particles cm<sup>-2</sup> yr<sup>-1</sup>). Sediment accumulation rates resulted in mean sample resolutions of 145 yrs (excluding the hiatus). Local fire events were distinguished from regional trends in biomass burning by decomposing the charcoal time series into background ‘noise’ and peak or local fire events occurring within approximately 1000 m of the lake site (Higuera et al., 2007; Lynch et al., 2004).

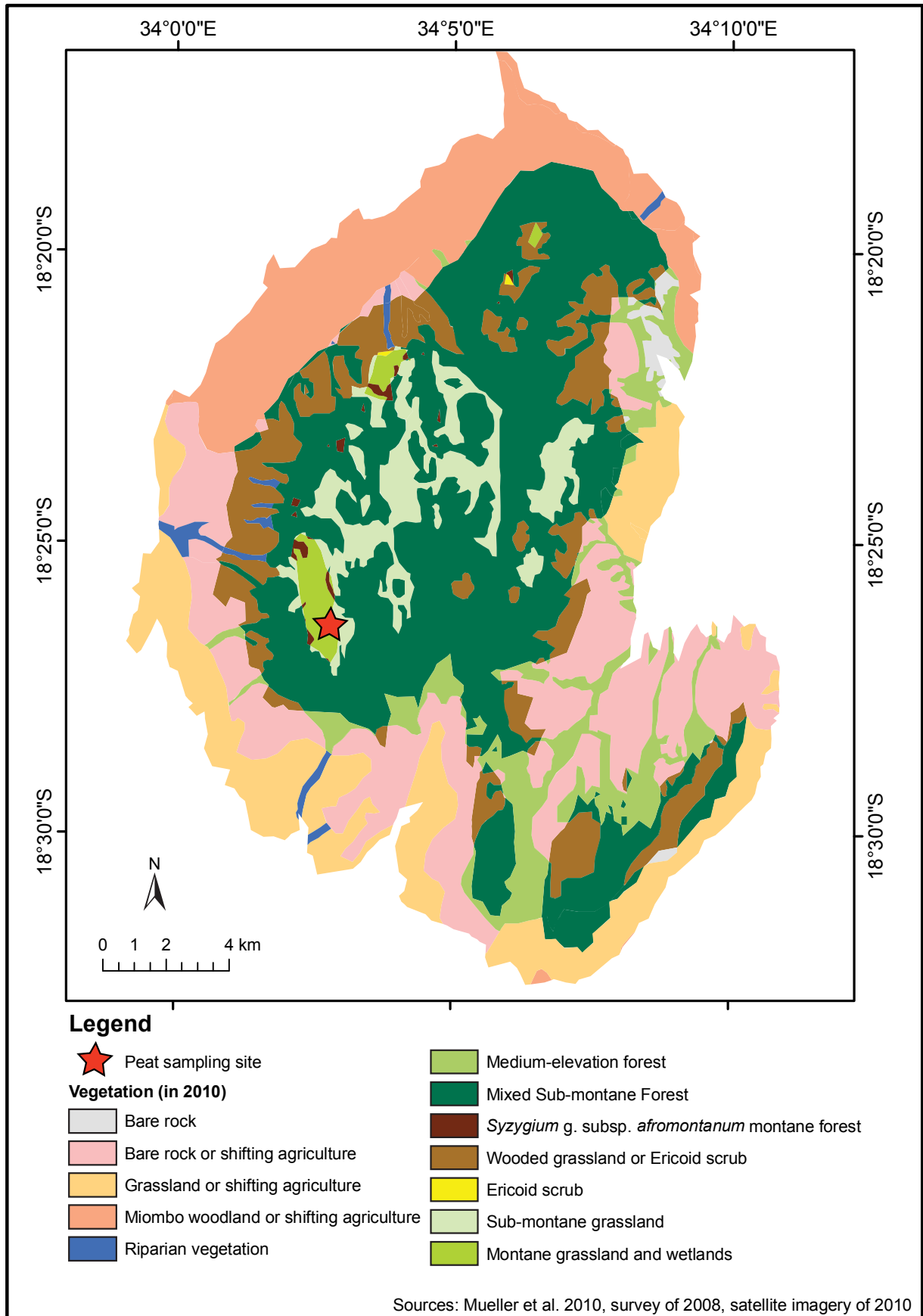
## 4. Results and discussion

### 4.1. Lithology, sedimentology and chronology

Lithology of the Mount Gorongosa core consisted of dark fibrous peat from 0.0 to 70.0 cm and then dark silty and sandy peat from 70.0 to 85.0 cm. Changes in core lithology from silty sand to sandy peat to dark peat indicating lacustrine conditions in the late Pleistocene transitioned to more palustrine conditions into the Holocene. Age chronologies derived from radiocarbon dating of bulk sediments suggest a basal date of c. 26.5 cal kBP and an extended hiatus at c. 48–49 cm (c. 22.5–7.2 cal kBP).



**Fig. 1.** Study area. Location of Mozambique and the East African Rift system (a); regional sites discussed in text and location of Mount Gorongosa, Sofala Province Mozambique (b); and topographic map of the Mount Gorongosa massif, major stream and rivers and location of the peat cores sampled from Mount Gorongosa wetlands (c, coring site indicated by the red star). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 2.** Dominant vegetation types (Müller et al., 2012) on the Mount Gorongosa massif, coring site indicated by the red star. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

## 4.2. Vegetation change

Pollen sample resolution varies from c. 270–900 years throughout the core except for the hiatus interval. The pollen profile (Figs. 3–4) was subdivided into five pollen zones (PZs) based on CONISS, a program designed for stratigraphically constrained cluster analysis. The palynomorphs were grouped according to their ecological habitats or other characteristics, e.g., forest, miombo woodland/savanna, or freshwater phytoplankton. The selections are based on references on the local and regional vegetation, especially Müller et al. (2012). A major transition occurs c. 24 cal kBP from *Podocarpus* forest, Ericaceae-heathland, and freshwater phytoplankton to relatively open grassy landscapes and forest patches with sparse arboreal elements (e.g., *Macaranga*, *Canthium*) and wetland taxa. Fern and lycopod spores (e.g., *Lycopodiella*, *Pteridium*) and fungal remains all increase during this transition suggesting a significant shift in ecosystem structure, composition, and associated disturbance regime. This development is interrupted by a hiatus 22.5–7.2 cal kBP. Since 7.2 cal kBP, a grassland/miombo forest mosaic accompanied by much more diverse subtropical trees (e.g., *Mimusops*, *Macaranga*, *Pavonia*, *Peddiea*), persists until pioneer and disturbance related taxa *Macaranga*, *Trema*, *Pteridium* and *Gelasinospora* become more prominent during the last two millennia.

### 4.2.1. Late Pleistocene: PZ 5 (79–67 cm, c. 26.9–24.9 cal kBP) Ericaceae-Zygnemataceae zone

The vegetation during the late Pleistocene c. 26 kBP is characterized by high percentages of Ericaceae pollen and moderate percentages of *Podocarpus* and grass pollen. High percentages of Ericaceae (c. 65%) indicate heathlands were widespread but declining towards the top of the zone. Carbutt and Edwards (2001, 2004) suggest cool and wet conditions are responsible for increases in the abundance of Ericaceae on the Drakensberg Escarpment. Mucina and Rutherford (2006) support a strong link between cool and humid conditions and Ericaceae. At Mount Gorongosa today, *Erica hexandra* is an element of the forest edge vegetation, a common shrub in the grassland that forms dense shrublands close to the coring location in association with *Morella*, *Rhus*, *Stoebe*, *Widdringtonia*, *Cliffortia* and *Anthospermum*. *Podocarpus* pollen increases towards the top of the zone where it reaches c. 40%. This suggests *Podocarpus* forests were widespread and expanding at the expense of Ericaceae heathlands. *Peddiea*-type pollen reach their highest abundance in PZ 5, when *Olea* pollen is also abundant and both decrease towards the top of the zone when *Podocarpus* percentages are increasing. Today, *Peddiea africana* is an important shrub in medium altitude-montane forests at Mount Gorongosa and is often associated with *Olea capensis* (Müller et al., 2012) suggesting other trees (e.g., *Macaranga*, *Celtis*, *Canthium*, *Mimusops*, *Englerophytum*, pollen of *Macaranga* and *Englerophytum*) were either missing or rare in the forest during that period. Miombo woodland taxa, namely *Brachystegia* pollen, are absent, indicating miombo woodlands were not established close to the site, probably due to low temperatures. The distribution of miombo forests is limited by frost and low minimum temperatures and are not found where minimum temperatures are much below  $-4^{\circ}\text{C}$  (Werger and Coetzee, 1978). Grassland is weakly developed during PZ 5, fluctuating between c. 15–25%.

High pollen abundance of fungi and freshwater algae suggest the water table was high during PZ 5. Zygnemataceae (e.g., zygospores of *Spirogyra*, *Zygnema*, *Debarya*, *Mougeotia*) peak at c. 25 cal kBP and then mostly decrease in abundance probably as a result of drier conditions. Zygnemataceae dwell in shallow, clean and oxygen-rich lakes and ponds but also in moist soils. Their zygospores (which allows the algae to cope with unfavourable

conditions) might be subaerially exposed during desiccation periods and may experience differential preservation (Van Geel and Grenfell, 1996). However, zygospores in our profile are well preserved and it seems possible that they were deposited in shallow but rising water conditions, probably mesotrophic-eutrophic pools. Typical swamp, bog and wetland elements like *Phragmites*-type and Cyperaceae are present but rare. Pollen of *Drosera*, another element of bogs, appears regularly. Spores of *Lycopodiella* (probably *L. sarcocaulon*, (Müller et al., 2012)), rise when algae are decreasing c. 26 cal kBP, and might signal a lower water table and swampy conditions with clubmosses. Fire activity may have suppressed the development of more closed-canopy forests and also benefitted several fern species (e.g., *Pteridium*, *Mohria*) which colonize disturbed areas (Figs. 4–5).

### 4.2.2. Late Pleistocene: PZ 4 (66–54 cm, c. 24.9–23.1 cal kBP) Podocarpus zone

Pollen zone 4 is characterised by the sudden spread of *Podocarpus* pollen, which reaches a pronounced peak (73%) c. 23.9 cal kBP, clearly signalling a high degree of available soil moisture. Ericaceae reach a minimum during the same time period and Poaceae pollen drop to c. 6%, indicating a contraction of heathland and spread of a rather uniform evergreen and moist podocarp forest with few other arboreal elements. *Phragmites* and *Spirogyra* increase, suggesting moist conditions. Fires are virtually absent in PZ 4 (Fig. 5).

### 4.2.3. Late Pleistocene-hiatus & Holocene warm period: PZ 3 (53–46 cm, c. 23.1–6.9 cal kBP, hiatus c. 48–49 cm, 22.5–7.2 cal kBP) Poaceae-Phragmites zone

Immediately below the hiatus (c. 22.9 and 22.5 cal kBP), a dramatic decrease in *Podocarpus* and Ericaceae pollen coincides with significant increase in grassland taxa (Poaceae, *Vernonia*, *Morella*), as well as much increased fire activity (Fig. 5), signalling the onset of warmer and probably drier conditions. This shift is accompanied by very low levels of algae and a peak of both *Osmunda* and *Lycopodiella* spores. Both *Lycopodiella* and *Osmunda*, thrive under warm conditions and intense light, and may have benefitted from a more warm and open, grassy environment (Reeb et al., 2012). Pollen of *Brachystegia*, a key element of miombo vegetation, appears for the first time. Pollen of warmth-loving subtropical trees like *Canthium* and *Macaranga* occur for the first time. Because *Brachystegia* is insect pollinated (as are many key miombo taxa) even low numbers of *Brachystegia* pollen suggest it was a forest component in the vicinity of the wetlands site (Campbell, 1996).

The core age-depth chronology and sedimentation rates clearly indicate an extended hiatus occurred c. 22.5–7.2 cal kBP. Pollen, spores and algae suggest drier conditions just before the hiatus and a terrestrial soil might have formed, leading to erosion. Immediately above the hiatus, similar conditions are encountered—with low *Podocarpus* and moderate but decreasing Ericaceae pollen percentages, low levels of algal cysts and increased fire activity (Fig. 5). Poaceae pollen percentages are low (c. 30%) but sharply increase at the transition to PZ 2, showing the spread and subsequent dominance of grassland. A *Phragmites* belt (probably *P. mauritanus*, growing in Gorongosa National Park, (Lynam et al., 2004)) forms from c. 7.2 cal kBP where *Phragmites* pollen have a prominent peak, probably as a consequence of a drop in the water table. Cyperaceae pollen increase to a moderate degree. Pollen of grassland elements like *Hypoestes* appear, Aizoaceae and Crassulaceae are typical indicators for dry conditions (Scott, 1982a). In contrast to the sample below the hiatus, pollen of warmth demanding subtropical forest and woodland taxa (*Mimusops*, *Pterocelastrus*, *Widdringtonia*, *Apoodytes*, *Acacia*, *Erythrina*, *Englerophytum*) and miombo elements appear regularly. The transition from Ericaceae and *Podocarpus* to

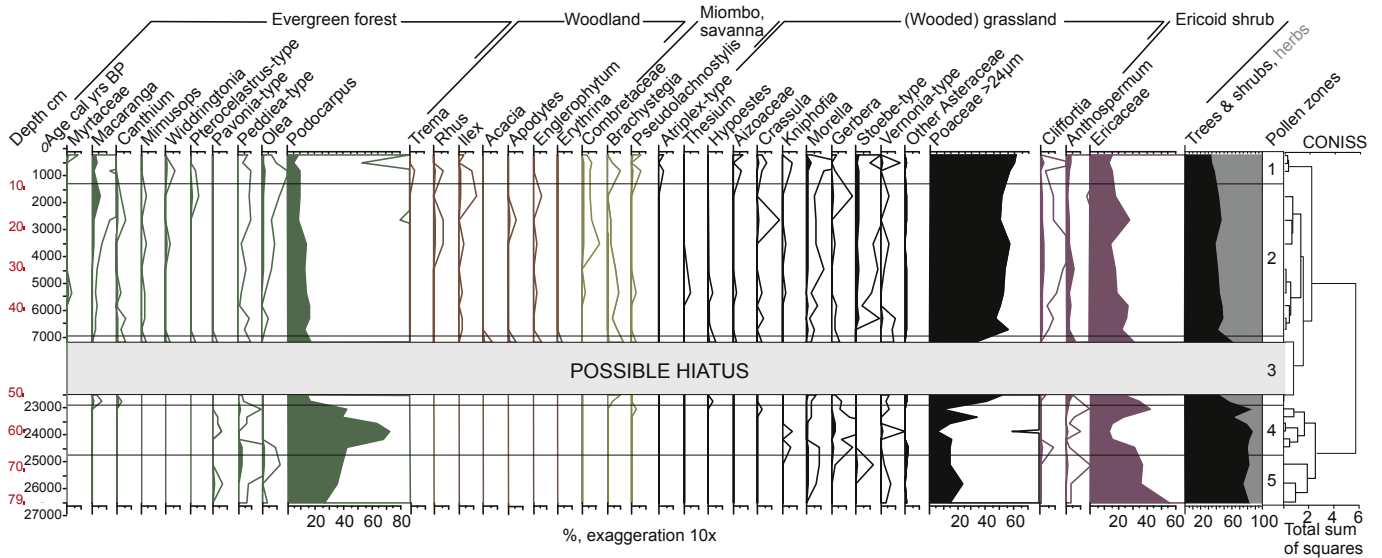


Fig. 3. Pollen diagram of select trees, shrubs and herbs from the Mount Gorongosa peat core.

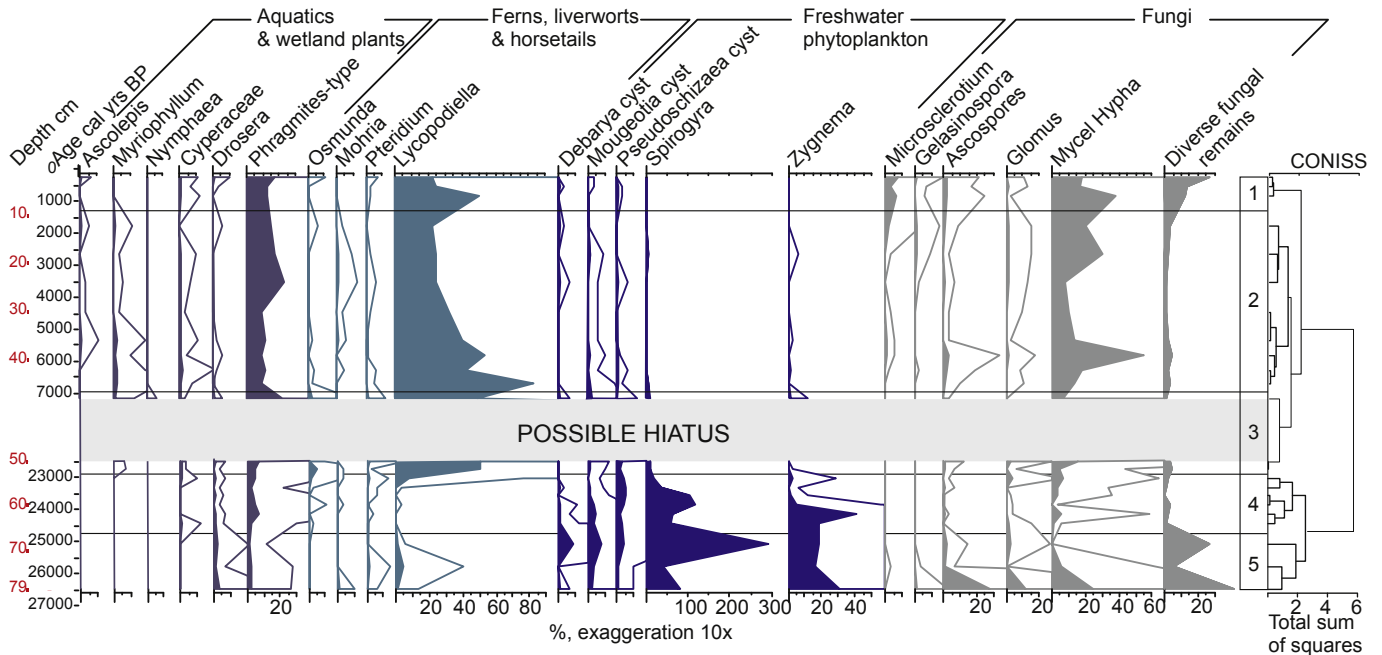


Fig. 4. Pollen diagram of select wetland elements, ferns & horse tails, freshwater plankton, and fungi from the Mount Gorongosa peat core.

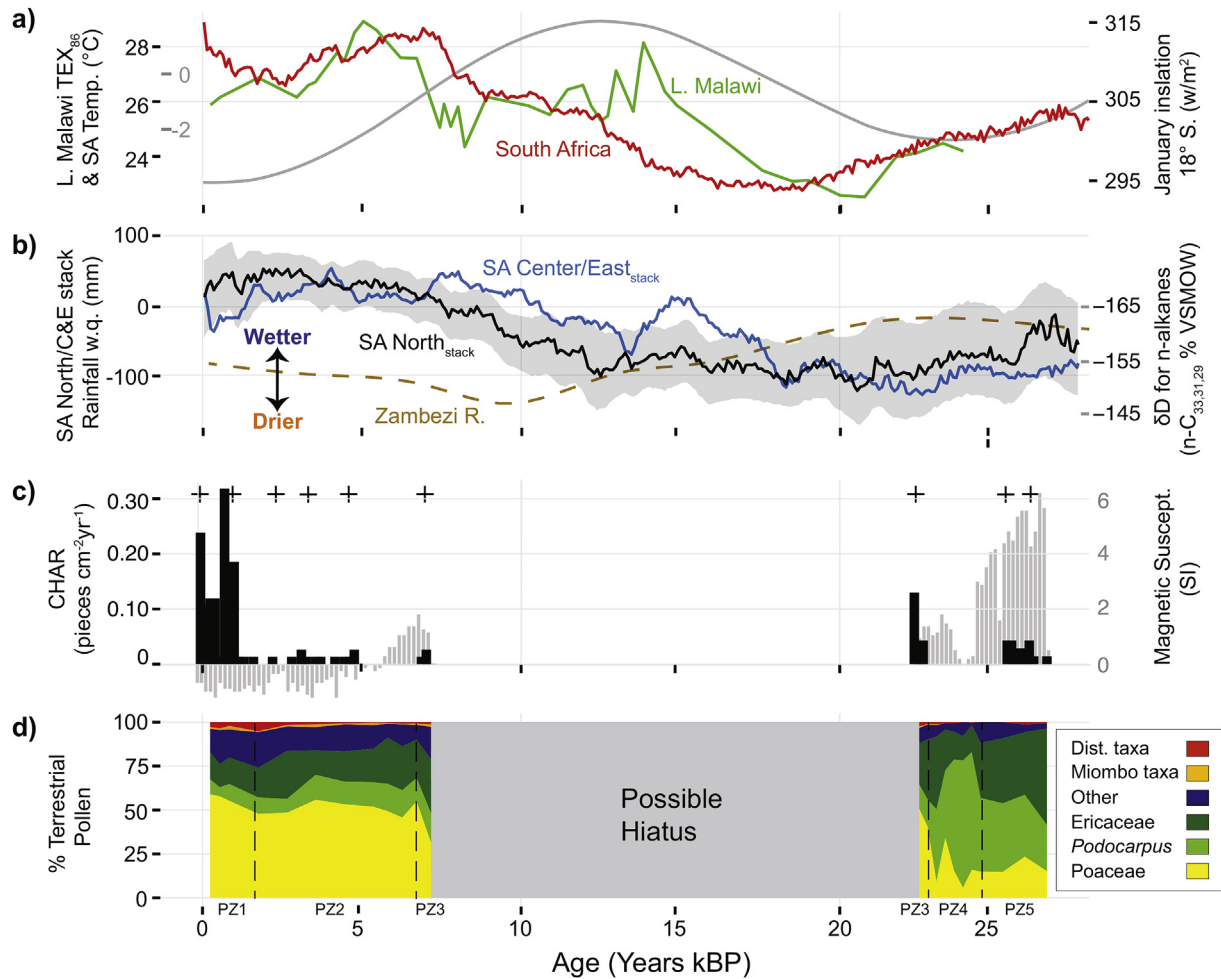
grasslands is likely related to both changing climatic conditions favouring grasslands and fire activity indicated by macroscopic charcoal influx (Fig. 5). Increases in macroscopic charcoal influx during this pollen zone indicate that biomass burning increased although fire activity could have occurred throughout the hiatus as grasslands expanded. *Pteridium*, often a dominant post-fire colonizer, likely established following increased fires associated with warmer and drier conditions.

4.2.4. Middle Holocene: PZ 2 (c. 45–10 cm; 6.9–1.3 cal kBP)  
Poaceae-Anthospermum-Lycopodiella zone

At the transition of PZ 2 to 1, *Podocarpus* pollen drops slightly and remains at this lower level throughout PZs 1 & 2. The decrease in *Podocarpus* pollen coincides with an abrupt increase in the

abundance of grass up to c. 55% at c. 6.7 cal kBP, indicating a substantial expansion of grasslands that persists today on Mount Gorongosa. Establishment of a montane grassland is further supported by the presence of pollen of other typical grassland elements including *Kniphofia* and *Vernonia*, *Hypoestes* and *Santalaceae*. In contrast, *Ericaceae* pollen declines but remains present at low percentages (c. 15%). In addition, some ericoid shrubs like *Anthospermum* and *Cliffortia* have their highest pollen percentages within PZ 2, showing that ericoid shrublands were still present but might have changed in composition. However, *Anthospermum* (most probably *A. ammannioides*) and *Cliffortia* spp. (*Cliffortia serpyllifolia*, *Cliffortia linearifolia*) also grow in grasslands, forests and wetlands and might indicate locally wet conditions near the site (Müller et al., 2012). *Stoebe*, often regarded as an indicator for cool fynbos





**Fig. 5.** Regional climate reconstructions, charcoal influx and changes in pollen percentages for dominant pollen groups from the Mount Gorongosa peat core. January solar insolation values (grey line,  $\text{watts/m}^2$ ) for 18° South (Berger and Loutre, 1991), paleotemperature reconstructions for Lake Malawi (green line) (Powers et al., 2005) and South Africa (red line) (Chevalier and Chase, 2015) (Fig. 6a); estimates of rainfall from northern (black line – grey shading represents 30% and 50% uncertainty) and central/eastern South Africa (blue line – uncertainty not shown for clarity but trends similar to North<sub>stack</sub>) (Chevalier and Chase, 2015); pollen and smoothing spline (dashed brown line) of historical deviation from present day moisture conditions as inferred from hydrogen isotope values ice-volume corrected ( $\delta\text{D}$ ) for three n-alkanes ( $n\text{-C}_{29,31,33}$ ) of sedimentary terrestrial leaf wax from a marine core (GIK16160-3) close to the Zambezi River delta (18.23°S, 37.89°E) (Wang et al., 2013) (Fig. 6b); Macroscopic charcoal influx ( $>125 \mu \text{ pieces cm}^{-2} \text{ yr}^{-1}$ ) and local fires (+) identified from decomposition of background from peak charcoal influx and magnetic susceptibility (grey bars) (Fig. 6c); changes in pollen percentages for major vegetation types (relative % change) for Poaceae (yellow), Podocarpus (light green), Ericaceae (dark green), miombo woodland taxa (orange-Brachystegia, Pseudolachnostylis, Combretaceae), disturbance taxa (red-Macaranga, Trema, Pteridium) all other terrestrial taxa (dark blue) (Fig. 6d). CONISS pollen zones indicated by black dashed lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Scott, 1982a, b), is prominent since c. 6.3 cal kBP. Only rare occurrence of *Stoebe*-type pollen in PZs 3–5, also recorded during the late Pleistocene at Mahwaqua (Neumann et al., 2014), is intriguing since it is prominent in certain southern African savanna sites like Wonderkrater (Scott, 1999b) and at Braamhoek in the Drakensberg Mountains (Norström et al., 2014) where *Stoebe*-type pollen is interpreted as an indicator for cool conditions. The reason for this incongruence is unclear and demands further research regarding the role of *Stoebe*-type as a climatic indicator.

Despite the decrease in *Podocarpus* pollen percentages, other forest and woodland elements that thrive in warmer conditions including *Alchornea*, *Mimusops*, *Canthium*, *Syzygium*, *Rauvolfia*, *Pterocelastrus*, *Widdringtonia*, *Acacia*, *Apodytes* and *Erythrina* and *Pavonia*-type occur in the pollen record, signifying a distinct change in forest composition. *Mimusops zeyheri*, found today along streams at Mount Gorongosa (Müller et al., 2012), prefers a hot climate with ample rainfall, often at the margins of evergreen forests or in open woodland (Coates-Palgrave, 2002). *Canthium oligocarpum* is an element of the sub-canopy in local evergreen montane forests

whereas *Widdringtonia nodiflora* and *Pterocelastrus echinatus* are dominant canopy species in the same forests, often in association with *Podocarpus latifolius* (Coates-Palgrave, 2002; Müller et al., 2012). Additionally, several prominent woodland elements appear for the first time in the Mount Gorongosa record c. 6.9 cal kBP. Frost-sensitive *Apodytes dimidiata* grows along streams at Mount Gorongosa in both forests and wooded grasslands, *Englerophyllum magalismontanum* dwells in diverse moist, wooded habitats and even miombo woodland as a sub-canopy species (Coates-Palgrave, 2002; Müller et al., 2012). Combretaceae pollen are absent before 5.4 cal kBP but then play a dominant role among the savanna taxa when other indicators for drier conditions like Crassulaceae increase. Scott (Scott, 1982a) notes that Combretaceae pollen are more prominent in dry types of savanna and are not well adapted to cool conditions. The appearance of savanna woodland taxa *Brachystegia* and *Combretaceae*, and changes in the composition of the forests taxa correspond with rising temperatures during PZ 2 which corresponds with rising temperatures at savanna sites further to the South (Scott et al., 2012). Overall, the low contribution of forest

pollen suggests vegetation consisted of a grassland/forest mosaic on Mount Gorongosa during PZ 2.

Algae are rather insignificant in PZ 2, whereas fungi, especially hypha and ascospores, spread in close association with the grasslands. Fungal hypha might, as indicated above, point to a higher water table and *Myriophyllum* pollen, increasing between 45 and 36 cm depth (c. 6.7–5.3 cal kBP), might signal shallow water in the vicinity of the site. Additionally, fungi are often saprophytic and thrive under warm conditions on and in leaves but also in the upper soil. Dark septate fungi may be of importance in seasonally dry grasslands because they are adapted to high temperatures and plants might benefit from their ability to fix N (Porrás-Alfaro et al., 2011). Rectangular microsclerotia as found in the Mount Gorongosa samples probably formed inside grass roots functioning as survival structures when the host plant died during dry seasons (Krikun and Bernier, 1990). *Gelasinospora* increases since c. 3.5 cal kBP. van Geel et al. (2011) recorded *Gelasinospora* cf. *cratiphora* from southern Kenya and is connected mainly to herbivore dung but also to charred substrate. The increase of *Gelasinospora* is also coincident with a renewed increase of charred particles suggesting fire may have helped promote its establishment.

Tree pollen and grass pollen abundance increase since c. 3.5 cal kBP (e.g. *Macaranga*, *Pterocelastrus* and *Ilex*), as *Podocarpus* and Ericaceae pollen abundances gradually decline. The growing influence of pioneer trees like *Macaranga* (Müller et al., 2012) and *Trema* together with a gradual spread of grasses and a strong increase in charred particles likely indicate human disturbance at the transition to PZ 1. *Gelasinospora* also shows a maximum c. 1.7 cal kBP which may be related to expansion of browsers/grazers or herding activity associated with increased land-use in the area as noted by Carrión et al. (2000) who recorded abundant *Gelasinospora* in Iron Age cow dung from South Africa (Neumann et al., 2014). Early farming communities in southern Mozambique can be dated to c. 2.0–1.4 cal kBP with evidence of agriculture, iron forging, animal husbandry and hunting-gathering practices (Morais, 1987; Sinclair, 1987). The increase in the abundance of pioneer species, animal dung spores, as well as rise in *Pediastrum*, an indicator of eutrophication, all suggest increasing human influence on Mount Gorongosa ecosystems during the last 1–2 millennia.

#### 4.2.5. Late Holocene: PZ 1 (9–2 cm, c. 1.3–0.2 cal kBP) *Atriplex* zone

Pollen samples representing the last c. 1300 years show an increase in grass pollen coincides with the highest levels of microscopic charcoal influx, suggesting fires burned large volumes of woody biomass. The increasing loss of forest elements (*Podocarpus* pollen reach a minimum c. 5% and most other tree pollen also decrease), expansion of grasslands and increased fire activity also coincide with regional intensification of land-use associated with Iron Age activities (Kay and Kaplan, 2015). Until c. 450 years BP pollen of *Brachystegia* can be detected in the record. Today miombo woodland occurs c. 600 m below the site and it seems unlikely that the heavy pollen of *Brachystegia* can be transported over such a large distance. Hence, *Brachystegia* might have grown closer to the site than today and its loss at the site may be a consequence of more recent human disturbance. The disturbance indicator *Pteridium*, but also *Atriplex*-type pollen produced by Chenopodiaceae, both increase during the last millennium. Chenopodiaceae often represent anthropogenic influences in the vicinity of settlements (Levyns, 1966; Neumann et al., 2011) but can also be an indicator for increased aridity. Hence, increases in pollen of Chenopodiaceae, Aizoaceae, Crassulaceae and Asteraceae can be linked to intensive land-use and/or increased aridity, both of which would have promoted the increased fire activity evident in the charcoal record during the last 1–2 millennia.

### 4.3. Climate-disturbance-vegetation interactions

Transitions from late-Pleistocene vegetation dominated by a *Podocarpus*/Ericaceae-heathland to a diverse forest and grassland mosaic in the middle Holocene to recent grasslands with early seral taxa highlight climate variability, disturbance and anthropogenic activities as important drivers of environmental change on Mount Gorongosa (Fig. 5). Pollen taxa for wetland, algal and fungal taxa suggest water levels were high c. 26.5–23.3 cal kBP (e.g. Zygnemataceae), decreasing since 23.3 cal kBP and then at intermediate but variable until 0.2 cal kBP. The cool, wet climate of the late Pleistocene/LGM likely contributed to low fire activity. As shown by analyses of macroscopic charcoal which record infrequent local fires and low peak magnitudes for fires occurring c. 26.9–22.9 cal kBP – an indication that these fires consumed low levels of woody biomass and/or fires were distant to the wetland site. The hiatus in peat deposition evident in the Mount Gorongosa core from c. 22.5–7.2 cal kBP coincides with a decrease in rainfall following the LGM at sites throughout southern Africa. The decrease of precipitation, suggested by the drop in *Podocarpus* pollen percentages and the spread of grassland and, to a lesser extent, miombo vegetation since c. 23.8 cal kBP may coincide with the decrease of precipitation modelled by Chevalier and Chase (2015) for northern South Africa but uncertainty associated with rainfall estimates for this time period are high (Fig. 5, North<sub>stack</sub> rainfall uncertainty).

Our record shows that the hiatus in peat deposition was accompanied by grassland expansion at the expense of Ericaceae-heathlands and low-severity fires. Following the hiatus in peat accumulation c. 7.2 cal kBP, pollen and charcoal data show repeated low-peak magnitude fires coincide with the dominance of a grassland/forest mosaic. The presence of *Nymphaea* and *Myriophyllum*, albeit low, pollen since c. 7.2 cal kBP suggest the period of dry conditions likely responsible for the hiatus was followed by an increase in moisture sufficient enough to support open water as a feature of the Mount Gorongosa wetlands for millennia. The development of a *Phragmites* belt in the middle Holocene indicated by sharp increases in the clubmoss *Lycopodiella* and sedges further suggest the water table rose during wetter conditions of the mid to late Holocene (Chevalier and Chase, 2015; Schefuss et al., 2011). Late-Holocene increases in pioneer and disturbance related taxa such as *Macaranga*, *Trema*, *Pteridium* and herbivore/human indicator *Gelasinospora* correspond with a dramatic increase in fires exhibiting the highest peak magnitude values of the Gorongosa record (10.2, 2.4 pieces cm<sup>-2</sup>).

Ordination of plant community assembly and change for the Gorongosa record (Fig. 6) shows distinct plant community transitions from late-Pleistocene Ericaceae-heathland/*Podocarpus* forests to grassland/miombo woodlands just before the hiatus and during the mid Holocene. Ordination cluster analysis also shows late Holocene vegetation is distinctly characterized by increasing presence of disturbance-related taxa (Fig. 6). Results from fitting environmental variables (temperature, precipitation, charcoal accumulation) onto the ordination of pollen taxa change over time suggest temperature ( $p < 0.001$ ,  $r^2 = 0.67$ ), and, to a lesser extent, charcoal accumulation and South Africa rainfall (not significant at  $p \leq 0.05$ ), acted as controls on vegetation community composition.

### 4.4. Regional comparison

A number of long-term records of environmental change exist for southern and eastern Africa but few between 15–20°S where important atmospheric convergence zones interact. Comparing the Mount Gorongosa record with montane records to the north and south highlights similarities and differences that result from

multiscale interactions between climate variability, disturbance regimes, land-use histories and local site conditions (Fig. 7).

#### 4.4.1. Late Pleistocene

Cold conditions during the late-Pleistocene promoted the dominance at Gorongosa of an Ericaceae-heathland and then afro-montane forest composed of *Podocarpus*, *Peddiea* and *Olea*. Moist conditions likely contributed to the long-term dominance of *Podocarpus*/Ericaceae-heathland mosaics as indicated by an abundance of algae (e.g., Zygnemataceae) in the pollen spectra. In particular the wettest period was recorded during the Last Glacial Maximum until c. 23.0 cal kBP when podocarp forests dominate the pollen spectra for c. 1300 yrs. Similarly, paleoecological records from two montane sites in South Africa, Mahwaqa Mountain (Neumann et al., 2014) and Braamhoek (Norström et al., 2014), suggest cool and moist conditions sustained afro-montane forests and Ericaceae-heathlands during the late Pleistocene although the hiatus at Mount Gorongosa precludes a direct comparison with these records during the Pleistocene-Holocene transition (Fig. 7). In central Africa, *Podocarpus* forests were expanding during a wet and cool Pleistocene (Dupont et al., 2001). A pollen record from Port Durnford at the east coast of South Africa shows exceptionally high *Podocarpus* percentages during a cool time period less than c. 70,000 years ago although podocarps are not an important element of coastal forest in the region today (Oschadleus et al., 1996).

#### 4.4.2. Pleistocene-Holocene transition

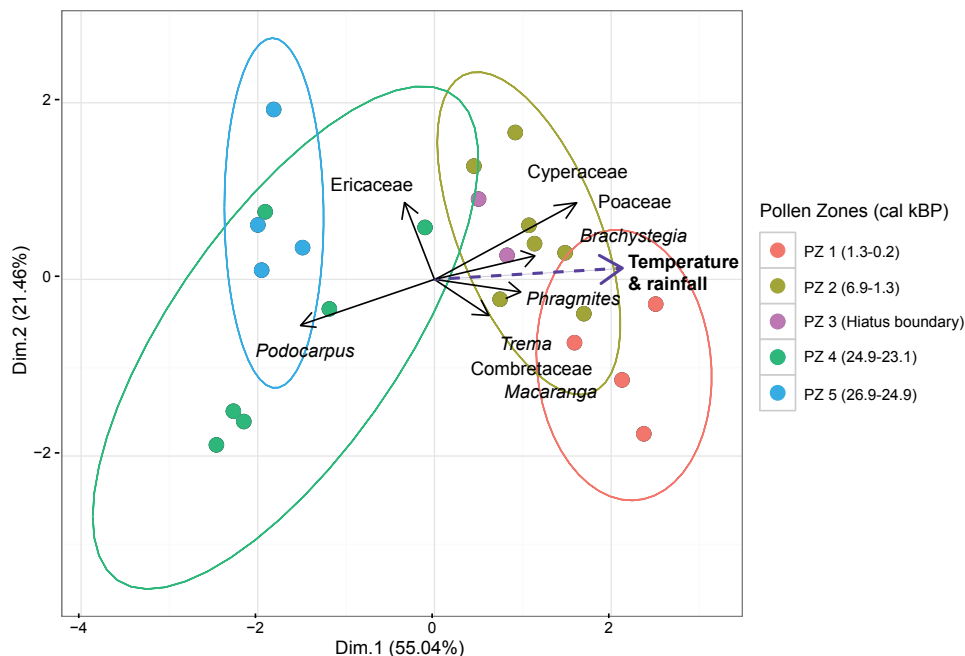
A significant decrease in rainfall evident in records throughout southern and eastern Africa might have been responsible for the hiatus in peat accumulation at the Mount Gorongosa site and a widespread expansion of grasslands at montane sites (Meadows and Linder, 1993). The hiatus at Mount Gorongosa parallels increases in Poaceae, Asteraceae and Chenopodiaceae at Braamhoek, South Africa and Norström et al. (2014) attribute the dominance of

more open grassland and herbaceous vegetation to drier conditions during the Pleistocene-Holocene transition. Additionally, late-Pleistocene palynological records from eastern Africa suggest drier conditions supported open afro-montane woodland savannah vegetation (Beuning et al., 2011; Bonnefille and Riollet, 1988; DeBusk, 1998; Garcin et al., 2006; Ivory et al., 2012; Vincens et al., 2003).

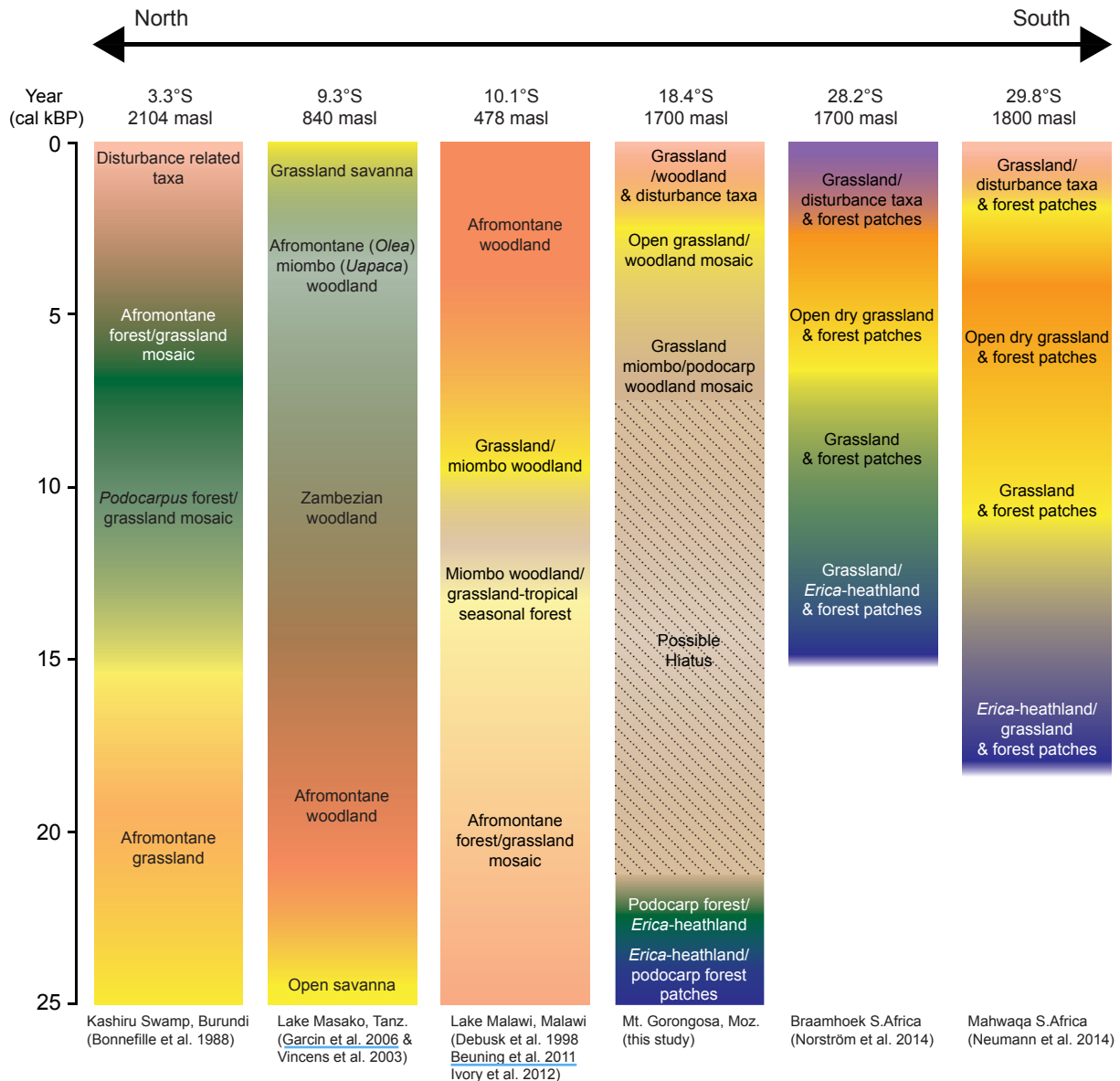
#### 4.4.3. The Holocene

The resumption of peat accumulation in the middle Holocene corresponds with increasing rainfall recorded at sites throughout southern Africa. This interval marks an expansion of grasslands and increased prominence of miombo woodland taxa (e.g. *Brachystegia*). As conditions become drier during the mid-Holocene in southern Africa, shifts in the seasonal position of the ITCZ and the African monsoon appear to provide increased moisture for sites in eastern Africa (Bonnefille and Chalié, 2000) resulting in the expansion of Zambezian/miombo woodlands at higher elevation sites in Tanzania (Garcin et al., 2006; Vincens et al., 2003) and Burundi which also sees an increase in *Podocarpus* (Bonnefille and Riollet, 1988) as well as lower elevation Lake Malawi (Beuning et al., 2011; DeBusk, 1998; Ivory et al., 2012). The development and persistence of a miombo woodland/grassland mosaic on Mount Gorongosa throughout the Holocene suggests that precipitation levels remained relatively stable once they increased from late-Pleistocene lows. Afro-montane woodland/savannas persist from the late Pleistocene into the late Holocene in eastern Africa until a rise in land-use intensity results in increased abundance of disturbance taxa.

Mount Gorongosa shows similarities with montane settings in both southern and eastern Africa although more so with sites in northern South Africa (e.g., Tate Vondo, Wonderkrater) that experienced similar patterns of rainfall variability. Late-Pleistocene Ericaceae-heathlands and *Podocarpus* forests that dominated the



**Fig. 6.** Ordination (Correspondence Analyses—CA) of dominant community types and drivers of vegetation change across pollen zones using R statistical programs *vegan* and *envfit* (R Development Core R Development Core Team, 2015). Ellipses identify position of dominant community types across the five pollen zones. Environmental variables were fit onto the ordination to evaluate correlation with community organization including: reconstructions of rainfall (South Africa, Zambezi River Delta (Chevalier and Chase, 2015; Schefuss et al., 2011)), and temperature (South Africa and L. Malawi (Chevalier and Chase, 2015; Powers et al., 2005)), January insolation (Berger and Loutre, 1991), macroscopic charcoal influx and peak magnitude (from this record). Dashed vector (purple) represents statistically significant ( $p < 0.001$  temperature) correlation between South Africa temperature and vegetation assembly over time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 7.** Major shifts in late Pleistocene – Holocene vegetation from sites in East and southern Africa (Beuning et al., 2011; Bonnefille and Riollot, 1988; DeBusk, 1998; Garcin et al., 2006; Ivory et al., 2012; Neumann et al., 2014; Norström et al., 2014; Vincens et al., 2003).

Mount Gorongosa flora show similarities to montane sites in southern Africa whereas slightly drier conditions promoted more open afromontane woodlands at montane sites in eastern Africa. Widespread drying beginning in the late Pleistocene coincides with the hiatus in peat accumulation at Mount Gorongosa and led to increases in miombo woodlands throughout southern Africa. The resumption of peat accumulation during the middle Holocene at Mount Gorongosa signals an expansion of grasslands and the arrival of miombo woodland taxa, a pattern seen at adjacent sites in both eastern and southern Africa. The transition at Mount Gorongosa from a late-Pleistocene Ericaceae-heathland to a grassland/woodland mosaic during the Holocene parallels estimated rainfall variability for sites in northern South Africa (Chevalier and Chase, 2015) except when *Podocarpus* forests were abundant at Mount Gorongosa in the late Pleistocene c. 26.5–24.9 cal kBP suggesting conditions were likely wetter than indicated by the record derived from northern South Africa sites. The relationship between shifts in the dominant vegetation and precipitation is consistent with previous research identifying aridity as an important driver of

vegetation change throughout southern and eastern Africa (Castañeda et al., 2007; Chevalier and Chase, 2015; Tierney et al., 2008) although the arrival of warmth-loving subtropical taxa on Mount Gorongosa in the late Holocene is likely related to warming temperatures. The Gorongosa record also lends further support for a late-Pleistocene to Holocene shift in the relative importance and influence of northern latitude (e.g., NH ice-extent and SSTs) versus southern latitude (e.g., Indian Ocean SSTs, insolation, north-south position of the ITCZ) and more local drivers of climatic variability (subtropical storm genesis and convective activity). The presence of an extended hiatus during the Pleistocene-Holocene transition precludes a more direct evaluation of this important interval and provides strong motivation for further research in this region.

## 5. Conclusions

The Mount Gorongosa record complements recent efforts to better resolve mechanisms and drivers of climatic variability in southern and eastern Africa during the last interglacial transition

(Chevalier and Chase, 2015) by providing a long-term record of environmental change for a region where few records exist. Our study confirms and contrasts with previous research investigating late Pleistocene – Holocene climate variability for southeast and southern Africa: 1) The dominance of *Podocarpus* forests in the late Pleistocene emphasizes the importance of this taxa as a relict of ancient Gondwanan rainforest flora which survived in moist regions across the Southern Hemisphere (Kooyman et al., 2014) and probably spread in Africa during the cool, more humid periods of the Pleistocene; 2) Grassland and miombo woodland taxa expansion occurred at least as early as the mid Holocene on Mount Gorongosa; 3) Changes in vegetation and the timing of the extended hiatus in our record reinforce aridity as an important driver of ecosystem dynamics in southeast Africa (Castañeda et al., 2007; Chevalier and Chase, 2015; Schefuss et al., 2011); 4) shifts in dominant vegetation and the hiatus in Mount Gorongosa peat accumulation indicate a wet (c. 27–22 kBP) – dry (c. 22–8 kBP) – wet (8 kBP–present) sequence of rainfall variability which is more consistent with records from southern (Chevalier and Chase, 2015) than eastern Africa (Castañeda et al., 2007; Schefuss et al., 2011; Tierney et al., 2008), with the important exception of an interval of inferred wet conditions during the late Pleistocene when *Podocarpus* forests dominate the Gorongosa record and algae indicate a high water table; 5) this sequence of rainfall variability is consistent with NH high latitude cooling leading to decreased western Indian Ocean SSTs and increased aridity during the LGM throughout much of southern and eastern Africa and an eventual increase in rainfall in the early Holocene as the influence of NH Atlantic forcing weakens and SH forcing (direct insolation, shifts in the ITCZ and tropical-subtropical storm genesis and convection) becomes the primary control on climate variability; 6) the dry interval in our record (indicated by a hiatus), however, contrasts with records suggesting latitudes 15–20°S received increased rainfall as the ITCZ shifted south (Schefuss et al., 2011); 7) the resumption of peat accumulation at Mount Gorongosa c. 7.2 cal kBP is consistent with an increasing role for direct insolation forcing on rainfall variability in the Holocene and; 8) large increases in charcoal influx and spread of disturbance indicators such as *Gelasinospora*, pioneer trees *Macaranga* and *Trema* and renewed increase of grass pollen in the last 1–2 millennia suggest Iron Age land-use activity had substantial impacts on vegetation dynamics during the late Holocene. Lastly, biomass burning during the past several decades has increased to levels that are unprecedented in the Mount Gorongosa record, and will likely fundamentally alter ecosystem dynamics on Mount Gorongosa (Ryan and Williams, 2011).

## Acknowledgements

We thank Gorongosa National Park ecologist Tongai Castigo, USDA staff Martin Sampson and University of Eduardo Mondlane student Hidigo Bape for assistance in the field and A. Niehus for the careful palynological preparation of the sediment samples. We thank E. Worobiec and L. Scott for fruitful discussions regarding pollen and spore types and vegetation history. We also thank two anonymous reviewers for their immensely helpful comments. Geochemical analyses were conducted at LacCore (National Lacustrine Core Facility), University of Minnesota-Twin Cities. This research was supported by National Geographic Committee for Research and Exploration grant# 8684-09.

## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2016.02.004>.

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