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Studies on late Quaternary environmental dynamics (vegetation, biodiversity, climate, soils, fire and human impact) on Mt Kilimanjaro

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Tag der mündlichen Prüfung:

Für meine Eltern

Sunflower field at the foot of Mt Kilimanjaro, Tanzania (February 2010)

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Zusammenfassung

Zur Rekonstruktion der jungquartären Landschaftsentwicklung am Kilimanjaro werden Sedimente aus Paläoböden am Mt Kilimanjaro untersucht, um die lokale und regionale Ökosystem-, Klima-, Feuerdynamik in einem größeren Rahmen zu verstehen. Desweiteren soll die Reaktion der Ökosysteme auf Umweltveränderungen erforscht werden, um die Beziehungen verschiedener Ökosysteme und ihre Rolle hinsichtlich der Entwicklung von „Biodiversity Hot Spots“ in Ostafrika aufzudecken. Die Ergebnisse tragen zu einem besseren Verständnis der heutigen und zukünftigen Dynamik von Ökosystemen bei. Sie sind außerdem eine wichtige Grundlage im Naturschutz, da sie bedeutende Informationen für die Aufrechterhaltung und das Management der hohen Biodiversität in den ostafrikanischen Hochländern liefern.

Die Durchführung von paläoökologischen Untersuchungen ist unerlässlich, da die Prozesse der Vergangenheit eine wichtige Rolle bei der Entwicklung der Ökosysteme und Biodiversität spielen. Die vorliegende Arbeit erforscht die spätquartäre Vegetation-, Klima- und Feuerdynamik am Kilimanjaro, um das Verständnis der dortigen Ökosystem zu vertiefen. Sowohl Pollen als auch weitere Klima-Proxies von zwei Sedimentkernen werden analysiert, um die Vegetationsdynamik vom frühen Spätglazial bis heute zu rekonstruieren und die jeweiligen Einflußfaktoren aufzudecken. Die Ergebnisse vom Maundi Krater, welcher auf 2780 m Höhe am südostlichen Hang des Kilimanjaros gelegen ist, stellen eines der längsten, terrestrischen Klimaarchive im tropischen Ostafrika dar, und ermöglichen den Einblick in fast 100 000 Jahre Vegetations- und Klimageschichte. Das WeruWeru Paläobodenprofil aus dem montanen Waldgürtel am Kilimanjaro ermöglicht die detaillierte Rekonstruktion der Reaktionsdynamik der Vegetation auf Veränderungen in der Umwelt. Die Ergebnisse beider Untersuchungen zeigen, dass Klimaveränderungen zu einer Verschiebung der montanen Vegetationsgürtel entlang des Höhengradienten des Mt Kilimanjaro geführt haben. Das Pollenarchiv des WeruWeru Profils dokumentiert starke Veränderungen in den höchsten Vegetationgürteln, dem Erikagürtel und dem oberen montanen Wald. Trotz markanter Klimaveränderungen scheint Mt Kilimanjaro aber auch als eiszeitliches Refugium für Waldarten gedient zu haben. Feuerereignissen spielten hinsichtlich der Ausbildung des Erikagürtels eine entscheidende Rolle. Hinweise auf verstärkte menschliche Aktivitäten können an keinem der beiden Untersuchungsstandorte festgestellt werden.

Die Pollenregen-Studie entlang des Höhengradienten am Kilimanjaro zeigt, dass es sehr entscheidend ist, die quantitative Beziehung zwischen Pollen-Niederschlag und moderner Vegetation zu untersuchen, um die Rekonstruktionen der Vergangenheit zu kalibrieren. Die Ergebnisse ermöglichen eine weitaus präzisere Interpretation der Vegetations- und Klimarekonstruktionen im tropischen Ostafrika.

Summary

Sediments of buried soils from different key areas at Mt Kilimanjaro are studied to reconstruct former and to predict future landscape dynamics on Mt Kilimanjaro. This contributes to a better understanding of local and regional ecosystems, climate, fire and soil dynamics in a larger context, ecosystem dynamics and their reaction on environmental changes, connections and disjunctions of different ecosystems and their role for the development of the biodiversity hot spots in East Africa. Mt Kilimanjaro represents one of the global centres of vascular plant diversity. It is one of the most biodiverse regions on earth. Despite the innate value and importance of the existing ecosystems, we are confronted with the progressing endangerment of these largely unexplored habitats. The implementation of palaeoenvironmental studies is crucial since past processes play a major role in the development of ecosystems and biodiversity. In the present study, investigations of late Quaternary vegetation, climate and fire dynamics are carried out in order to gain a deeper understanding of modern and future ecosystem dynamics.

Palynological and multi-proxy analyses of two sediment records are used to reconstruct past vegetation dynamics and to reveal influencing factors. The pollen, charcoal and sedimentological record from the Maundi Crater, located at 2780 m elevation on the south-eastern slope of Mt Kilimanjaro, is one of the longest terrestrial records in equatorial East Africa, giving an interesting insight into the vegetation and climate dynamics back to the early last Glacial period. The WeruWeru pollen record from a montane forest site at 2650 m provides detailed reconstruction of the vegetation response to environmental changes during the Late Glacial and the Holocene. Our results suggest that past climate change caused the vegetation belt to shift along the elevational gradient. The pollen archives reveal shifts in the upper vegetation zones (ericaceous zone and montane forest zone) of at least 1100 m but underline the role of Mt Kilimanjaro as a glacial refuge for montane forest species similar to that of the Eastern Arc Mountains. Fire played an important role in controlling the development and elevation of the ericaceous zone and the tree line around Maundi crater. During the Holocene no anthropogenic impact can be observed, since neither higher fire activity nor a spread of hemerophilic plants is recorded.

The modern pollen-rain study along the elevational gradient on Mt Kilimanjaro reveals that it is crucial to establish a modern pollen-rain – vegetation relationship for the calibration and interpretation of a fossil pollen record from a mountain site. The results facilitate the confident use of fossil pollen data to reconstruct more precisely potential vegetation and its dynamics in East African montane forests and also to refine past climate reconstructions in this region for a more accurate comparison of data and modelling.

Chapter 1

General Introduction

The Tropics are currently the region most influenced by the rapid population growth and the profound changes in land use. Also from a climate point of view the tropical areas are very sensitive and they play a key role in understanding the globe's present and past climate phenomena (Thompson *et al.*, 2002). During the past decades tropical ecology has become an important focus of scientific research. In order to understand and assess the development as well as trends of the present vegetation under changing environmental conditions, it is inevitable to unearth the vegetation and climate history.

Why do we investigate the palaeoecology and palaeoclimate in the Tropics?

The role of the Tropics in palaeoecological research has gained strong interest in the past decades. This was especially motivated by advances in tropical environmental and climate dynamics on the one hand, and the emergence of questions calling attention to the role of the Tropics in palaeoecology on the other hand. Three properties of the tropical vegetation and climate dynamics are of particular importance in palaeo-research (Chiang, 2009): the sensitivity of the tropical ecosystems and climate to change, the ability of tropical systems to reorganize and the ability of the tropical climate to project its influence globally.

A major part of the tropical climate's sensitivity can be attributed to the nature of tropical moist convection. This convection is extremely sensitive to the prevailing climatic conditions. According to Pierrehumbert (2000) it is rather instable and responds rapidly to the changing environment. It is mainly the margins of convective regions, i.e. the boundary between convecting and non-convecting zones that are most sensitive to change (Lintner and Neelin, 2007). The position of convective zones in the Tropics is extremely sensitive to spatial gradients in sea surface temperature (SST) (Chiang and Koutavas, 2004) and is controlled by the inter-hemispheric gradient in tropical SST. A change of only 1 Kelvin in the gradient influences the migration of the Intertropical Convergence Zone (ITCZ) sufficiently to have severe implications for rainfall patterns (Hastenrath and Heller, 1977).

This sensitivity of the tropical convective climate can be translated into a larger context: the sensitivity of regional tropical climates to change. One example of regional climate variations that are highly sensitive to changes is the African and Asian monsoon. Particularly the monsoons display extreme year to year excursions. Tropical SST conditions over the neighbouring oceans – the tropical Atlantic for the West African monsoon and the Indian ocean for the Asian monsoon – are understood to influence the development of the monsoon and its large-scale circulation (Xie, 1999).

The tropical convection itself and the global convection cells communicate, or teleconnect, tropical climate changes to the extra-tropics (Hoskins and Karoly, 1981). Teleconnections are correlation patterns of large–scale atmospheric circulations which involve precipitation and temperature relationships. When considering the force of SSTs for extra-tropical teleconnections, the spatial gradients of tropical SSTs are much more important that the magnitude of SST changes since they are responsible for shifts in convection centres. Thus, the Tropics play an important role of globalizing climate change. The most pronounced response of the tropical hydrological cycle during stadials during the last Glacial was a major decrease in the Asian and West African monsoon (Wang *et al.*, 2001; Weldeab *et al.*, 2007). This demonstrates clearly that changes to tropical climate do usually not stay confined to the Tropics.

It is widely established that climate is a major determinant of vegetation structure and ecosystems function, but the extent to which vegetation influences climate is far less certain (Hoffmann and Jackson, 2000). Because plants are the primary source for water and carbon flux between the land and atmosphere, vegetation has an important role in the climate system. This role has been particularly well documented in the lowland Tropics, where several modelling studies have demonstrated that large-scale deforestation may lead to decreased precipitation and increased temperature (Dickinson and Kennedy, 1992; Polcher, 1995; Zhang and Henderson-Sellers, 1996; Lean and Rowntree, 1997).

The large annual fluxes of carbon between terrestrial ecosystems and the atmosphere make these systems especially prone respond to climate changes and to influence the global carbon balance (Schuur, 2003). It is still under on-going debate whether tropical forests are currently sequestering carbon (Grace *et al.*, 1992; Keller *et al.*, 1996; Mahli *et al.*, 1998; Phillips *et al.*, 1998; Clark, 2002), and how these ecosystems will respond in the future to global climate change (Kindermann *et al.*, 1996;

Braswell *et al.*, 1997; Cox *et al.*, 2000). Determining the sensitivity of tropical ecosystems to climate is critical for understanding their potential for carbon cycling and the response to changes in temperature, precipitation, and other factors such as CO_2 fertilization.

Climatic changes may also have tremendous effects on species distributions and the functioning of ecosystems. We will not be able to predict these effects with certainty, but a better understanding of the ecosystems will improve and refine our predictions. The effects of climate change are expected to be particularly pronounced in mountain areas (Price, 2005). The alpine ecosystems are the most conspicuous ecotones in mountains worldwide and they are to a great extent controlled by climate. Therefore these ecosystems have been proposed as potential indicators for the response of ecosystems to climatic change (Smith and Young, 1987; Slaytor and Noble, 1992), and they can serve as indicators of past and present climatic trends (Van der Hammen and Cleef, 1986; Kupfer and Cairns, 1996).

The main effect of the expected rapid climate change (IPCC, 2007) at landscape scales will be changes in the geographical patterns and environmental gradients that will immediately alter the function of ecosystems; in the long term, this will determine the future extent of vegetation types and their biodiversity (Hughes, 2000). Although the degree of climate change is predicted to be largest at mid and high latitudes, the impact of climate change in the Tropics will also be significant and alter both the function (Silver, 1998) and distribution of vegetation types. Depending on the degree of climate change and the sensitivity of ecosystems, these changes will significantly impact the biodiversity (Markham, 2012).

The investigation and reconstruction of former vegetation dynamics unravels the ecosystem responses to climate change in the past and adds to the understanding of the state and functioning of today's ecosystems. Further, this knowledge will allow for a more refined and comprehensive prediction of future changes in biodiversity and bio geographical patterns.

Our understanding of vegetation in the past comes mainly from the examination of macrofossils (e.g. wood and leaves) and microfossils (e.g. pollen and spores) found in sedimentary records. The potential for microscopic fossils to provide an insight into past vegetation change on a landscape scale was pioneered by Von Post (1916) and has been subsequently used to understand changes in vegetation and biodiversity patterns as well as to address conservation issues (Willis *et al.*, 2007). The analysis of fossil pollen and spores (palynology) is now widely used to answer ecological questions linking past vegetation and environmental change as well as its response to the occurrence of fires, human impact and animal activity.

Palynology – some general aspects on methods and applications

Palynology is defined as the "study of dust" (Greek: παλύνειν/palynein - to scatter) or "particles that are strewn" (Faegri and Iversen, 1989). It is one of the most widely used research tools in Quaternary studies. It is useful to think of pollen analysis as a remote sensing instrument, which records the past and present composition of vegetation. It is defined as ' a technique for reconstructing former vegetation by means of pollen grains it produced' (Faegri and Iversen, 1989). Pollen analysis has been used to document long-term vegetation dynamics ever since the success of Von Post's pioneering experiments in 1916 (Von Post, 1916; 1946).

Several ecological principles are in favour of this scientific approach: The enigmatic and multifarious world of colourful flowers in seed plant aims at the dispersion of their pollen, which is a fine to coarse powder containing the male reproductive cells (Raven *et al.*, 2000). The single pollen grains are morphologically distinct for each plant species so that it is possible to identify plant species by only investigating the pollen grains (Faegri and Iversen, 1989). Further, the bio-geographical distribution of every individual plant species is determined by a set of environmental parameters which limits its spatial spread (Willig *et al.*, 2003; Francis and Currie, 2003).

The basic assumption of palynology is that the number of pollen grains deposited per unit time, at a given point, is directly related to the abundance of the associated species in the surrounding vegetation (Dimblebly, 1957; Davis, 1963). The general principles of pollen analysis can be outlined as follows (Birks and Birks, 1980):

- pollen grains are produced in large quantities during the natural reproductive cycles of many plants
- relative vegetation composition can therefore be inferred from the pollen grains released into the environment, as these are a function of the number of parent plants
- the majority of pollen grains produced by plants never fulfil their reproductive function, and when deposited within sediments they may be preserved as fossils
- fossil grains may be extracted from sediments and identified down to family/genus/species level
- the stratigraphic level at which grains are extracted corresponds with particular periods in the past.

Any change in climatic parameters indispensably causes a change in the plant species composition and a latitudinal of elevational shift of vegetation belts. This close connection between climate and ecosystems allows the palynological reconstruction of past vegetation belt distribution on the slopes of mountains, such as Mt Kilimanjaro.

Palaeoecological research on a tropical mountain ecosystem in East Africa

Mountain systems are especially susceptible to climate change. The elevational gradient and the involved gradient of climatic parameters only allow rather narrow ecological niches (Körner, 2003b). That means that even minor environmental changes have a great impact on the vegetation composition. This unique feature makes mountains ecosystems particularly vulnerable (Huber *et al.*, 2005). Global warming is expected to enable species to migrate to higher elevational and potentially cause extinction in the alpine zones due to competitive exclusion (Pauli *et al.*, 2012). Hence, these systems receive special attention in conservation. However, any change in the environment causes a change in vegetation composition of these ecosystems which is consequently also recorded in the pollen deposition. Due to this inherit characteristic of ecosystems to translate environmental changes directly into a pollen record they are especially suitable as archives in palaeoecological and palaeoclimate research.

Kilimanjaro is an ancient volcano which is an ideal archive for past changes in the East African climate system. Mt Kilimanjaro is not only the highest mountain of Africa but also the highest free-standing mountain in the world. Since it is not surrounded by other high mountain ranges the climate record captured in the palaeo-ecological archives on Mt Kilimanjaro is unmasked and hence likely to be very representative for tropical East Africa. It possesses an impressive wealth of different habitats ranging from hot and dry savannas at the foot of the mountain, over traditional coffee and banana plantations in the Chagga home gardens, the afro-montane forest zone with Africa's most altitudinous cloud forests at 4100 m asl, the alpine zone up to the barren nival zone just below the snout of the glaciers (Hemp, 2006a). This variety of different vegetation belts along the elevational gradient allows the reconstruction and detection of montane forest belt shift upslope and downslope. Especially the retreating glaciers of Mt Kilimanjaro are a clear indication for the changing climate in tropical East Africa (Thompson *et al.*, 2002; Kaser *et al.*, 2004). Rising temperatures and decreasing precipitation have changed the hydrology on Mt Kilimanjaro causing severe water shortfall for the Chagga population inhabiting the savannas at the foot of the mountain (Hemp, 2009). Obviously, this lack of water supply together with temperature rise and increased human activities on the mountain has also a major impact on the ecosystems (Chan *et al.*, 2008). These profound changes in the environment give rise to many controversial discussions about past, present but also future climate change (IPCC, 2007). For understanding the ecosystems functioning today we need to investigate past ecosystems and their evolution in a changing environment. Only once we understand the state and dynamics of past ecosystems under certain past climate conditions we will be able to make any reliable predictions concerning their stability or dynamics under different climate change scenarios of the future.

Study region – an overview

Geography

Mt Kilimanjaro (3°049 S, 37°219 E) is located in the highlands of equatorial East Africa in north-eastern Tanzania at the border to Kenya. With its three peaks Shira (4005 m asl), Mawenzi (5140 m asl) and Kibo (5895 m asl) the Kilimanjaro massive is not only the highest mountain in Africa but also the highest free-standing mountain in the world overtopping its surrounding by more than 5000 m (Kaser *et al.*, 2004). The massive is of strato-volcanic origin and has a diameter of 80 by 50 km. Mt Kilimanjaro is located roughly 370 km south of the equator and at about as distant from the Indian Ocean located to the east. The nearest by town is Moshi at 812 m asl (about 206,780 inhabitants in 2011, (Moshi Municipal Council, 2012)) which is located at the foot of the southern slope of Mt Kilimanjaro.

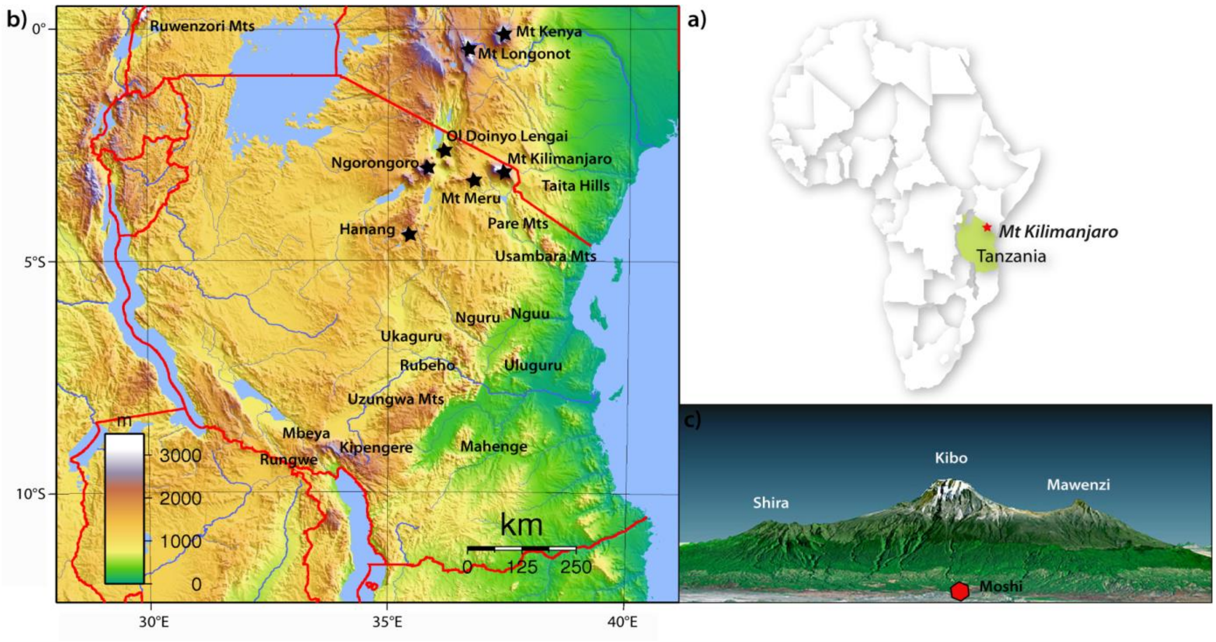

Figure 1: a) The location of Tanzania and Mt Kilimanjaro in equatorial East Africa, b) Topographic map of Tanzania. Names of mountain areas are indicated, stars (★) represent mountains of volcanic origin, all other mountains ranges except for the Ruwenzori Mts, belong to the Eastern Arc, c) The Kilimanjaro massive with its three peaks: Shira, Kibo and Mawenzi. The town Moshi is located on the southern foot of Kilimanjaro. Sources: worldofmaps.net (Fig.1b), NASA (Fig.1c).

Along with Mt Kilimanjaro there are only two other mountains in East Africa that reach elevations in which glaciers are formed: Mt Kenya (5199 m asl) in Kenya, which is located about 325 km north of Kilimanjaro, and the Ruwenzori Mountains on the border between Uganda and the Democratic Republic of the Congo, with heights of up to 5109 m. Besides the mountains of young volcanic origin a chain of ancient crystalline Precambrian basement mountains, stretching from the Taita Hills in Kenya to the Udzungwa Mountains in south-central Tanzania, called the Eastern Arc. This mountain range was uplifted at least 30 million years ago (Lovett and Wasser, 1993). The Eastern Arc Mountains are partly covered with forests and are recognized as one of the globally important „Hot-Spots“ for forest biodiversity (Newmark, 2002; Burgess *et al.*, 2007).

Geology

The East African Rift System (or Great Rift Valley) is an active continental rift zone in eastern Africa that appears to be a developing divergent tectonic plate boundary (Baker *et al.*, 1972). The rift is a narrow zone in which the African Plate is in the process of splitting into two tectonic sub-plates called the Somali Plate and the Nubian Plate (Fig.2). This rifting of the sub plates has started more than 30 million years ago when plumes of superheated rock rose beneath the earth's crust, bulging and thinning it. The crust fractured and created valleys surrounded by mountains and escarpments. The East African Rift System is not one continuous formation but a series of rift valleys of related origin. It runs from the Afar Triple Junction in the Afar Depression southward through eastern Africa (Chorowicz, 2005). The rift consists of two main branches: the Western Rift and the East Rift Valley. These result from the actions of numerous faults which are typical of all tectonic rift zones. The Western Rift Valley includes the Albertine Rift, and further south the valley of Lake Malawi. The Eastern Rift Valley includes the Main Ethiopian Rift, running eastward from the Afar Triple Junction, which continues south as the Kenyan Rift Valley (eastern branch). Although the volcanic area is by far smaller in northern Tanzania than in those to the north, there are major features such as Ngorongoro crater, one of the largest calderas on Earth, Oldoinyo Lengai, the world's only active carbonatite volcano and Mt Kilimanjaro, the highest mountain on the African continent (Dawson, 2008).

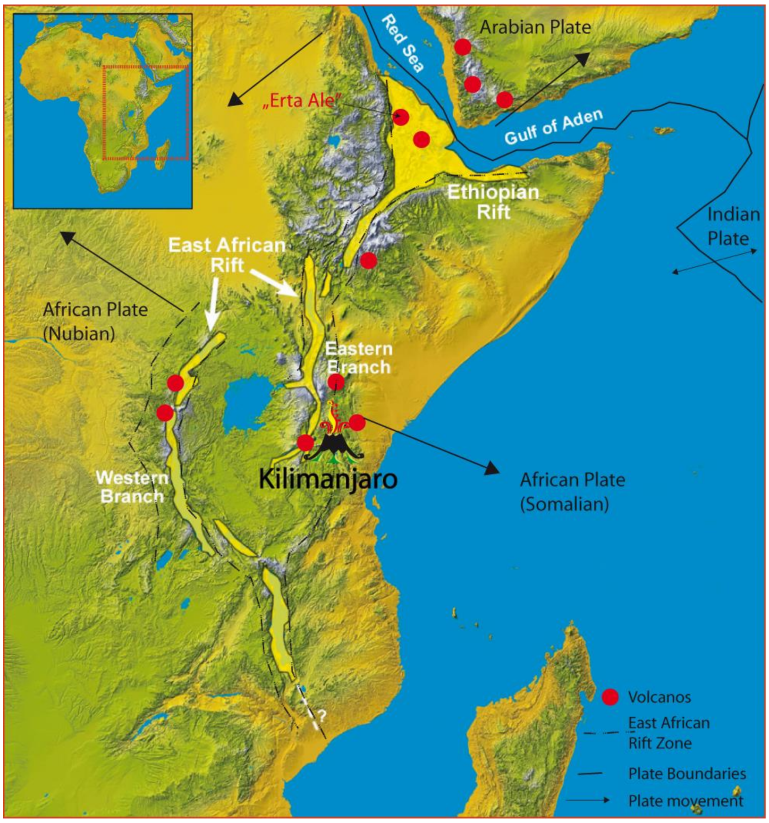

Figure 2: Geology of the East African Rift System. Yellow areas indicate the rift zones as created by the spreading of the Nubian and the Somalian plates. Sources: The basemap is a Space Shuttle radar topography image by NASA. Illustration after Wood and Guth (2012).

Mt Kilimanjaro was formed about 3 million years ago during the formation if the Great Rift Valley (Frisch *et al.*, 2010). About 1 million years ago the volcanic activities centred on the three points, Shira, Mawenzi and Kibo (see Fig.1) (Downie *et al.*, 1956). Shira was the first to become extinct. Soon after Shira's extinction, Mawenzi started to form following a further eruption within the Shira caldera. 460 ka ago an enormous eruption just west of Mawenzi caused the formation of Kibo. Continual subterranean pressure forced Kibo to erupt several times more until reaching a maximum height of about 5900 m (Siebert and Simkin, 2002). A further eruption from Kibo 100 ka later led to the formation of Kilimanjaro's characteristic shape. Kibo has not been active in modern times, but steam and sulphur are regularly seen coming from the crater at the summit (Richard, 1945).

Soils

The soils on the volcanoes of the East African Rift system developed on ash. Characteristic for these soils types are a high organic matter and volcanic glass content, good rootability and high water storage properties with a high rate of phosphate-fixation (Wada, 1985). According to the USDA soil taxonomy the dominating soil type which developed on Mt Kilimanjaro is the Andisol (or 'Andosol' according to FAO standard) (Soil Survey Staff, 2010). The parent material is mainly volcanic ash, but also tuff, pumice, cinders and other volcanic ejecta. Andisols develop in undulating to mountainous environment of humid, arctic to tropical regions with a wide range of vegetation types. They typically show an AC- or ABC-profile (Zech and Hintermaier-Erhard, 2002). The soils on the southern slope of Kilimanjaro exhibit are high accumulation rate of organic material. The low decomposition rate of litter as well as the cool and humid climate conditions are responsible for the low mineralization rate, and hence a low nutrient availability (Schrumpf, 2004).

Climate

The climate dynamics in tropical Africa are complex, responding to a variety of ocean-atmosphere processes associated with both the Indian and the Atlantic Ocean (Camberlin *et al.*, 2001). A mixture of Atlantic and Indian Ocean related mechanisms account for trends in moisture balance in the central and eastern African tropics (Fig.3). In the easternmost part of tropical Africa, the hydroclimate is oreographically insulated from the influence of the Atlantic ocean by the Congo Air Boundary (CAB) (Sepulchre *et al.*, 2006). Therefore, it is primarily influenced by the Indo-Pacific climate dynamics. The El-Niño-Southern-Oscillation (ENSO) and the Indian Ocean Zonal Mode (IOZM) have a particularly strong impact on the precipitation patterns during the short rainy season (October, November, December) (Nicholson, 1996; Camberlin *et al.*, 2001). On geological timescales, changes in the annual insolation alter the climate in East Africa through the modification of monsoonal intensity (Abram *et al.*, 2007; Tierney *et al.*, 2011).

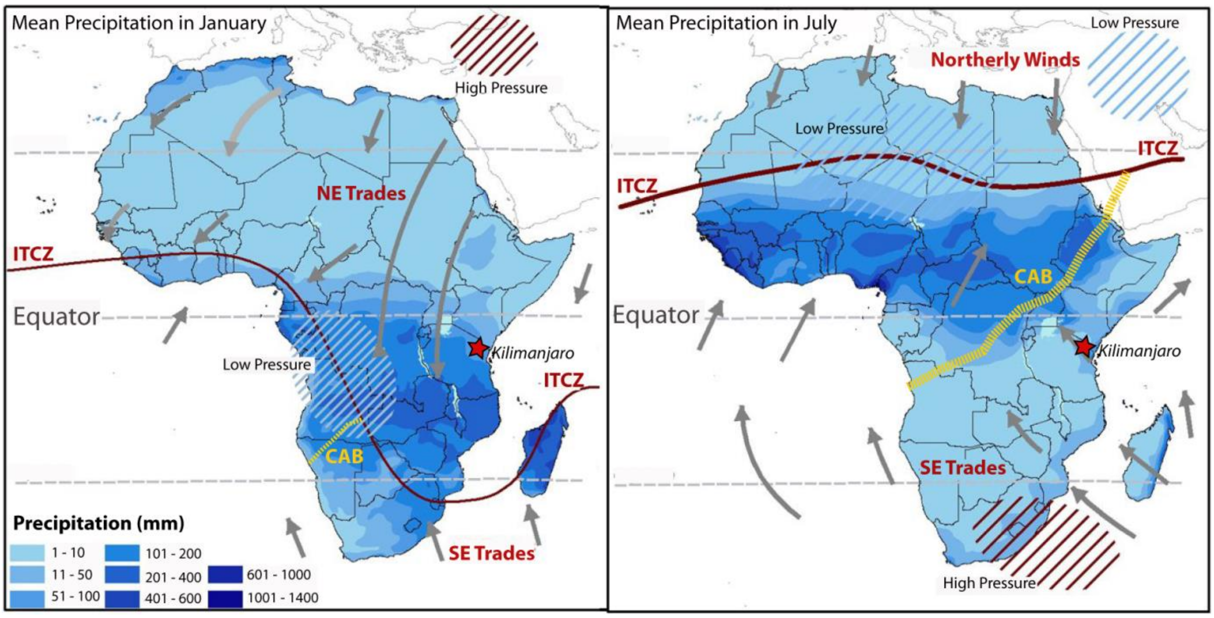

Figure 3: Mean January and July precipitation in Africa. During the southern hemisphere summer the ITCZ is located in the south following the area of highest insolation. That convergence line is extended from south west by the Congo air boundary (CAB) and the area over this region is unstable air and produces extensive cloudiness and severe thunderstorms. The ITCZ is shifted to the north during the northern hemisphere summer bringing high rainfall to central and northern Africa. The position of the ITCZ also determines the direction of predominant either north-easterly (NE) or south-easterly (SE) trade winds. Adapted after UNEP, Nairobi

Over Southeast Asia and East Africa the climate, and especially the precipitation pattern, is influenced by the monsoon system (Fig.3 and Fig. 4). The warming over the Asian continent induces a low surface pressure zone that drives the moisture transport and hence brings rain into Southeast Asia and East Africa. North-easterly and south-easterly trade winds which are driven from the high surface pressure regions of the Subtropics towards the low pressure zone near the equator converge onto the Intertropical Convergence Zone (ITCZ). This again gives rise to a narrow zonal band of high precipitation north of the equator.

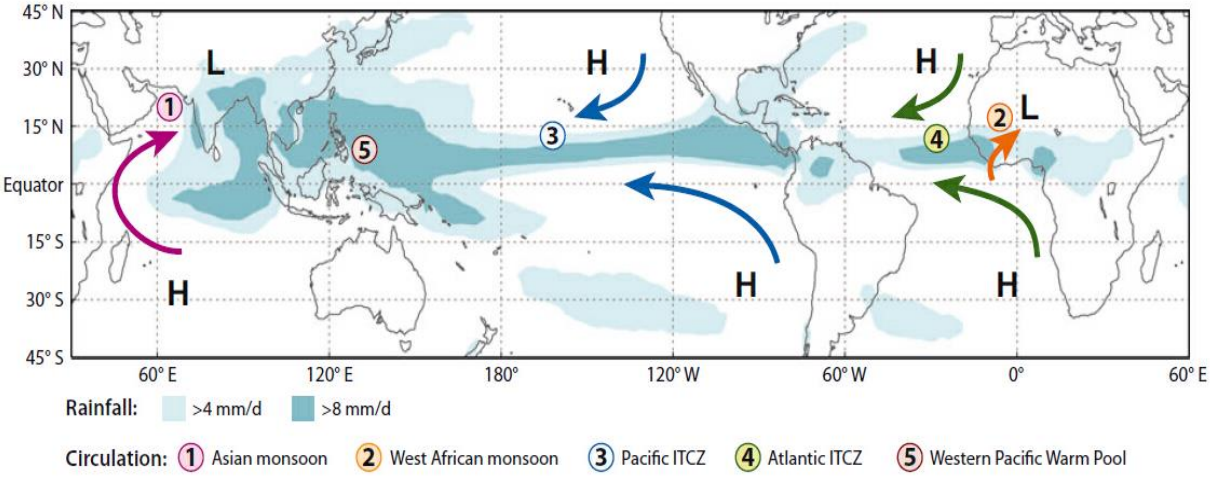

Figure 4: Regional perspective on the tropical climate. The figure shows the precipitation patterns in July/August and the surface wind systems associated with the Asian and West African monsoon. Trade winds originating in the Subtropics of the Pacific and Atlantic which flow into the Intertropical Convergence Zone (ITCZ) are also depicted. High seas surface temperatures (SST) cause convection over the western Pacific warm pool. L and H indicate the locations of low and high surface pressure systems. (Source: Chiang, 2009)

According to Köppen and Troll/Pfaffen (Müller, 1989) the Kilimanjaro area is characterized by a seasonally dry, tropical climate. Due to the influence of the position of the ITCZ and its proximity to the equator, Mt Kilimanjaro is characterized by a bimodal rainfall pattern and experiences four hydrological seasons per year: one short dry season in January and February, a long rainy season from March to May, a long dry season from June to September followed by a short rainy season in November and December.

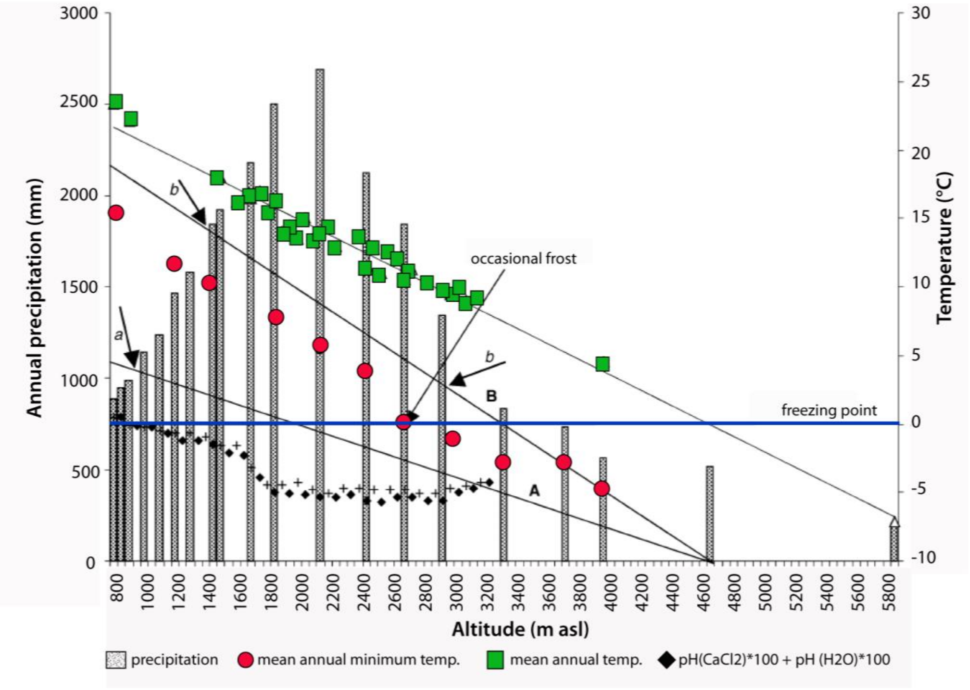

Figure 5: Mean annual precipitation and temperature combined from three transects on the central southern slope of Mt. Kilimanjaro. Line A: linear regression of mean annual temperature, line B: linear regression of mean annual temperature. Intersection of line and precipitation (arrow a) indicates transition from sub-humid to humid conditions, intersection of line b (arrows b) indicates that of humid and per-humid conditions (after Hemp, 2006a).

The climate on Mt Kilimanjaro is further dependent on the elevation on the mountain and the exposition of the mountain side (Fig.5). The foothills of the southern slopes receive a mean annual precipitation (MAP) of 800–900 mm and the lower slopes at 1500 m receive 1500–2000 mm. The forest belt between 2000 and 2300 m receives partly over 3000 mm (Hemp, 2001), which is more than on other high mountains of East Africa. In the alpine zone the precipitation decreases to 200 mm. Due to the prevalence of SE trade winds the southern slope is generally wetter than the northern slope (Hemp, 2006a). The mean annual temperature (MAT) is 24°C at the southern foothills at about 800 m asl and decreases linearly by 0.56 °C per 100 m altitude difference to -7.1 °C at 5895 m asl (Walter *et al.*, 1975; Thompson *et al.*, 2002). Frosts can occur above 2700 m asl. Despite the dominance of south-easterly or north-easterly winds, depending on the season, the wind system on Mt Kilimanjaro is further influence by katabatic and anabatic winds along the mountain slopes. While strong uphill winds prevail during the day, this pattern is reversed during the night when the cool air moves downhill (Hemp, pers.com.).

Vegetation

Despite tropical climate conditions only 2 % of the land surface of equatorial East Africa are covered with forests and these are mostly limited to mountainous regions (Bjørndalen, 1992). Today’s vegetation of Mt Kilimanjaro harbours about vascular 3000 plant species (Hemp, 2006a; Hemp, 2006b).

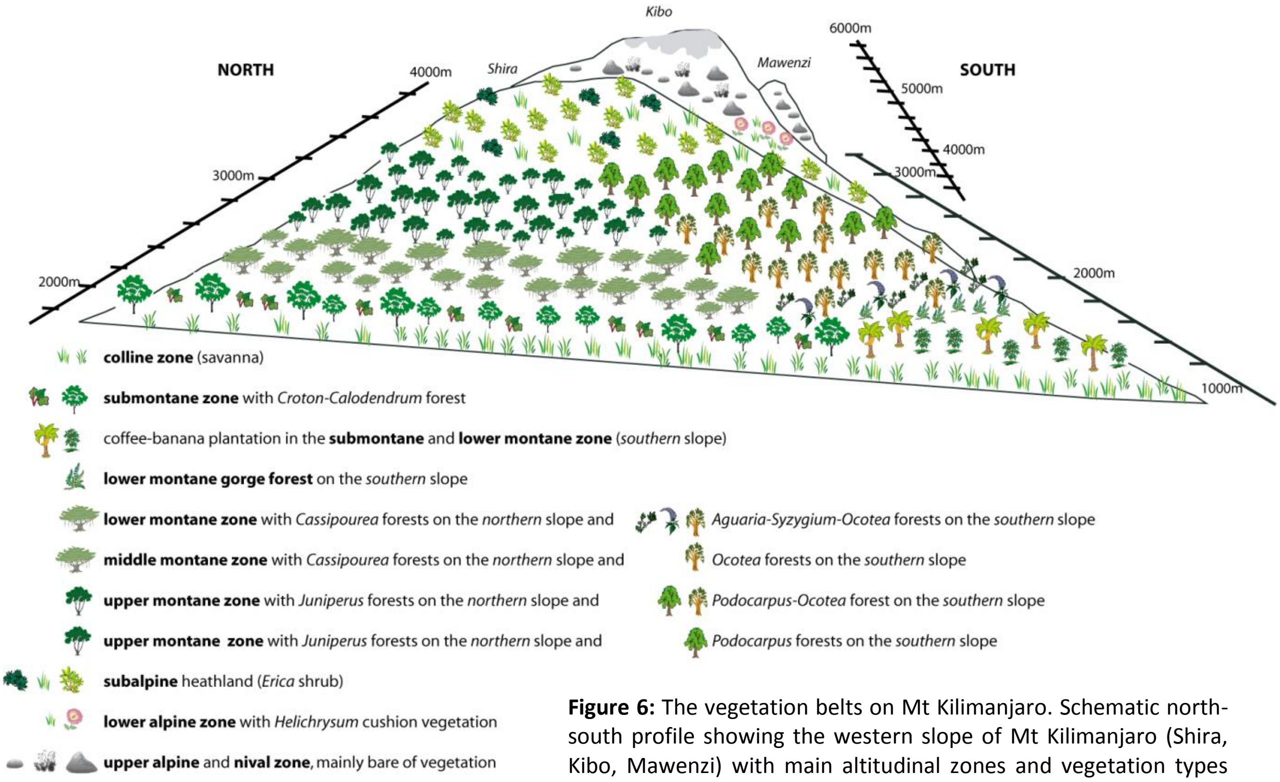

Figure 6: The vegetation belts on Mt Kilimanjaro. Schematic north-south profile showing the western slope of Mt Kilimanjaro (Shira, Kibo, Mawenzi) with main altitudinal zones and vegetation types (after Hemp, 2006a).

On the southern slope of Mt. Kilimanjaro several vegetation zones can be differentiated (Hedberg, 1951; Hemp, 2006a):

Figure 7: Colline savanna zone with sunflower fields.

Colline savanna zone: Between 700 and 1100 m asl a dry and hot savanna zone stretches around the mountain base (Fig.7). The mean annual temperature is 24 °C, and the precipitation reaches about 1000 mm/a. Today most of this area is used for crop production (maize, beans and sunflowers fields) or as pasture land. Remnants of the former vegetation include savanna woodlands with *Acacia* (Fabaceae), *Grewia* (Malvaceae), *Terminalia* and *Combretum* (Combretatceae) but also riparian forests with species such as *Ficus vallis-choudae* (Moraceae) and *Lecaniodiscus fraxinifolius* (Sapindaceae). On the south-eastern side dry forests with the succulent *Euphorbia quinquecosta* and *E. candelabrum* (Euphorbiaceae) as well as some deciduous species such as *Commiphora baluensis* (Burseraceae) and *Haplocoelum foliosum* (Sapindaceae) can be found. Only around Lake Challa, at the south-eastern foot of Mt Kilimanjaro, remnants of the pristine savanna woodland vegetation are still present.

Submontane forest zone (Fig.8):

Due to the favourable climate (mean annual temperature (MAT): 19 °C, mean annual precipitation (MAP): 1600 mm), today the main zone of agri- and horticulture with banana and coffee plantations extends from 1000 up to 1800 m. This zone has been inhabited by the Chagga, a Bantu tribe, for several centuries. Remnants of the former forests of this zone have survived only in the deepest valleys and gorges. This forest vegetation is highly divers and includes species such as *Entandrophragma excelsum* (Meliaceae), *Heinsenia diervilleoides*, *Hallea rubrostipulata*, *Mitragyna rubrostipulata* (all Rubiaceae), *Newtonia buchananii (*Mimosaceae), *Leptonychia usambarensis* (Sterculiaceae*)*, *Strombosia scheffleri* (Loganiaceae), *Dasylepis integra* (Flacourtiaceae), *Garcinia tansaniensis* (Clusiaceae) and *Polyscias albersiana* (Araliaceae). In the western parts of the mountain the comparatively dry submontane forest below 1600 m is dominated by *Olea europaea* ssp. a*fricana* (Oleaceae), *Croton megalocarpus* (Euphorbiaceae*)*, *Calodendrum capense* (Rutaceae) and *Diospyros abyssinica* (Ebenaceae).

Figure 8: Submontane forest belt with mostly semi-decidious forest.

Figure 9: Mid montane forest belt with mostly evergreen trees and a many ferns and epiphytes.

Montane forest: The montane forests of Mt Kilimanjaro border the cultivated zone on the southern and south-eastern slopes between 1700 and 1800 m and surround the whole mountain. Within the montane forest belts three sub-belts can be distinguished: lower, mid and upper montane forest.

The lower montane zone ranges from 1600 to 2100 m asl (MAT: 16 °C, MAP: 2000-2700 mm). Between 1500 and 1800 m asl the lower montane forest *Ocotea usambarensis* (Lauraceae) is the most abundant tree species. It is associated with *Agarista salicifolia* (Ericaceae), *Syzygium guineense* (Myrtaceae), *Macaranga capensis* var.

kilimandscharica (Euphorbiaceae), and *Polyscias fulva* (Araliaceae).

The mid montane forest belt (Fig.9) (2100-2800 m asl) receives the highest amount of rainfall on the whole mountain (MAP: 1910 to 3050 mm) and has a mean annual temperature range 10.4 to 14.4 °C. These favourable climate conditions give rise to a high richness in ferns and epiphytes. The frost susceptible tree fern *Cyathea manniana* is very abundant below 2700 m asl which is the elevation at which frost starts to occur occasionally during the night. In the lower part of this belt the camphor-tree *Ocotea usambarensis* forms monospecific stands.

In the upper part it is associated with *Podocarpus latifolius*.

Above 2800 m asl the dominance of *Podocarpus latifolius* (Podocarpaceae) is characteristic for the upper montane forest belt which forms together with *Hagenia abyssinica* (Rosaceae) and *Prunus africana* (Rosaceae) form the tree canopy (Fig.10). Monodominant stands of *Erica excelsa* (Ericaceae) play also an important role in this zone, replacing *Podocarpus* and *Hagenia* forests after fire, forming the actual upper closed forest line on the southern slope of Kilimanjaro at 3250 m (Hemp and Beck, 2001).

Figure 10: Upper montane forest zone with abundant *Hagenia abyssincia*

Figure 11: Subalpine moorlands and *Erica* shrub lands below the Mawenzi peak

Subalpine zone (Fig.11): Between 3100 and 3900 m the forests of *Erica excelsa* are gradually replaced by *Erica*-shrub with the dominant species *Erica arborea* and *Erica trimera*, *Protea caffra* and *Euryops dacrydioides.* In the south-eastern parts moorland vegetation, formed by tussock grass and characterised by giant lobelias, fringes the forest. The mean annual temperature ranges between 4.2 to 8.7 °C. This belt receives relatively little rainfall (MAP: 700 to 1500 mm) which facilitates the occurrence of fires.

Alpine zone: At an altitude of about 3900 m the *Erica* heathlands grade into a *Helichrysum* cushion vegetation that extends up to 4500 m. Due to the rather hostile climate conditions (MAT: 4.2 to 0.7 °C, MAP: 500 to 700 mm) these altitudes are poor in vegetation. Open grasslands with cushions of *Helichrysum newii* and *citrispinum, Senecio meyeri-johannis* and *Pentaschistis borussica* (all Asteraceae) and bogs with *Carex monostachya* and *Dendosenecio kilimanjari* (Fig. 12) *are* characteristic for this zone.

Figure 12: Alpine bog with *Carex monostachya* and stands of the endemic *Dendrosenecio kilimanjari.*

Nival zone: Above 4800 m the mean annual temperature is below 0 °C and annual precipitation is low (MAP: < 500 mm). The boulder slopes is only sparsely vegetated by lichens and mosses. The top of Kibo (5895 m asl) is still partly covered with glaciers.

Due to drier climate conditions, the vegetation zones on the northern slope of Kilimanjaro are shifted upslope and harbour a partly different species composition (see Fig.6). Savanna woodlands with *Acacia* div. sp. (Mimosaceae), *Terminalia* div. sp. (Combretaceae), *Grewia* div. sp. (Malvaceae) and *Combretum* div. sp. (Combretaceae) characterize the *colline zone* between 1400 and 1600 m asl. In the *submontane zone* (1600-2000 m asl) a similar Croton-Calodendrum forest grows as on the western slope. In the lower *montane forest zone* (2000-2500 m asl) *Cassipourea malosana* (Rhizophoraceae), *Teclea simplicifolia*, *Fagaropsis angolensis* (Rutaceae) and *Olea capensis* are abundant. Above 2500 m up to 3100 m asl, a *Juniperus-Podocarpus*-forest (*Juniperus procera,* Cupressaceae), *Podocarpus latifolius, Hagenia abyssinica)* replaces the lower montane forest. Monospecific stands of Erica *excelsa* can also be found. Since with increasing elevation climatic conditions (in particular rainfall) become similar to the conditions on the southern slope, the plant distribution above 3100 m asl the subalpine *Erica*-shrub as well as the alpine and nival zones harbour a similar flora as found on the southern slope.

Missing Bamboo Belt

An interesting feature of the forests of Mt Kilimanjaro is the absence of a bamboo zone, which occurs on all other tall mountains in East Africa with a similarly high rainfall (Fig.14). Stands of *Sinarundinaria alpina* (Poaceae) are favoured by elephants and buffaloes but on Mt Kilimanjaro these mega-herbivores occur on the northern slopes, where it is too dry for a large bamboo zone to develop. *Sinarundinaria alpina* needs at least 1250 mm of annual rainfall (Dale, 1940; Lind and

Morrison, 1974). In contrast to the dry northern slope, these wetter climate conditions exist on the southern slope of Mt Kilimanjaro. Similar climate conditions can be found on the southern slope of Mount Kenya, where, however, a bamboo belt has developed (White, 1950). The existence of a bamboo belt seems to be closely related to the presence of mega-herbivores as observed on other East African mountains. Mega-herbivores are excluded from Mt Kilimanjaro‘s wet southern slope forests by topography and humans, who have cultivated the foothills for at least 2000 years. Hence, the interplay of biotic and abiotic factors could explain the lack of a bamboo zone on Kilimanjaro (Hemp, 2006c).

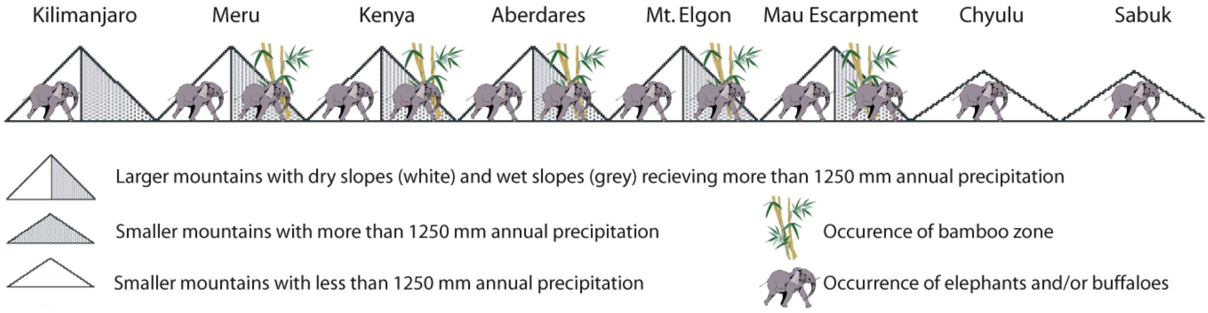

Figure 13: Occurrence of bamboo zones, mega-herbivores and areas of high annual precipitation (>1250 mm) on several mountains in East Africa. A bamboo zone occurs only on wet slopes, which are inhabited by elephants and buffaloes (adapted after Hemp, 2006c)

Anthropogenic Impact

For the past 2000 years humans have been inhabiting the slopes of Mt Kilimanjaro (Odner, 1971a; 1971b). While ethnographic studies by Widenmann (1899) report 50,000 to 60,000 Chagga people on Mt Kilimanjaro in 1895, in 2002 the census counted already over 1 million people (National Bureau of Statistics and Central Census Office, 2003). Especially during the last decades the human population increased dramatically. The highest population density is found at altitudes between 1000 and 1800 m, with densities varying from 500 to 1000 people per km² in some areas (Timberlake, 1986). Within this submontane zone, the Chagga have transformed the native forests into so called ‘home gardens’. The Chagga home gardens are traditional, densely planted ‘banana forests’ with a scattered upper tree layer. Typical is their multi-layered vegetation structure similar to a tropical forest, which integrates numerous multipurpose trees and shrubs with food crops and stall-fed animals (Fernandes et al., 1984). Most commonly encountered are dense ‘banana forests’ with a scattered upper tree layer. Due to this rather sustainable and well developed agroforestry system degradation in this vegetation belt is rare, despite the enormous population (Hemp, 2006b).

Palynological and Palaeoecological research on tropical East Africa – state of knowledge

Compared to the tropical regions in South America, Asia or Australia, only few palynological studies are available for tropical Africa, and even less from tropical East Africa. On the one hand this is due to the lack of suitable study sites, especially terrestrial ones, which could provide sufficient pollen preservation; on the other hand, extensive vegetation studies are also sparse in East Africa which means that the documentation of the pollen and spore flora has only recently been set on sound footing by a few research groups (Lézine, 2001; Vincens *et al.*, 2007).

Early Last Glacial – pre-Last Glacial Maximum (LGM)

Only few palaeoenvironmental records from East Africa extend beyond 42 ka BP (Coetzee, 1967; Taylor, 1990; Street-Perrott *et al.*, 1997; Olago *et al.*, 1999; Schüler *et al.*, 2012). Most of them are pollen records and they present useful data for the reconstruction of East Africa's palaeoenvironment beyond the LGM. During the period prior to 42 ka BP the climate is characterized by warmer conditions. Between 42 ka BP and 30 ka BP the shift of montane vegetation belts to lower elevations marks a change to cold and dry conditions (Kiage and Liu, 2006). Much of this evidence is obtained from pollen and diatom data as well as charred grass cuticles and is verified by carbon isotope ($\delta^{13}C$) records (Olago, 2001). Before the LGM cool conditions prevailed in East Africa with temperatures being 2–4.1°C colder than present (Coetzee, 1967; Olago, 2001).

Last Glacial Maximum (LGM)

During the LGM East Africa's environment was generally cool and punctuated by episodes of prolonged desiccation (Kendall, 1969; Street and Grove, 1979; Beuning *et al.*, 1997). For the Rukiga Highlands in Burundi Bonnefille and Chalié (2000) suggest a 2 to 5 °C temperature drop. A record from Lake Albert, Uganda and Democratic Republic of Congo (Fig.15), documents two episodes of lake level low stands of at least -46 m below the present lake levels during the LGM (18 – 20 ka BP). Palaeoenvironmental proxies from Lake Victoria also document a low stand at ca 15.4 ka BP. This very dry period in Lake Victoria reduced the lake level to at least -66m below present. This dry phase at 18 – 20 ka BP (Lake Albert) and ca 15.4 ka BP (Lake Victoria) could be synchronous with the LGM. Palaeopedological and palaeoecological results from the southern slopes of Mt Kilimanjaro suggest a climate driven downhill decent of the ericaceous belt of about 1000 m due to cold and dry climate conditions during the LGM (Hemp and Beck, 2001; Zech, 2006; Schüler *et al.*, 2012). This is underpinned by a multi-proxy study from Mt Kenya suggesting the expansion of C4 grasses on African mountains during the LGM (Wooller *et al.*, 2001; Street-Perrott *et al.*, 2007).

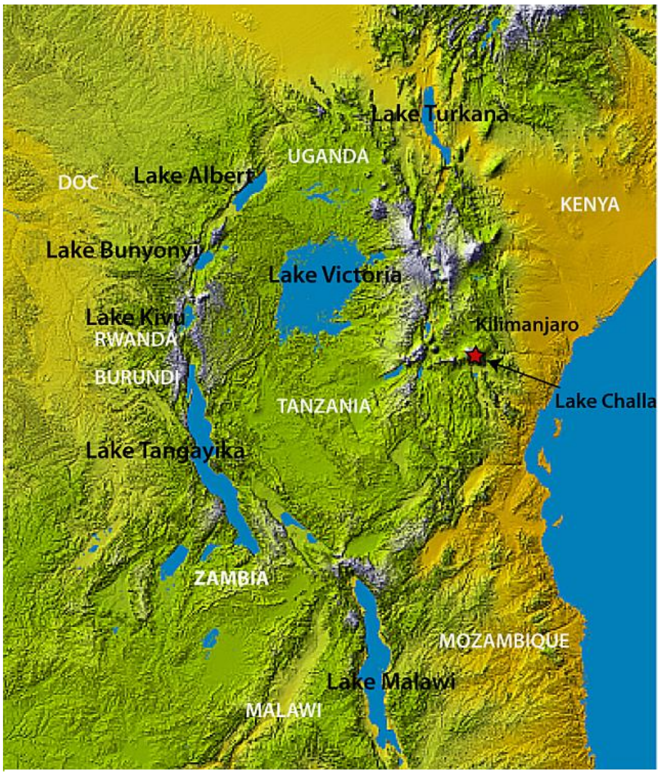

Figure 14: The East African Lakes. Lake Turkana is located in Kenya; Lake Albert and Lake Bunyonyi are located at the border of Uganda with the Democratic Republic of Congo (DOC); Lake Victoria is part of Uganda and Tanzania; Lake Tanganyika borders Tanzania, Burundi and the DOC; Lake Malawi abuts the countries Malawi, Zimbabwe and Tanzania. Lake Challa is located at the border of Tanzania with Kenya. Source: The basemap is a Space Shuttle radar topography image by NASA.

Dry climate conditions are characteristic for the final period of the LGM. The palaeoecological records of the East African Lakes indicate a distinct water table low stand. At Lake Tanganyika, located at the border between Congo, Tanzania, Burundi and Zambia, this low stand was dated to about 21 ka calibrated (cal) BP (Gasse *et al.*, 1989). Desiccation is recorded from Lake Victoria, Tanzania/Uganda/Kenya, at 20.5 ka cal BP (Talbot and Livingston, 1989), Lake Albert, Uganda/DOC at about 22 ka cal BP (Beuning *et al.*, 1997), and Lake Rukwa, Tanzania, at 20 ka cal BP (Barker *et al.*, 2002). For the same time period similar trends were observed at Lake Malawi (DeBusk Jr, 2003), Tanzania/Malawi/Mozambique and in the Magadi-Natron Basin, Kenya/Tanzania (Hillaire-Marcel and Casanova, 1987). Also studies from the Ruwenzori Mountains, DOC/Uganda (Livingston, 1967), the Kalambo Falls, Zambia/Tanzania (Van Zinderen Bakker, 1969), from the valleys around Mufo, Angola (Van Zinderen Bakker and Clark, 1962), and the Zaire-Basin, DOC (Caratini and Giresse, 1979; Jansen *et al.*, 1984) suggest dry and cold conditions for the late phase of the LGM. According to Kutzbach and Street-Perrott (1985) this aridity was a consequence of the prevalent lower tropical land and sea surface temperatures caused by enlarged polar ice sheets (Western Pacific sea surface temperatures 2 to 3°C cooler than at present: Thunell *et al.*, 1994; Lea *et al.*, 2000) and a modified chemical composition of the atmosphere. The reduced ocean evaporation caused a weakening of the global hydrological cycle, and hence, also of the East African Monsoon system which largely determines the terrestrial precipitation patterns (Gasse, 2000). For the Rukiga Highland in Burundi Bonnefille and Chalié (2000) suggest a reduction in precipitation by 32 %.

16 ka until 11.5 ka cal BP – Deglaciation

The end of the Pleistocene in Eastern and Central Africa was generally characterized by a shift to warmer and more humid climate conditions which also marks the beginning of the African Humid Period. For the early stage of this time period the pollen record of Sacred Lake, Mt Kenya, still indicates a vegetation dominated by Poaceae and *Artemisia* (Asteraceae) (Coetzee, 1967).

Sedimentological evidence indicates that the period of maximum aridity occurred just before 13.5 ka cal BP, at a time when there was a change from C4-dominated to a C3-dominated vegetation community (Olago *et al.*, 1999); this is supported by the abundant occurrence of *Artemisia* after 14.5 ka cal BP which indicates dry conditions. An increase in *Cliffortia* and, later, *Hagenia,* which replaced the open grassland vegetation, indicate a slight climatic amelioration. An increase in *Celtis* which is currently found on the plateau and at lower altitudes in the forests of Mt Kenya might indicate moister conditions in the lowlands around 12.3 ka BP.

A short relapse into dry conditions after 13 cal ka BP is reported from the Empakai Crater, Tanzania (Ryner *et al.*, 2006), the Rumuiku Swamp on Mt Kenya (Rucina *et al.*, 2009). This dry spell corresponds to the Younger Dryas Period of the northern hemisphere and is also well documented by East African lake-level fluctuations (Roberts *et al.*, 1993). This arid phase found an abrupt end around 11 cal ka BP (Kendall, 1969; Hamilton, 1982). An increase in tree taxa around Lake Victoria (Van Zinderen Bakker, 1972) and the lake-level rise in e.g. Lake Tanganyika (Vincens *et al.*, 1993) are clear indicators for the return of humid conditions.

Based on seismic-reflection stratigraphy and organic biomarker molecules in the sediment record of Lake Challa near Mt Kilimanjaro, Verschuren *et al.* (2009) suggest that monsoon rainfall in this region varied at half-precessional, 11.5 ka intervals, in phase with orbitally controlled insolation forcing. According to the authors the south-easterly and north-easterly monsoons that advect moisture from the western Indian Ocean were strengthened around 11 cal ka BP, and hence, led to increased precipitation on land.

11.5 ka until 5 ka cal BP – Early to Mid-Holocene

The Holocene African Humid Period occurred between ca. 9 and 6 cal ka BP (Ritchie *et al.*, 1985; Roberts, 1998) but humid conditions had initially commenced by ca. 14.5 cal ka BP (deMenocal *et al.*, 2000). The beginning of the Holocene is marked by the peak of the African Humid period as indicated by several lake-level studies (e.g. Van Zinderen Bakker, 1972; Roberts *et al.*, 1993; Chalié and Gasse, 2002; Verschuren, 2003). The ice core record from Mt Kilimanjaro shows very high accumulation rates also indicating wet climate conditions between 11 ka and 4 cal ka BP (Thompson *et al.*, 2002). Coetzee (1967) reports an upward shift on vegetation zones at Sacred Lake, Mt Kenya, after 10 ka cal BP due to increased temperatures and precipitation. Forest pollen types like *Hagenia* become exceedingly dominant and marked declines of *Erica*, the dominating taxon in the Ericaceous zone, occur. A pollen record from Lake Turkana suggests an extension of highland forest coupled with high fern abundance also indicating increased rainfall over tropical East Africa (Owens *et al.*, 1982).

However, this period was punctuated by severe dry spells lasting several hundreds of years, centred at 8.2 ka, 6.6 ka, and 4 ka BP (Gasse, 2000). Gupta *et al.* (2003) suggest that these droughts have mechanistic links to millennium-scale climate variability in the North Atlantic region but their timing has not been sufficiently constrained to explore this in detail.

5 ka until present – Mid to Late Holocene

DeMenocal (2000) reports an abrupt termination of the African Humid Period around 5.5 cal ka BP. A change to cooler and especially drier conditions in the second half of the Holocene was also observed in the ice core record from Mt Kilimanjaro (Thompson *et al.*, 2002). While the rapid increase of $\delta^{18}O$ in the ice indicate a fast temperature decrease between 5 and 4 cal ka BP, high dust concentrations containing elevated concentrations of chemical species e.g. fluoride (F) and sodium (Na) propose pronounced dry conditions after 4 cal ka BP. Lake level records from Lake Rukwa, Tanzania (Talbot and Livingston, 1989), Lake Victoria, Tanzania (Van Zinderen Bakker, 1972), and Lake Cheshi, Zambia (Stager, 1988), show an abrupt dry episode around 3 ka BP. This abrupt desiccation event during 4.5 – 3.5 ka BP has been recognized across tropical Africa (Hamilton, 1982; Street-Perrott and Harrison, 1985; Street-Perrott and Street, 1990; Maley and Brenac, 1998; Elenga *et al.*, 2000; Bonnefille and Chalié, 2000; Barker *et al.*, 2004). This aridity has been associated with decline in the base flow of the White Nile (Talbot and Brendeland, 2001). It could also be linked to the collapse of the Old Kingdom in the Nile Valley (Hassan, 1997; Barker *et al.*, 2004). This sudden shift to drier and more seasonal environmental conditions at around 4 ka BP has also been recorded at different sites on the island of Madagascar (Burney, 1993).

The pollen record from Lake Tanganyika shows increasingly arid conditions after 5 ka BP causing the replacement of forest by open grassland in the surrounding area (Msaky *et al.*, 2005). The Lake Bogoria pollen sequence documents an abrupt disappearance of high altitude forest pollen such as *Hagenia abyssinica*, *Hypericum*, *Stoebe*, and Ericaceae, and an increase in more drought-adapted taxa such as *Podocarpus*, *Juniperus*, *Acacia* and *Dodonaea* after 4.5 ka BP (Vincens, 1986). A sharp increase in *Podocarpus* was observed after 4.5 ka BP at Mt Kenya (Street-Perrott and Perrott, 1993) and a similar rise in Mt Elgon at about 3.5 ka BP (Hamilton, 1982). This probably signifies the onset and establishment of dry conditions in the region.

During this same period there was a rise in dry forest taxa such as *Olea* and *Prunus* (Coetzee, 1967; Street-Perrott and Perrott, 1993; Olago, 2001). The sharp increase in *Podocarpus* at about 4.5 ka BP at the Mt Kenya site (Street-Perrott and Perrott, 1993) and around 3.5 ka BP at Mt Elgon (Hamilton, 1982) corresponds with the third abrupt dry event recorded in the Mt Kilimanjaro ice core record (Thompson *et al.*, 2002).

General objectives and outline of chapters

The broad context of this research is the need to understand how tropical African forest ecosystems responded to the impacts of past climate change. 20 % of the earth´s terrestrial surface are covered by mountain ecosystems which expand across large elevational gradients with different climatic and biogeographic zones (Körner, 2003a). Tropical mountain areas have unique ecosystems and they are global biodiversity hotspots (Myers *et al.*, 2000), but they are severely threatened by climate and land use change, with considerable consequences for biodiversity, ecosystem functioning and human societies. The steep climate gradient and the occurrence of varied ecosystems makes tropical mountains convenient for ecological research investigating the effects of past, present and future environmental change (Körner, 2000; Nogués-Bravo *et al.*, 2008). This holds true in particular for Mt Kilimanjaro with its altitudinal range of over 5000 m and its climatic and vegetation zones ranging from hot and dry tropical savannas to the cold and rather hostile afro-alpine grasslands. In order to unearth new scientific information, the specific aim of this particular research is the reconstruction of the Late Quaternary vegetation and climate dynamics on Mt Kilimanjaro based on palynological and sedimentological data. The results can help improve the predictability of both, the future ecosystem response to environmental change and the impact of anthropogenic climate change on rainfall, fire regimes and carbon sinks. In this context, this study pursues in particular the two following research topics:

1) *The investigation of past vegetation, climate and fire dynamics at different study sites on Mt Kilimanjaro.*

   This task aims at the complementation of previous investigations in Tropical East African Mountains. The new data contributes to the establishment of a basis for more detailed comparison between different study sites. The reconstruction of past vegetation changes and identification of environmental conditions and their impact on local and regional ecosystem dynamics are of main interest. More specifically, the following fundamental but yet open questions were approached:

   - How did the vegetation respond to environmental change?
   - What changes in biodiversity can be observed?
   - How did the floristic composition of the different vegetation types change in space and time?
   - Did Mt Kilimanjaro serve a refuge for montane forest species during the last Glacial?
   - What was they dynamic of vegetation belt shift under past climate change conditions?
   - How frequent were fire events and how did they impact the vegetation?
   - Is there any evidence for anthropogenic impact on Mt Kilimanjaro?

2) *The investigation of the relationship between modern pollen rain data and present vegetation patterns along the elevational gradient of Mt Kilimanjaro.*

   Since past shifts in the distribution of vegetation types are reconstructed from fossil pollen assemblages, the exact relationship between modern vegetation and modern pollen compositions is crucial for calibration of the fossil pollen records. Such calibration studies which quantitatively relate pollen with elevation or climatic parameters are still lacking in tropical Africa. One key objective of this project, therefore, is to establish exact pollen-vegetation and pollen-climate relationships, from which transfer functions can be developed for detailed reconstruction of past vegetation and climate states from fossil pollen records.

The chapters are predominantly prepared as manuscripts for submission to peer-reviewed journals. The specific objectives of the chapters are as follows:

Chapter 2 deals with the pollen analysis of the Maundi crater located at 2780 m asl on the south-eastern slope of Mt Kilimanjaro. This study provides first palynological data extending back into the early last Glacial (~90 ka BP) and therefore presents one of the longest terrestrial pollen records in East Africa covering almost a full glacial-interglacial cycle of vegetation and climate history.

Chapter 3 provides insight into how present vegetation is reflected in the modern pollen rain along the elevational gradient of Mt Kilimanjaro. To investigate the representation of plant families in the pollen-trap samples the % abundance differences between local vegetation cover and the pollen rain are calculated. The similarity between paired pollen-trap samples within each plot gives an indication for how representative it is for the surrounding vegetation. The results indicate whether plant taxa are strong or weak pollen producers, and/or subject to long-distance pollen transport. These quantitative results are crucial for calibration of the fossil pollen records.

In ***Chapter 4*** the palynological and sedimentological outcome of the WeruWeru 26 (WW26) palaeo-soil profile record is presented. The study site is located at 2650 m asl, in the montane forest on the southern slope of Mt Kilimanjaro. The record describes the last ca 50 ka of past vegetation and climate dynamics in high resolution and therefore allows detailed reconstruction of the vegetation response to environmental changes.

The development of mathematical transfer functions, as described in ***Chapter 5***, allows ‘translation’ of fossil pollen data to specific climate data, by comparing the composition of pollen rain collected in traps with the surrounding vegetation and local climatic conditions. For the development of the pollen-climate transfer functions for the Kilimanjaro elevational gradient between 800 and 3200 m, weighted-averaging partial least square regression models (WA-PLS) were used.

In ***Chapter 6*** the most important outcomes of this research are summarized and synthesized, and fundamental conclusions are drawn. Further, the issue of uncertainties is shortly addressed and finally some perspectives for palaeoecological research in East Africa are envisioned.

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Chapter 2

Vegetation, climate and fire-dynamics in East Africa inferred from the Maundi Crater pollen record from Mt Kilimanjaro spanning the early last Glacial

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Abstract

The pollen, charcoal and sedimentological record from the Maundi Crater, located at 2780 m elevation on the south-eastern slope of Mt Kilimanjaro, is one of the longest terrestrial records in equatorial East Africa, giving an interesting insight into the vegetation and climate dynamics back to the early last Glacial period.

Our sediment record has a reliable chronology until 42 ka BP. An extrapolation of the age-depth model, as well as matching with other palaeo-records from tropical East Africa, suggest a total age of about 90 ka BP at the bottom of the record. During the last Glacial the distribution as well as the composition of the vegetation belts classified as colline savanna, submontane woodland, montane forest, ericaceous belt, and alpine vegetation changed.

The early last Glacial is characterized by high amounts of Poaceae and Asteraceae pollen suggesting a climatically dry but stable phase. Based on the absence of pollen grains in samples deposited around 70 ka BP, we assume the occurrence of distinct drought periods. During the pre-LGM (Last Glacial Maximum) a higher taxa diversity of the ericaceous and montane zone is recorded and suggests a spread of forest and shrub vegetation, thus indicating a more humid period. The taxa diversity increases steadily during the recorded time span. The decent of vegetation zones indicate dry and cold conditions during the LGM and seem to have been detrimental for many taxa, especially those of the forest vegetation; however, the early last Glacial seems to have been markedly drier than the LGM. The reappearance of most of the taxa (most importantly *Alchemilla*, Araliaceae, *Dodonea, Hagenia, Ilex*, *Myrsine*, Moraceae, and Piperaceae) during the deglacial and Holocene period suggest a shift into humid conditions. An increase in ferns and the decrease in grasses during the Holocene also indicate increasing humidity.

Fire played an important role in controlling the development and elevation of the ericaceous zone and the tree line. During the Holocene no increased anthropogenic impact around the Maundi crater can be observed, since neither higher fire activity nor a spread of hemerophilic plants is recorded.

This pollen archive reveals shifts in the upper vegetation zones (ericaceous zone and montane forest zone) of at least 1100 m but underlines the role of Mt Kilimanjaro as a glacial refuge for montane forest species similar to that of the Eastern Arc Mountains.

Keywords: Tanzania, Pollen, Charcoal, late Quaternary, Vegetation Zones, Kilimanjaro, climate change

Introduction

During the past decades the famous snow topped mountain rising from the East African savannas has repeatedly caught attention and given rise to many discussions concerning present and past climate change. Especially recently, the retreating glaciers of Mt Kilimanjaro (Thompson, 2000; Gasse, 2002; Thompson et al., 2002) indicate a marked change in regional environmental and climate conditions (Hemp, 2005).

Mt Kilimanjaro (3°049 S, 37°219 E) is the highest mountain in Africa and the highest solitary mountain in the world overtopping its surroundings by more than 5000 m.

With its range of different climate and vegetation zones (700 – 5895 m asl), including dry and hot savanna, montane forest and alpine vegetation above the tree line, Mt Kilimanjaro is a suitable object for studying the influence of climate change on vegetation. Reconstructing the vegetation dynamics of the past is of particular interest as Mt Kilimanjaro is a critical water catchment for both Tanzania and Kenya. Changing climatic conditions could have major impacts on several millions of people depending on the water of Mt Kilimanjaro (Hemp et al., in press). The melting glaciers have nearly no impact on the water balance, as the water mainly originates from the forest belt, which is the mountains' vegetation formation most susceptible to climate change (Hemp, 2005).

Since the monsoon system is a major driver for precipitation amount and pattern, its activity is considered as one of the driving factors in climate change in the past but also today. Nagai et al. (1995) suggested that the intensity of the southeast trade wind bringing the moisture was reduced during glaciation. Changes in ocean and wind dynamics of the western Pacific influence the climate conditions, and hence, influence the vegetation in tropical East Africa (Marchant et al., 2006; Chan et al., 2008). Based on lipids and δD analysed in the sediment samples of Maundi crater, Zech et al. (2009) suggest the prevalence of dry conditions during the early last Glacial/pre-LGM period. Lake level records from Lake Malawi propose periods of extreme aridity between 135 –75 ka BP causing a 95% reduction in water volume. Also, pollen and diatom records from Lake Malawi indicate severe drought events until about 95 ka BP (Cohen et al., 2007; Scholz et al., 2007). Cohen et al. (2007), as well as Scholz et al. (2007), interpret this period of aridity to be far more extreme than any period recorded in equatorial Africa during the LGM suggesting cool and semi desert conditions at Lake Malawi. Such climatic conditions were also proposed for Lake Abhé, at the southern border between Djibouti and Ethiopia, between 70 - 60 ka BP (Gasse, 1977).

For the period >42 ka BP Taylor (1990) suggests climate conditions similar to today. Pollen and diatoms, as well as lake level records from Lake Malawi, Lake Bosumtwi (West Africa) and Lake Tanganyika (East Africa), also suggest diminishing aridity after 70 – 60 ka BP indicated by rising lake levels and an increase in montane forest taxa (Scholz et al., 2007). Other records from East Africa (Rukiga Highlands, southwest Uganda (Taylor, 1990), Mt Kenya (Olago et al., 1999; 2001), Lake

Albert, Ethiopia (Lézine, 1982) and Kashiru Swamp, Burundi (Bonnefille and Riollet, 1988)) report the ericaceous belt position to be about 1050 m lower than today between 42 – 30 ka BP. Palaeo-pedological results from the southern slopes of Mt Kilimanjaro suggest palaeo-climatically driven fluctuations and changes of the vegetation zone. The downhill decent of the ericaceous belt of about 1000 m coincides with cold and dry periods like the LGM (Hemp and Beck, 2001; Zech, 2006). Early assessments of the LGM interpreted this elevational shift to have resulted solely from lowered temperature (~-6°C, Hamilton, 1972). Later, pollen-based reconstructions considering the combined effect of changes in temperature and precipitation (Bonnefille et al., 1990; Bonnefille et al., 1992; Vincens et al., 1993) suggested that the decent of vegetation zones was due to glacial climate being both, cooler (by 3-4 °C) and drier (~30 % less precipitation). Carbon isotope analysis of leaf waxes from Mt Kenya (2350 m asl) showed a significant expansion of C4 grasses during the last glacial period (Street-Perrott et al., 2004). Multi-proxy studies from Mt Kenya confirmed the expansion of C4 grasses on African mountains during the LGM (Wooller et al., 2001; 2003; Street-Perrott et al., 2007), however, this could not be shown for Mt Kilimanjaro (Zech et al., 2011).

Geochemical and sedimentological data from Lake Tanganyika, southwest Tanzania, show very dry conditions during the late Pleistocene (31 - 18 ka BP), and wetter conditions before and after that period. The interval from 60-50 ka BP was comparatively wet, similar to modern conditions. Intermediate aridity prevailed from 50-32 ka and was followed by intense aridity from 32 - 18 ka BP (Felton et al., 2007). Based on a record of hydrological variability during the past 25 ka BP in Lake Chala at the south-eastern foothills of Mt Kilimanjaro, Verschuren et al. (2009) propose that monsoon rainfall varied at half-precessional (~11.5 ka BP) intervals in phases with orbital controlled insolation forcing. The Lake Chala record implies moist conditions in equatorial East Africa during the periods >25 - 20.5 ka BP (excl Heinrich event 2), 14.5 - 8.5 ka BP (excl Younger Dryas) and since 4.5 ka BP. The LGM drought was immediately followed by a wet phase.

Studies on Lake Albert, the northernmost lake in Great Rift Valley at the border between Uganda and the Democratic Republic of Congo, suggest lake level low stands due to dry conditions during the LGM, from 20 - 18 ka and at 12.5 ka BP (Beuning et al., 1997).

Based on ice core data, Thompson et al (2002) distinguish two climate phases at Mt Kilimanjaro: warmer and wetter conditions than today from 11 to 4 ka BP ago and relatively dry and cool conditions over the past 4 ka BP. These results agree with several continental and marine records, showing that the monsoon circulation and related rainfall over the northern tropics and equatorial East Africa were considered stronger during the early to mid-Holocene (Gasse, 2000).

δ^{18}O isotope records from Mt Kenya (Barker et al., 2001) and Mt Kilimanjaro (Thompson et al., 2002) show similarities with a strong isotope depletion at 6.5 - 5.2 ka BP. However, the authors interpret their results differently. Thompson et al. (2002) suggest a substantial cooling for this time period, whereas Barker et al. (2001) argue that they reflect exceptional heavy snowfall events.

Like Mt Kilimanjaro itself, the Eastern Arc Mountains stand out due to their high biodiversity in animals as well as plants. More than 800 vascular plants, 10 % of which are trees, are known to be endemic to that area (Burgess et al., 2007). Most of these species belong to forest ecosystems which are restricted to higher elevations today. It is unknown yet whether the high number of endemic species in this area evolved during times of closed forest covers between the Eastern Arc Mountains and adjacent mountain systems or after their separation by savanna ecosystems as we find it today (Hemp et al., 2009; Voje et al., 2009; Hemp et al., 2010).

The Eastern Arc Mountains have been proposed to be one of the several moist refugia in Africa during the last glaciation. Pollen records show shifts from cooler and moister climate conditions prior to the LGM to generally dry and cool conditions during the last part of the glacial period ~20 ka BP (Mumbi et al., 2008). Similar conditions have been recorded from a number of studies in East Africa (Coetzee and Rogers, 1982 (South Africa); Van Zindereren Bakker and Coetzee, 1988; Marchant *et al.*, 1997 (Uganda)). However, shifts of C3 and C4 plants reveal contradictive results for equatorial East Africa (Street-Perrott et al., 1997 (Mt Kenya and Mt Elgon); Ficken et al., 2002 (Mt Kenya); Mumbi et al., 2008 (EAM, Tanzania)). Some studies from the eastern highlands of central Africa recorded the persistence of arboreal taxa such as *Ilex, Myrica, Olea, Podocarpus* and *Syzygium* throughout the LGM (Bonnefille and Riollet, 1988 (Burundi); Bonnefille et al., 1990 (African tropics); Jolly et al., 1997 (Burundi, Rwanda, W Uganda)). Moist forests were generally present during the LGM along the East African Mountains according to Anhuf et al. (2006).

In this paper we present the first palynological results of East African vegetation and climate history spanning back to the last Glacial. In our research we assessed vegetation, climate and fire dynamics of Mt Kilimanjaro based on pollen and charcoal data. We set out to provide more detail on past environmental change in tropical East Africa, give new insights into biodiversity and vegetation patterns and derive information on potentially responsible climatic factors.

Regional setting and study area

Mt Kilimanjaro is a relict of an ancient volcano which was formed as part of the East African spreading zone. It is located 300 km south of the equator in Tanzania, near the border with Kenya and about 300 km west of the Indian Ocean (Fig. 1a). It rises from savanna plains at 700 m up to its glaciated summit at 5895 m asl.

The Mt Kilimanjaro area is characterized by a typical tropical day-time climate. Due to its equatorial location, the precipitation pattern follows the position of the intertropical convergence zone (ITCZ) and is strongly influenced by the activity of the Indian monsoon system. According to Köppen and

Troll/Pfaffen (in Müller, 1989), Mt Kilimanjaro can be assigned to a seasonal dry tropical climate with two pronounced wet seasons: a short one in November/December and a longer one from March to May. Annual precipitation is modified by elevation and exposure to prevailing winds blowing inland from the Indian Ocean and varies on the wet southern slope from 500 mm at the mountain foothills to about 3000 mm at 2200 m asl. Higher up, at altitudes of 2700 m, 3000 m and 4000 m asl, rainfall amounts to roughly 70 %, 50 % and 20 %, respectively of this annual maximum (Hemp, 2001b; Hemp, 2006c). The northern slopes, on the lee side of the mountain, receive much less annual rainfall. The mean annual temperature decreases from 23.4 °C at the foothills in Moshi, 813 m asl (Walter et al., 1975) linearly to -7.1 °C at the summit (Kibo) (Thompson et al., 2002). The lapse rate is about 0.6 °C/100 m which is typical for tropical mountains (Lauer, 1976). Frost can occur from 2700 m upwards (Hemp, 2006a).

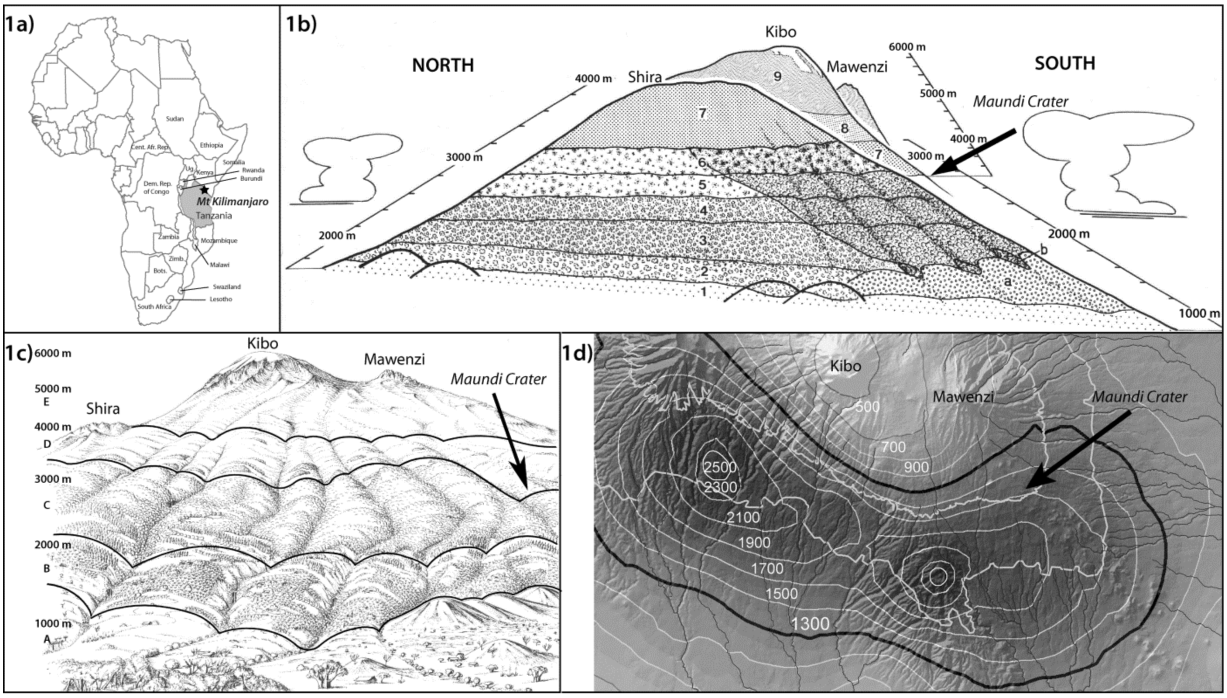

Figure **1a:** Map of Africa and location of Mt Kilimanjaro, Tanzania.
1b: Schematic north-south profile showing the western slope of Mt. Kilimanjaro (Shira, Kibo, Mawenzi) with main altitudinal zones, vegetation types and location of Maundi Crater (arrow). 1: colline (savanna) zone; 2: submontane zone with *Croton-Calodendrum* forest; a: coffee-banana plantations in the submontane zone on the southern slope; b: submontane gorge forests on the southern slope; 3: lower montane zone with *Cassipourea* forests on the northern slope and *Agauria-Syzygium-Ocotea* forests on the southern slope; 4: middle montane zone with *Cassipourea* forests on the northern slope and *Ocotea* forests on the southern slope; 5: upper montane zone with *Juniperus* forests on the northern slope and *Podocarpus-Ocotea* forests on the southern slope; 6: subalpine zone with *Juniperus* forests on the northern slope and *Podocarpus* forests on the southern slope; 7: subalpine zone with heathlands (*Erica* bush); 8: lower alpine zone with *Helichrysum* cushion vegetation; 9: upper alpine and nival zone, mainly bare of vegetation. Changed after Hemp (2006a).
1c: Altitudinal vegetation zones on the southern slope of Mt. Kilimanjaro and location of Maundi Crater (arrow). A: colline savanna zone, B: submontane cultivation zone, C: montane forest zone, D: subalpine zone, E: alpine zone. On the south-eastern slope, where Maundi crater is located, the closed forest line is depressed due to frequent fires.
1d: Rainfall distribution on the south eastern slope of Kilimanjaro. Climatically, Maundi crater is still part of the southern slope receiving about 1500 mm of annual rainfall. Changed after Hemp (2006c).

Covering about 5000 km^2, Mt Kilimanjaro has several different bioclimatic zones (Fig. 1b/1c): A dry and hot colline savanna zone surrounds the mountain base between 700 and 1100 m asl. Most of this area is used for crop production (maize, beans and sunflowers) or as pasture land. Remnants of the former savanna vegetation with *Acacia, Terminalia, Grewia, Combretum* woodlands are encountered mainly around Lake Chala in the eastern foothills and on the north-western side of the mountain. The submontane and lower montane forest belt between 1000 and 1800 m have been converted to coffee-banana fields in the "Chagga home gardens", a special type of agroforestry. Here, the human population reaches a maximum density of more than 500 persons per km^2. Remnants of the former forests of this zone, with *Newtonia, Strombosia and Entandrophragma,* are hardly found outside of deep valleys and gorges. Montane tropical rain and cloud forests cover an area of about 1000 km^2 on Mt Kilimanjaro. The lower parts of the forests on the wetter southern slope are characterized by the dominance of the camphor tree (*Ocotea usambarensis*). However, wide areas of these forests have been logged. Above the camphor belt the forest is dominated by *Podocarpus latifolius, Hagenia abyssinica* and *Erica excelsa*. On the drier northern slope, forests are comprised of *Croton-Calodendrum* at lower elevations, followed by *Cassipourea* at mid-altitudes and *Juniperus* stands at higher altitudes. Above ca. 3100 m asl, the cloud forests are replaced by *Erica* heathlands. *Erica trimera* forest remnants at 4000 m indicate the upper potential natural forest line. Above this altitude, the *Erica* heathlands change into *Helichrysum* dwarf cushion vegetation that extends up to 4500 m asl. The highest altitudinal region is very poor in vegetation and the top of Kibo, the main summit, is covered with glaciers. For a more detailed description of these vegetation types see Hemp (2001b; 2006a; 2006c).

The Maundi Crater (3°10'27.5''S, 37°31'05.8''E) is located on the south-eastern slope of Mt Kilimanjaro at 2780 m asl, receiving about 1500 mm of annual rainfall with a mean annual temperature of 9 °C (Fig. 1b/1c/1d). Due to the prevailing SE monsoon, the Maundi crater is dominated by the climate conditions of the southern slope of Kilimanjaro (Hemp 2006a) (Fig. 1d). Likewise, the vegetation composition typical for the wetter southern slope also occurs around the crater (Fig. 1b/1c). The centre of the crater forms a small swamp which is dry during most of the year. However, during the rainy seasons the centre of the swamp can be filled with shallow water temporarily. The crater has a diameter of about 60 m and is 20-30 m deep. The bedrock material consists of porphyric rocks (Downie et al., 1956). On the north-western side of the crater rim a low-stature *Erica* forest with trees such as *Erica excelsa, Myrsine melanophloeos* and *Schefflera volkensii* grows. In the shrub layer young *Podocarpus, Ilex* and *Xymalos* trees indicate the regeneration of a *Podocarpus* forest after fire. The herb layer is dominated by ferns (*Asplenium* ssp., *Dryopteris* ssp.), *Lycopodium clavatum, Alchemilla volkensii,* and *Rubus steudneri*. The swamp on the bottom of the crater consists mainly of *Carex conferta*, whereas *Festuca obturbans* and *Helichrysum* ssp. dominate the vegetation of the inner slopes. At an elevation of 2780 m asl the Maundi Crater is located in an area where the closed forest grades into open *Erica* bush, i.e. in the interface between the upper montane forest and the subalpine heath land. The term “subalpine” is applied to the transition zone between the broad leaf montane forest and the alpine *Helichrysum* scrub vegetation (the tree line-ecotone sensu Körner, 2003b). It corresponds closely to the “ericaceous belt” of Hedberg (1951) (for the definition of the different altitudinal zones on Kilimanjaro compare Hemp, 2006a). Due to frequent fires on the south-eastern slope the actual upper forest line is strongly depressed, whereas the potential tree line on Kilimanjaro lays at 4000 m (Hemp, 2005).

Material and methods

Material collection, pollen, charcoal and sediment analysis

In total 74 sediment samples were taken from a soil pit in the centre of the dry crater. Samples from 0 - 240 cm were hand collected and the samples from 240 – 646 cm were obtained by downward coring in the same spot first using an Eijkelkamp piston corer (50 cm length, 4 cm diameter) and for the lower more compacted part of the profile an Edelman corer. Samples were collected at about every 10 cm, transferred and transported in plastic tubes, and kept under cool conditions. For pollen and charcoal analysis a sample volume of 0.5 cm^3 was prepared in the lab applying the standard method (Faegri and Iversen, 1989). The extracted pollen samples were mounted in glycerine jelly for pollen identification and counting. At least 300 pollen grains were counted for each sample. For pollen analysis, the determination was carried out using light microscopy with 400x and 1000x magnification. The references consulted included our own reference pollen collection of Tanzania of about 1500 taxa, the online African Pollen Database (Lézine, 2001), and African Tropical Pollen book (Assemien et al., 1974). The charcoal particles were counted on the pollen slides. Charcoal selection was restricted to fragments that are black, completely opaque and angular (Swain, 1973). Each charcoal particle > 10µm was counted using the grid count method (Patterson et al., 1987).

Data Analysis

In total 19 samples had to be omitted (40, 45, 55, 70, 77, 112, 120, 398, 400, 408, 423, 438, 448, 458, 468, 478, 488, 498, 508, 518 cm) from the data analysis since pollen grains were absent in these samples. The data gaps are grey-shaded in the pollen diagram. In total 11 samples (Tab. 1) were AMS dated in the 14C laboratory of Poznan/Poland and at the Physical Institute of the University Erlangen-Nürnberg/Germany, then calibrated with the online version of CalPal (Danzeglocke et al., 2009). We used a linear age-depth model to infer the time scale for the pollen diagram and the chronostratigraphy (Fig. 2, Tab. 1). According to Fig. 2 a sampling distance of 10 cm provides a time resolution of ca. 1 ka. The lower part of the core dates prior 40 ka and age estimates there are derived by linear extrapolation.

Pollen Diagram

The pollen diagram was compiled and analysed with the program Psimpoll (Bennett, 1998). The percentage diagram is based on the pollen sum which includes all pollen taxa and excludes fungi and fern spores. For the calculation of the 7 pollen zones the CONISS (Constrained cluster analysis by sum-of-squares) method was used. Samples without pollen were excluded from the CONISS to avoid biases. Pollen and spore diversity refers to the total number of morphologically distinct pollen and spore types identified. The classification of pollen taxa into vegetation zones (savanna, submontane forest, montane forest, ericaceous vegetation and alpine vegetation) was based on studies of Hemp (2006a). Based on the growth form of plant taxa, we further assigned the pollen taxa to groups of herbs, trees, shrubs and lianas (see Tab. 2 in electronic supplements for more detailed information).

Multivariate Data Analysis

The multivariate data analyses were accomplished with the programs CANOCO and CanoDraw for Windows (ter Braak and Šmilauer, 1997; Leps and Šmilauer, 2003). After a detrended correspondence analysis (DCA) had revealed a gradient length of 1.714 (1st PCA axis), we applied a principle component analysis (PCA) as recommended by Leps and Smilauer (2003) for data sets with short environmental gradients. The species data was standardized and log transformed. The ordination diagram was centred by species and the scaling is focused on inter-sample distance. In order to compare the results of the pollen diagram with the multivariate data analysis, we performed a PCA with the full data set including all species and sample. For the detailed analysis of samples dated to the Glacial after the data gap between 423 and 518 cm, we performed a partial PCA ordinating all species but only samples belonging to this time period (see supplements).

Results

Lithostratigraphy

Fig. 3 informs about the lithostratigraphy of the record based on proxies like colour, TOC, and grain size data. Sand (63-2000 µm) and silt (2-63 µm) contents often fluctuate abruptly with sand contents varying between 10 to more than 90 %. The clay fraction remains generally low (<10-20 %). Silt contents are highest in the upper 20 cm (ca. 70 %), and relatively high between 65-125 cm and in the lower half of the record.

The upper 122 cm of the profile are mainly black to brownish black and generally very rich in organic matter.

Stratification is caused by yellowish layers of smeary silty consistence between 15-21 cm and 40-45 cm depth (tephra?), and by a greyish, silty sandy laminated mottled gleyic horizon between 55-70 cm, deposited above a boggy silty sandy layer between 70 and 122 cm.

Table 1: Radiocarbon dates for the Maundi record. OM = organic matter.

Labcode	Depth (cm)	Material	^{14}C Age ka	±	Age ka BP	±
Poz-29391	20	Bulk OM	2.2	35	2.2	96
Erl-11563	35	Alkali insoluble	5.3	45	6.1	86
Erl-11564	50	Alkali insoluble	6.5	52	7.4	47
Erl-11565	75	Alkali insoluble	8.0	54	8.9	100
Erl-11566	90	Alkali insoluble	9.4	58	10.6	65
Erl-11567	117	Alkali insoluble	11.9	64	13.8	144
Poz-24901	160	Bulk OM	15.6	80	18.9	224
Por-29390	190	Bulk OM	18.0	90	21.7	365
Poz-24902	240	Bulk OM	28.3	200	32.7	335
Poz-24970	295	Bulk OM	38.4	1400	42.9	1040
Poz-29391	315	Bulk OM	36.8	600	41.8	418

Both, the gleyic and the boggy layer document humid conditions. Sand maxima up to more than 90 % characterise the sediments in 25-60 cm depth above the gleyic horizon. Those from 135 - 155 cm consist of sandy gravels. Between 155 and 383 cm mainly brownish colours dominate with strongly varying sand and silt contents. Between 383 to 410 cm depth yellowish, smeary silty and TOC-poor sediments (tephra?) occur. In the lower third of our record black and brown colours vary. The TOC-rich layer between 440 to 500 cm depth correlates with increased silt contents, whereas the TOC-maximum in about 590 cm correlates with high sand contents. In summary, grain size data and soil colour indicate that the southeast exposed slopes of Mt. Kilimanjaro in 2780 m asl experienced at least partly abrupt ecological changes. A significant correlation between TOC and texture fractions could not be detected.

Chronology

The age-depth model (Fig. 2) based on 11 AMS dates (Tab. 1) reveals a close to linear relationship ($R^2 = 0.9815$) between core depth and calibrated age BP until about 42 ka BP (~300 cm). Samples from >300 cm are out of the radiocarbon dating range. Though, a linear extrapolation beyond 42 ka BP suggests an age dated to the early last Glacial at the bottom of the core (646 cm). This assumption will be further discussed lateron.

Pollen diagram

The percentage pollen diagram (Fig. 4) depicts pollen taxa assigned to the different vegetation zones (cp. Table 2). The percentages are based on a total pollen count of about 300 grains.

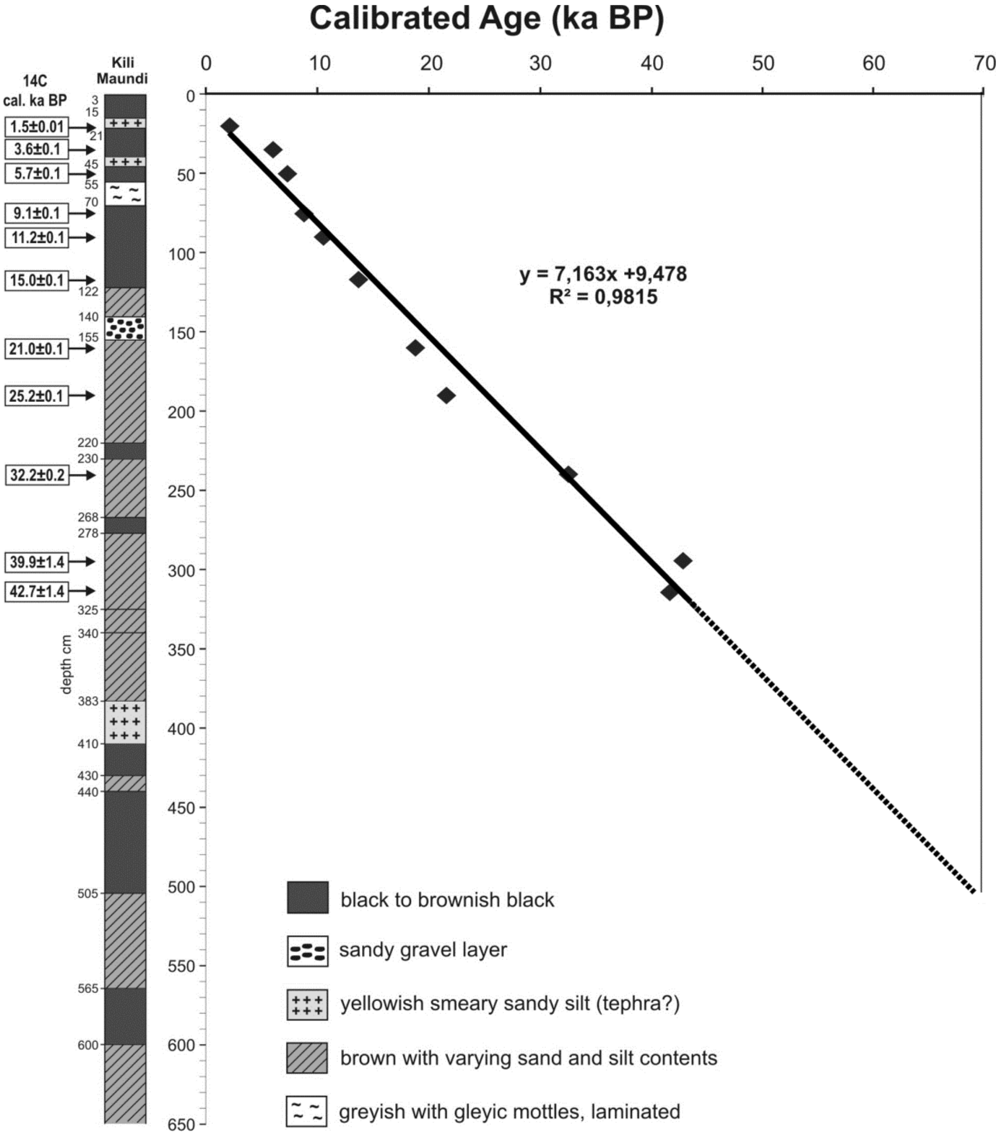

Figure 2: Stratigraphy of the Maundi record and calibrated age model based on the radiocarbon dates from Table 1. Age estimates >42.7 ka BP are derived by linear extrapolation.

The pollen preservation remained stable throughout the recorded time period. The most recorded pollen types are from the montane, the ericaceous and the alpine zone. Signals from savanna and submontane forest taxa were generally rare. Their high signals in the pollen profile make an origin from a remote source unlikely. A pollen rain transect study in-progress confirms that the signal of Poaceae and Asteraceae is local and does not originate from savanna vegetation. Therefore we assigned Poaceae and Asteraceae to the alpine zone, indicating open, species-poor vegetation dominated only by *Helichrysum*, *Festuca* and other grass species. The grey shaded zones in the diagram represent samples in which no pollen grains could be found.

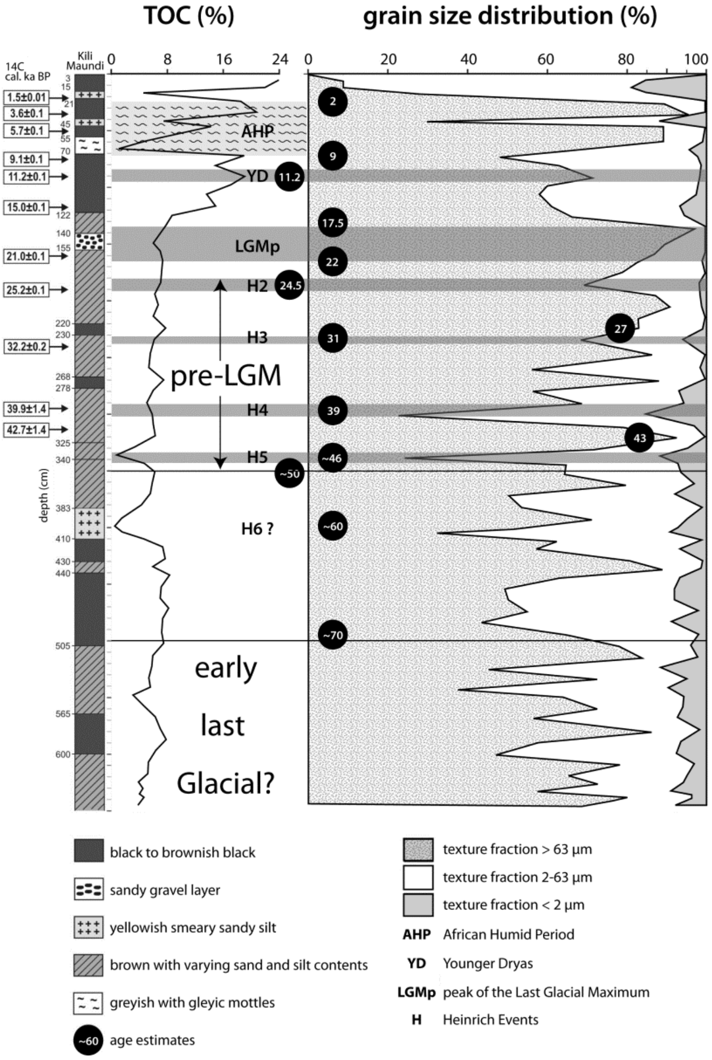

Figure 3: Depth profiles of total organic carbon (TOC) and texture fractions. Age estimates >42.7 ka BP are derived by linear extrapolation (s. Fig. 2)

Concise description of the pollen zones

Pollen Zone M-1a (ca. 90 – 75 ka BP): Pollen grains of Poaceae (70 %) and Asteraceae (5-15 %) clearly dominate. Few records of taxa assigned to the ericaceous zone (*Artemisia, Erica*) and the montane forest (*Myrica, Podocarpus*) are also present. *Ranunculus* is well represented, comprising up to 10 % of the pollen percentage. The percentage of herbal pollen taxa clearly predominates over shrubs and trees. Charcoal concentration is low in the deposits. The number of pollen and spore types range between 7 and 17.

Pollen Zone M-1b (ca. 75 – 60 ka BP): In most of the samples pollen grains were absent. The only pollen-containing sample shows high percentages of Poaceae and Asteraceae, though lower than in the previous zone. The herbal taxa predominate over shrubs, lianas and trees. Montane forest taxa, *Podocarpus* and *Myrica*, are present as well as *Leonotis* of the submontane forest and fern spores. The percentage of tree taxa increases.

Pollen Zone M-2a (ca. 60 – 42 ka BP): This zone is depicted by a lower percentage of Poaceae pollen and an invariant signal of Asteraceae in comparison with zone M-1a. The data shows a distinct increase of *Erica* accompanied by a first appearance of *Myrsine* and *Geranium* pollen. Percentages of *Myrica* and *Podocarpus* as taxa of the montane forest increase. Several taxa of the montane (*Hagenia, Moraceae, Olea, Piperaceae*) and submontane (*Vitex*) forest as well as of savanna (Combretaceae, *Euphorbia*) are recorded for the first time. The percentage of herb pollen declines, instead especially shrubs but also tree taxa increase. A very distinct increase in charcoal particles can be observed which persists throughout the pollen zone but fluctuates strongly.

Pollen Zone M-2b (ca. 42 – 25 ka BP): The composition of taxa remains stable. Poaceae (on average 50 %) decline slightly compared to zone M-2a, while Asteraceae pollen shows a small increase. *Erica* and *Artemisia* (ericaceous zone) as well as *Podocarpus* and *Myrica* (montane forest) are persistently well represented. Most other taxa that were not present so far occur for the first time during this zone; however they remain constantly at values lower than 5 % of the pollen sum. In samples of the upper part of this zone fern and fungi spores become more abundant. The percentage of shrub taxa temporarily reaches up to 20 %. Also, liana pollen increases whereas values of herb and tree taxa decline slightly. A steady increase in the number of pollen and spore types can be observed. The charcoal concentration is very low throughout this zone.

Pollen Zone M-2c (ca. 25 – 17 ka BP): Poaceae pollen increases on average to about 65 %; Asteraceae account for about 10 % of the pollen sum. *Alchemilla* and *Artemisia* are represented with up to 5 %. Taxa of the montane (*Podocarpus*) and the submontane (*Fabaceae*) forest decrease or become temporarily absent from the record. Spores show a sharp decline. Herbal taxa predominate again over shrub and tree taxa, and the liana signal is very much reduced. However, proportionally the herbal taxa do not reach as high values as in zone M-1a. Charcoal concentration remains low.

Pollen Zone M-3a (ca. 17 – 5.5 ka BP): This zone comprises three series of pollen-free samples which intersperse the remaining pollen record. The lower part of the pollen zone shows a significant decrease in Poaceae and Asteraceae compared to the preceding pollen zone in favour of an increase in taxa of the ericaceous zone (*Artemisia, Erica, Geranium*, Proteaceae) and the montane forest (*Podocarpus, Myrica*, Piperaceae). The percentage of fern and fungi spores also rises considerably.

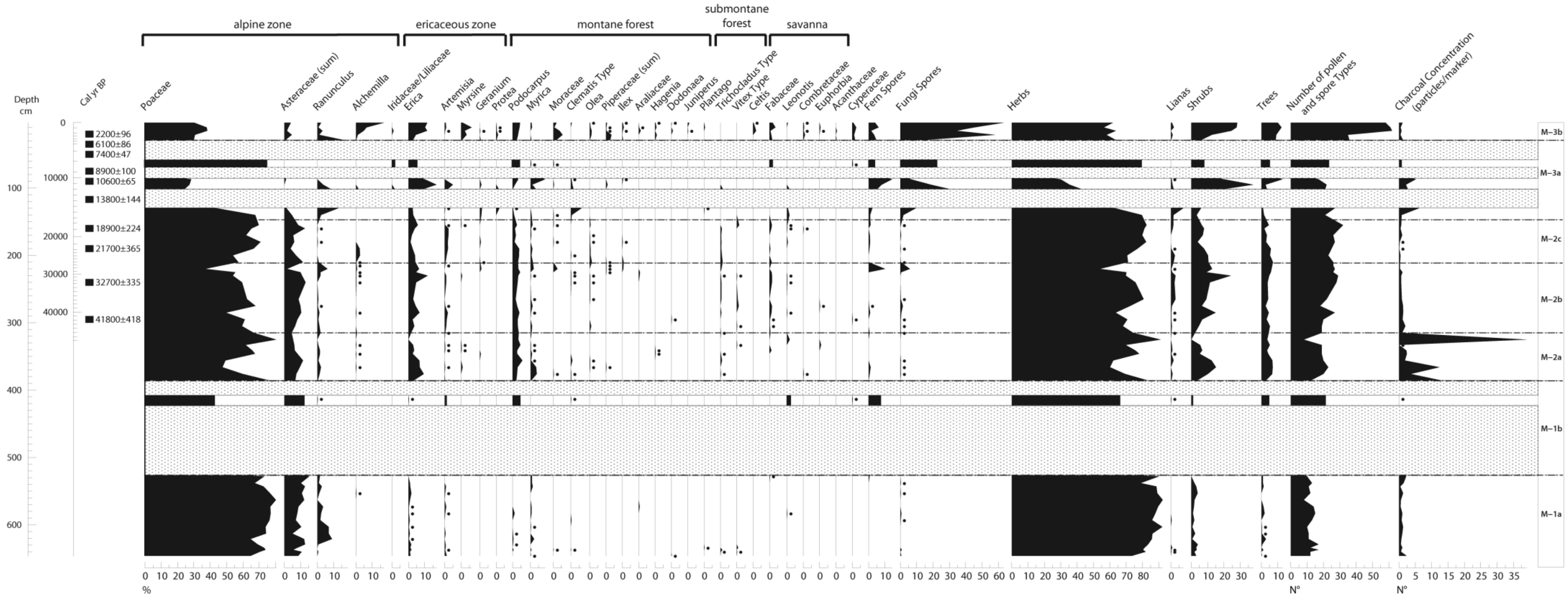

Figure 4: Percentage pollen diagram of selected taxa, charcoal concentration and number of all identified pollen and spore taxa. The taxa % between the data gaps are represented as bars to avoid that data progression reaches 0 % where percentage data is absent. % is based on a total pollen count of at least 300 grains per sample. Low % values are represented by a dot.

The central part of the pollen zone is characterized by a maximum in Poaceae pollen and fungal spores. The charcoal concentration is slightly increased in the older part of this zone but low again in the upper part. The number of pollen and spore types declines.

Pollen Zone M-3b (ca. 5.5 – 0 ka BP): The percentage values of Asteraceae and Poaceae are reduced (5 % and ~35 %, respectively). Cyperaceae pollen occurs for the first time. Pollen grains of taxa of the montane forest (Moraceae, *Olea*, Piperaceae, *Podocarpus*) and the ericaceous zone (*Erica,* Proteaceae) become generally more abundant. *Myrsine* increases markedly.

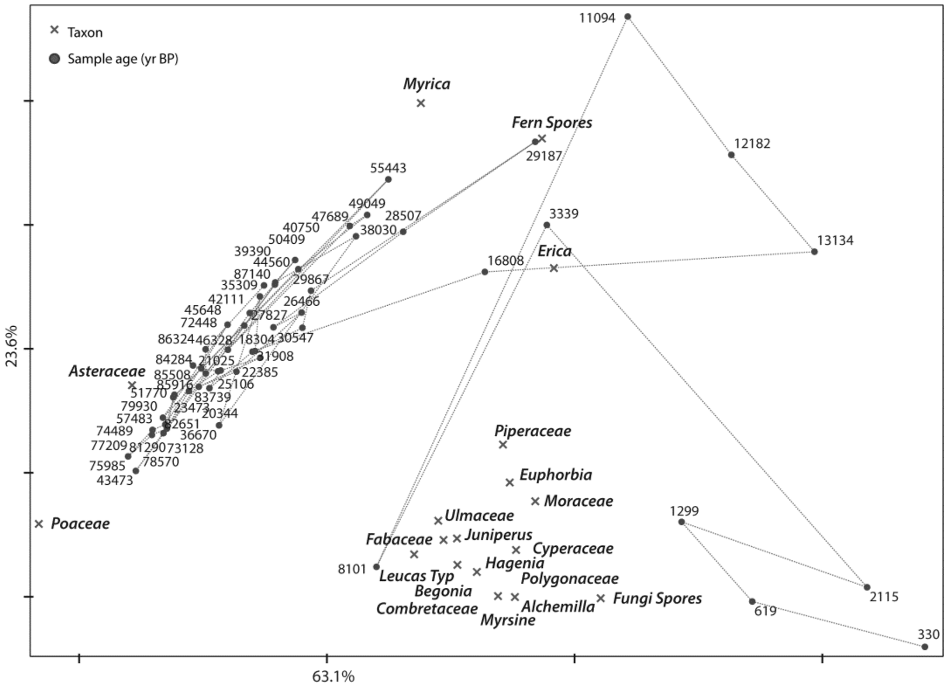

Figure 5a: Principle Component Analysis (PCA) of all Maundi samples labelled with age (yr BP). 50 % of the taxa that contribute most to the ordination pattern are plotted. Samples are connected in series to clarify the dynamic. The % values on the axes indicate the explained variation.

The same applies for *Ranunculus* and *Alchemilla*, representatives mainly of the alpine zone. The amount of pollen and spore types reaches a maximum. Charcoal concentration declines. Fungi spores peak in abundance and also fern spores are frequent.

Multivariate Data Analysis

The ordination diagram of the PCA (Fig.5a) shows a clear division of samples on the right and on the left quadrants. Poaceae and Asteraceae are strongly negatively correlated with all other taxa. *Erica* and *Myrica* are positioned in the upper right quadrant; their occurrence is strongly correlated with fern spores and samples from the early Holocene. Samples from the late Holocene are correlated with forest taxa such as Moraceae, Piperaceae and *Hagenia* but also with Cyperaceae and fungi spores. The relative distance between samples stands for the differences in pollen taxa composition. Therefore, samples that are positioned close to each other have a similar pollen taxa composition. The position of the plotted taxa indicates the correlation with the samples. If the distance is short the correlation between taxon and sample is high.

(The partial ordination diagrams of the sub data sets from the early last Glacial, pre-LGM and LGM, and Deglacial and Holocene are provided in the supplements Fig. 5b, 5c, 5d).

Interpretation and Discussion

As a result of favourable topographic and climate conditions Maundi crater is a site where sediments have accumulated over a long period of time. Due to the defined crater catchment area the majority of the pollen and spores are most likely to have originated from vegetation growing on the adjacent hill-sides. In East African montane areas the natural vegetation shows a distinct altitudinal zonation (Hemp, 2006a). Therefore, the pollen assemblage in Maundi crater will not originate from plants from a broad spectrum of altitudes. As a result, past changes in climate will have had a notable effect on the altitudinal occurrence of taxa and these changes are likely to be represented in the pollen record. Hence, at any period of time, the natural vegetation around Maundi crater should be a reasonably sensitive indicator of climatic conditions on Mt Kilimanjaro.

Approaches of multivariate data analysis, the conventional pollen diagram and the lithostratigraphy reveal partly marked changes of the environmental conditions and the vegetation at Mt Kilimanjaro since the early last Glacial.

Lithostratigraphy

The interpretation of the lithostratigraphy (cp. section 4.1 and Fig. 3) rests upon the assumption that high sand contents at the bottom of the crater primarily indicate accelerated erosion along the crater slopes due to high rainfall intensities, likely related to the strengthening of the SE Monsoon, or due to cryogenic processes during cold spells. Increased silt contents most likely document a dominance of increased wind-blown input during more dry and/or cool conditions e.g. due to intensified northerly trade winds. We are aware that fire events might also influence these processes, but their effect should be more short-termed.

As up to now no reliable chronology is available for the lower half of the record (>315cm), our interpretation of this segment remains speculative. The sediments between 650 to about 500 cm were probably deposited during the early last Glacial (here older than 70 ka BP). They are relatively rich in silt, indicating dry conditions in agreement with the palynological findings.

The sediment deposits in about 500 to 350 cm core depth contain even more silt and were most likely deposited between the end of the early last Glacial and about 50 ka BP. The lower part of this section (500-440 cm) is characterised by dark colour, a long lasting high silt accumulation and by the absence of preserved pollen indicating pronounced aridity and probably cooler conditions supporting the conservation of humus. This interpretation is in agreement with a strong enrichment of δD values of long-chain alkanes indicating dominating grassland vegetation in this part of the core, interpreted by Zech et al. (2009) as evidence of a late Pleistocene mega drought (see also Scholz et al., 2007).

In the sediments between 350 to 185 cm, deposited during the pre-LGM (here ca. 50 to 25 ka BP), the intensity of the silt maxima more or less continuously decreases upward, fluctuating with abrupt sand maxima, likely indicating moderate humidity in comparison with the core section between 500 to 350 cm. The pronounced sand maxima in ~320 and ~205 cm depth might indicate for even more humid intervals around 43 and 27 ka BP. The silt maxima, interpreted as indicators for more arid and cooler conditions, partly correlate with enriched δD values (Zech et al., 2009) and with the chronology of the Heinrich Events 2-5 (Fig. 3) which are also documented in other archives of equatorial Africa (Hessler et al., 2010).

Following our depth-age model (Fig. 2) the sand maxima in 165 to 135 cm were deposited between 22-17.5 ka BP, documenting the peak LGM and apparently correlating with increased runoff phenomena described by Verschuren et al. (2009) from Lake Chala between 22-18 ka BP. Since it is well documented that this period was cold and dry in most parts of East Africa (eg. Felton et al., 2007) most likely cryogenic processes in combination with a scarce vegetation cover promoted sand erosion along the crater slopes.

Increased silt accumulation between 125-70 cm gives evidence of moderately arid conditions and an accelerated aeolian input between ca. 17-9 ka BP (Fig. 3), comprising deglaciation, the Late Glacial and parts of the early Holocene. The TOC-richness of these silty, boggy sediments does not contradict the conception of generally moderate aridity because this period was still substantially cool causing an increase in effective soil moisture through decreased evaporation. In addition, the litter of *Erica*, expanding during this time, is rich in tannins, promoting the accumulation of soil organic matter. The high sand content in about 90 cm depth correlates with a positive shift of alkane δD values (Zech et al., 2009), thus providing evidence of the Younger Dryas event. This interpretation is opposite to what has recently been inferred from Lake Chala at the foothills of Mt Kilimanjaro, where Verschuren et al. (2009) provided evidence for increased runoff between 14-9 ka BP.

The high sand contents between 65-25 cm depth likely indicate accelerated erosion between about 9-2 ka BP (Fig. 3) in agreement with the lowest δD values (=pronounced humidity) in the study of (Zech et al., 2009), and with the well documented regional evidence of an “African Humid Period”.

The laminated lake sediments in 70-55 cm indicate that increased precipitation has stimulated erosion intensity at least at the beginning of this humid phase, but we cannot exclude that human disturbances also contributed, probably towards the end of this phase.

The uppermost 20 cm of the record have the highest silt contents. According to our above mentioned assumptions and the significant enrichment of δD values of long-chain alkanes (Zech et al., 2009) we assume that these silty sediments document a shift to more arid conditions during the last 1.5 ka.

Pollen Record

Early last Glacial (Zone M-1a and M-1b)

During the early last Glacial abundant Poaceae and Asteraceae as well as low taxa diversity, representing abundant species-poor open *Helichrysum* cushion vegetation of the alpine zone, indicate very dry and relatively cool conditions. Alpine *Helichrysum* vegetation occurred at this time probably more than 1100 m lower than today (Hemp and Beck, 2001; Zech, 2006; Anhuf et al., 2006). Inferring from actual climate data (Hemp, unpb. data) this would mean a decrease in mean annual temperature and precipitation of at least 5-6 °C and 1100 mm, respectively. Such a change in temperature and precipitation would have caused a substantial elevational downward shift of vegetation zones at Mt Kilimanjaro. This is also supported by the absence of ferns and fungi at Maundi crater which depend on humid conditions. The low abundances of *Erica* and *Artemisia* as the only present taxa of the ericaceous zone indicate the strongly reduced or much lower distribution of the ericaceous zone. The same applies for *Podocarpus* and *Myrica* of the montane forest. The low occurrence of ericaceous vegetation in comparison to the alpine zone and limited charcoal deposition during the early last Glacial indicate insufficient plant-fuel to maintain extensive fires, and hence cool and very dry conditions. The absence of pollen grains in the samples from 508 to 418 cm might consequently be interpreted as severe drought events causing the crater to dry out completely and hence hamper pollen preservation. Results of lipid and δD analyses in the sediment samples of Maundi crater by Zech et al. (2009) also propose very dry conditions during this time. Lake level records from Lake Malawi propose periods of extreme aridity between 135 – to 75 ka BP (Scholz et al., 2007) supported by pollen and diatom records from Lake Malawi (Cohen et al., 2007). Also Olago et al. (1999) report cool and dry conditions from Mt Kenya during the early last Glacial (Fig.6). The fossil diatoms suggest saline waters associated with lower water depth. The pollen record shows a predominance of grass. Arboreal and herbaceous components are divers but sparsely represented (Cohen et al., 2007). Our results would be in agreement with Cohen et al. (2007) as well as with Scholz et al. (2007) who interpret this period of aridity to be far more extreme than any period recorded in equatorial Africa during the LGM. Gasse (1977) proposed this also for Lake Abhé, Ethiopia between 70 to 60 ka BP.

The differentiation of pollen taxa into groups of herbs, trees, shrubs and lianas allows a more detailed interpretation of the vegetation dynamics. Herbal taxa are mainly representatives of the open grassland vegetation whereas trees and lianas are forest elements. The forest-grassland transition is predominantly composed by shrubs (esp. *Erica* spp). Hence, the high occurrence of herbs and low abundance of ligneous taxa at Maundi crater supports the assumption of dry and cool conditions and suggests abundant alpine vegetation around the crater due to the downward shift of vegetation zones.

The concurrence of our data set with others obtained from tropical Africa suggesting the end of this arid episode around 70 – 60 ka BP (Gasse, 1977; Cohen et al., 2007; Scholz et al., 2007) evidences that the beginning of the pre-LGM (M-2a) could be dated to around 60 ka BP. This is in agreement with the results of our age-depth model (Fig. 2) suggesting an age of 55 – 60 ka BP for 400 cm core depth, the upper limit of the pollen depleted zone.

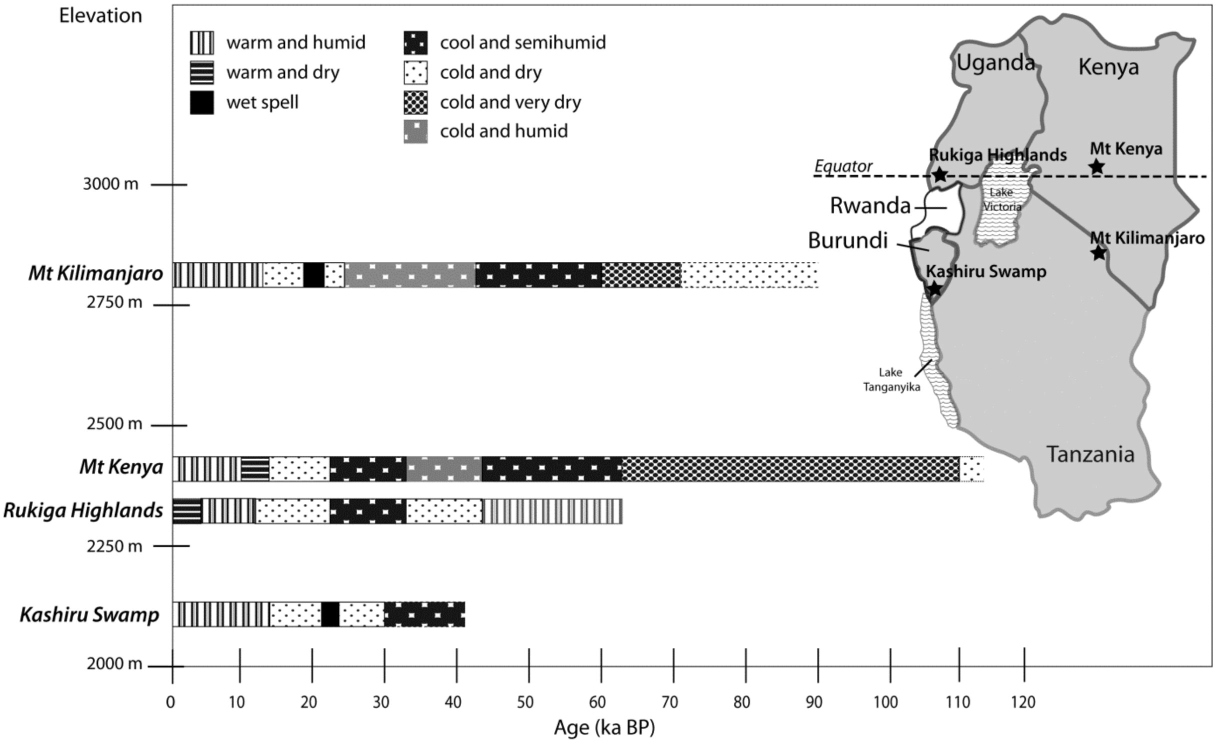

Figure 6: Comparison of the climate dynamic inferred from the Maundi record, with the climate reconstructions from records of Mt Kenya (Olago, 1999), Rukiga Highlands, Uganda (Taylor, 1990) and Kashiru Swamp, Burundi (Bonnefille and Riollet, 1988).

Pre-LGM (Zone M-2a and M-2b)

The period of the pre-LGM (~60 to 25 ka) until the LGM period (25 to 15 ka) appears rather stable. Taxa diversity increases steadily, however taxa composition of the different vegetation zones, although fluctuating, remains stable. The savanna and submontane forest taxa are more abundantly recorded in our archive which might indicate increased wind system activity as part of the warming, expansion of submontane forest, as well as a colonization of the savanna by herbs and shrubs due to more favourable climatic conditions.

During the pre-LGM earlier than 42 ka, the open grassland taxa are comparatively less abundant in favour for a slight increase in taxa belonging to the ericaceous and montane forest zone. In combination with the slightly higher occurrence of fern spores and an increasing diversity, we suggest more humid and warmer conditions for this period. Such a palaeo-environment would have allowed the spread of ericaceous taxa as well as some montane tree species, such as *Podocarpus* and *Myrica.* These taxa are rather frost and drought tolerant compared to other tropical montane forest species and hence could have withstood occasional extreme climate events. Taylor (1990) suggests similar climatic conditions as today for the >42 ka BP period. The abundance of montane forest taxa (especially *Myrica, Podocarpus, Clematis*) and taxa of the ericaceous belt (*Erica* in particular) indicates an upward shift of vegetation zones, but we do not interpret our results such as that the vegetation zones exceeded their present elevation. Pollen, diatom and lake level records from Lake Malawi (Cohen et al., 2007), Lake Bosumtwi (West Africa), Mt Kenya (Olago et al., 1999) and Lake Tanganyika (Tanzania) (Scholz et al., 2007) also suggest diminishing aridity after 70 – 60 ka BP. Other records from East Africa report an ericaceous belt position about 1050 m lower than today between 42 – 30 ka BP (Mt Kenya, (Olago et al., 1999; 2001), Lake Albert, Ethiopia (Lézine, 1982) and Kashiru Swamp, Burundi (Bonnefille and Riollet, 1988). For the Rukiga Highlands of Uganda Taylor (1990) suggests climate conditions similar to today (Fig.6).

Between ~ 60 - 42 ka BP we observe an increased fire activity in the Maundi record. Today fires play an important ecological role in the upper areas of Mt Kilimanjaro. Fire in upper montane *Podocarpus* forests changes species composition and structure favouring *Erica excelsa* because this tree is able to re-sprout from stumps after fire. The presence of *Erica* enhances the fire risk, since even fresh *Erica* wood burns well, which in turn prevents the *Podocarpus* forest from re-establishing. This leads to monodominant *Erica excelsa* forests. During long periods of dry climate with recurrent fires, the *Erica* forest boundary moves downslope and advances upslope during wet periods. At high fire frequency, the closed *Erica excelsa* forest degrades into open bush land of ca. 1.5 m height, dominated by *E. trimera* and *E. arborea* between 2800 and 4000 m asl (the potential tree line). Continuously high frequency of fires destroys this bush, resulting in grassland or *Helichrysum* cushion vegetation, which is the climatic climax vegetation at altitudes above 4000 m (Hemp and Beck, 2001; Hemp, 2005). In this subalpine transition zone below 4000 m (cp. Section 2.) floristic elements of the alpine and montane zone are mixed. Before 42 ka BP the charcoal record does obviously follow the same pattern. Whitlock et al. (2010) recently conceptualized the characteristics of fire activity in different biomes and discuss climate versus plant fuel limitation. Following this concept our results suggest that fire activity (frequency, size, intensity) was increased before 41 ka BP, leading to plant fuel limitation, and hence preventing *Erica* vegetation to develop and spread. This explains that peaks of charcoal in the Maundi record correspond to high percentages of *Erica* pollen, whereas the highest charcoal peaks are congruent with grass pollen. Consequently high percentages of Asteraceae and grasses without high fire activity are indicative of a cold alpine climate. Until 42 ka BP the fires seem to have oscillated between phases of moderate activity allowing and facilitating the spread of *Erica* vegetation and phases of high activity preventing it. The relative increase of shrubs (mainly *Erica*) and trees (mainly *Podocarpus* and *Myrica*) also indicates an upward movement of vegetation zones and the spread of the ericaceous zone over the alpine vegetation approaching Maundi crater. This implies an increase of plant fuel availability and facilitates fire activity as indicated also by the charcoal record. During the mid and late Glacial the low fire activity stabilized the proportion of ericaceous to alpine vegetation.

During the later pre-LGM phase between 33 - 25 ka the occurrence of several montane forest taxa (Araliaceae, Moraceae, Piperaceae, *Ilex*) as well as fungi and ferns suggest humid and comparatively warm climate conditions. The increase in shrubs and trees indicate a shift of vegetation zones to higher elevations. Since alpine *Helichrysum* vegetation and montane *Podocarpus* forest are today separated by at least 800 m in altitude, we assume a respective upward movement of vegetation zones compared to the early last Glacial and LGM but located at lower elevation than today. The ericaceous zone becomes more wide spread and the higher abundance of lianas (taxa of montane forest) indicates that the floristic composition of the forest becomes more divers. This coincides with the general increase in taxa diversity. Forest vegetation approached the Maundi crater as indicted by higher percentages of tree taxa, especially *Podocarpus, Myrica* and *Erica*. In the Eastern Arc Mountains, Mumbi et al. (2008) observe an altitudinal shift of montane forest from 1700 - 1800 m asl (38 ka BP) to 1800 - 1900 m asl (35 – 29 ka BP). The pollen record from Kashiru Swamp (2104 m asl), Burundi Highlands (Bonnefille and Riollet, 1988), shows a similar pattern. Here, a higher abundance of tree taxa, such as *Podocarpus* and *Erica*, as well as ferns indicate more humid conditions than during the LGM. The pollen and δ13C record from Mt Kenya (Olago et al., 1999) also suggests cool and humid conditions during the period preceding the LGM (Fig.6). High lake level stands during this period were reported from Lake Tanganyika (Felton et al., 2007), the Nakuru-Elmenteite Basin (Richardson and Dussinger, 1986), Lake Manyara and Lake Albert (Beuning et al., 1997), and palaeo-lake Suguta (Casanova et al., 1988).

LGM (Zone M-2c)

The dominance of open grassland taxa such as Poaceae and Asteraceae during the LGM (~ 25 – 17 ka BP) suggests dry and cool climatic conditions. The only montane forest taxa that could be recorded previously, during the pre-LGM period, such as *Podocarpus* and *Myrica,* decline. The low abundance of ferns and fungi also indicate locally as well as regionally dry conditions. A dry LGM for equatorial East Africa is also suggested by several other studies (Coetzee, 1967; e.g. Bonnefille and Riollet, 1988; Aucour et al., 1994; Wooller et al., 2000; Olago, 2001; Zech, 2006; Felton et al., 2007; Mumbi et al., 2008) and is assumed to be partly caused by the reduced Asian and African Monsoon activity (Barker et al., 2001). The diminishing forest vegetation and high abundance of herbs evidence the cool and dry conditions during the LGM causing a downward shift of vegetation zones and hence a higher abundance of alpine vegetation around the crater. It seems that the climate conditions are not very detrimental for the bushy ericaceous vegetation since its decline is insignificant. This supports the assumption that the LGM was not such an extremely dry period as the early last glacial when forest and ericaceous vegetation was largely reduced.

Between 24-21 ka BP, the occurrence of *Ilex, Olea, Podocarpus* and other arboreal taxa as well as a decrease in Poaceae and Asteraceae suggest a short wet spell. Within the ericaceous zone, the decrease of herbaceous taxa in favour of ligneous *Erica* might indicate an expansion of *Erica* over the alpine grassland. Bonnefille and Riollet (1988) also observe this short wet phase in their Kashiru swamp record by an increase in arboreal taxa, especially *Podocarpus, Olea* and *Macaranga*. The difference in elevation between the Maundi crater (2780 m asl) and the Kashiru Swamp (2104 m asl) and hence the affiliation to the ericaceous zone or the montane forest zone, respectively, explains the differences in taxa representation. This short wet period was also observed at Lake Chala at the foot of Mt Kilimanjaro (Verschuren et al., 2009; Sinninghe Damsté et al., 2011). In contrast this wet spell was not observed in the Rukiga Highlands of Uganda (Taylor, 1990) and at Mt Kenya (Olago et al., 1999) (Fig.6). Hence, this might be an event only observed on the southern side of the equator and might indicate a shift of the ITCZ and enhanced monsoon activity during this time period. However, due to the rather low resolution of our data set such short events can only be vaguely interpreted.

Deglacial and Holocene (Zone M-3a and M-3b)

The results indicate a shift to more humid conditions directly after the LGM. The frost tolerant ericaceous zone, in particular *Erica* and *Artemisia*, spread while the abundance of montane forest taxa still remains rather low. This is supported by a general decline of herbs and an increase in shrubs and trees. The spread of taxa of the ericaceous zone is accompanied by an increase of charcoal concentration which might again be a result of the easily inflammable fuel provided by *Erica* (cp. the discussion in 5.2.2). The early Holocene seems to have experienced more humid but still cool conditions which enabled the development of the ericaceous zone but prevented the montane forest taxa from ascending.

This coincides with the Antarctic Cold Reversal (ACR) (Blunier et al., 1997), which is recorded as a humid period in Lake Chala (Sinninghe Damsté et al., 2011). A trend to more humid conditions was also observed on the Burundi Highlands (Bonnefille and Riollet, 1988) (Fig. 6). The concurrent minimum summertime insulation suggests orbital precession as a main driver of the East African climate (Garcin et al., 2007; Verschuren et al., 2009).

The pollen diagram as well as the PCA results show an increase in Cyperaceae (likely to be represented by *Carex conferta* and *C. monostachya* which also constitute the bog today), ferns, and fungi during the Deglacial (~17 -12 ka BP) and early Holocene (~11.5 to 8 ka BP), indicating that the area around the Maundi crater experienced a shift into wetter conditions.

A study on the stable isotope composition of n-alkanes by Sinninghe Damasté et al. (2011) revealed a dominance of C4 plants around Lake Chala during the last Glacial period which is replaced by a more mixed C3/C4 plant composition during the Holocene. The beginning of this trend coincides with the start of enhanced monsoonal rainfall.

The data gaps in our record from about 8 to 5.5 ka BP could indicate a dry spell which would be in agreement with the results from Lake Chala (Verschuren et al., 2009). But the results of the lipid analyses of the Maundi core sediments (Zech et al., 2009) do not coincide with this interpretation because they allow the conclusion that the mid Holocene environment has been relatively wet. However, the mid Holocene remains unclear due to the missing data sets.

The late Holocene is characterized by the highest taxa diversity of the whole record. The ericaceous zone is well developed, however the records of the montane forest taxa indicate the ascent of this vegetation zone closer to the study site (at 2780 m asl). Especially Piperaceae, which represent understory and epiphytic taxa, but also *Hagenia*, a poor pollen-producer (but definite arboreal taxon) of the upper montane forest suggest montane forest next to the Maundi crater. Since *Myrica* and *Hagenia* are light demanding taxa their increase indicates the colonization of the ericaceous zone. The increase in fungi and Cyperaceae implies locally wet conditions. In combination with the forest ascent and the further spread and development of the ericaceous and the alpine zone, we can assume humid and increasingly warmer environmental conditions which are probably close to what we find at this elevation today. Similar tendencies for the late Holocene were found e.g. by Vincens (1986; 1989; 1991) in Kenya and from the Tanganyika Basin, at Mt Kenya (Olago et al., 1999) and the Rukiga Highlands, Uganda (Taylor, 1990) (Fig.6).

Implications

The Maundi record is one of the longest terrestrial records from equatorial East Africa, giving an important insight into the vegetation and climate dynamics back to the early last Glacial. From palynological studies on East African Mountains it is well-known that altitudinal shifts of the vegetation zones took place during the past and were mainly controlled by climatic factors like temperature and precipitation (Flenley, 1979; Hamilton, 1982; Lamb et al., 2003). After the return to more humid conditions during the pre-LGM the tree line on Mt Kilimanjaro seems to have been higher than during LGM. This shift was also recorded on other east African mountains in this period (Coetzee, 1967; Vincens, 1986; Bonnefille and Riollet, 1988; Marchant *et al.*, 1997). Despite the documented dry conditions during the LGM, montane forest taxa are strongly reduced but not absent from the Maundi record. A record from the upper montane forest zone at 2600 m asl in the Eastern Arc Mountains also shows that the LGM climatic conditions seem to have been a detrimental factor to some taxa, but did not cause a whole ecosystem shift (Finch et al., 2009). This provides support for the supposed long-term environmental stability of the Eastern Arc and their function as a glacial refugia (e.g. Fjeldså and Lovett, 1997; Mumbi et al., 2008). Mt Kilimanjaro obviously had a similar function as glacial refugium for montane forest species.

The downward shift of vegetation zones during the LGM seems to have caused changes in taxa composition within the vegetation zones but did not lead to elimination neither of vegetation zones, nor of major taxa dominating these zones today. Unlike major parts of western equatorial Africa, where the humid forest area was reduced by 84 % (Anhuf et al., 2006), the mountains of east equatorial Africa seem to have received sufficient precipitation to sustain most of their forest taxa, even throughout the LGM. The stabilizing effect of the moisture carrying Indian monsoon is probably the most important prerequisite enabling the east African mountain systems to have served as glacial refugium for montane forest taxa which makes the area to one of the world’s biodiversity hotspots today. This means that a reduction of precipitation in East Africa as a result of Global Warming will be the most influential factor for ecosystem changes and loss of biodiversity.

Summary and Conclusions

The vegetation and climate history harboured by Maundi record from Mt Kilimanjaro unravels new and interesting aspects of the last glacial palaeo-environment of East Africa. The study site, located at the transition between the montane forest zone and the forest line-ecotone, offers the unique possibility to observe the dynamic of the forest line. In our study we reveal major shifts in the upper vegetation zones of Mt Kilimanjaro during the last glacial period. Alpine vegetation was replaced by subalpine ericaceous vegetation and montane forest, representing a movement of at least 1100 m. Nonetheless, persisting montane forest around the Maundi crater suggests only a comparatively moderate climatic variability during LGM. Therefore Mt Kilimanjaro played a similar role as a glacial refugium for montane forest species as the Eastern Arc Mountains do.

Very dry and cool conditions prevail during the early last Glacial, probably interspersed with extreme drought events. During the pre-LGM period humidity increased, allowing ericaceous and forest vegetation to spread and causing and an upwards shift of vegetation zones. This period appears slightly more humid depicted by less open vegetation and an increase in *Myrica, Erica, Podocarpus* and fungi as well as ferns. The diversification of floristic composition, especially in the forest, is supported. This short wet spell was observed only south of the equator and might indicate a sudden shift of the ITCZ and an enhancement of the south-eastern monsoon. The LGM is characterized by dry and cold climatic conditions which are indicated by the dominance of Poaceae and Asteraceae. The taxa of the montane forest indicating warm and humid conditions decline. The transition from the glacial period to the Holocene is marked by a shift into wetter conditions, but it remains rather cool. This is indicated by the spread of frost tolerant taxa, as well as ferns and fungi. During the Holocene the climate becomes increasingly warm and wet and ericaceous vegetation surrounds the crater, replacing the alpine vegetation. An ascent of montane forest is indicated by montane forest climax species. Today, fire determines the position of the forest-line on Kilimanjaro and maintains it at around 2600m asl on the south eastern slope, just below the Maundi crater. During the last Glacial, especially the development of an ericaceous zone was strongly controlled by fire activity. Spread and decline of this vegetation zone oscillated depending on climate and fuel controlled fire dynamics. Hence, regular fires had a stabilizing effect on the vegetation composition. Despite the increased fire occurrence during the past century, fires were relative rare during the Holocene, giving no indication for increased anthropogenic influence on the study area.

Further high resolution records of Mt Kilimanjaro are needed, in particular for the Holocene. The results will surely allow a more elaborate comparison with other East African palaeo-archives and they will provide more elaborate and applicable knowledge for conservation and management issues.

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Supplementary Material

Table 2: List of identified pollen taxa. The submontane forest includes taxa from riverine forests. The letter in the third column indicates the growth form: H = Herb, T = Tree, S = Shrub, L = Liana.

SAVANNA

ACANTHACEAE	Blepharis	H
ACANTHACEAE	Justicia/Monechma	H
AIZOACEAE	Aizoaceae undiff.	H
ASTERACEAE	Schkuria Type	T
BIGNONIACEAE	Bignoniaceae undiff.	T
BORAGINACEAE	Heliotropium	H
BRASSICACEAE	Farsetia ramosissima Type	H
CAPPARACEAE	Cleome	H
CAPPARACEAE	Gynandropsis Type	H
COMBRETACEAE	Combretaceae undiff.	
COMBRETACEAE	Combretum	S
EUPHORBIACEAE	Euphorbia	H
FABACEAE	Abrus Type	L
FABACEAE	Lonchocarpus Type	H
LAMIACEAE	Hyptis Type	H
LAMIACEAE	Leonotis Type	H
MALVACEAE	Sida Type	
MENISPERMACEAE	Cocculus Type	H
SANTALACEAE	Osyris Type	S
SCROPHULARIACEAE	Striga Type	H

SUBMONTANE FOREST

ASTERACEAE	cf Achyrothalamus	H
ASTERACEAE	cf Blepharispermum	H
EUPHORBIACEAE	cf Margaritaria	T
FABACEAE	Aschynomene Type	H
FABACEAE	Calpurnia Type	H
HAMMAMELIDACEAE	Trichocladus Type	S
MELIACEAE	Meliaceae undiff.	T
MENISPERMACEAE	Cissampelos Type	L
SAPINDACEAE	Blighia Type	T
SAPINDACEAE	Paullinia pinnata	L
SAPOTACEAE	Aningeria adolfi-friderici Type	T
ULMACEAE	Celtis Type	T
VERBENACEAE	Vitex strickeri Type	L

MONTANE FOREST

APIACEAE	Apiaceae undiff.	H
APIACEAE	Oenanthe	H
AQUIFOLIACEAE	Ilex mitis	T
ARALIACEAE	Araliaceae undiff.	T
ARALIACEAE	Polyscias	T
ARALIACEAE	Schefflera	T
BALSAMINACEAE	Impatiens	H
BEGONIACEAE	Begonia	H
CLUSIACEAE	Garcinia	T
CONNARACEAE	Connaraceae undiff.	L
CUPRESSACEAE	Juniperus	T
EUPHORBIACEAE	Macaranga	T
ICACINACEAE	Icacinaceae undiff.	T
LOGANIACEAE	Strychnos Type	T
MIMOSACEAE	Acacia/Albizia Type	T
MORACEAE	Moraceae undiff.	H
MYRICACEAE	Myrica	T
OLACACEAE	Strombosia Type	T
OLEACEAE	Olea	T
PIPERACEAE	Peperomia Type 15µm	H
PIPERACEAE	Peperomia Type 8µm	H
PIPERACEAE	Piper Type verrucat	H
PIPERACEAE	Piper Type	H
PLANTAGINACEAE	Plantago	H
PODOCARPACEAE	Podocarpus	T
PROTEACEAE	Protea Type	T
RANUCULACEAE	Clematis	L
RANUCULACEAE	Thalictrum	H
ROSACEAE	Hagenia abyssinica	T
RUBIACEAE	Psychotria Type	T
SAPINDACEAE	Dodonaea	S

ERICACEOUS ZONE

ASTERACEAE	Artemisia	S
ERICACEAE	Erica	S
ERICACEAE	Erica Type I	S
ERICACEAE	Erica Type II	S
ERICACEAE	Erica Type III	S
GERANIACEAE	Geranium	H
MYRSINACEAE	Myrsine	S
PROTEACEAE	Protea	S

ALPINE ZONE

ASTERACEAE	Helichrysum Type	H

BORAGINACEAE	Lithospermum afromontanum	H
IRIDACEAE	Iridaceae undiff.	H
IRIDACEAE	Gladiolus watsonii Type	H
IRIDACEAE	Iridaceae Type 24µm	H
IRIDACEAE	Iridaceae/Liliaceae Type	H
POACEAE	Poaceae <10µm large anulus	H
POACEAE	Poaceae <10µm small anulus	H
POACEAE	Poaceae 10-20µm large anulus	H
POACEAE	Poaceae 10-20µm small anulus	H
POACEAE	Poaceae 20-30µm large anulus	H
POACEAE	Poaceae 20-30µm small anulus	H
POACEAE	Poaceae undiff.	H
POLYGONACEAE	Polygonaceae undiff.	

OTHER

APOCYNACEAE	Apocynaceae undiff	T
ARECACEAE	Arecaceae	T
ASTERACEAE	cf Carthamus	H
ASTERACEAE	cf Centaurea	H
ASTERACEAE	Asteraceae undiff.	H
ASTERACEAE	Emilia Type	H
ASTERACEAE	Subf. Asteroideae	H
ASTERACEAE	Senecio Type	H
BEGONIACEAE	Begoniaceae undiff.	H
BRASSICACEAE	Brassicaceae undiff.	H
CASUARINACEAE	Casuarina	T
CARYOPHYLLACEAE	Caryophyllaceae undiff.	H
CARYOPHYLLACEAE	Polycarpa eriantha Type	H
COMMELINACEAE	Commelinaceae undiff.	H
CONNARACEAE	Connarus	L
CONVOLVULACEAE	Convolvulaceae undiff.	H
CYPERACEAE	Cyperaceae undiff.	H
EUPHORBIACEAE	Euphorbiaceae undiff.	
EUPHORBIACEAE	Croton	T
EUPHORBIACEAE	Phyllantus Type	H
FABACEAE	Fabaceae undiff.	H
FABACEAE	Dahlbergia Type	S
FABACEAE	Desmodium Type	S
FLACOURTIACEAE	Flacourtiaceae undiff.	
HYPERICACEAE	Hypericum Type	S
LAMIACEAE	Lamiaceae undiff.	H
LAMIACEAE	Basilicum Type	H
LAMIACEAE	Leucas Type	H
MELASTOMATACEAE	Melastomataceae undiff.	H
MENISPERMACEAE	Menispermaceae undiff	L
MIMOSACEAE	Mimosa Type	H
OLEACEAE	Jasminum Type	S
OXALIDACEAE	Oxalis Type	H
RESEDACEAE	Caylusea Type	H
RHAMNACEAE	Scutia Type	S
ROSACEAE	Sorbus group	S
RUBIACEAE	Rubiaceae undiff.	H
RUBIACEAE	Oldenlandia Type	S
SCROPHULARIACEAE	Scrophulariaceae undiff.	H
SOLANACEAE	Solanum Type	
STERCULARIACEAE	Sterculariaceae undiff.	

FERN SPORES

ASPLENIACEAE	Asplenium Type
ATHYRIACEAE	Cystopteris Type
CYATHEACEAE	Cyathea
LYCOPODIACEAE	Huperzia Type
POLYPODIACEAE	Pleopeltis Type
PTEROPHYTES	Trilete Type
PTEROPHYTES	Monolete Type

FUNGI SPORES

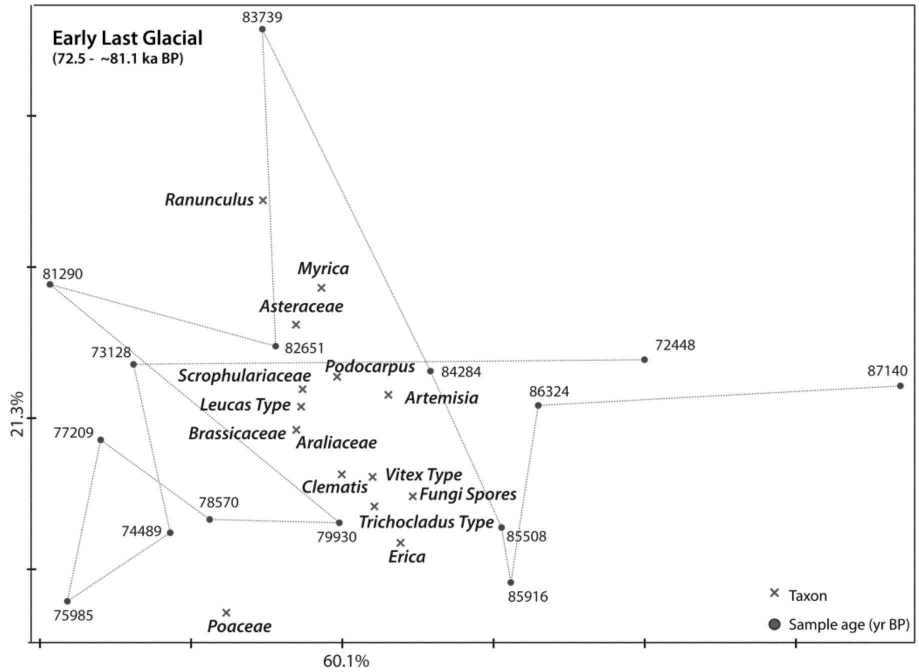

Figure 5b: Ordination diagram of the principle component analysis (PCA) of the samples dated to the early last Glacial (87140 – 72448 yr BP). The species data was standardized and log transformed. The ordination diagram was centred by species and the scaling is focused on inter-sample distance. The % values on the axes indicate the explained variation. The relative distance between samples stands for the differences in pollen taxa composition. The position of the plotted taxa indicates the correlation with the samples. The ordination diagram shows that the vegetation composition was rather stable during the early last Glacial. The predominance of taxa from the alpine and ericaceous zone indicates dry and cool conditions.

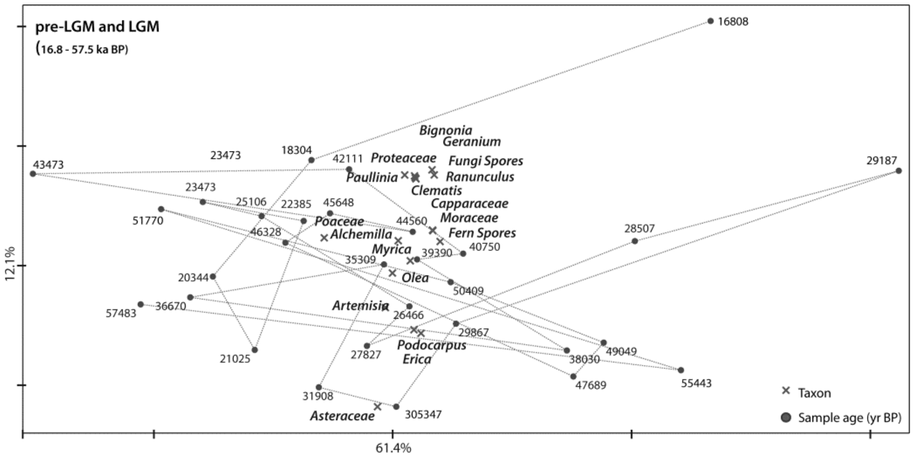

Figure 5c: Ordination diagram of the principle component analysis (PCA) of the samples dated to the pre-LGM and the LGM (57483 – 16808 yr BP). The diagram was centred by species and the scaling is focused on inter-sample distance. The % values on the axes indicate the explained variation. The relative distance between samples stands for the differences in pollen taxa composition. The position of the plotted taxa indicates the correlation with the samples. The % values on the axes indicate the explained variation. The ordination diagram shows that the pre-LGM was a rather stable phase concerning the vegetation composition. Montane forest taxa (e.g. Moraceae, Capparaceae, *Olea, Podocarpus, Protea*) are more abundant indicating wetter conditions than in the early last Glacial. The samples from the LGM are more positively correlated with Poaceae, Asteraceae and some taxa from the Ericaceous Zone (*Erica, Artemisia*) indicating cool and dry conditions. After the LGM we can observe the predominance of taxa from the Ericaceous zone and the montane forest as well as ferns proposing a fast shift into the more humid climate conditions of the Deglacial.

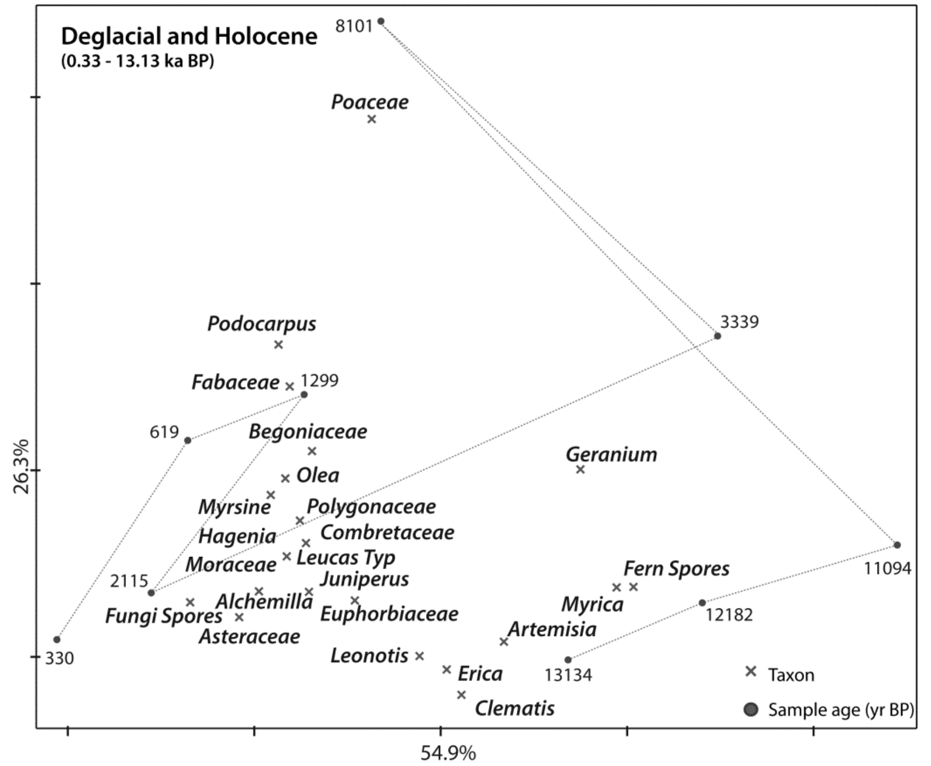

Figure 5d: Ordination diagram of the principle component analysis (PCA) of the samples from the Deglacial and the Holocene (13134 – 330 yr BP) with an 80 % species fit range. The diagram was centred by species and the scaling is focused on inter-sample distance. The % values on the axes indicate the explained variation. The relative distance between samples stands for the differences in pollen taxa composition. The positions of the plotted taxa indicate the correlation with the samples. The % values on the axes indicate the explained variation. The correlation of the samples from the Deglacial and early Holocene to the taxa of the ericaceous zone (*Erica, Artemisia,* and *Geranium*) indicates that the open grassland vegetation around Maundi crater was replaced by heathland. During the mid and late Holocene the montane forest taxa (most importantly *Podocarpus, Olea, Hagenia*, Moraceae, Begoniaceae, *Juniperus*) become more abundant indicating an upward shift of the forest belt approaching the Maundi crater. This proposes increasingly warm and humid climate conditions over the course of the Holocene. The lack of data from the mid Holocene hampers more detailed interpretation for this period.

Chapter 3

Pollen-rain - vegetation relationship along an elevational gradient between 1900 and 3200 m on Mt Kilimanjaro, Tanzania

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(To be submitted)

Abstract

Aim

The establishment of a modern pollen-rain – vegetation relationship in different vegetation zones along an elevational gradient in an afro-montane ecosystem. We investigated the relationship between vegetation and pollen-rain, the taxa level needed to be able to differentiate between forest zones based on the modern pollen-rain assemblage, biodiversity patterns, and pollen and spore drift.

Location

Forest transect along the WeruWeru River between 1900 and 3200 m elevation on the southern slope of Mt Kilimanjaro, Tanzania.

Method

Analysis of modern pollen-rain traps and vegetation inventory data of montane forest plots every 100 m elevation. We applied multivariate data analysis (principle component analysis) to assess the relationship between vegetation and modern pollen-rain and quantified the representativeness of forest belts in the pollen traps by calculating a transfer factor.

Results

At our study site it is possible to analyse the pollen-rain on plant family level in order to derive the forest zone of the surrounding vegetation. The plant families are differently represented in the modern pollen depending on various reproduction factors. This can be quantified as a transfer factor which can be applied to calibrate palaeo-pollen data. The diversity trend captured in the modern pollen-rain reflects the plant diversity. The pollen and spore dispersal is strongly influenced by the regional wind patterns.

Conclusions

The modern pollen-rain study revealed that it is crucial to establish a modern pollen-rain – vegetation relationship for the calibration and interpretation of a fossil pollen record from a mountain site. Our results facilitate the confident use of fossil pollen data to reconstruct more precisely potential vegetation and its dynamics in East African montane forests and also to refine climate past reconstructions in this region for a more accurate comparison of data and modelling.

Keywords: Modern pollen-rain, pollen analysis, tropical montane forest, vegetation zonation, East Africa

Introduction

Modern pollen analogues are essential tools for palaeoecological reconstructions (Birks and Birks, 1980b; Huntley *et al.*, 2011). The relationship between vegetation and pollen trap data is essential for the calibration of palaeo-records. However, only few of such calibration studies which quantitatively relate pollen with altitude and climatic parameters exist. Modern pollen-rain studies in tropical Africa have been carried out to differentiate between different biomes along latitudinal gradients (Jolly *et al.*, 1998; Elenga *et al.*, 2000b; Vincens *et al.*, 2006; Watrin *et al.*, 2007; Lézine *et al.*, 2009; Lebamba *et al.*, 2009) as well as along altitudinal gradients (Bonnefille *et al.*, 1993; Vincens *et al.*, 1997).

The comparison between pollen-rain and plant distribution is essential for a more precise vegetation and climate reconstruction in Africa, as it identifies taxa that have high correspondence between pollen and plant distribution patterns. However, the relationship between pollen assemblage and vegetation is not straight forward since differences in pollen production and dispersal cause some plant taxa to be over-represented in pollen records while others are underrepresented (Tauber, 1967; Prentice, 1985; Sugita, 1993; Jackson and Lyford, 1999).

A major obstacle to progress in tropical palynology is the high diversity of species, and hence, pollen types. Much of the potential information in the record is lost among the 'unknowns' and there is a general lack of understanding of the proportional representation of species (Bush and Rivera, 2001).

In the tropical forests of Barro Colorado Islands, Panama, Bush and Rivera (2001) found that wind-pollinated plants are generally over-represented while animal-pollinated plants are under-represented.

Not clear is to what degree the pollen assemblages represent local versus regional vegetation. A substantial portion of pollen deposited in small collection basins, or under a closed canopy, originates from vegetation growing close to the site, while pollen from a more distant source often overshadows the local signal in large basins (Tauber, 1967; Jacobson and Bradshaw, 1981; Prentice, 1985; Sugita, 1993; Jackson and Lyford, 1999).

Studies of closed canopy sites have shown strong representation in assemblages by pollen from non-local (>100 m) and even distant sources, if non-local vegetation includes an abundance of taxa that produces large quantities of easily dispersed pollen (Sugita, 1993; Jackson and Wong, 1994; Calcote, 1995; Jackson and Kearsly, 1998).

In the study in the Congo Basin Elenga *et al.* (2000a) suggest that the pollen-rain and floristic composition of the vegetation is not linked to altitudinal or precipitation gradients but to hygromorphy and soil type. Only a few taxa show a good correlation between plant cover and pollen abundance. Arboreal taxa dominate in the pollen-rain and the plant diversity is poorly reflected. The results by Elenga *et al.* (2000a) also propose that in dense forest, most pollen grains originate from a distance of 20-50 m only.

The work by Lebamba *et al.* (2009) on different forest types in Cameroon, Gabon and Congo evidences the ability of modern pollen data to predict accurately the present potential vegetation in tropical African lowland forest ecosystems in terms of biomes. This could also been shown by Reese and Liu (2005) for the major vegetation zones of the central Andean region of South America.

Marchant and Taylor (2000) investigated the pollen representativeness of montane forest taxa in south-west Uganda. A close relationship between the modern pollen-rain and the plant abundance was not reflected in all cases. The subsequent reassessment of the Holocene pollen record of the Mubwindi Swamp showed that the suggested dominance of *Olea* and *Podocarpus* around the swamp was erroneous (Marchant *et al.*, 1997; Marchant and Taylor, 1998). Also taxa such as *Celtis*, Ericaceae, *Faurea*, *Hagenia*, *Macaranga*, *Nuxia*, *Olea*, *Podocarpus* and *Schefflera* were probably significantly less important components of the surrounding vegetation over the late Holocene than indicated by their pollen record.

A modern pollen-rain - vegetation relationship from the Ecuadorian Andes revealed that the altitudinal vegetation gradient of lower montane forest, upper montane forest, subpáramo and páramo is well reflected in the modern pollen-rain data (Niemann *et al.*, 2010). The results indicate that a high number of pollen and spore taxa are characteristic for one vegetation type or reflect the altitudinal distribution of genera and families of modern vegetation. Pollen spectra from mature forests in Central America accurately reflect changes in actual forest types (Bush, 2000). Upslope transport of pollen of wind pollinated species is evident in the sparsely vegetated montane samples. However, the corresponding downslope transport of these prolific pollen producers is masked by local pollen production.

In our study we address several of the still open questions by investigating the modern pollen-rain - vegetation relationship along an elevational gradient on the southern slope of Mt Kilimanjaro between 1900 and 3200 m asl. Such a relationship between the vegetation composition and pollen-rain is essential for the calibration of available and future palaeo-records from Mt Kilimanjaro (Schüler *et al.*, 2012) as well as East Africa in general.

By analysing modern pollen and vegetation inventory data of plots at 100 m elevation intervals, we investigate how the pollen record represents the forest zones and quantify the relationship between vegetation cover and pollen-rain concerning the taxa composition. Since the identification of tropical pollen grains to a generic or species level remains difficult (Elenga *et al.*, 2000a) we apply multivariate data analysis in order to detect the adequate taxonomic level of pollen grain identification for reliable results on the corresponding vegetation. By comparing plant and pollen abundances we assess biodiversity patterns as well as pollen and spore dispersal along the elevational gradient. This paper provides also a prediction of which species are most likely to be represented in African montane forest palaeo-records.

Study Area

Mt Kilimanjaro (Fig. 1a) is located 300 km south of the equator in Tanzania on the border with Kenya between 2°45 and 3°25 south and 37°00 and 37°43 east. Mt Kilimanjaro is a more or less eroded relic of an ancient volcano with three peaks (Shira, Mawenzi and Kibo) rising from the savanna plains at 700 m elevation to a snow- and ice-clad summit of 5895 m altitude (Fig. 1b). Its diameter from northwest to southeast is about 90 km. The investigated transect is located inside the forest belt at the southern slope of Kilimanjaro (Fig. 1c). It ranges from 1900 m up to the upper forest border at 3200 m and runs in the vicinity of the river WeruWeru.

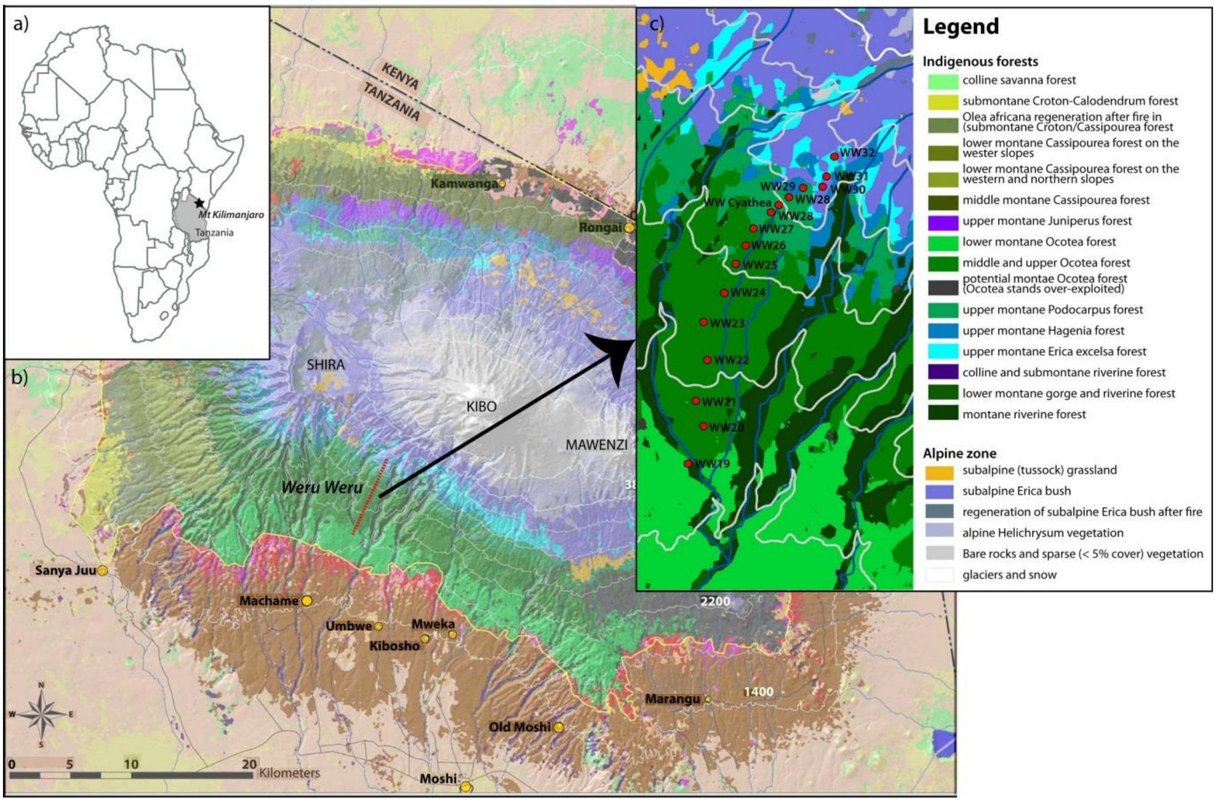

Figure 1 a) Map with location of Mt Kilimanjaro, Tanzania.
b) Land use and vegetation map of Mt Kilimanjaro. Red dotted line indicates the pollen trap transect.
c) The WeruWeru pollen trap transect from 1900 m to 3200 m asl on the SE slope of Mt Kilimanjaro.

Vegetation

Covering about 5000 km², Kilimanjaro has several completely different bioclimatic zones (Fig. 1b): A dry and hot colline savanna zone surrounds the mountain base between 700 and 1100 m asl. Most of this area is used for crop production or as pasture land. Remnants of the former savanna vegetation with *Acacia, Terminalia, Grewia, Combretum* woodlands are encountered mainly around Lake Chala in the eastern foothills and on the north-western side of the mountain. The submontane and lower montane forest belt between 1000 and 1800 m have been converted to coffee-banana fields in the "Chagga homegardens", a special type of traditional agroforestry. Remnants of the former forests of this zone with *Newtonia, Strombosia and Entandrophragma* are hardly found outside of deep valleys and gorges.

The pollen trap transect (Fig. 1c) starts in the lower montane forest zone (LMF), where *Macaranga kilimandscharica, Agauria salicifolia* and *Ocotea umsabarensis* are the dominant tree species. This part of the transect is influenced by human activities such as fodder and wood collection and grazing by cattle.

Most plots are located in the middle montane forest zone (MMF), which starts in the Weru-Weru area at 2200 m elevation. In this zone humidity reaches its maximum, indicated by the wealth of epiphytes and ferns, in particular filmy ferns and tree ferns. *Ocotea umsabarensis*, *Xymalos monospora* (Monimiaceae), *Ilex mitis* (Aquifoliaceae), and *Schefflera volkensii* (Araliaceae) build up the tree layer.

In the upper montane forest zone (UMF) above 2800 m the gymnosperm *Podocarpus latifolius* (Podocarpaceae), *Hagenia abyssinica* (Rosaceae) and *Prunus africana* (Rosaceae) form the tree canopy. Monodominant stands of *Erica excelsa* (Ericaceae) play also an important role in this zone, replacing *Podocarpus* and *Hagenia* forests after fire, forming the actual upper closed forest line on the southern slope of Kilimanjaro at 3250 m.

Above 3250 m, the cloud forests are replaced by *Erica* heathlands. *Erica trimera* forest remnants at 4000 m indicate the upper potential natural forest line. Above this altitude, the *Erica* heathlands change into *Helichrysum* dwarf cushion vegetation that extends up to 4500 m. The highest altitudinal region is very poor in vegetation and the top of Kibo, the main summit, is covered with glaciers. For a more detailed description of these vegetation types see Hemp (2001b; 2006a; 2006c).

Climate

Mean annual precipitation at the lowest pollen plot at 1950 m is about 2670 mm and increases to over 3050 mm between 2050 and 2350 m. At higher elevation, precipitation decreases to 1480 mm at 3250 m. The mean annual temperature decreases from 14.3 °C at 1950 m to 7.1 °C at 3250 m with a lapse rate of 0.6 °K. Frost starts at 2950 m during cool nights in July and August (Hemp, 2006a). The predominance of the southeasterly trade wind at Mt Kilimanjaro is modified by the mountain's topography causing strong downhill winds during the evening hours and weaker uphill winds during day-time (Hemp & Zimmermann, unpubl.).

Material and Methods

Floristic inventories

On the WeruWeru transect research plots in 100 m altitudinal intervals with vegetation records, soil profiles, rain gauges and data logger for temperature and humidity were established in 2005. For our study we used the 15 plots between 1950 and 3250 m, since the forest below 1900 m is heavily disturbed and frequented by people collecting fire wood and fodder. The plots measured 50 x 50 m. The plot size was chosen with respect to the minimum area calculated with the nested plot method (as suggested by Mueller-Dombois *et al.*, 1974). Three plots were located within the lower montane forest (LMF: 1900 to 2100 m asl), eight in the middle montane forest (MMF: 2200 m asl to 2800 m asl including one additional plot at the upper distribution border of *Cyathea manniana*) and four in the upper montane forest (UMF: 2900 to 3200 m asl). Plant taxa abundances were estimated using the Braun-Blanquet cover-abundance scale (1964) for vegetation analysis.

Modern pollen-rain sampling and laboratory methods

In total 30 pollen traps were installed 10 cm above the ground along the elevational transect used for the floristic inventories (see above) in February 2010. Two traps were installed at every vegetation plot. The same pollen trap type was used as suggested by Behling *et al.* (2001) and Niemann *et al.* (2010) using 50 ml test tubes with 3 ml glycerine and synthetic cotton and a net as cover. 26 pollen traps could be recollected in February 2011 (Table 1).

Chemical preparation of samples followed the standard method of Faegri and Iversen (1989). The pollen residue obtained was kept in distilled water until mounted into glycerol jelly for pollen analysis. For each sample at least 300 pollen grains were counted forming the pollen sum of 100%. Fern spores were also counted and expressed as percentages of the pollen sum. Pollen and spore identification was based on the reference collection of about 2000 slides of the Department of Palynology and Climate Dynamics, Göttingen University, the African Pollen Database (Lézine, 2001) and relevant literature (Assemien *et al.*, 1974).

Table 1: Location and forest type of the plots used for the vegetation survey and the installation of 2 pollen traps along the SE slope of Mt Kilimanjaro. The number of traps installed in 2010 and recollected in 2011 is given.
LMF: Lower montane forest; MMF: Mid montane forest; UMF: Upper montane forest

Plot	**Altitude (m asl)**	**Coordinates**		**N° traps 2010**	**N° Traps 2011**	**Vegetation Zone**	
		°S	°E				
WW 19	1952	03°09'34.6''	37°15'38.4''	2	2	LMF	*Ocotea-Agauria* forest consistant of *Ocotea usambarensis* associated with *Agaria salicifolia, Syzygium guineense, Macaranga kilimandscharia* and *Polyscias fulva*
WW 20	2030	03°09'11.3''	37°15'49.9''	2	1	LMF	
WW 21	2143	03°08'52.5''	37°15'43.1''	2	1	LMF	
WW 22	2255	03°08'28.3''	37°15'53.8''	2	2	MMF	*Ocotea Podocarpus* forest, consisting of *Ocotea usambarensis* associated with *Podocarpus latifolius* and the tree fern *Cyathea manniana*
WW 23	2378	03°08'06.8''	37°15'51.9''	2	2	MMF	
WW 24	2489	03°07'46.3''	37°16'03.5''	2	2	MMF	
WW 25	2568	03°07'31.5''	37°16'07.7''	2	2	MMF	
WW 26	2681	03°07'18.1	37°16'17.7''	2	2	MMF	
WW 27	2798	03°07'06.9''	37°16'23.6''	2	2	MMF	
WW C.	2800	03°07'06.5''	37°16'25.9''	2	1	MMF	
WW 28	2879	03°06'58.5''	37°16'30.9''	2	1	MMF	
WW 29	3009	03°06'44.8''	37°16'40.2''	2	2	UMF	*Podocarpus-Ocotea* forest with prevailing *Podocarpus latifolius*
WW 30	3087	03°06'39.9''	37°16'51.6''	2	2	UMF	
WW 31	3176	03°06'33.6''	37°17'06.7''	2	2	UMF	*Hagenia-Podocarpus* forest with *Podocarpus latifolius, Hagenia abyssinica* and *Pruns africana*
WW 32	3255	03°06'21.5''	37°17'09.0''	2	2	UMF	

Multivariate data analysis

For the multivariate data analysis the program CANOCO was used (ter Braak and Šmilauer, 1997). A principle component analysis (PCA) based on the percentage data of the pollen-rain and the vegetation of the plots was applied to investigate the similarity between pollen traps within one plot, the relationship between vegetation and pollen-rain, and the taxa level needed to be able to differentiate between forest zones based on the modern pollen-rain assemblage.

The PCA was based on 150 identified pollen types. The species data was square root transformed as suggested by Leps and Šmilauer (2003). For the analysis of the taxa level another PCA based on the corresponding plant families was performed. The pollen types were pooled into 67 plant families.

Representativeness of plant families in the modern pollen-rain

For the data analysis the identified pollen types were pooled on family level. Some pollen types are difficult to determine at genus level but can easily be assigned to a plant family. Merging pollen types into families allows for a larger data set since the pollen grains that could not be determined at genus but at family level do not have to be excluded from the data set. To investigate how the vegetation is represented in the pollen traps we compare the percentages of plant families present in the vegetation cover and in the pollen-rain. This was done separately for every forest zone (LMF, MMF, and UMF) for all plant families present in both data sets. To enable calibration according to the relationship between the percentage of the family within the pollen trap and the surrounding vegetation, we generate a transfer factor (TF = (% taxa in vegetation)/ (% taxa in pollen-rain)). This factor, which can also be applied to fossil pollen data (Marchant and Taylor, 2000) compensates differences in representativeness of pollen. The comparison of the transfer factors of the different forest zones also allows further ecological conclusions.

A pollen percentage diagram was compiled with the software C2 Version 1.7.2 (Juggins, 2011), illustrating the most important taxa (Appendix S1). Pollen taxa were assigned to forest zones in accordance with Hemp (Hemp, 2006a).

Assessing biodiversity

Plant diversity was assessed by comparing the number of plant families in the pollen traps and in the corresponding vegetation plot. This comparison was also done on generic and specific level of plant taxa and pollen types.

Pollen and spore dispersal

For assessing pollen and spore dispersal we made a comparison between the abundance of Cyperaceae and *Cyathea* in the vegetation and in the modern pollen-rain. Those two taxa are very abundant and most likely to capture the wind pattern in their pollen/spore distribution. Cyperaceae release their pollen around-the-clock and the sporangia of *Cyathea* are opened only during the drier climate conditions during day-time. Both taxa have defined borderlines of their distribution within the studied altitudinal transect which facilitates the detection of pollen/spore shifts. In each case the vegetation cover and the pollen/spore data were plotted against the altitude. For the vegetation cover we applied a moving average to the data set (window size of 2) to smooth out short-term fluctuations caused by the transformation of the Braun-Blanquet scale into percentage values, and to highlight long-term trends.

Results

Multivariate data analysis

The principle component analyses (PCA) of the modern pollen-rain data give information on the differences between individual pollen traps and between different vegetation plots derived from the modern pollen-rain data.

In Fig. 2a the PCA of the individual pollen traps based on the pollen types is shown. The ordination axes represent cumulatively 50.2 % of total variance in the data set (1st PCA axis: 30.0 %; 2nd PCA axis: 20.2 %). Samples of the same plot (same elevation) are clustered. Further, samples of the pollen traps ranging from 1900 to 2100 m asl are grouped as well as samples from 2200 to 2400 m asl, 2500 to 2800 m asl, and 2900 to 3200 m asl. The separation between the clusters of 2500 to 2800 m asl, and 2900 to 3200 m asl is very distinct.

Fig. 2b shows the pooled modern pollen-rain samples per plot based on the pollen grain types. The 1st PCA axis represents 33.3 % of the total variance in the data set; the 2nd axis represents 24.6 % (cumulatively 57.9 %). The samples of 1900 to 2100 m asl are clustered in the upper left corner of the diagram and are most strongly correlated with the abundance of *Macaranga* (Euphorbiaceae), Acanthaceae, *Ocotea* (Lauraceae) and *Tabernaemontana* (Apocynaceae).

Samples of 2200 to 2800 m asl are located in the lower half of the ordination diagram and are correlated with the abundance of Piperaceae, Rubiaceae (*Psychotria, Pauridiantha*), *Begonia* (Begoniaceae), *Podocarpus* (Podocarpaceae), *Schefflera* (Araliaceae), *Ilex* (Aquifoliaceae) and Cyperaceae

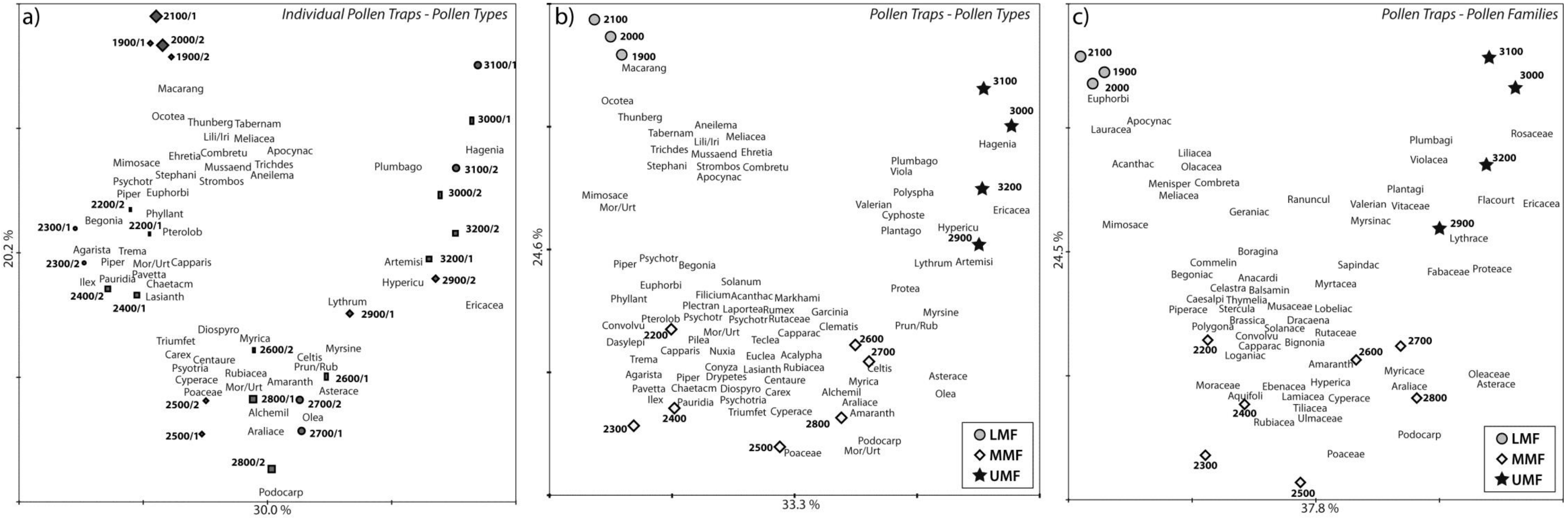

Figure 2 Ordination diagram of the principle component analysis (PCA)
a) PCA of the individual pollen traps based on the pollen types (best fit 10-100%)
b) PCA of the pollen trap plots based on the pollen types (best fit 10-100%)
c) PCA of the pollen trap plots based on the pollen families

The pollen trap samples of 2900 to 3200 m asl are positioned in the upper right quadrant of the diagram. They are correlated with the modern pollen-rain types of *Hagenia* (Rosaceae), *Erica* (Ericaceae), *Artemisia* (Asteraceae), *Viola* (Violaceae) and *Hypericum* (Hypericaceae). Two subgroups are noticeable. Samples of 2900 and 3200 m asl are clustered and correlated with *Erica* and *Hypericum*, whereas the samples of 3000 and 3100 m asl are correlated stronger with *Hagenia*.

In Fig. 2c the PCA of the pollen traps based on the pollen types pooled into their corresponding plant families is shown. 37.8 % of the total variance is given by the 1st PCA axis; 24.5 % by the 2nd PCA axis (cumulatively 62.3 %). The pattern of the sample distribution is similar to the one revealed by the PCA based on the pollen types (Fig. 2b). Samples of 1900 to 2100 m asl are most strongly correlated with Euphorbiaceae, Lauraceae, Acanthaceae, Apocynaceae, Begoniaceae and Mimosaceae. Pollen samples from plots of 2200 to 2800 m asl are clustered in the lower part of the ordination space. The samples are correlated with Aquifoliaceae, Araliaceae, Moraceae, Tiliaceae, Podocarpaceae, Poaceae and Cyperaceae. Pollen trap samples of 2900 to 3200 m asl are positioned in the upper right quadrant of the diagram and are correlated with Proteaceae, Ericaceae, Rosaceae and Violaceae.

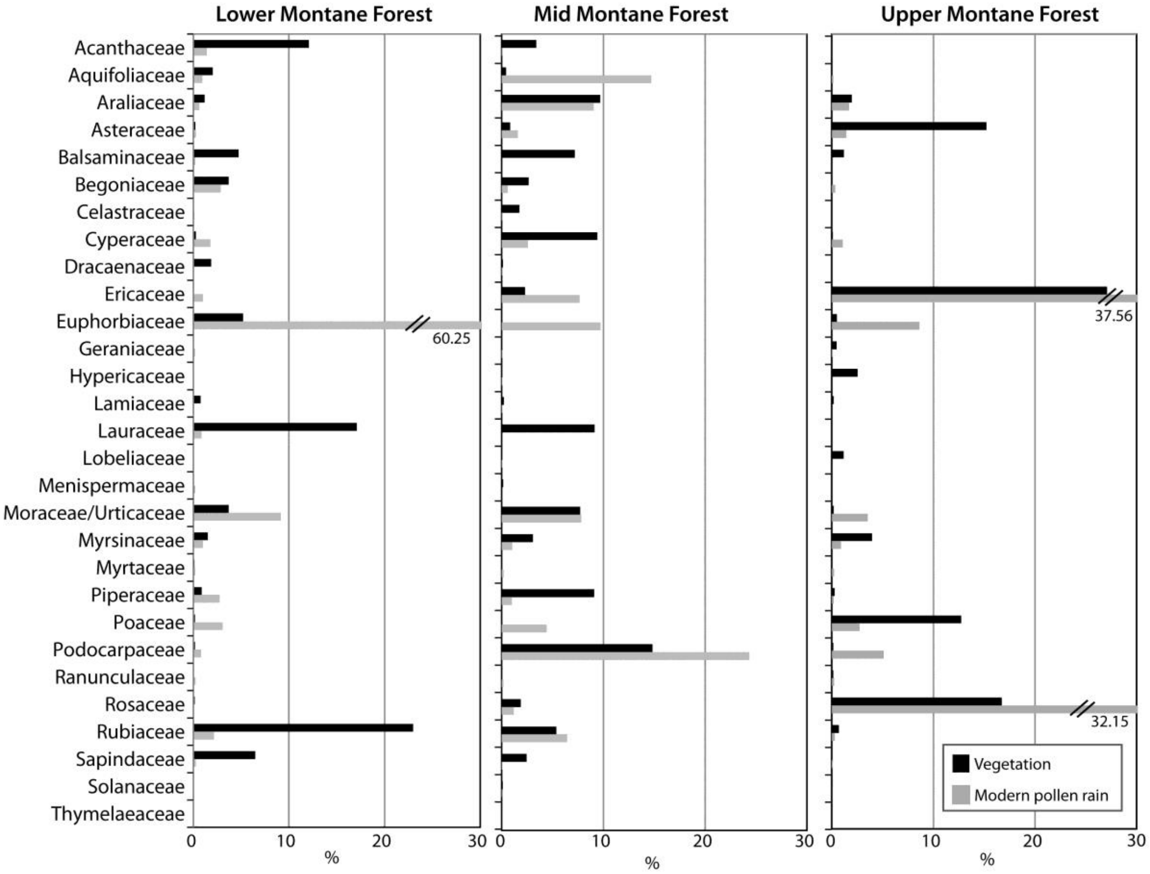

Figure 3: Summary histogram comparing percentage data on family level of the modern pollen-rain and plant taxa in vegetation plots for the different montane forest zones.

Representativeness

The percentage pollen diagram is shown and described in the electronic supplements (see supplementary information). The representativeness of plant families in the modern pollen-rain in comparison with their abundance in the surrounding vegetation is shown in Fig. 3 and summarized as potential transfer factors (TF) in Tab. 2. A TF close to 1 means that the percentage of a plant family in the pollen record is about equal to the one in the vegetation. TF values <1 indicate over-representation in the pollen record and TF values >1 mean under-representation. In the LMF the percentage of Euphorbiaceae is much higher in the pollen record (60.25 %) than in the vegetation (5.20 %). The TF is very low (0.09). In contrast, the pollen percentage of Lauraceae (0.86 %) and Rubiaceae (2.17 %) is lower than in the vegetation (Lauraceae: 17.09 %; Rubiaceae: 22.99 %) as also indicated by their high TFs (19.94 and 10.60, respectively). In the MMF the pollen record shows high percentages for Aquifoliaceae (14.71 %), Euphorbiacea (9.71 %), Moraceae/Urticaceae (7.83 %), and Podocarpaceae (24.33 %) whereas for Cyperaceae (2.58 %), Lauraceae (0 %), Piperaceae (1.00 %) the pollen percentages are clearly lower than the families' abundances in the vegetation. While pollen percentages in the UMF are high for Ericaceae (37.56 %), Rosaceae (32.15), Euphorbiaceae (8.64 %), Moraceae/Urticaceae (3.54 %), and Podocarpaceae (5.12 %) they are low for Cyperaceae (1.07 %), Piperaceae (0.18 %) and Poaceae (2.73 %) in comparison with their abundance in the surrounding vegetation.

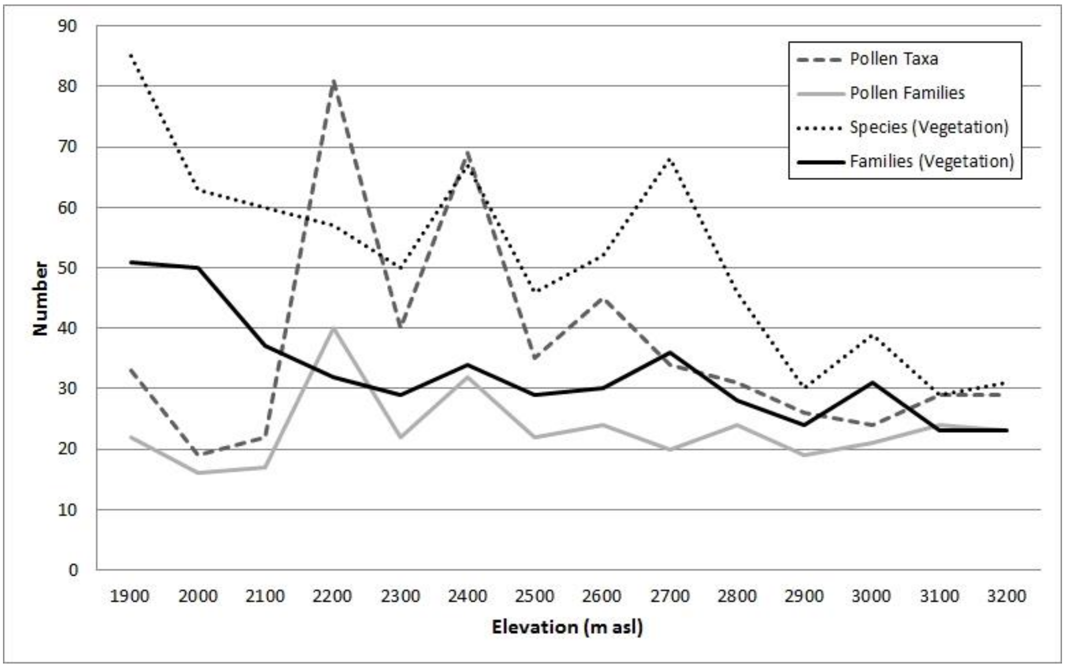

Figure 4: Number of plant species and pollen taxa plotted along the elevational gradient. Additionally, the number of families derived from the species and the pollen taxa are given.

Table 2: Information on representativeness given for all plant families that were recorded at least once in the pollen traps. The transfer factors are shown when the family is present within the pollen record and the vegetation survey. The average transfer factor is only calculated if the family is present in all forest zones.
Empty cell: taxa recorded neither in vegetation nor in pollen-rain; st: recorded in vegetation but not in the modern pollen-rain (silent taxon); x: not in vegetation but in pollen record; TF<1: over-represented in pollen record; TF>1: under-represented in pollen record; TF~1: equivalently represented in pollen record

	LMF	MMF	UMF
Acanthaceae	8.54	58.83	
Aquifoliaceae	2.15	0.03	x
Araliaceae	1.83	1.07	1.15
Asteraceae	0.82	0.53	10.55
Balsaminaceae	20.82	st	st
Begoniaceae	1.29	4.35	x
Celastraceae	0.29	17.18	
Cyperaceae	0.15	3.65	0.10
Dracaenaceae	20.42	1.98	
Ericaceae	x	0.30	0.72
Euphorbiaceae	0.09	0.003	0.06
Geraniaceae	x	x	4.20
Hypericaceae	st	x	st
Lamiaceae	st	2.73	st
Lauraceae	19.94	st	
Lobeliaceae		x	st
Menispermaceae	x	st	
Moraceae/Urticaceae	0.41	0.98	0.06
Myrsinaceae	1.52	2.95	4.36
Myrtaceae	0.60	x	x
Piperaceae	0.32	9.09	1.58
Poaceae	0.05	x	4.66
Podocarpaceae	0.21	0.61	0.03
Ranunculaceae	0.14	0.23	0.64
Rosaceae	st	1.57	0.52
Rubiaceae	10.60	0.84	2.31
Sapindaceae	23.75	28.33	x
Solanaceae		3.36	st
Thymelaeaceae	x	st	

Biodiversity

The plant diversity shows a decreasing trend with increasing elevation in the vegetation. This is also found in the modern pollen-rain (Fig. 4). In the vegetation the highest number of species (85) and families (51) is recorded at 1900 m asl. The number of species reaches another maximum at 2700 m asl (69 species) and then decreases to 31 species in 23 families at 3200 m asl. The diversity found in the modern pollen-rain has its minimum at 2000 m asl with only 19 pollen types in 16 plant families, it reaches 81 pollen types in 40 families at 2200 m asl and then decreases again to 29 pollen types in

23 plant families at 3200 m asl. The pollen diversity is generally lower than the diversity in the vegetation but converges to it with increasing elevation. At 2200 m and at 3100 m asl the number of plant families recorded in the modern pollen-rain exceeds slightly the number of families in the vegetation.

Pollen and spore dispersal

A comparison of the percentage of Cyperaceae pollen in the record along the elevational gradient with the abundance of Cyperaceae in the surrounding vegetation cover (Fig. 5a) shows different distribution patterns. Cyperaceae contribute between 2 and 10 % to the modern pollen-rain up to an elevation of 2400 m asl.

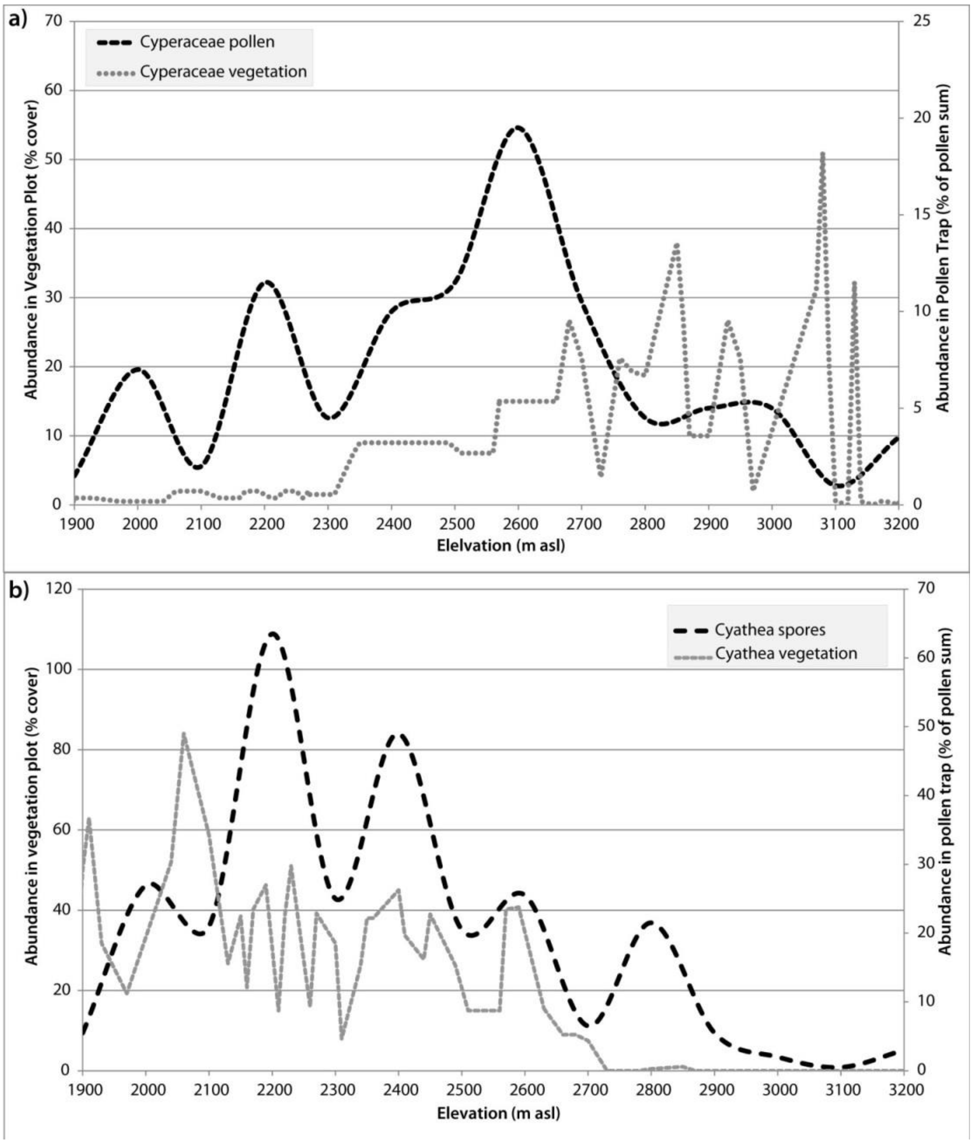

Figure 5 Comparison between the plant abundance in the vegetation and the percentage in the pollen record.
a) Cyperaceae
b) *Cyathea*

At 2600 m asl they reach the maximum of 20 % followed by a strong decrease of Cyperaceae pollen to less than 5 % at higher elevations. In the vegetation Cyperaceae are most abundant around 3100 m asl showing a 50 % vegetation cover. Between 2400 m and 3000 m asl the abundance fluctuates between 5 and 38 %. At lower elevations Cyperaceae only represent 1 to 2 % of the vegetation.

Fig. 5b depicts the abundance of *Cyathea* spores in the pollen traps and the vegetation cover along the altitudinal gradient. While in the vegetation *Cyathea* can only be found up to about 2800 m asl, it still occurs in the spore signal at 3200 m asl (and potentially even higher). The pattern of abundance along the altitudinal gradient shows a phase-shift between vegetation and pollen record. The abundance of *Cyathea* in the vegetation lags the occurrence in the spore record by about 100 m of altitude. While *Cyathea* shows about 60 % vegetation cover at 1980 m asl, this maximum can only be observed at about 2200 m asl in the spore record.

Interpretation and Discussion

The PCA of the individual pollen traps (Fig. 2a) reveals only minor differences of modern pollen-rain assemblages between the pollen traps within one plot. That means that the individual pollen traps are similarly representative for the surrounding vegetation.

Some differences between the pollen traps e.g. at 3100 m asl are caused by the abundance of *Hagenia*. *Hagenia* is a strong pollen producer but due to the relatively large pollen grains the pollen dispersal over larger distances is rather low (Jackson and Lyford, 1999). Hence, the dominance reflected in the modern pollen-rain is a very distinct but locally restricted sign of the presence of single *Hagenia* trees. This is to be considered whenever *Hagenia* appears as dominant taxa in a sample. The close similarity of taxa composition within pollen traps of one plot is an essential prerequisite for any further investigations.

The PCA also shows that the pollen traps are not only representative for the vegetation of the direct surrounding but also for the corresponding vegetation zone described by Hemp (2006) along the elevational gradient of Mt Kilimanjaro (see also pollen diagram in Appendix S1). The resemblance of samples of the same forest zone (LMF, MMF and UMF) is much higher than in-between the forest zones.

In the LMF *Macaranga kilimandscharica* (Euphorbiaceae), a wind pollinated species, is very abundant in the vegetation and the major component of the pollen-rain record. The fact that it is strongly over-represented in the LMF is also because *Macaranga* is a strong pollen producer.

The MMF is generally characterized by abundant Cyperaceae, Rubiaceae, Moraceae, Urticaceae, Piperaceae, Araliaceae, *Podocarpus* and *Ilex*. However, two forest sub-types, as described by Hemp (2006a), can be detected in the modern pollen-rain: the lower MMF (2200 to 2400 m asl) is characterized by abundant *Schefflera* (Araliaceae), *Begonia*, *Ilex* and several Rubiaceae taxa (*Psychotria, Pauridiantha)*. The dominance of *Podocarpus* and Urticaceae (*Pilea*) in the pollen-rain represents the vegetation cover of the upper MMF (2500 to 2800 m asl). *Podocarpus* is most abundant at 2700 to 2800 m asl which is also reflected in the modern pollen-rain. Also, *Prunus* and *Rubus* (Rosaceae) can be used as indicator taxa for this upper MMF in the pollen record.

The UMF above 2900 m asl is dominated by *Hagenia* and *Erica* as a result of forest fires during the past. The abundance of *Hypericum, Valeriana* and Violaceae in the pollen-rain also indicates a more open forest structure. Especially, *Artemisia, Geranium, Protea* and *Myrsine* are typical taxa of the Erica zone which replaces the UMF above 3200 m asl.

The comparison of forest zonation based on the modern pollen-rain reveals similar patterns for pollen types as for plant families. That shows that the plant family composition is already very decisive when trying to distinguish between LMF, lower and upper MMF and UMF along the elevational gradient. Therefore, our results support the suggestion by Minckley and Whitlock (2000) that it is not always necessary to use the full suite of pollen taxa present if the goal is to reconstruct vegetation at the level of vegetation type or zone.

Even though the dominant plant families in the pollen-rain are not in all cases also the abundant ones in the vegetation, their occurrence facilitates the detection of forest zones as is also suggested by Niemann *et al.* (2010). The more detailed ecological interpretation and floristic characterization within the forest zones can then be continued based on key taxa. Nevertheless, some aspects have to be taken into account. First, plant families consist in most cases of many species, which can have different ecological demands. Second, the pollen productivity and dispersal vary between species. As many tropical trees are animal pollinated the relationship between pollen deposition and plant distribution is not linear.

The representativeness of a plant family adds important qualitative information for the interpretation. The results show that the representativeness of a plant family is not the same for every forest zone (each spanning an elevational difference of 300 to 500 m). However, Ericaceae and Euphorbiaceae are strongly over-represented in the pollen record of the forest zones. Both families are strong pollen producers which would lead to such a representativeness pattern. Their pollen grains also seem to be subject to long-distance dispersal since they are also recorded in plots where they do not appear in the vegetation.

Taxa that have a high TF value and that also occur as silent taxa (present in the flora but unrecorded in pollen rain) such as Hypericaceae or Balsaminaceae indicate weak pollen production. Taxa which appear with a low TF in one forest zone and are silent in other zones suggest that their pollen is wind transported.

The over-representativeness of Ericaceae, Rosaceae (*Hagenia*), Euphorbiaceae (*Macaranga)* and partly *Podocarpus* and Araliaceae coincides with the finding of Marchant and Taylor (2000) who could show that these taxa are probably significantly less important components of the surrounding vegetation than indicated by their sub-fossil pollen.

The elevational gradient of plant diversity shows a hump-shaped elevational species richness pattern which is known from other elevational gradient studies on mountain systems and it is assumed to be related to the overlap of distributional ranges and the absence of extreme life conditions (Becker *et al.*, 2007). This range-overlap-effect is known to be particularly pronounced in the transition zone from montane forests to alpine vegetation (Kessler, 2001; Körner, 2003b). On Mt Kilimanjaro this was shown for overall vascular plant diversity and in particular for pteridophytes in relation to habitat variety, which is a major controlling factor of species richness. At the upper forest border fires start to become important on Mt Kilimanjaro, creating a mosaic of different fire induced successional stages of forest, shrub and tussock grassland stands. Here, high community (beta) diversity in the fire-influenced areas of the upper montane zone leads to a higher species (alpha) diversity as compared to the closed undisturbed forest at lower altitudes and the monotonous *Erica* bush at higher altitudes (Hemp, 2001b; Hemp, 2006d).

We can observe a similar overlap-effect in the pollen diversity pattern. Highest values for pollen diversity are found in forest type transition zones where the taxa composition in the vegetation changes substantially. This is the case at 2100 m to 2200 m asl, the transition from LMF to MMF, and at 3100 m to 3200 m asl where the montane forest is replaced by ericaceous and alpine vegetation.

The diversity trend captured in the modern pollen-rain reflects the plant diversity in the vegetation. Substantial differences in numbers of taxa are probably due to the high proportion of insect-pollinated plants in the tropics (Bawa, 1983) which are mostly not or only rarely recorded in the pollen-rain. Towards more open vegetation in the UMF and the *Erica* belt the pollen diversity reflects the plant diversity much better. It seems that our results in tropical montane vegetation confirm the finding by Tauber (1967) who proposed that under closed canopy cover the pollen assemblage is a more local signal whereas in more open areas a wider range is recorded. That leads to the conclusion that the pollen diversity reflects the plant diversity pattern independent of the investigated taxa level but that it can only be interpreted in consideration of the specific vegetation type and surrounding flora. Unlike the findings by Elenga (2000a) our results propose a good reflection of diversity patterns in the modern pollen-rain.

The comparison of Cyperaceae in the pollen record with their vegetation cover reveals that the abundance is not directly reflected by the pollen-rain recorded. The results suggest a downwards shift of the distribution pattern reflected in the pollen-rain. The maxima of the Cyperaceae abundance at 3100 m, 2850 m and 2700 m asl are recorded about 500 to 600 m lower in the pollen-rain. Cyperaceae, which are wind pollinated, have rather light and non-sticky pollen so that they can be transported by air currents. Hence, this shift of Cyperaceae pollen signal could be caused by strong downward winds which prevail on the slopes of Mt Kilimanjaro during evening time. In contrast, the spores of *Cyathea* are large (80-120 µm) and not easily transported over long distances. The spore record of *Cyathea* reflects an average shift by only 100 m elevation, however in upward direction. While the highest occurrence in the vegetation is at 2850 m asl, *Cyathea* spores can still be found in the pollen traps at 3200 m asl. This could be explained by the characteristic of ferns to release their spores under dry environmental conditions which prevail during day time which is also the time period of upward winds along the slopes of Mt Kilimanjaro. Hence, our results do not only suggest a positive correlation between the pollen/spore drift and wind direction but also between drift distance and the wind force.

Our results show that even in closed canopy sites there is a representation of non-local (>100 m) sources. This agrees with the findings by Sugita (1993), and Jackson and Wong (1994). However, we could show that this does not only include taxa that have a high pollen production.

In his study in forest habitats in Panama and Costa Rica Bush (2000) also observed wind dependent pollen transport for sparsely vegetated montane zones. In contrast to his findings we do not observe a masking effect by local vegetation in the downslope transport into more dense vegetation.

Conclusion

Our modern pollen-rain study along the elevational gradient on Mt Kilimanjaro has revealed that it is crucial to establish a modern pollen-rain – vegetation relationship for the calibration and interpretation of a fossil pollen record from a mountain site. At our study site it is possible to analyse the pollen-rain on plant family level in order to derive the forest zone of the surrounding vegetation and with this to assess the climatic conditions, which is important for the interpretation of palaeo-records. Even the separation in lower and upper mid montane forest zone is possible by modern pollen-rain. The occurrence of plant families along the altitudinal gradient are differently represented in the modern pollen depending on various reproduction factors. This can be quantified as a transfer factor which will be applied to calibrate palaeo-pollen data in future studies. The diversity trend captured in the modern pollen-rain reflects the plant diversity in the vegetation; but we observed differences in the taxa richness. The pollen and spore dispersal seems to be strongly influenced by the regional wind patterns. This needs to be considered when deriving past distribution ranges from pollen-records.

Our results facilitate the confident use of fossil pollen data to reconstruct more precisely potential vegetation and its dynamics in East African montane forests and also to refine climate past reconstructions in this region for a more accurate comparison of data and modelling.

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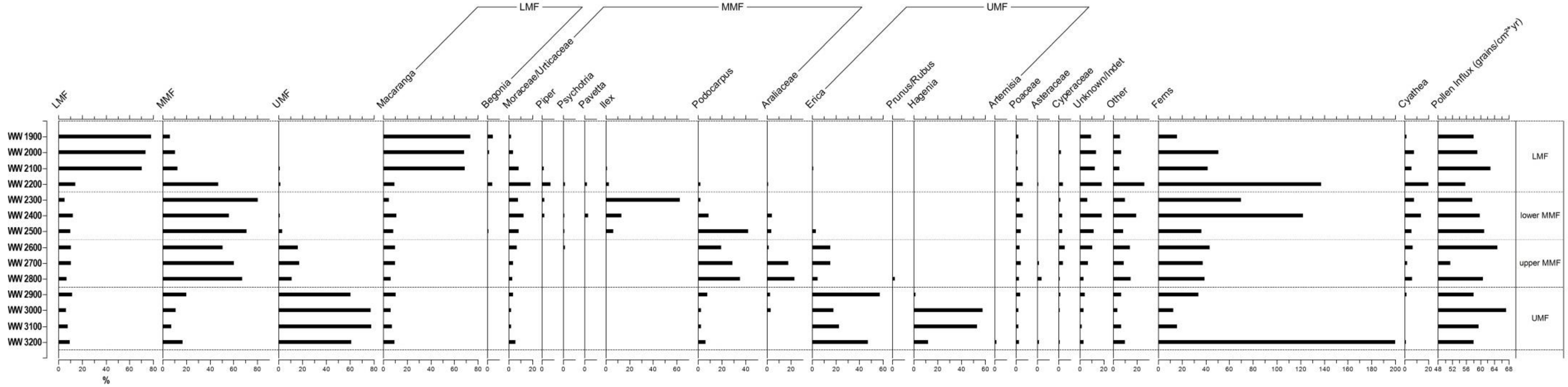
Supplementary Material



S1: Pollen percentage diagram of modern pollen-rain (WeruWeru transect: 1900 - 3200 m asl), showing sums of forest zones, lower montane forest (LMF), mid montane forest (MMF) and upper montane forest (UMF), and selected pollen taxa grouped into these forest zones. The two respective pollen data sets per plot were merged. Grouping of taxa was based on (Hemp, 2006a). The pollen sum includes all pollen types except for the spores. Fern spores were calculated based on the pollen sum. The diagram shows that it is possible to distinguish between forest zones based on the pollen type assemblage. Taxa associated with the LMF in the modern vegetation such as *Macaranga* and *Begonia* were also major elements of the modern pollen-rain between 1900 – 2200 m asl. Major pollen taxa of the MMF (e.g. *Podocarpus, Ilex,* Araliaceae) and of the UMF (e.g. *Erica, Artemisia, Alchemilla, Hypericum*) are also abundant in the corresponding forest belts of the vegetation. This shows that the modern pollen rain reflects the vegetation zones and their floristic composition of the elevational gradient on Mt Kilimanjaro. Hence, the results are in accordance with the outcome of the multivariate data analysis. The downslope shift of the pollen signal by 100 m as revealed by the comparison between the plant abundance in the vegetation and the pollen record (Fig. 5) can also be seen in the pollen diagram. Taxa associated with the MMF as *Piper, Psychotria*, and *Pavetta* show a pollen displacement into the uppermost LMF. The same applies for taxa of the UMF as *Alchemilla, Prunus/Rubus* and *Hypericum* which show an elevational displacement into the uppermost MMF. This pattern is most evident in taxa with a limited distribution range. These results agree with the findings of Cyperaceae pollen shift (Fig. 5) and support the dependence of pollen distribution patterns on predominant wind direction and speed.

Chapter 4

Unravelling > 40 000 years of vegetation and climate dynamics on Mt Kilimanjaro: a pollen and sediment record from the montane forest

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Abstract

This pollen and sediment record of past vegetation and - climate dynamics in tropical East Africa generally extends back to about 50 ka BP. The WeruWeru study site is located in the montane forest at an elevation of 2650 m on the southern slope of Mt Kilimanjaro. The palynological and sedimentological analyses were performed in high resolution and therefore allow detailed reconstruction of the vegetation response to environmental changes during the Late Glacial and the Holocene.

Our results suggest that past climate change caused the vegetation belt to shift along the elevational gradient. During the Glacial the major taxa which from the montane forest today were present. That indicates that Mt Kilimanjaro served as forest refugia. The pollen record further proposes the presence of more drought tolerant *Cassipourea* forests during the early Holocene. In the course of the Holocene, the taxa of montane forest of the wetter southern slope, which also form the forests today, become more abundant Apart from the pollen data, also the results of the geochemical analysis of the soils profile suggest different phases of enhanced wind intensities and rainfall which can be associated with enhance monsoonal activities observed at other study sites in tropical East Africa. Further, the palynological study gives no indication for the presence of a bamboo belt on the southern slope of Mt Kilimanjaro as it is found on other East African mountains with suitable climate conditions. Although, fires occur regularly throughout the investigated time period, they do not seem to play an important role in the vegetation dynamics. The succession of different forest types proposes that past environmental changes did not only cause an elevational shift of vegetation but also profound re-structuring of the forest ecosystems. Hence, this reconstruction of former vegetation and climate dynamics unravels the ecosystem responses to climate change in the past and adds to the understanding of the state and functioning of the ecosystems of Mt Kilimanjaro.

Keywords: pollen, East Africa, climate, forest belts, montane vegetation, Glacial, XRF

Introduction

It is widely established that climate is a major determinant of past and present vegetation structure and ecosystem functions, but the extent to which vegetation influences climate is far less certain (Hoffmann and Jackson, 2000). Global temperatures are rising, and climate change is driving biodiversity changes worldwide (Parmesan and Yohe, 2003). Species extinctions, changes in abundance, and shifts in species ranges are profoundly altering ecological communities and ecosystem services (Lovejoy and Hannah, 2005). Tropical species are adapted to relatively uniform and narrow temperature conditions, which consequently makes them to the most sensitive species to climate change (Feeley and Silman, 2010). Species in tropical montane ecosystems are likely to be even more vulnerable than lowland species, because changes in climatic conditions appear to be more pronounced at higher elevations (Vuille *et al.*, 2008). With exceptionally high environmental heterogeneity across relatively short spatial scales, Mt Kilimanjaro is a region of unparalleled diversity and endemism and a global centre of speciation (Myers *et al.*, 2000; Hemp, 2006a; 2006b). Restricted range size of many tropical species is likely to make them especially prone to extinction (Lovejoy and Hannah, 2005; Hemp, 2009; Herzog *et al.*, 2011). With climate warming the tropical East African mountain forests appear to be among the Earth's most ecologically vulnerable regions to climate change (Malcolm *et al.*, 2006).

The investigation and reconstruction of former vegetation dynamics unravels the ecosystem responses to climate change in the past and adds to the understanding of the state and functioning of today's ecosystems (Chiang, 2009). Any change in climatic parameters indispensably causes a change in the plant species composition and a latitudinal of elevational shift of vegetation belts. This close connection between climate and ecosystems allows the palynological reconstruction of past vegetation belt distribution on the slopes of mountains, such as Mt Kilimanjaro. Climate does not only have an influence on vegetation patterns but it is also a primary control of the soil profile characteristics (Berry *et al.*, 2006). Since geochemical composition of soils is strongly influenced by source area composition, wind transportation and post depositional weathering and pedogenesis (Chen *et al.*, 2006), *X-ray fluorescence (XRF)* data can add valuable information about past environmental changes and complement the pollen data.

The specific aim of this particular research is the reconstruction of the Late Glacial and Holocene vegetation and climate dynamics on Mt Kilimanjaro based on palynological and sedimentological data.

One interesting feature of the forests of Mt Kilimanjaro is the absence of a bamboo zone, which occurs on all other tall mountains in East Africa with a similarly high rainfall. Stands of *Sinarundinaria alpina* (Poaceae) are favoured by elephants and buffaloes but on Mt Kilimanjaro these mega-herbivores occur on the northern slopes, where it is too dry for a large bamboo zone to develop. *Sinarundinaria alpina* needs at least 1250 mm of annual rainfall (Dale, 1940; Lind and Morrison, 1974). In contrast to the dry northern slope, these wetter climate conditions exist on the southern slope of Mt Kilimanjaro. The existence of a bamboo belt seems to be closely related to the presence of mega-herbivores as observed on other East African mountains (Hemp, 2006b). Mega-herbivores are excluded from Mt Kilimanjaro's wet southern slope forests by topography and humans, who have cultivated the foothills for at least 2000 years.

Hence, this study focusses on the environmental and vegetation dynamics of the mountain ecosystems on the southern slope of Mt Kilimanjaro, Tanzania, with the particular aim to trace the existence and development of a bamboo zone. This high-resolution multiproxy palaeoecological analysis of the paleosol profile in the montane forest of the WeruWeru area is used to provide detailed insights into palaeoenvironmental variations. This will allow the identification of past climate influences and their potential impacts of the vegetation. The results can help improve the predictability of future ecosystem response to environmental change.

Study Site

Mt Kilimanjaro is a relict of an ancient volcano which was formed as part of the East African spreading zone. It is located 300 km south of the equator in Tanzania, near the border with Kenya and about 300 km west of the Indian Ocean (Fig. 1a). It rises from savanna plains at 700 m up to its glaciated summit at 5895 m above sea level (asl).

Vegetation

Mt Kilimanjaro has several different bioclimatic zones (Fig. 1b/1c): the dry and hot colline savanna belt surrounds the mountain base between 700 and 1100 m asl. Most of this area is used for crop production (maize, beans and sunflowers) or as meadows. Remnants of the former savanna woodlands (*Acacia, Terminalia, Grewia, Combretum)* are encountered mainly around Lake Chala in the eastern foothills and on the north-western side of the mountain. The submontane and lower montane forest belts between 1000 and 1800 m have been converted to coffee-banana fields, a special type of agroforestry called 'Chagga home gardens'. Remnants of the former forests of this belt (*Newtonia, Strombosia and Entandrophragma)* are mainly restricted to deep valleys and gorges. Montane tropical rain and cloud forests on Mt Kilimanjaro cover an area of about 1000 km^2. The WeruWeru 26 study site (03°07'18.1'' S, 37°16'17.7'' E) is located at 2650 m asl on the southern slope of Mt Kilimanjaro in the WeruWeru river area (Fig.1b/1c/1d). In the lower montane belt (1800-2000 m asl) of the WeruWeru area *Macaranga kilimandscharica*, *Agarista salicifolia* and *Ocotea* *umsabarensis* are the dominant tree species. This part of Kilimanjaro's forests is influenced by human activities such as fodder and wood collection and grazing by cattle.

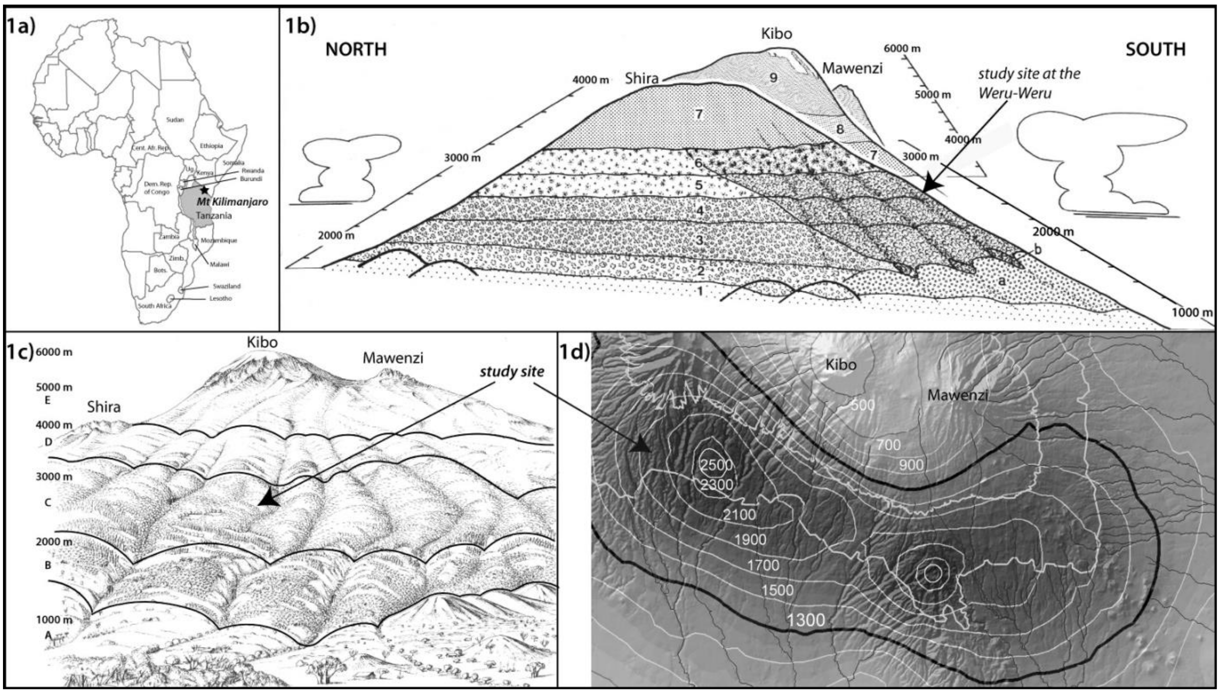

Figure 1: **a:** Map of Africa and location of Mt Kilimanjaro, Tanzania.

b: Schematic north-south profile showing the western slope of Mt. Kilimanjaro (Shira, Kibo, Mawenzi) with main altitudinal zones, vegetation types and location of Maundi Crater (arrow). 1: colline (savanna) zone; 2: submontane belt with semi-deciduous *Croton-Calodendrum* forest; a: coffee-banana plantations in the submontane belt on the southern slope; b: semi-deciduous submontane gorge forests on the southern slope; 3: lower montane belt with *Cassipourea* forests on the northern slope and *Agarista-Syzygium-Ocotea* forests on the southern slope; 4: middle montane belt with *Cassipourea* forests on the northern slope and evergreen *Ocotea* forests on the southern slope; 5: upper montane belt with *Juniperus* forests on the northern slope and *Podocarpus-Ocotea* forests on the southern slope; 6: subalpine belt with *Juniperus* forests on the northern slope and *Podocarpus* forests on the southern slope; 7: subalpine belt with heathlands (*Erica* shrub); 8: lower alpine belt with open *Helichrysum* cushion vegetation; 9: upper alpine and nival zone, mainly bare of vegetation. Changed after Hemp (2006a).

c: Altitudinal vegetation zones on the southern slope of Mt. Kilimanjaro and location of WeruWeru record a 2650 m asl (arrow). A: colline savanna zone, B: submontane cultivation zone, C: montane evergreen forest zone, D: subalpine zone, E: alpine zone

d: Rainfall distribution on the south eastern slope of Kilimanjaro. Changed after Hemp (2006b).

The study site at 2650 m is located in the mid montane belt which starts in the WeruWeru area at 2000m and end at 2800 m elevation. In this belt humidity reaches its maximum, indicated by the wealth of epiphytes and ferns, in particular filmy ferns and tree ferns. Evergreen forest species such as *Ocotea umsabarensis*, *Xymalos monospora* (Monimiaceae), *Ilex mitis* (Aquifoliaceae), and *Schefflera volkensii* (Araliaceae) build up the tree layer.

In the upper montane belt above 2800m the gymnosperm *Podocarpus latifolius* (Podocarpaceae), *Hagenia abyssinica* (Rosaceae) and *Prunus africana* (Rosaceae) form the tree canopy. Monodominant stands of *Erica excelsa* (Ericaceae) play also an important role in this zone, replacing *Podocarpus* and

Hagenia forests after fire, forming the actual upper closed forest line on the southern slope of Kilimanjaro at 3250 m.

Above this altitude, the *Erica* shrub land changes into *Helichrysum* dwarf cushion vegetation that extends up to 4500 m asl. The highest altitudinal region is only sparsely vegetated and the top of Kibo, the main summit, is covered with glaciers. More detailed description of these vegetation types are given by Hemp (2001; 2006a; 2006b).

Soil

In the montane belt of the WeruWeru area dark A horizons typically overlie brunified B horizons (Schrumpf, 2004). According to the Soil Taxonomy these soils can be classified as Andosols (Soil Survey Staff, 2010). Middle and lower parts of the soil profiles are often characterized by sequences of buried black, brown and mottled grey horizons and reddish iron pans which indicate hydromorphic processes. The basis of these paleosoils s is mostly formed by mottled grey clays above the volcanic parent material. Further uphill, the soils become less deep but still reveal polygenetic features up to an altitude of about 3150 m (Zech, 2006).

Climate

Due to its equatorial location the Mt Kilimanjaro area is characterized by a typical tropical day-time climate. The precipitation pattern follows the position of the intertropical convergence zone (ITCZ) and is strongly influenced by the activity of the Indian monsoon system. According to Köppen and Troll/Pfaffen (in Müller, 1989), Mt Kilimanjaro can be assigned to a seasonal dry tropical climate with two pronounced wet seasons: a short one in November/December and a longer one from March to May. Annual precipitation is modified by elevation and exposure to prevailing winds blowing inland from the Indian Ocean and varies on the wet southern slope from 500 mm at the mountain foothills to about 3000 mm at 2200 m asl. At higher altitudes of 2700 m, 3000 m and 4000 m asl, rainfall amounts to roughly 70 %, 50 % and 20 %, respectively of this annual maximum (Hemp, 2001; Hemp, 2006b). The northern slopes receive less annual rainfall. The mean annual temperature decreases from 23.4 °C at the foothills in Moshi, 813 m asl (Walter et al., 1975) linearly to -7.1 °C at the summit (Kibo, 5895 m asl) (Thompson et al., 2002). The lapse rate is about 0.6 °C/100 m which is typical for tropical mountains (Lauer, 1976). Frost occurs from 2700 m upwards (Hemp, 2006a).

The study site (Fig. 1b/1c) is located on the south-eastern slope of Mt Kilimanjaro, receiving about 2230 mm of annual rainfall with a mean annual temperature of 9 °C. Due to the prevailing SE monsoon, this area is dominated by the climate conditions of the southern slope of Kilimanjaro (Hemp 2006a) (Fig. 1d).

Material and method

Sampling and pollen analysis

In total 76 samples were taken from a 165 cm long WeruWeru 26 (WW26) sediment core. The core was obtained from a soil pit by hammering five 50 cm long metal cases consecutively into the pit wall. Due to the high content of un-decomposed material it was only possible to extract sediment from 15 cm below the soil surface downwards. The material was wrapped into plastic foil and kept under cool and dark conditions until transported back to the University of Göttingen. Samples were taken every 2 cm between 15 and 165 cm. For pollen analysis a sample volume of 0.5 cm³ was prepared in the lab applying the standard method (Faegri and Iversen, 1989). For calculation of pollen concentration one tablet of *Lycopodium clavatum* spores (18584 +/- 371) was added before sample processing. 29 samples (between 15 and 27 cm, and between 53 and 95 cm core depth) had to be prepared with the doubled amount of *Lycopodium* markers due to their high pollen concentration. The extracted pollen samples were mounted in glycerine jelly for pollen identification and counting. At least 300 pollen grains were counted for each sample. Pollen determination was carried out using light microscopy with 400x and 1000x magnification. The references consulted included our own reference pollen collection of Tanzania of about 1500 taxa, the online African Pollen Database (Lézine, 2001), and the African Tropical Pollen book (Assemien et al., 1974).

X-ray fluorescence spectroscopy (XRF)

Non-destructive XRF scanning was performed at the Geography Institute at the University of Bremen. An ITRAX Corescanner (COX Analytical Systems) provided semi-quantitative analyses of the chemical composition (Croudace *et al.*, 2006) at 0.1 cm depth intervals between 6 and 164 cm (ITRAX Corescanner instrument settings: Mo X-ray tube at 30kV, 26mA, step size 1mm, count time 20s). Due to the rough sediment surface no continuous XRF scanning was possible, therefore measurements with a validity of 0 (no measurement possible) were excluded from further analysis. A Detrended Correspondence Analysis (DCA) was performed with the all element analysed by the XRF scan in order to derive the length of the underlying environmental gradient (Jongman *et al.*, 1987; ter Braak and Šmilauer, 1997). Afterwards we applied a principle component analysis (PCA). The variables were standardized and centred.

Chronology

In total 13 samples (Tab. 1) were AMS dated; 11 at the Physical Institute of the University Erlangen-Nürnberg/Germany. Two samples were AMS dated by Beta Analytic in Miami, Florida/USA. Five AMS sates were derived from bulk samples, and eleven dates from charcoal particles. According to the results, samples from 17 to 52 cm core depth can be assigned to the Holocene. Samples between 66 and 158 cm core depth belong to the Late Pleistocene.

Table 1: List of radiocarbon dates and calibrated ages from WeruWeru 26

Lab Code	Depth (cm)	Sample description	14C Age (B.P.)	B.P. Error	cal. Age (B.P.)
Erl-16288	17-18	bulk	907	42	832
Erl-16968	23-24	charcoal	1715	45	1625
BETA 330270	41-42	bulk	2550	30	2682
Erl-16289	47-48	charcoal	81	42	110
Erl-16969	49-50	charcoal	-594	126	NA
BETA 330271	51-52	bulk	6060	40	6915
Erl-16970	66-67	bulk	35971	475	41111
Erl-16285	77-78	charcoal	40068	676	44008
Erl-16971	83-84	charcoal	31744	300	36231
Erl-16286	95-96	bulk	27619	221	31734
Erl-16972	101-102	charcoal	44724	1011	47892
Erl-16973	105-106	charcoal	22727	262	27400
Erl-16287	157-158	charcoal	47604	2642	NA

Pollen analysis

The pollen diagram was compiled and analysed with the program C2 (Juggins, 2011). The percentage diagram is based on the pollen sum which includes all pollen taxa and excludes fungi and fern spores. For the calculation of zones the CONISS (constrained cluster analysis by sum-of-squares) method was used. Samples without pollen were excluded from the CONISS to avoid biases. The classification of pollen taxa into vegetation zones (savanna, semi-deciduous and evergreen forest, *Erica* shrub and open vegetation) is based on studies of Hemp (2006a).

Results

Chronology

Thirteen AMS radiocarbon dates (Table 1) provide the chronological control for the sediment core from the WeruWeru soil profile. The six dates in the upper ~60 cm of the profile indicate Holocene deposits. The sediments between ~60 and ~160 cm soil depth seem to be of glacial origin. Due to the high amount of fine roots and the very brittle sediment properties in some parts of this core it is very likely that some dates are caused by contamination. This applies probably to the dates that indicate a substantially younger age (grey coloured in Fig. 3 and Fig. 4) than the surrounding ones. The abrupt change in age scale between 52 and 66 cm, from 6.9 to 41.1 calibrated (cal) ka BP strongly proposes the loss of sediment in-between. This period is marked as hiatus in the following pollen and XRF data.

XRF spectroscopy and pollen analysis

The rather short gradient length revealed by the DCA (1.717) suggests that a PCA is most likely to bring out the most influencing elements and relevant patterns inherent in the chemical composition.

The PCA (Fig. 2) of the most important elements analysed by XRF spectroscopy shows a gradient along PC1 (first principle component) which represents 28.0 % of the variability of the data set. While Mg, Al, incoherent/coherent scatter and Fe are more correlated with PC1, Rb , K and Ti are more correlated with PC2 (representing 17.4 % of the data variability), all other element show a correlation with both PCs. Ca and Fe are positively correlated with PC1. Contrariwise, Rb, Sr, Pb and Zr and negatively correlated with this PC.

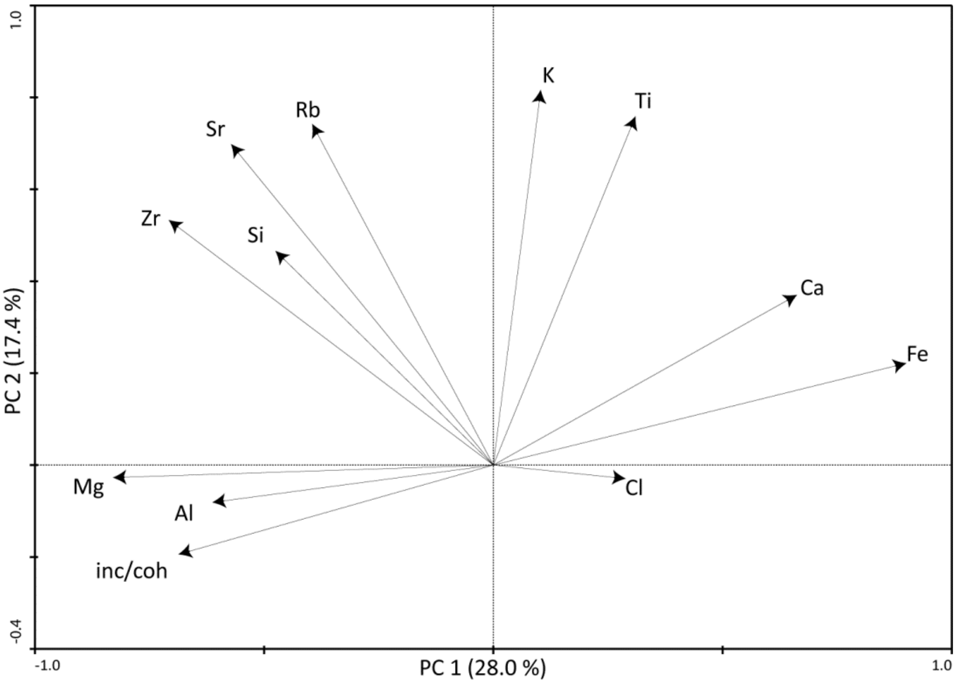

Figure 2: Principle Component Analysis (PCA) of the most important elements. The first principle component 1 (PC 1) represents 28.0 % of the total variability of the chemical composition; the second principle component (PC 2) represents 17.4 %. The ratio between the incoherent (Compton) and coherent (Rayleigh) scatter, inc/coh, represents the variation of relative proportion of light to heavy elements, thus it is a semi quantitative indicator of organic matter (Jenkins, 1999).

Figure 3 depicts the percentage pollen diagram including the sums of the most representing taxa grouped into the corresponding vegetation types. The calculation of the pollen zones (WW29 I – VI) is based on the pollen data but they are also plotted into the diagram of the XRF data (Fig. 4) which shows the element ratios and inc/coh.

Zone WW26-I (164 – 123 cm): Pollen grains in this zone are absent. Inc/coh drops from a ratio of 5 down to 3 and then increases again. The Zr/Rb ratio remains rather constant between 15 and 30. Rb/Sr fluctuates strongly between 0.2 and 1.2. The Fe/Ti ratio starts off at values between 5 and 10; between 140 and 130 cm depth the ratio peaks with values around 30.

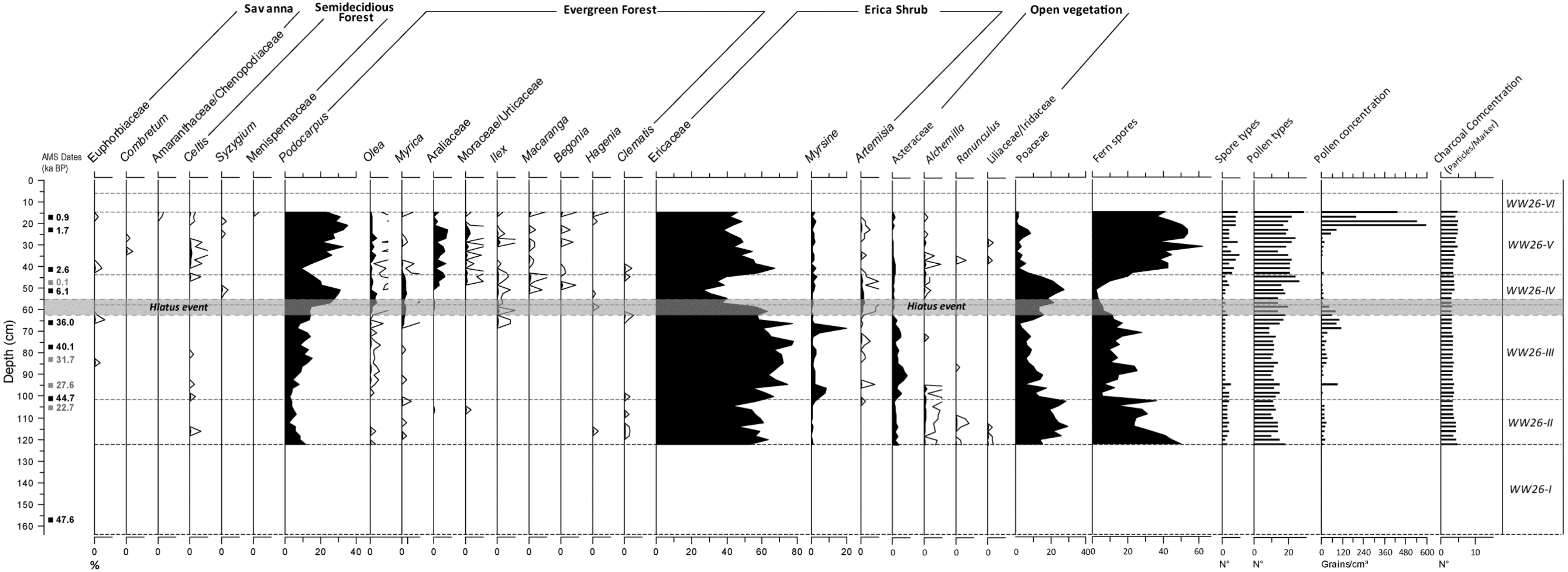

Figure 3: Percentage pollen diagram of selected taxa, charcoal concentration and number of all identified pollen and spore taxa from the Weru Weru sediment record. The most important and frequent taxa are grouped into potential natural vegetation types of (colline) savanna, (submontane) semi-deciduous forest, (montane) evergreen forest, (subalpine) Erica shrub and open vegetation. % is based on a total pollen count of at least 300 grains per sample. Low % values are multiplied by 10 and shown as exaggeration line. The grey bar between 55 and 63 cm core depth indicates the likely period for an hiatus event.

Zone WW26-II (123 – 102 cm): The pollen signal from the savanna and the semi-deciduous forest (*Celtis*) are very low. Evergreen forest pollen accounts for about 18 %, mainly represented by *Podocarpus,* and a few records of *Olea, Myrica*, Moraceae/Urticaceae, *Hagenia* and *Clematis*. Taxa of the Erica zone such as Ericaceae and *Myrsine* constitute most (50 to 60 %) to the pollen signal. The sum of open vegetation taxa is about 2 %. Poaceae pollen grains a very abundant (~18-28 %). And Asteraceae are present with ~3 %. Fern spores represent 30 to 50 %. The pollen concentration is constant. The inc/coh ratio is around 4.5. Zr/Rb shows a sharp increase to 150 and decreases again to values between 40 and 80. Rb/Sr is low (<0.3). The values for Fe/Ti (~ 10) remain stable.

Zone WW26-III (102 – 58 cm): The pollen signal of the savanna taxa (Euphorbiaceae) is still low; the semi-deciduous forest is also only represented by *Celtis*. The sum of the evergreen forest belt increases from 10 to 20 %, which is mainly caused by a rise in *Podocarpus, Olea* and *Myrsine* but also by the first appearance of *Ilex*. Araliaceae and Moraceae/Urticaceae, which were present in the previous zone, disappear. Taxa of the Erica belt are the major component of this zone accounting for more than 60 % of the pollen. *Myrsine* shows a clear increase and *Artemisia* pollen grains become more abundant. Poaceae, *Alchemilla* and Liliaceae/Iridaceae decline in the pollen record. The sum of the open vegetation also shows a slight decrease. Asteraceae pollen grains are more abundant and account for about 6 to 10 %. The abundance of fern spores varies strongly between 5 and 30 %. Although initially low, the pollen concentration shows an abrupt peak at 95 cm core depth starts increasing in the upper third of the zone. After a first increases to a ratio of about 5 inc/coh levels off between 4.5 and 5. Zr/Rb varies strongly (40 to 80) in the lower half of this zone, at 72 cm it drops to a ratio of around 20. Rb/Sr remains low (<0.3). The value for Fe/Ti (~ 10) remains stable but increases at about 65 cm to 15.

Zone WW26-IV (58 – 44 cm): Pollen grains from the savanna and the semi-deciduous forest are rare. Taxa of the evergreen forest (especially *Podocarpus, Olea* and *Myrsine*) increase considerably and account for up to 40 % of the pollen record. Araliaceae and Moraceae/Urticaceae also increase towards the end of this zone. *Macaranga* and *Begonia* appear for the first time. While Ericaceae decline strongly *Artemisia* increases. The taxa sum of the *Erica belt* decreases to about 30 %. Taxa of the open vegetation slightly increase and Poaceae pollen are much more abundant (about >20 %). Asteraceae pollen declines to 3 %. The abundance of fern spores also drops to about 2 % and rises again strongly (25 %) towards the upper part of this zone. The pollen concentration is consistently low in this zone. Inc/coh remains at a ratio of 4.5. Zr/Rb shows an abrupt peak of 180 at 48 cm and drops back to the initial value of 20. Rb/Sr shows an increasing trend with fluctuation towards the upper part of this zone. Fe/Ti increases strongly from 10 to 49 which is also the maximum value recorded.

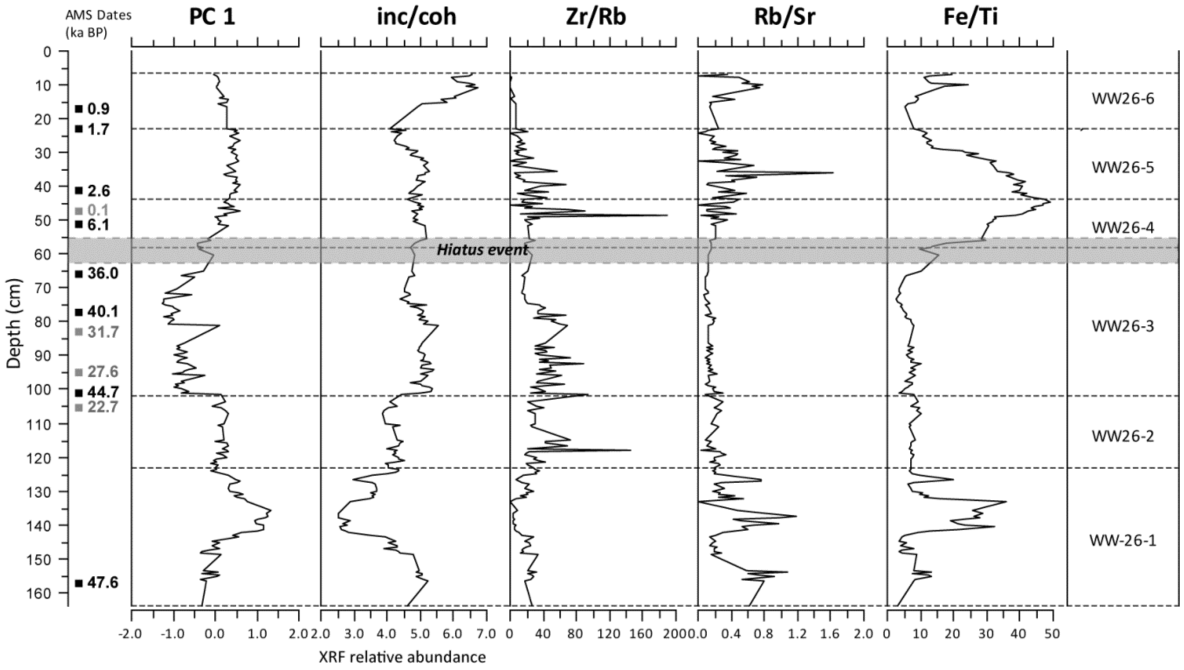

Figure 4: Profiles of the Principle Component 1 (PC1) and the XRF elemental analyses of the sediment from WeruWeru at 2650 m. XRF data are plotted as ratios. The ratio between incoherent and coherent scatter can be interpreted as a measure of organic content.

Zone WW26-V (44 – 23 cm): Pollen grains of the savanna and the semi-deciduous forest become slightly more abundant but remain generally rare. After an abrupt decline at the lower part of this zone (12 %), taxa of the evergreen forest increase again (40 %). Besides *Podocarpus* (~ 30 %), especially Araliaceae, Moraceae/Urticaceae and *Ilex* pollen grains become more abundant. The contribution of *Myrica* (~ 1 to 2 %) is low in comparison to the previous zone. The taxa sum of the Erica shrub reaches ~ 70 % at the lower part of the zone and decreases again to 50 % in the upper part of the zone. Changes in Ericaceae pollen grains are mostly responsible for this trend. Poaceae pollen grains decline to <10 %. By contrast fern spores reach peak values of 60 % and are continuously abundant in this zone. The pollen concentration, initially low, increases strongly in the uppermost samples reaching the highest values overall of this record. Inc/coh slightly declines to 3.5. Zr/Rb fluctuates strongly between 0 and 50. Sr/Rb varies between 0 and 0.8 with a peak (1.6) at 34 cm profile depth. A strong decrease is recorded in Fe/Ti which drops from the peak value of 49 down to 8.

Zone WW26-VI (23 – 6 cm): Pollen grains in this zone are absent. Inc/coh rises to 6, while Zr/Rb goes towards zero. Rb/Sr and Fe/Ti show a sharp increase in the uppermost samples of this zone.

The plotted principle component (PC1) plotted with the XRF elemental ratios (Fig. 4) shows an oppositional trend to inc/coh. The pollen and spore diversity increases towards younger samples. Bamboo pollen grains were not represented at all. The pollen concentration is highest in the uppermost samples above 23 cm core depth. It is also elevated between 67 and 63 cm depth, just below the assumed hiatus. The charcoal concentrations are relatively constant throughout the sediment record.

Interpretation and discussion

The combination of a high resolution pollen record and XRF data from a montane forest site on Mt Kilimanjaro allows detailed reconstruction of vegetation and climate during the late Glacial and the Holocene. The high number of radiocarbon dates permits the chronological placement of the hiatus to the LGM period and the Deglaciation. Since the geochemical composition of soils is strongly influenced by source area composition, wind transportation and post depositional weathering and pedogenesis (Chen *et al.*, 2006), the XRF data add valuable information about past environmental changes and complement the pollen data. The first principle component (PC1) reduces all allochtonous minerogenic input parameters to one proxy (Shotyk *et al.*, 2001; Guyard *et al.*, 2007). The ratio between the incoherent (Compton) and coherent (Rayleigh) scatter, inc/coh, represents the variation of relative proportion of light to heavy elements, thus it is a semi quantitative indicator of organic matter (Jenkins, 1999). The fact that PC1 shows an opposite trend to the organic matter content (inc/coh) suggests that PC1 can be interpreted as an indicator of minerogenic input. Therefore, an increase in this PC1 indicates an increase in runoff or aeolian supply.

The Rb/Sr ratio may be used as an indicator of chemical weathering in relict palaeo-soil profiles (Dasch, 1969) and seems to respond to the intensity of pedogenesis (Chen *et al.*, 1999). Chemical weathering during periods of warmer and more humid climate conditions would have increased concentrations of relatively insoluble components by the removal of soluble minerals from the soil. Therefore, a relative enrichment of Rb over Sr can happen in paleosoils due to the removal of Na- and Ca- containing minerals. Some acid leaching experiments have shown that the major factor in the increase of an Rb/Sr ratio is loss of strontium during weathering (Chen *et al.*, 1998). This means that the Rb/Sr ratio can be used to estimate pedogenic intensity which is related to monsoon conditions. During periods of enhanced monsoon activity winds bring moist air from the Indian Ocean and increase the precipitation on the East African continent and result in changes in soil geochemistry and the vegetation. Low pH and anoxic conditions due to increased rainfall might cause an upward migration of Fe as acidic and reducing conditions are most favourable for metal solubilisation (Chuan *et al.*, 1996).

During the earliest period recorded in the WeruWeru profile (165 to 123 cm), which can be assumed to date around 47 ka BP, an increase of minerogenic input and a concurrent decrease in organic matter indicates a shift to wetter conditions. The rise in Fe/Ti, indicating a relative increase in Fe, proposes anoxic and acidic soil conditions. Also the relatively high Rb/Sr ratio suggests increases soil weathering due to a rather humid climate. Zr is enriched in heavy minerals in sediments, especially in zircon (ZrSiO4) (Fralick and Kronberg, 1997). Rb is a typical dispersed element that is not associated with any specific Rb-bearing mineral but is present in K-containing minerals (Heier and Billings, 1970). The two elements are closely related to grain-size fractions in fine-grained siliciclastic sediments (Dypvik and Harris, 2001). Zr is enriched in the coarser fraction, whereas Rb tends to be enriched in the finer fraction. As a result, Zr/Rb ratios increase remarkably from the finest to the coarsest fraction. Aeolian dust deposition as well as erosion events as caused by high rainfall events lead to a change in the grain size fractions. Hence, the increased grain size may be an indicator for higher (monsoonal) wind intensities and/or increased precipitation.

The driest conditions occurred between 44 and 40 ka BP with very low minerogenic input, and hence increased organic material in the soil. Also, the low Rb/Sr and Fe/Ti ratios propose drier conditions. The vegetation indicates a warming trend. The *Erica* shrub spreads and *Myrsine* as well as *Artemisia* become more abundant elements within this vegetation type. Consequently, ferns and alpine vegetation were pushed back. It seems that the climate conditions were not yet warm enough and too dry for montane forest taxa to ascend. Although *Podocarpus* and *Olea* remain frequent, other forest taxa are not recorded during this period anymore (*Hagenia, Clematis*, Moraceae/Urticaceae). This may be due to a change in composition of the forest plant community characterized by dominance in more drought tolerant taxa such as *Podocarpus* and *Olea* and a decline in more drought sensitive taxa. The continuous abundance of these two taxa throughout cool and dry climate conditions was also recorded from the Rukiga Highlands in Uganda (Taylor, 1990) and the Kashiru Swamp, Burundi (Bonnefille and Riollet, 1988). However, both sites also show abundant *Hagenia* throughout the late Glacial which is not the case for the montane forest of Mt Kilimanjaro as indicated by this WeruWeru record and Maundi crater (Schüler *et al.*, 2012b).

After about 39 ka BP the XRF data suggest a weakening of the winds and increasingly wetter climate conditions. This trend was also recorded at Lake Malawi (Brown *et al.*, 2007). Due to the absence of data during the LGM and the deglacial in our soil profile we can only speculate on what caused this hiatus. Since it is generally known from tropical East Africa that the LGM was a very dry and cold phase followed by an abrupt onset of very wet conditions (Taylor, 1990; Olago, 2001 and literature herein; Schüler *et al.*, 2012b), the concurrence of rather loosely vegetated soil as well as sudden and strong precipitation events is very likely to have caused major erosion, and hence the loss of surface sediment.

Very abundant ferns as well as the spread of montane forest indicate increasingly warm and wet climate conditions during the mid to late Holocene. *Podocarpus, Olea*, Moraceae and Araliaceae dominate the forest plant community. This taxa composition could also indicate the presence of *Cassipourea* forests which do presently not exist on the northern slopes of Mt Kilimanjaro. These *Cassipoura* forests (with *Cassipourea malosana*, *Tecleas implicifolia*, *Fagaropsis angolensis* and *Olea capensis*) are today typically found in the lower and middle montane forest belt of the drier, northern slope of Mt Kilimanjaro. Their abundance on the southern slope in the early to mid-Holocene proposes the prevalence of substantially drier climate conditions during this time period. Yet, it needs to be investigated whether the high proportion of *Podocarpus* found in the pollen record during this time, could be *Podocarpus falcatus* which is today exclusively found on the northern slopes. The shift from abundant *Myrica* during the early Holocene to forests with high abundance of Araliaceae and *Macaranga* replacing *Myrica* in the mid Holocene was also observed on Mt Kenya (Olago *et al.*, 1999) and in the montane forests of southwest Uganda (Taylor, 1990). The order of taxa occurrence during the Holocene demonstrates the gradual upward shift of forest zones. *Iex*, today primarily recorded found in the mid montane forest (2300 – 2600 m asl) on Kilimanjaro, occurs earliest in the pollen record, followed by *Macaranga* and *Begonia* which are both most abundant in the lower montane forest (1900 – 2200 m asl) (Hemp, 2006a). Ivory et al. (2012) also recorded the persistence of more drought tolerant taxa *Podocarpus, Erica*, and *Olea* during drier periods at Lake Malawi and more abundant closed-canopy, drought-intolerant trees as *Macaranga* and Moraceae as well as shade-loving herbs (Urticaceae) during more humid times. Taxa of the submontane, semi-deciduous forest (such as *Celtis* and *Syzygium*) also ascend to higher elevations.

The XRF data (Rb/Sr and Fe/Ti) indicate wet soil conditions in the early to mid-Holocene, which immediately follows the late Glacial in our record due to the hiatus. The high abundance of montane forest which was fostered by more humid climate conditions supports this assumption. *Ilex aquifolia,* known to require moist and shady environments (Peterken, 1966; Ellenberg *et al.*, 1991), became abundant which indicates that forests were already at a late successional stage. Taylor (1990) also reports *Ilex* only with the beginning of the early Holocene.

Several proxies have been proposed to reflect variations of monsoon climate in the continental and atmospheric systems. Grain size variations of the coarse dust fraction indicate the relative wind strength. The Zr/Rb ratio may be interpreted as a proxy of mean grain size and may therefore serve as an index of strength of monsoon winds. However, at our study site an increase of grain size could also originate from the input of erosional material which could be caused by increased precipitation. Hence, the information derived from the Zr/Rb ratio has to be accomplished by the Fe/Ti ratio, which is as measure of anoxic and acidic soil conditions, and consequently wetter soil conditions. We can observe two phases of enhanced wind intensity and/or increased precipitation at the WeruWeru. The first phase dates between approximately 40 to 46 ka BP. The combinations of increased relative grain size and rather oxic soil conditions (according to low Fe/Ti) propose enhanced monsoonal winds. This coincides with findings by Trauth *et al.* (2003) who record enhanced North African Monsoon between 25ka BP and 50 ka BP. Brown et al. (Brown *et al.*, 2007) also report intensified north-easterly winds at Lake Malawi which they propose to be triggered by a southwards displacement of the Intertropical Convergence Zone. A stronger monsoon activity at Kilimanjaro is also demonstrated by wetter conditions at the onset of this period around 47 ka BP as indicated by high minerogenic input as well as anoxic and acidic soil conditions. Despite no clear evidence for high lake levels in the Central Kenyan Rift (Lakes Naivasha, Nakuru, and Elmenteita) between 60 and 30 ka BP (Richardson and Dussinger, 1986; Trauth *et al.*, 2001; 2003), cool and rather humid conditions around 45 ka BP are also reported from Maundi crater on Mt Kilimanjaro (Schüler *et al.*, 2012b) and from Mt Kenya (Olago *et al.*, 1999). While strong monsoon winds continued after ~ 45 ka BP, the climate conditions gradually became drier. Rb/Sr ratio suggests low soil weathering intensity probably due to less precipitation and a general cooling. The amount of minerogenic input decreased and the vegetation was characterized by open *Erica* shrub land with a high abundance of grasses, Asteraceae and ferns. Montane forest was shifted to lower elevation on Kilimanjaro. The assumption that the vegetation zones were generally shifted downslope was also proposed for Mt Kilimanjaro by Zech (2006).

The second phase of increased mean grain size during the mid-Holocene coincides with wetter soil conditions. Therefore, this observation may be due to an increase in rainfall and resulting erosion. According to the elevated Rb/Sr and Fe/Ti ratios and more abundant and divers montane forest as well as ferns the stronger winds are accompanied by increasingly wetter conditions. Increased northerly winds are reported from Lake Malawi around 4 ka BP (Konecky *et al.*, 2011). At ~ 4 ka Thompson et al. (2002) observe a most distinct dust input in the northern ice field of the Kilimanjaro and the $\delta 18O_{ice}$ record of the ice core suggests this to be caused by very abrupt cooling. In contrast, the 25 ka branched isoprenoid tetraether (BIT) index of Lake Challa at the eastern foot of Kilimanjaro suggests heavy convective precipitation around 5 ka (Verschuren *et al.*, 2009), while the Challa $\delta 18O_{diatom}$ record also indicates aridity (Barker *et al.*, 2011). Considering the cooler mid-late Holocene climate suggested by the Tanganyika TEX86 record (Tierney *et al.*, 2008), one explanation is that evaporation was greatly enhanced because a weak south eastern monsoon resulted in a reduced long rainy season and protracted main dry season. Short but strong precipitation events during the rainy season causing temporarily swampy soil conditions on the slopes of Kilimanjaro might explain the elevated Fe/Ti and Rb/Sr ratios in the soil profile while prolonged dry seasons repressed taxa typical for humid montane forest.

The late Holocene is characterized by the predominance of montane forest mainly represented by *Podocarpus, Olea*, Araliaceae and Moraceae/Urticaceae. Ferns are very abundant indicating persistently very humid conditions which are also supported by the XRF data (Rb/Sr and Fe/Ti).

Indicators of open vegetation (Poaceae, and Asteraceae) are strongly reduced suggesting a closed canopy cover and rather dense forest vegetation. Since Erica shrub decreases proposing an extended distance of this vegetation type to the study site, and submontane taxa increase which indicates the approximation of this forest type, we assume a general ascend of vegetation along the slope. The taxa contribution of the youngest sample dated to the late Holocene about 1 ka BP in this record is in accordance with the modern pollen-rain from this site (Schüler *et al.*, 2012a) indicating that the forest composition resembled the one found here today.

Although, fires occur regularly throughout the investigated time period, they do not seem to play an important role in the vegetation dynamics.

Regarding the existence of a bamboo belt, as it is found on other East African mountains with suitable climate conditions and the presence of mega-herbivores (elephant and buffalos); Mt Kilimanjaro seems to be an exceptional case. Despite the present suitably humid conditions of its southern slope, the palaeoecological reconstructions have shown that a bamboo belt did not exist on, at least not during the last Glacial. Based on our WW26 data we can assume that the climate was too dry and possibly too cold for bamboo until 2 ka BP, when humans started to settle on Kilimanjaro. This would support the theory that a interplay by biotic and abiotic conditions (missing mega-herbivores due to anthropogenic influence and climatic conditions) are the reason for the missing bamboo belt on Kilimanjaro.

Conclusions

This study presents the palynological and sedimentological outcome of the WeruWeru 26 palaeo-soil profile record. The record of this study site is located in the montane forest on the southern slope of Mt Kilimanjaro describes the last ca 50 ka of past vegetation and climate dynamics in high resolution and therefore allows detailed reconstruction of the vegetation response to environmental changes. Our results suggest that past climate change caused the vegetation belt to shift along the elevational gradient. Nevertheless, during the Glacial the major taxa of the montane forest today were present which means that Mt Kilimanjaro served as a forest refugia as reported from other Easter Arc Mountains. Our results also indicate the presence of more drought tolerant *Cassipourea* forests at the study site during the early Holocene which today only exists on the northern slopes. In the course of the Holocene, the taxa of montane forest of the wetter southern slope, which also form the forests today, become more abundant. This succession of different forest types proposes that past environmental changes did not only cause an elevational shift of vegetation but also profound re-structuring of the forest ecosystems. Apart from the pollen data, also the results of the geochemical analysis of the soils profile suggest different phases of enhanced wind intensities and rainfall which can be associated with enhance monsoonal activities observed at other study sites in tropical East Africa. Further, the palynological study give no indication for the presence of a bamboo belt on the southern slope of Mt Kilimanjaro as it is found on other East African mountains with suitable climate conditions. This investigation and reconstruction of former vegetation and climate dynamics unravels the ecosystem responses to climate change in the past and adds to the understanding of the state and functioning of the ecosystems of Mt Kilimanjaro. This knowledge will allow for a more refined and comprehensive prediction of future changes in biodiversity and biogeographical patterns.

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Chapter 5

Weighted-Averaging Least Square Regression (WA-PLS) pollen-based temperature and precipitation inferences for the montane forest of Mt Kilimanjaro during the last Glacial and the Holocene

(To be submitted)

Abstract

The relationship between modern pollen rain taxa and measured environmental variables was explored along the elevational gradient of the southern slope of Mt Kilimanjaro, Tanzania. Pollen assemblages in 28 pollen traps positions on 14 vegetation plots were identified and their relationship with measured environmental variables was examined using multivariate statistical methods. Canonical correspondence analysis revealed that the mean annual temperature (MAT) and mean annual precipitation (MAP) each accounted for significant fractions of the variation in pollen taxa. A training set with 107 modern pollen taxa was used to derive transfer functions for MAT and MAP using weighted-averaging-partial-least-squares (WA-PLS) techniques. The models were developed to infer the mean precipitation and mean temperature estimates of the Late Glacial and the Holocene on Mt Kilimanjaro. Therefore, the transfer functions were applied to a fossil pollen record from the montane forest of Mt Kilimanjaro to reconstruct the past vegetation and climate dynamics.

Keywords: pollen, climate reconstruction, transfer function, modern pollen-rain, East Africa, montane forest

Introduction

Many environmental issues, like global warming or altered precipitation patterns, have increased the interest in fossil species assemblages as indicator of the palaeo-environment. In palaeoecology the direct measurement of environmental variables is impossible; consequently there is the need to resort to indirect methods. Fossil taxa assemblages can provide a record of the palaeoenvironment since each biological species requires particular environmental conditions for regeneration, establishment and growth. Today, this principle idea is primarily used in biomonitoring (Spellerberg, 1991). Nevertheless, it is also possible to infer the past environmental conditions at a site from the species composition that occurred there. Fossil taxa records are valuable for obtaining a historical perspective of current environmental problems such as acid rain (Battarbee, 1984) and global warming (Fritz *et al.*, 1991; Walker *et al.*, 1991).

The use of numerical techniques in palaeoecology, including transfer functions, requires several assumptions: a) climate is the main cause of changes in the pollen record, b) vegetation of the past, as reflected in the observed pollen assemblage, has responded in a constant way to climate and has thus been in equilibrium with the climate and c) the relationships implicit in the mathematical technique used to estimate the transfer function represent adequately the relationship between climatic variables and pollen. Webb and Bryson (1972), who were the first to develop transfer function for the pollen assemblage in lake sediments, developed their transfer function based only on 8 pollen types since they excluded many pollen types for a variety of reasons (local origin, function of human disturbance, pollen under- or overrepresentation of taxa). Bonnefille et al. (1992), who made quantitative estimates of glacial temperatures from palynological data in Burundi also eliminated taxa with values less than 2 % and taxa that occurred in less than 10 % of the total number of samples.

As mentioned above, it requires a representative training set consisting of data on species assemblages and associated environmental measurements. Relationships between species and environmental variables are generally nonlinear. Because of Shelford's law of tolerance (Odum, 1971) and niche-space partitioning (Whittaker *et al.*, 1973), species abundance or probability of occurrence is often a unimodal function of the environmental variables.

Palaeoecological transfer functions share the several characteristics (Sachs *et al.*, 1977). They produce calibrated quantitative estimates of environmental parameters of a past environment. They make use explicit algebraic methods to formulate these estimates. The applied algorithms rely on multivariate techniques to analyse multicomponent fossil data. The transfer functions are calibrated from a training data set, an adequate sample of modern distributional data. The calibrated function is then applied to older samples to estimate environmental parameters for past times.

In palaeoecology, the weighted averaging (WA) method gained popularity because it combines niche-space partitioning with empirical predictive power (Birks *et al.*, 1990; Fritz *et al.*, 1991; ter Braak and Juggins, 1993). Ter Braak and Juggins (1993) could show that the addition of a partial least square regression (PLS) to the weighted averaging (WA) method could even further improve the predictive power. They demonstrated that the application of weighted averaging partial least square regression (WA-PLS) could reduce the prediction error by up to 70 %. The main advancement of the WA-PLS procedure is that it is unimodal-based (since it is based on the niche-space partitioning concept and ecological optima of species) unlike the PLS which is linear-based (ter Braak and Juggins, 1993; Birks, 1995).

This study aims at the development of a plausible and significant transfer functions through the calibration of the relationships between pollen assemblages, vegetation belts and climate in the Kilimanjaro area. The transfer functions are then applied to the fossil WeruWeru 26 pollen record to reconstruct the past vegetation and climate dynamics of equatorial East Africa and compare the results to other climate reconstruction from equatorial East Africa.

Study Site

Mt Kilimanjaro is a relict of an ancient volcano which was formed as part of the East African Rift Zone. It is located at the border to Kenya 300 km south of the equator in Tanzania and about 300 km west of the Indian Ocean (Fig. 1a). It rises from savanna plains at 700 m up to its glaciated summit at 5895 m asl.

Vegetation

Mt Kilimanjaro has several different bioclimatic zones (Fig. 1b/1c): the dry and hot colline savanna zone surrounds the mountain base between 700 and 1100 m asl. Most of this area is used for crop production (maize, beans and sunflowers) or as meadows. Remnants of the former savanna woodlands (*Acacia, Terminalia, Grewia, and Combretum)* are encountered mainly around Lake Chala in the eastern foothills and on the north-western side of the mountain. The submontane and lower montane forest belts between 1000 and 1800 m have been converted to coffee-banana fields, a special type of agroforestry called “Chagga home gardens”. Remnants of the former forests of this belt (*Newtonia, Strombosia and Entandrophragma)* are mainly restricted to deep valleys and gorges. Montane tropical rain and cloud forests on Mt Kilimanjaro cover an area of about 1000 km^2. The WeruWeru 26 (WW26) study site (03°07’18.1’’ S, 37°16’17.7’’ E) is located at 2650 m asl on the southern slope of Mt Kilimanjaro in the WeruWeru river area (Fig.1b/1c). In the lower montane zone

(1800-2000 m asl) of the WeruWeru area *Macaranga kilimandscharica*, *Agauria salicifolia* and *Ocotea umsabarensis* are the dominant tree species. This part of Kilimanjaro's forests is influenced by human activities such as fodder and wood collection and grazing by cattle. WW26 is located in the mid montane zone, which starts in the WeruWeru area at 2000m and end at 2700 m elevation. In this zone humidity reaches its maximum, indicated by the wealth of epiphytes and ferns, in particular filmy ferns and tree ferns. Evergreen forest species such as *Ocotea umsabarensis*, *Xymalos monospora*, *Ilex mitis* and *Schefflera volkensii* build up the tree layer. More detailed description of these vegetation types are given in Chapter 1 and are published by Hemp (2001; 2006a; 2006b).

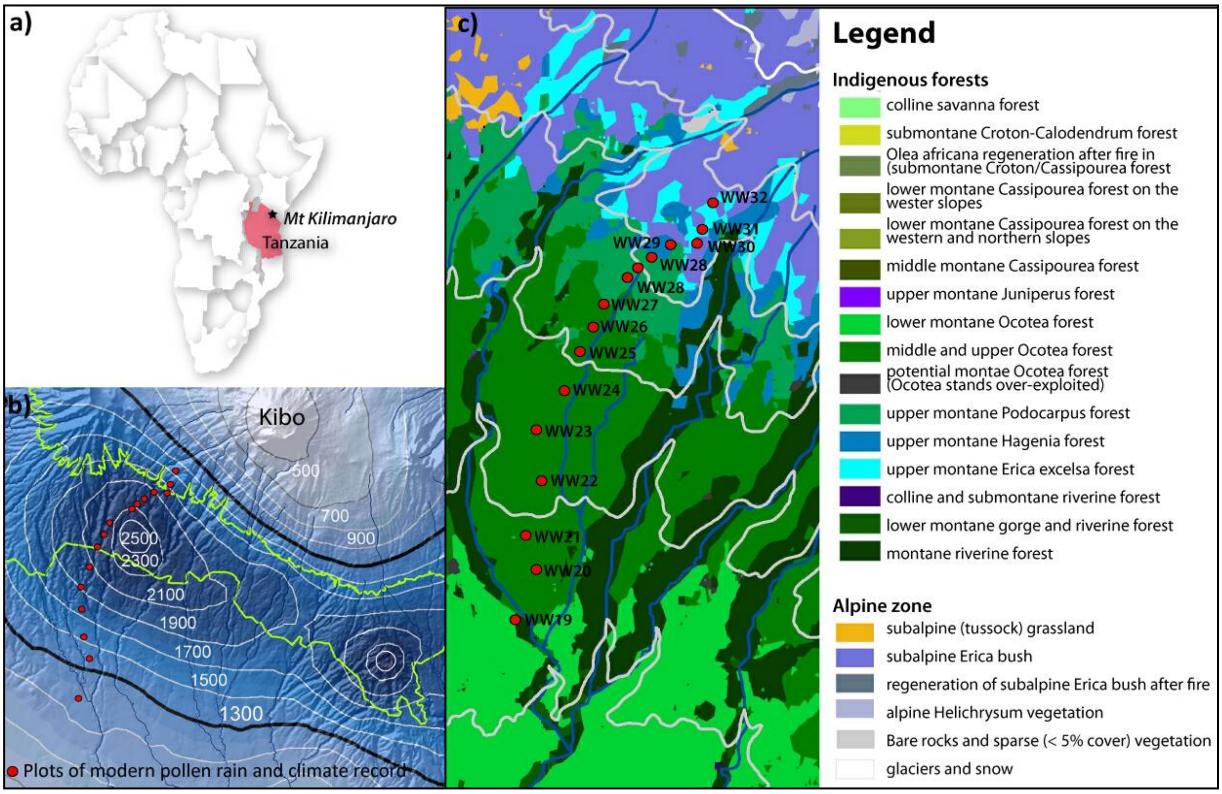

Figure 1: a) The study site Mt Kilimanjaro in northern Tanzania. b) Mean annual precipitation gradient on the southern slope of Mt Kilimanjaro. Red circles indicate the WeruWeru transect sites, where the modern pollen-rain and the climate variables were recorded. c) The vegetation types found on the southern slope of Mt Kilimanjaro. Again, red circles indicate the WeruWeru transect sites.

Climate

Due to its equatorial location the Mt Kilimanjaro area is characterized by a typical tropical day-time climate. The precipitation pattern follows the position of the intertropical convergence zone (ITCZ) and is strongly influenced by the activity of the Indian monsoon system. According to Köppen and Troll/Pfaffen (in Müller, 1989), Mt Kilimanjaro can be assigned to a seasonal dry tropical climate with two pronounced wet seasons: a short one in November/December and a longer one from March to May. Annual precipitation is modified by elevation and exposure to prevailing winds blowing inland from the Indian Ocean and varies on the wet southern slope from 500 mm at the mountain foothills to about 3000 mm at 2200 m asl (Fig.1b). At higher altitudes of 2700 m, 3000 m and 4000 m asl, rainfall amounts to roughly 70 %, 50 % and 20 %, respectively of this annual maximum (Hemp, 2001; Hemp, 2006b). The northern slopes receive less annual rainfall than the southern slopes. The mean annual temperature decreases from 23.4 °C at the foothills in Moshi, 813 m asl (Walter et al., 1975) linearly to -7.1 °C at the summit (Kibo, 5895 m asl) (Thompson et al., 2002). The lapse rate is about 0.6 °C/100 m which is typical for tropical mountains (Lauer, 1976). Frost occurs from 2700 m upwards (Hemp, 2006a).

Material and Method

Material collection and sample preparation

The pollen and climate data sets used for the training data set included the 14 plots of the WeruWeru transect on the southern slope of Kilimanjaro (see also Chapter 3). The modern pollen-rain was captured in pollen traps installed on 14 montane forest plots every 100 m elevation between 1900 and 3200 m asl. On each plot the rainfall was recorded using dipping bucket rain gauges and in parallel funnel-gauges. Data loggers were used for temperature. The instruments were accurate within ± 1 mm and ± 0.1°C, respectively. Mean annual precipitation (MAP) and mean annual temperature (MAT) were calculated based on data from the years 2005 to 2010.

For the climate parameter reconstruction the developed transfer functions were applied to the data set of the WW26 sediment core (see Chapter 4) containing in total 76 samples. Chemical preparation of all pollen samples followed standard methods (Faegri and Iversen (1989). The extracted pollen samples were mounted in glycerine jelly for pollen identification and counting. At least 300 pollen grains were counted for each sample. Pollen determination was carried out using light microscopy with 400x and 1000x magnification. Pollen identification referred to collections at Göttingen University and the African Pollen Database (Lézine, 2001). The pollen sum was used for the calculation of the pollen taxa abundance (in %). The fern spore abundance (%) was computed based on the pollen sum but it is not included in it.

Numerical analyses

An ordination derives quantitative information on the relationship among species, environmental variables and sites (Legendre and Legendre, 1998). In quantitative environmental reconstructions the first step is to examine whether linear or unimodal methods are appropriate for the available training set in relation to the environmental variables of interest (Birks, 1995). For this purpose the modern pollen rain data set was analysed by Detrended Correspondence Analysis (DCA) to estimate the lengths of environmental gradient inherit in the data. To visualize the response of each pollen taxa to the climate variables, the taxa percentage at each site/elevation was plotted again the climate parameters measured at these sites. A local regression function (alpha: 0.45) was fitted to visualize the response trend. Further, in order to estimate the explanatory power of MAT and MAP, two Canonical Correspondence Analyses (CCA) were performed using each climate parameter as sole constraining variable. This ordination method is preferably applied to data of species abundance and relative frequency that have a large number of zero values (Legendre and Legendre, 1998). DCAs and CCAs were carried out using CANOCO 4.54 (ter Braak and Šmilauer, 1997; ter Braak and Šmilauer, 2002). For the statistically significant environmental variables, pollen-based inference models were developed using weighted-averaging-partial-least-squares (WAPLS) models (ter Braak & Juggins, 1993). The optimum number of components is usually determined on the basis of the prediction errors in the test set (RMSEP: Root Mean Square Error of Prediction). In applications like the present one, large test sets are not available; instead the prediction errors are simulated by cross-validation. The goal of cross-validation is to estimate the expected level of fit of a model to a data set that is independent of the data that were used to train the model. The leave-one-out (or jack-knifing) cross-validation involves using a single observation from the original sample as the validation data, and the remaining observations as the training data (Picard and Cook, 1984). This is repeated such that each observation in the sample is used once as the validation data. The number of WA-PLS components to use for the model is based on the lowest RMSEP value.

Since it is not easily possible to quantitatively estimate to what degree pollen taxa abundance represents rather a function of local origin and/or pollen under- or overrepresentation, WA-PLS calibration functions were developed on non-transformed and transformed species data for a comparison. Finally, the models were used to reconstruct MAT and MAP based on the WW26 pollen data set. 54 pollen taxa were present both, in the modern pollen-rain/training data set and the WW26 pollen record, hence 54 pollen taxa were used in the model. The WA-PLS procedure and the reconstruction was computed using a C2 (Juggins, 2011).

Results

MAP and MAT along the WeruWeru transect

Figure 2 shows the trend of MAP (Fig.2a) and MAT (Fig.2b) along the elevational gradient between 1900 and 3200 m asl of the southern slope of Mt Kilimanjaro. Starting off with 2750 mm (at 1900 m asl) the MAP peaks at 2300 m elevation with about 3450 mm rainfall. It then gradually decreases with increasing elevation to 1600 mm at 3200 m asl. MAT (Fig.2b) shows a linear decrease in temperature uphill. While the MAT reaches 14.2 °C at 1900 m asl, in drops to 7.06 °C at 3200 m asl.

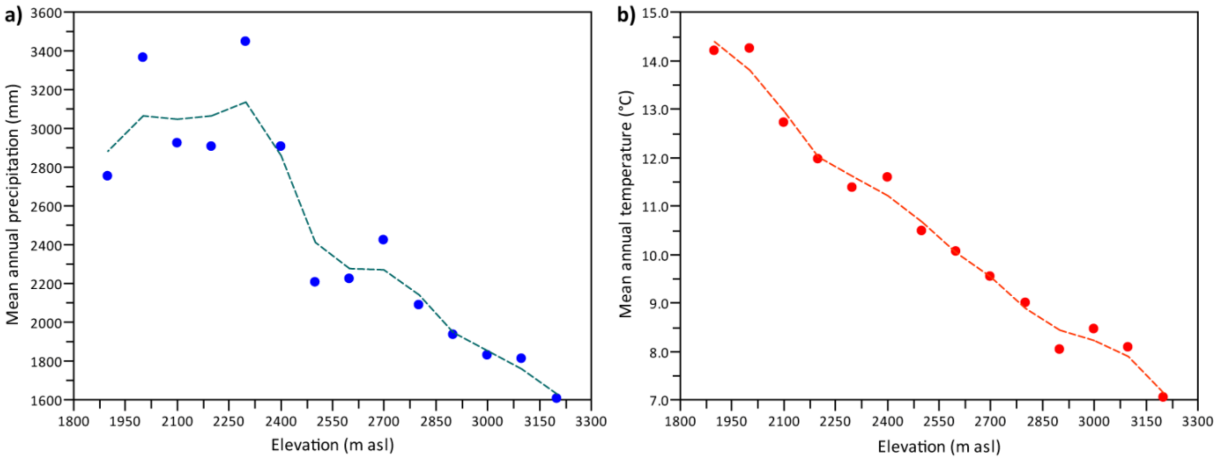

Figure 2: Trend of mean annual precipitation (MAP) and mean annual temperature (MAT) along the elevational gradient of the WeruWeru transect between 1900 and 3200 m asl on the southern slope of Mt Kilimanjaro. A local regression function (alpha: 0.45) was fitted to visualize the trend of the climate variables a) MAP gradient b) MAT gradient.

Pollen taxa response to MAP and MAT

In Figure 3 the response of the individual pollen taxa to MAP (Fig.3a) and MAT (Fig.3b) are depicted. Araliaceae pollen grains are most abundant on the plots with 2090 mm and at 2420 mm MAP (23% of the recorded pollen sum and 18 % respectively). Lowest abundance values are recorded at sites with rainfall of 1610 to 1830 mm/a and with MAP > 2900 mm. The abundance varies strongly at sites between 2000 and 2600 mm MAP. *Macaranga* pollen grains show an abundance of about 5 to 15 % at every site (MAP range: 1600 to 3450 mm) except for three; at locations with 3670,2920 and 2750 mm MAP this pollen taxon is very abundant (70 to75 %). The abundance of *Ilex* is consistently low (<8 %) up to about 2500 mm MAP, between 2500 and 3000 mm *Ilex* increases slightly (up to 16 %). This taxon reaches a maximum of 64 % at 3440 mm; however *Ilex* has a zero record at 3370 mm MAP. *Erica* pollen grains decrease with increasing MAP. It drops from 25 to 57 % between 1600 and 2000 mm MAP to <18 % between 2000 and 2500 mm rainfall. At higher precipitation the abundance of *Erica* pollen is < 5%. *Olea* pollen has the highest abundance at 1930 mm MAP. At lower and higher precipitation the abundance decreases gradually. *Podocarpus* pollen grains show a similar response to MAP with highest occurrence of 43 % at 2210 mm MAP. The abundance decreases gradually with higher and lower MAP.

The MAT plot (Fig.3b) shows that Araliaceae pollen grains are abundantly recorded (18 to 24 %) at plots with 9 to 10 °C MAT. At all other sites with MAT < 9°C and > 10 °C the abundance of Araliaceae pollen is <5 %. *Macaranga* pollen grains show an abundance of about 5 to 15 % at every sites with MAT <12 °C. Between 12 and 14.3 °C this pollen taxon is very abundant (70 to75 %). The abundance of *Ilex* pollen is consistently low (0 to 1 %) at sites with MAT below 10.2 °C. Between 10.3 and 12.8 °C *Ilex* pollen grains are recorded more often with a maximum of 43 % at 11.4 °C. At sites with MAT > 12.5 °C the taxon is rare.

The abundance of *Erica* pollen grains decreases with increasing MAT. This taxon is strongly recorded at sites with MAT <8 °C. Between 8 and 10.5 °C *Erica* varies between 5 to 24 %. This taxon is not or rarely recorded at sites with MAT >11.4 °C. *Olea* pollen grains show a slight increase in abundance (0.3 to 1.0 %) between 7 and 10.5 °C. Then, with increasing MAT (> 11 °C), *Olea* decreases and is not recorded at sites with MAT > 12.6 °C. *Podocarpus* pollen grains are not very common at sites with MAT <9 °C (<9 %). They are most abundant between 9 and 11 °C and then the record of *Podocarpus* pollen decreases with increasing MAT.

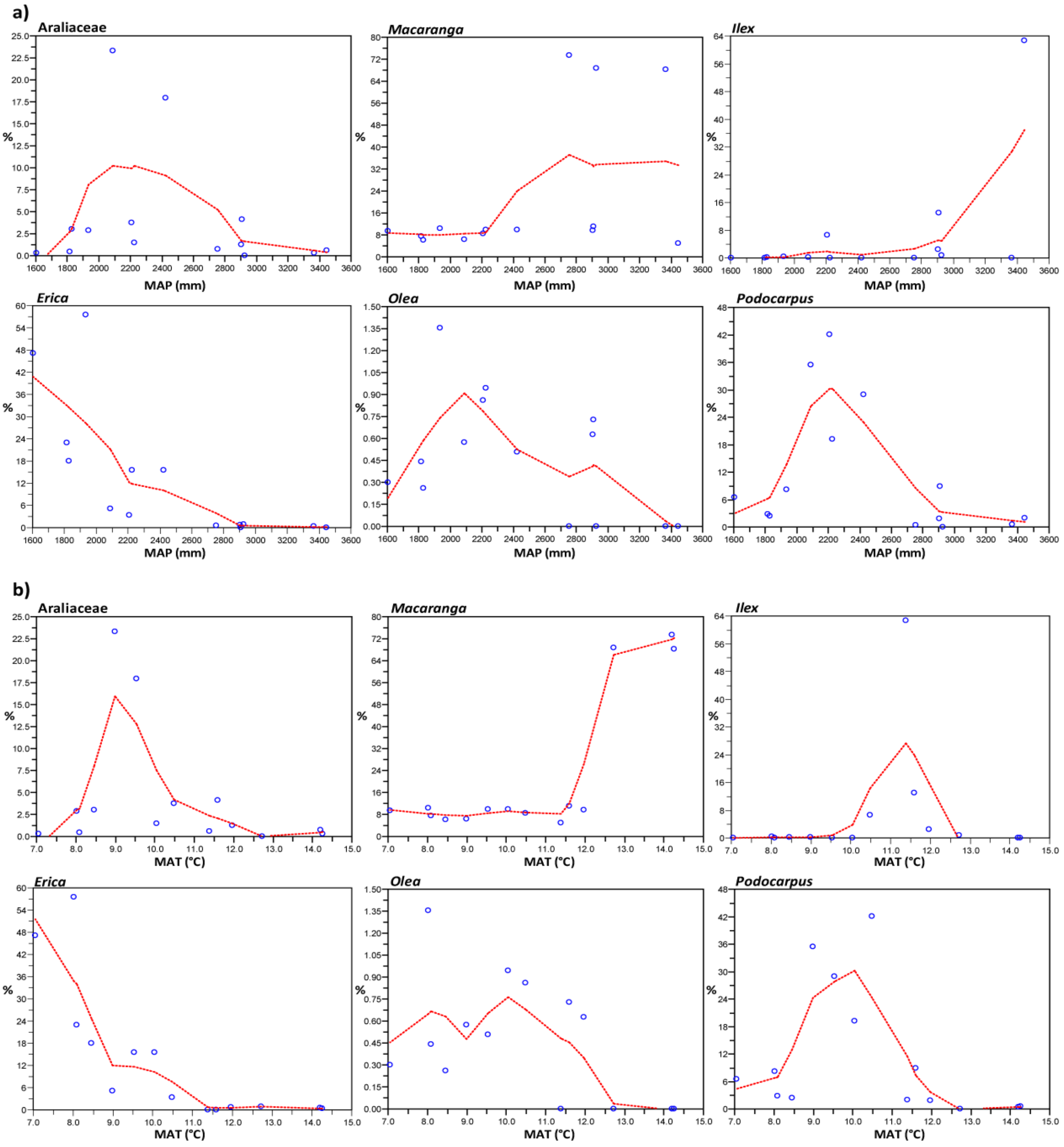

Figure 3: Response curves of the pollen taxa to the climate variables mean annual temperature (MAT) and mean annual precipitation (MAP) along the WeruWeru transect between 1900 and 3200 m asl. The taxa percentage at each site/elevation was plotted again the climate parameters measured at these sites. A local regression function (alpha: 0.45) was fitted to visualize the response trend a) Taxa responses to MAP b) Taxa responses to MAT.

Detrended Correspondence Analysis (DCA) of the modern pollen-rain data

The DCA of the untransformed modern pollen-rain data revealed a length of environmental gradient of 2.493 inherit in the data. This result and the predominantly unimodal response of single pollen taxa suggested to continue with a CCA (a unimodal based constrained ordination).

Canonical Correspondence Analysis (CCA)

The CCA biplots (Fig.4a/b) represent simultaneously the ordination of samples (sites labelled with elevation in m asl) and pollen taxa and their relationship to environmental variables. In the ordination diagrams, the environmental variables (MAP and MAT) are represented by arrows, the point direction indicates increasing values of the respective parameter.

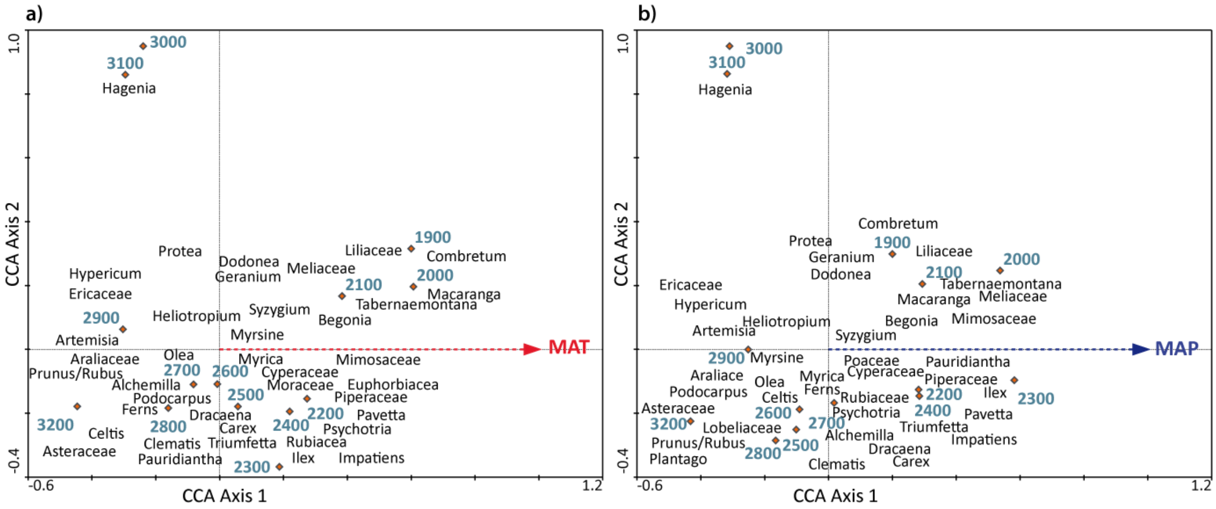

Figure 4: Biplots of the Canonical Correspondence Analyses (CCA) of the modern pollen-rain data set from the WeruWeru transect. a) CCA of the pollen taxa, the plots and the mean annual temperature (MAT) as climate variable. The Eigenvalues are 0.295 (CCA Axis 1) and 0.147 (CCA Axis 2). b) CCA of the pollen taxa, the plots and the mean annual precipitation (MAP) as climate variable. The Eigenvalues are 0.272 (CCA Axis 1) and 0.144 (CCA Axis 2).

The proximity of pollen taxa and sites to any climate parameter is a relative measure for the correlation between those data point. Sites that a closer positioned to MAT, or MAP respectively, experience a higher MAT or MAP. Taxa that show a positive correlation with one of the climate parameters are most abundant at sites with high values of this parameter.

Araliaceae and Ericaceae pollen grains e.g. show a negative correlation with both MAP and MAT whereas *Macaranga* is positively correlated with these climate parameters. In contrast, the occurrence of *Hagenia* pollen grains does not seem to be correlated neither with MAP nor with MAT. *Ilex* is more strongly correlated with MAP than with MAT, the opposite is the case for *Podocarpus* pollen grains which are slightly more correlated with MAT. Taxa that are positioned close to the centre of the ordination diagram do either not show a clear preference for any climate variable and/or do not contribute to the variance of the whole data set (hence, the dispersion of taxa within the ordination space).

Table 2: Summary of the CCA (first two axes) with the two climate variables MAP and MAT

Climate Variable		**1st CCA axis**	**2nd CCA axis**	**Total inertia**
MAP	Eigenvalues	0.272	0.416	1.827
	Species-environment correlation	0.849		
	Cumulative percentage variance of species data	14.9	37.7	
MAT	Eigenvalues	0.295	0.442	1.318
	Species-environment correlation	0.8837		
	Cumulative percentage variance of species data	16.1	40.3	

The summary of the CCA (Tab.1) shows that the first two CCA axes with MAP as single constraining variable accounted for 37.7 % of the cumulative variance in the pollen data. For the MAT constrained CCA this is 40.3 %. The correlation between pollen taxa and the climate variables is 0.849 for MAP and 0.884 for MAT.

Climate reconstruction of the WW26 using Weighted-Averaging Least Square Regression (WA-PLS)

Table 2 shows the performance expressed by the Root Mean Square Error of Prediction (RSEMP) of the models based of different types of transformation of the training data set. The RMSEP is not standardized, but is expressed in terms of the original variables. It is the average error of the predicted value to the actual value, expressed as the square root of the mean sum of the square errors. The number of WAPLS components used for the model was based on the lowest RMSEP value (*).

Table 3: Values of Root Mean Square Error of Prediction (RSEMP) given for the reconstructed climate variables MAP and MAT. The RSEMPs are given for the different number of components calculated for the WA-PLS model. * indicates the lowest RSEMP value which is an indication for good model performance. The units are mm for MAP and °C for MAT.

Reconstructed climate variable	**training data set transformation**	**RMSEP Comp. 1**	**RMSEP Comp. 2**	**RMSEP Comp. 3**	**RMSEP Comp. 4**	**RMSEP Comp. 5**
MAP	untransformed	485.08	480.39*	544.63	521.39	514.19
	Square root	354.24*	377.97	385.70	391.10	394.76
	log	318.85*	333.75	357.73	360.81	363.39
	untransformed, N<2 excl.	485.59	482.75*	596.66	599.88	591.22
MAT	untransformed	1.48*	1.53	1.75	1.76	1.74
	Square root	1.28	1.15	1.15	1.13*	1.14
	log	1.24	1.178*	1.15	1.120	1.122
	untransformed, N<2excl.	1.48*	1.56	1.92	2.03	2.02

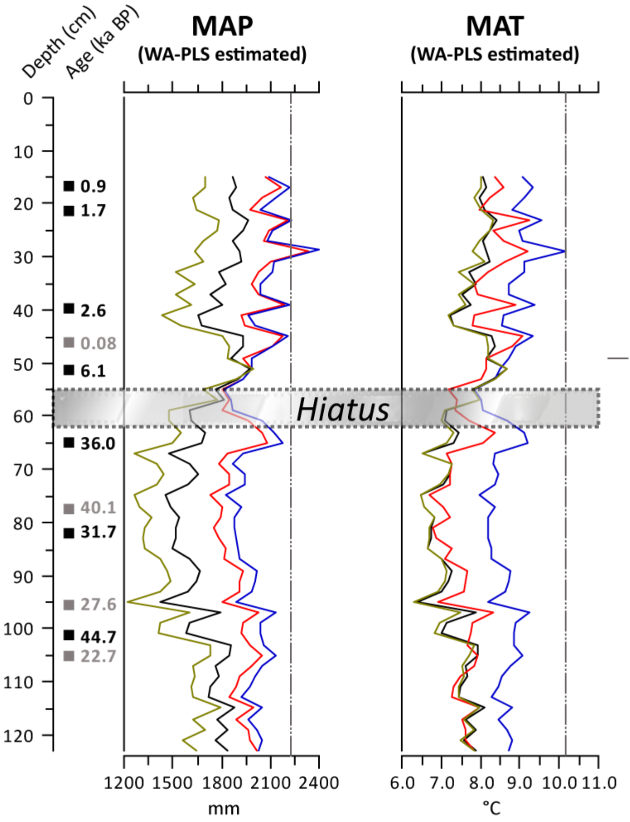

Figure 5: Reconstruction of mean annual precipitation (MAP) and mean annual temperature (MAT) of the WW26 pollen data set using weighted-averaging-least square regressions (WA-PLS). The model was run using different types of training data transformation: untransformed data including all taxa, untransformed data omitting rare taxa (N<2), square-root transformation and log transformation. As a reference, the present MAT (10.05 °C) and MAP (2230 mm) for the study site WW26 at an elevation of 2650 m are given (dashed, grey line). For further details on age/depth scale and pollen record, see Chapter 3.

The highest RSEMP values in MAP and MAT result from modelling the untransformed training data set, independent of whether rare pollen taxa (N<2) were excluded or not (RSEMP > 480.39 mm for MAP, and >1.48 °C for MAT). For reconstructed MAP based on square-root transformed data the RSEMP is lower (354.24 -394.76 mm), the same outcome is observed for MAT (RSEMP 1.13 – 1.15 °C). Lowest RSEMP values in the MAT and MAP reconstruction are derived from modelling log transformed data.

The WA-PLS reconstruction of MAP and MAT for the WW26 pollen record (Fig.5) shows the estimates based on the training data set (modern pollen-rain data). Due to sediment loss, the sequence assumed to be the Last Glacial Maximum (LGM) is missing (for details see Chapter 3). Except for at 29 cm core depth, MAT values of all reconstructions are lower than the reference the present MAT of the reconstructed site WW26 at an elevation of 2650 m. The MAP estimates of the untransformed training data set are low (1200 to 2000 mm). Omitting very rare pollen taxa (N<2) results in an even lower MAP estimate. Square-root and log transformation of the data leads to generally higher MAP estimates (1800 to 2400 mm). The fluctuations along the depth axis are very similar for both estimates. However, estimated based on the log transformed data tend to exceed square-root transformed based MAP estimates.

The MAT values of the different reconstructions are generally lower than the present MAT of the reconstructed site WW26. The MAT estimates of the untransformed training data set and the untransformed data with omitted rare pollen taxa (abundance < 2%) are lowest (6.2 to 8.5 °C). The fluctuations along the depth axis are very similar for both estimates. Square-root transformation of the data leads to slightly higher MAT estimates especially in the upper 60 cm of the pollen record. Between 100 and 120 cm core depth, the estimates based on untransformed data exceed MAT estimates from square-root transformed data. Highest MAT estimates (8.0 to 10.5 °C) results from WA-PLS modelling based on the log-transformed training data. The relative MAT estimate fluctuations along the record are similar for square-root and log transformed data.

Interpretation and Discussion

The results of the climate record along the WeruWeru transect on the southern slope of Mt Kilimanjaro between 1900 and 3200 m elevation have shown that the MAP and MAT follow the typical climate gradient observed from mountains located in dry tropical region (Lauer, 1976). While the MAT shows a linear trend along the elevational gradient, the MAP shows a normal distribution with a maximum in mid-altitudes at Kilimanjaro (Hemp, 2006a). Since the investigated gradient starts at an elevation of 1900 m asl, this unimodal trend is not very strong reflected in our results.

The response of the pollen taxa to the climate variables differs substantially between taxa. Despite the fact that the majority of pollen taxa seems to follow a normal distribution along the gradient of either climate variable, there are taxa that show a rather directional trend such as *Macaranga* vs. MAT, *Erica* vs. MAT and MAP, and *Ilex* vs. MAP. However, keeping in mind Shelford's law of tolerance (Odum, 1971) and niche-space partitioning (Whittaker *et al.*, 1973), species abundance is usually a unimodal function of the environmental variable. Despite potential differences in pollen dispersal patterns between species (as suggested in Chapter 3), this unimodal distribution would also hold true for the pollen record. Hence, it can be assumed that directional trends in the taxa abundance along the elevation gradient recorded in this study are rather caused by the incomplete inventory of the climate gradient. This is supported by the fact that the precipitation gradient is not fully captured as can be seen from the recorded MAP (Fig.2) and when compared to Hemp (2006a). The evaluation of unpublished data of A. Hemp (600 forest relevées from Kilimanjaro) reveals that all these taxa have an unimodal distribution regarding abundance and biomass along the climatic gradient.

Assuming that the patterns of taxa abundance are not sole caused by pollen dispersal performance, the climate optima of the taxa differ. Taxa such as *Ilex* seem to have a rather narrow MAT optimum area whereas *Olea* seems to be rather tolerant and display a broader MAT optimum. This unimodal response of taxa was further supported by the long environmental gradient revealed by the DCA. The CCA revealed that MAP and MAT are important environmental variables explaining the distribution of the pollen taxa. The first two CCA axes with MAP as single constraining variable accounted for 37.7

% of the cumulative variance in the pollen data. For the MAT constrained CCA this was 40.3 %. In both cases the explained variance of the pollen data set is very high. The high correlation between pollen taxa and the climate variables indicates a strong relationship between species and environment. Based on these outcomes, quantitative inference models for these variables from the pollen assemblages were developed. We used WA-PLS to reconstruct past MAT and MAP from the WW26 pollen data set.

Based on the assumption that MAT and MAP have not significantly changed in the Kilimanjaro area during the past six centuries, the ideal model reconstruction for the youngest sample of the WW26 pollen record, dated to about 0.6 ka BP, should be close to these climate parameters measured today. At the study site at 2600 m elevation the MAP is 2220 mm and the MAT 10.05 °C. The model results which approximate these measurements most are the log transformed based reconstructions of MAP and MAT. The WA-PLS model computes a MAP of 2096 mm which is a 5.86 % offset. For the MAT, which is predicted to be 8.92 °C, this offset is larger (11.24 %). All models based on the untransformed training data set performed not as well. The fact that excluding rare taxa results in the largest deviation of modelled data to observed MAP and MAT, proposes that the rare taxa play an important role in the representivity of the pollen taxa composition and their correlation with climate parameters. This is further supported by findings from the montane vegetation of Mt Kilimanjaro demonstrating that several pollen taxa are over or underrepresented due to differences in plant pollen productivity and possibly wind-caused pollen drift (Schüler et al, submitted; cp. Chapter 3). The application of log and square-root transformation to the training data set lead to smaller prediction errors in the reconstruction. A square root transformation normalizes data that is slightly positively skewed and when the variance of samples is approximately equal to the mean. A logarithmic transformation is used when there is a strong positive skew or for count data where the variance is greater than the mean. This transformation does not only produce a more normalised distribution but also removes the dependence of the variance on the mean (Cook and Wheater, 2000). Since not only the most abundant pollen taxa show a good correlation with MAP and MAT but also taxa that have a low occurrence (e.g. *Olea*), square-root and log transformations amplify the weight of rare taxa. The fact that the reconstructions with a log or square-root transformed training data set do not only produce the smallest prediction errors but also the most likely temperature and precipitation range, means that the information inherent in taxa that are only infrequently recorded must not be neglected but rather these rare taxa must receive special attention and should be reinforced prior to model application.

During the Holocene the relative MAT fluctuations (based on the log transformed training data) are between -0.31 and -1.42 °C (between 15 to 53 cm core depth). Due to the missing sequence in our reconstructed pollen record we cannot draw any conclusions about MAP and MAT during the LGM.

During pre-LGM (~43 to ~ 37 ka BP) the relative change in MAT was -1.78 and -1.34 °C. This means that it was on average 1.6 °C cooler than today. Before this period, our model suggests again warmer conditions, on average 1.3 °C cooler than today, but 0.3 °C warmer than during the pre-LGM. The relative changes of MAP during the Holocene (based on the log transformed training data) are between -252.24 and +216.68 mm. During pre-LGM (~43 to ~ 37 ka BP) this relative change in MAP was between -325.91 and -185.17 mm. This proposes an average reduction in MAP of 262 mm which is 12.5 % less than today (maximally -325.91 mm, or – 15.55 % respectively). Before this period, our model suggests an average MAP reduction by 174 mm (-8.3 %) compared to today.

Pollen-based reconstructions from Kashiru Swamp, Burundi, considering the combined effect of changes in temperature and precipitation (Bonnefille et al., 1992; Vincens et al., 1993) suggest a glacial climate being by 3-4 °C cooler and drier (~30 % less rainfall) than today. None of our models support such large amplitudes in MAP and MAT. However, when considering the prediction error (RSEMP MAP: 318.85 mm; RSEMP MAT: 1.178 °C; both for log-transformed training data), the values of most extreme MAP and MAT values (driest and coldest climate event) would also account to a 30 % reduction in precipitation and 3 °C cooling at 55 cm core depth.

However, the fact that Bonnefille et al. (1992) eliminated rare taxa could also be responsible for the differences in temperature reconstructions. Our results show, that the importance of rare taxa must not be underestimated but should be considered carefully when developing a WA-PLS model based on palynological data. In addition, it could make a difference that the climate gradient used by Bonnefille *et al.* (1992) for calibrating the model was based on longitudinal and latitudinal gradients rather than an elevational climate gradient like in the present study. In this context the reconstruction/prediction of the species‘ response to changing climate is complicated by the fact that taxa in different regions and at different elevations respond in different ways depending on their ecology, environment, and evolutionary traits (Daniels and Veblen, 2004).

Further, outlier samples, such as samples with unusual pollen assemblages or unusual combination of environmental variables, or a pollen assemblage with poor relationship to MAP and/or MAT can strongly affect the predictive power of transfer functions (Birks *et al.*, 1990; Hall and Smol, 1992) or eventually the respective reconstruction. As can be observed in the response function of individual pollen taxa to MAP and MAT outlier samples probably play a role in our data set. In future reconstructions these samples could be detected either by samples that have extreme (more than 5 times) influence and very high squared residual chi-squared distance as detected by CCA with the environmental variable as the sole constraining variable (Birks *et al.*, 1990; Lotter *et al.*, 1997); and by sample scores that are situated outside the 95% confidence limits about the sample score means a DCA of the species data (Hall and Smol, 1992). Hutson (1976) points out that failure of transfer functions due to environmental conditions that have no modern analogue may be cryptic, but that chances for discovery are increased if more than one transfer function algorithm is applied to a given set of samples. Hence, there is an urgent need of modern pollen rain studies in Eastern Africa in order to establish pollen-climate relationships that show a strong and stable correlation. Further, it needs to be explored in more detail which taxa are to be included and how they are weighted in the calibration and eventually also in the reconstruction. This will strongly improve the model performances and lead to much better predictions of climate parameter variations based on fossil pollen distribution.

Conclusions

It is possible to compute objective transfer functions relating the distribution of fossils to the distribution of the climatic parameter of interest. However, this implies the existence of an adequate set of fossil samples and a representative training data set, hence, meaning good data on the distribution of environmental parameters under modern conditions. This relationship can then be used to estimate the climate values under past conditions. This computation is crucially dependent on a strong and stable correlation between climate parameter variations and fossil distribution. If these constraints are satisfied, the transfer functions derived through WA-PLS yield comparable results. Our best fit model (with the smallest root mean square error of prediction) is the one based on log-transformed modern pollen rain data.

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Chapter 6

Synthesis

All studies presented in the previous chapters contribute to an increase in knowledge of late Quaternary palaeoenvironmental conditions in equatorial East Africa and more specifically in the Mt Kilimanjaro area. Further, the new palaeoecological data and research approaches contribute to a better understanding on how tropical mountain ecosystems and climate vary naturally and respond to changes in environmental forcing.

Discussion of the research outcomes

The results of the palaeoenvironmental investigation on Mt Kilimanjaro provide important insight into tropical African forest ecosystems and their response to the impacts of past climate change. The specific aim of this particular research was to reconstruct the late Quaternary vegetation and climate dynamics on Mt Kilimanjaro based on palynological and sedimentological data.

Investigation of past vegetation, climate and fire dynamics on Mt Kilimanjaro

Apart from achieving comprehensive understanding of the past vegetation changes and identification of environmental conditions and their impact on local and regional ecosystem dynamics in the Mt Kilimanjaro area, this part of the research also aimed at the complementation of previous investigations in Tropical East African Mountains. Th***e*** new data from Mt Kilimanjaro contribute to the establishment of a basis for more detailed comparison between different study sites. Long climate records from tropical continental regions are an important complement to the well-known polar climate records contained in ice cores from Greenland and Antarctica, as they are crucial to resolve long-standing questions about the long-term periodicity of low-latitude climate changes, and about the relative importance of tropical and high-latitude climate processes in translating external climate forcing into region-specific climate change.

The study on Maundi provides first palynological data extending back into the early last Glacial (~90 ka BP) and therefore presents one of the longest terrestrial pollen records in East Africa covering almost a full glacial-interglacial cycle of vegetation and climate history. The reconstructions reveal major shifts in the upper vegetation zones of Mt Kilimanjaro during the last glacial period. The open alpine vegetation was replaced by subalpine ericaceous vegetation and montane forest, which represents an elevational shift of vegetation belts of about 1100 m. Studies of buried soils on Kilimanjaro suggest a long history of climatically-driven fluctuations in the altitudinal distribution of vegetation zones (Zech, 2006). During cold and dry periods like the Last Glacial Maximum, 23 to 19 ka ago, the upper treeline descended by about 1000 m. Other records from East Africa also report a glacial ericaceous belt position about 1050 m lower than today (Kashiru Swamp, Burundi: Bonnefille and Riollet, 1988; Uganda: Taylor, 1990; Mt Kenya: Olago *et al.*, 1999). Multi-proxy studies on Mt Kenya showed a significant expansion of high-altitude C4 grasslands on Mt Kenya (Wooller et al., 2001; 2003). However, this could not be shown for Kilimanjaro (Zech et al., 2011), indicating that the Mt Kenya pattern cannot be generalized to East Africa's other high mountains.

Also regarding the existence of a bamboo belt, as it is found on other East African mountains with suitable climate conditions and the presence of mega-herbivores (elephants and buffalos); Mt Kilimanjaro seems to be an exceptional case. Despite the present suitably humid conditions of its southern slope, the palaeoecological reconstructions have shown that a bamboo belt did not exist, at least not during the past about 40 ka BP. Based on our WW26 data we can assume that the climate was too dry and/or too cold for bamboo until 2 ka BP, when humans started to settle on Kilimanjaro. This would support the theory that an interplay by biotic and abiotic conditions (missing mega-herbivores due to anthropogenic influence and climatic conditions) are the reason for the missing bamboo belt on Kilimanjaro. Further, none of the investigated sites show influence of direct anthropogenic impact as could have been derived from the occurrence of hemerophytes and crop plants as well as the abundance of disturbance indicator taxa. Latter could have also indicated the activity of mega-herbivores. However, none of these factors seem to have had a distinct impact on the vegetation.

Persisting montane forest around the Maundi crater suggests only a comparatively moderate climatic variability during LGM. Therefore Mt Kilimanjaro played a similar role as a glacial refugium for montane forest species as the Eastern Arc Mountains do. The downward shift of vegetation zones during the LGM seems to have caused changes in taxa composition within the vegetation zones but did not lead to elimination neither of vegetation belts, nor of major taxa dominating these belts today. Unlike major parts of western equatorial Africa, where the humid forest area was reduced by 84 % (Anhuf et al., 2006), the mountains of east equatorial Africa seem to have received sufficient precipitation to sustain most of their forest taxa, even throughout the LGM. The stabilizing effect of the moisture carrying Indian monsoon is probably the most important prerequisite enabling the east African mountain systems to have served as glacial refugium for montane forest taxa which makes the area to one of the world's biodiversity hotspots today. This means that a change of precipitation will be the most influential factor for ecosystem changes and loss of biodiversity at Kilimanjaro.

Very dry and cool conditions prevailed during the early last Glacial, probably interspersed with extreme drought events. During the pre-LGM more humid conditions allowed the ericaceous and forest vegetation to spread and caused an upwards shift of vegetation zones. When comparing the vegetation dynamics from Maundi crater with other East African mountains during the same time period (Burundi: Bonnefille and Riollet, 1988; Uganda: Taylor, 1990; Mt Kenya: Olago *et al.*, 1999) it appears that this short wet spell is observed only south of the equator and might indicate a sudden shift of the ITCZ and an enhancement of the south-eastern monsoon.

There is no doubt that changes in lake level, pollen and other proxy records reflect changes in the climate and vegetation of many study areas in tropical East Africa. However, the understanding of the forcing mechanisms behind the palaeoenvironmental changes in tropical regions remains a challenge. Although the Milankovich cycles are certainly one explanation for the changes (Tyson, 1999; Olago, 2001; Stager *et al.*, 2003; Kiage and Liu, 2006), they are unlikely to be responsible for centennial and decadal-scale changes. Hence, more studies are needed to further investigate the possible causal mechanisms.

Some explanations have been offered identifying these mechanisms. One hypothesis is based on the intensity of the south-east summer monsoon and the Congo air boundary (CAB) that influences the amount und pattern of precipitation in East Africa (Hamilton, 1982; Nicholson, 1996; Vincens *et al.*, 2003). Since the south-east monsoon is driven by the seasonal movement of the ITCZ, dramatic changes must have occurred during times of intense aridity recorded in the East African lakes. A very weak summer monsoon could have been responsible for the intense aridification (*ca* 20-18 ka BP, 12.5 ka BP, and after ~4 ka BP), resulting in very low lake levels as recorded in Lakes Albert, Lake Victoria, and Lake Naivasha. In fact, many records from terrestrial sites in Asia and from the Arabian Sea, which correspond with those from the African sites, suggest significant century-scale monsoon weakening events, especially during the early to mid-Holocene (Van Campo *et al.*, 1982; Street-Perrott and Street, 1990; Van Campo and Gasse, 1993; Gasse and Van Campo, 1994; Overpeck *et al.*, 1996). Such fluctuations in the south-eastern summer monsoon may explain some abrupt climate changes evident in the palaeoecological record from East Africa. Variations in the summer monsoon are closely linked to changes in global circulation patterns. Most evident are temperature changes which are associated with events such as the deglaciation and the Younger Dryas in the northern hemispheric mid-latitudes as well as sea surface temperatures (SST). There is also increasing evidence that the changes in the monsoon and in the ITCZ are linked to SST (Gasse, 2000) as well as to the nature of the thermohaline circulation (THC) (Nyberg *et al.*, 2002).

The pollen record from Maundi crater further showed, that during the last Glacial, especially the development of an ericaceous zone was strongly controlled by fire activity. Spread and decline of this vegetation zone oscillated depending on climate and fuel controlled fire dynamics. Hence, regular fires had a stabilizing effect on the vegetation composition. Despite the increased fire occurrence during the past century, fires were relative rare during the Holocene, giving no indication for increased anthropogenic influence. The pollen record from WW26 did not show any major impact of fire frequency on the vegetation.

While the LGM is characterized by dry and cold climatic conditions which are indicated by the dominance of Poaceae and Asteraceae at the Maundi site and the presence of mainly ericaceous vegetation at the WW26 site, the transition from the glacial period to the Holocene is marked by a shift into wetter but still cool conditions.

During the Holocene the climate becomes increasingly warm and wet and ericaceous vegetation surrounds the crater, replacing the alpine vegetation. The pollen records from Maundi crater and WW26 show an ascent of montane forest as indicated by montane forest climax species. The WW26 pollen record further proposes the presence of more drought tolerant *Cassipourea* forests during the early Holocene. Also the results of the geochemical analysis of the soils profile suggest different phases of enhanced wind intensities and rainfall which can be associated with enhance monsoonal activities observed at other study sites in tropical East Africa. Today *Cassipourea* forests are only present on the drier northern slopes of Mt Kilimanjaro, which means that past environmental changes did not only cause an elevational shift of vegetation but also profound re-structuring of the forest ecosystems.

The pollen-based reconstructions on Mt Kilimanjaro have shown that in the past taxa tended to respond sometimes individually, sometimes in groups to environmental change. Since these pollen taxa refer in most cases to genus or even family level, and since pollen taxa represent only a part of the formerly existing vegetation, such changes are in many cases interpreted as shifts in whole vegetation types or belts. The classification of vegetation into distinct types or belts makes the investigation of temporal and spatial ecosystem dynamics feasible, and interactions between climate and vegetation scientifically accessible. Nevertheless, we should keep in mind that such classifications are – event though regularly used – an expedient implement that we apply to our data but they are not necessarily appropriate for any scientific question. Especially in vegetation and climate reconstructions, single taxa and their particular spatial and temporal abundance may carry a lot more information about the past environment than we have so far been able to deduce. In future palaeoecological and palaeoclimate studies we should turn more attention to the information displayed by individual species. But for this we will need to focus on today's patterns. Besides a profound knowledge of the ecology and association of recent taxa, the observation of the response of nature to the rapid recent (anthropogenic) climate change enables us to draw our conclusions and apply this newly gained knowledge for interpreting the past. The past is not only the key to the future but also vice versa!

Establishment of a modern pollen rain- vegetation relationship and pollen based climate reconstructions on Mt Kilimanjaro

Since past shifts in the distribution of vegetation types are reconstructed from fossil pollen assemblages, the exact relationship between modern vegetation and modern pollen compositions is crucial for the calibration of the fossil pollen records. Such calibration studies which quantitatively relate pollen with altitude or climatic parameters are still lacking in tropical Africa. One key objective of this research, therefore, was to establish exact pollen-vegetation and pollen-climate relationships, from which transfer functions can be developed for detailed reconstruction of past vegetation and climate states from fossil pollen records.

The accomplished modern pollen-rain study provides insight into how present vegetation is reflected in the modern pollen rain along the elevational gradient of Mt Kilimanjaro. The results indicate that it is crucial to establish a modern pollen-rain – vegetation relationship for the calibration and interpretation of a fossil pollen record from a mountain site. At our study site it is possible to analyse the pollen-rain on plant family level in order to derive the forest belt of the surrounding vegetation and with this to assess the climatic conditions, which is important for the interpretation of palaeo-records. Even the separation of thin elevational belts such as lower and upper mid montane forest zone is possible by modern pollen-rain. The occurrence of plant families along the altitudinal gradient is differently represented in the modern pollen depending on various reproduction factors. This can be quantified as a transfer factor which will be applied to calibrate palaeo-pollen data in future studies. The diversity trend captured in the modern pollen-rain reflects the plant diversity in the vegetation; but we observed differences in the taxa diversity. The pollen and spore dispersal seems to be strongly influenced by the regional wind patterns. This needs to be considered when deriving past distribution ranges from pollen-records. Our results facilitate the confident use of fossil pollen data to reconstruct more precisely potential vegetation and its dynamics in East African montane forests and also to refine climate past reconstructions in this region for a more accurate comparison of data and modelling.

The development of mathematical transfer functions allows the 'translation' of fossil pollen data into specific climate data, by comparing the composition of modern pollen rain collected within the surrounding vegetation and local climate conditions. For the development of the pollen-climate transfer functions along an elevational gradient between 1900 and 3200 m at Mt Kilimanjaro, weighted-averaging partial least square regression models (WA-PLS) were used. The outcome of this attempt is that it is possible to compute objective transfer functions relating the distribution of fossils to the distribution of the climatic parameter of interest. However, this implies the existence of an adequate set of fossil samples and a representative training data set, hence, meaning good data on the distribution of environmental parameters under modern conditions. This relationship can then be used to estimate the climate values under past conditions. This computation is crucially dependent on a strong and stable correlation between climate parameter variations and fossil distribution. If these constraints are satisfied, the transfer functions derived through WA-PLS yield comparable results.

Pollen samples with unusual taxa assemblages, unusual combination of environmental variables, or a pollen assemblage with poor relationship to the climate variables can strongly affect the predictive power of transfer functions and eventually the respective reconstruction. Transfer functions can also produce reconstruction with a low fit due to past environmental conditions that have no modern analogue. As mentioned above, our palaeoecological results of the WW26 pollen record suggests the presence of *Cassipourea* forest during the early Holocene. This forest type is not captured in the elevational modern pollen rain gradient since it does not exist on the southern slope of Mt Kilimanjaro today. Therefore the presence of *Cassipurea* forest in the pollen record may lead to strong temperature and precipitation deviations in the quantitative reconstruction. Samples harbouring such conditions may appear cryptic, but chances for discovery are increased if more than one transfer function algorithm is applied and, of course, if the training data set is enlarged.

Hence, there is an urgent need of more elaborate modern pollen-rain studies in Eastern Africa in order to establish pollen-climate relationships with a strong and stable correlation. Further, it needs to be explored in more detail which taxa are to be included and how they are weighted in the calibration and eventually also in the reconstruction. This will strongly improve the model performances and lead to much better predictions of climate parameter variations based on fossil pollen distribution.

Implications

Based on the tendency of many tropical species to move upslope, species on Mt Kilimanjaro may be directly threatened by climate-induced range shifts in several ways. This might include the disappearance or decline of species in the lowlands and at lower elevations due to upslope movement of species, the extinction of high elevation species since there are no options for migration, and the inability of species to shift into a suitable geographic range either due to geographical barriers or insufficient dispersal capability (Herzog *et al.*, 2011).

Mt Kilimanjaro still harbours one of the most diverse tropical montane forests ecosystems in the world and many of these species are predicted to migrate towards wetter and cooler habitats as the lowlands heat up. As the highest mountain range in Eastern Africa, Mt Kilimanjaro may represent one of the few East African refuge areas for many tropical forest species. Because no species from lower latitudes or from lower elevations are available to replace species that move upslope, montane tropical rainforests are expected to suffer a net loss of species (Colwell *et al.*, 2008). Species on tropical mountains like Mt Kilimanjaro are likely to be highly vulnerable to climate change because their ecological (thermal) niche is not as broad as of species in cooler areas (Feeley and Silman, 2008). Further, high elevation species may go extinct with climate change since latitudinal migration is not possible. Typically, the total colonisable area on mountains decreases at higher elevations simply due to the mountain's shape which potentiates the problem (Körner, 2003). Hence, high montane species, and particularly high elevation species, become extinct unless they adapt rapidly to changing environmental conditions or they colonize nearby higher mountain ranges.

So far, few data exist regarding mountaintop extinctions in tropical regions. Raxworthy et al. (2008) predicted a 10 % loss amphibian and reptile species on a high massif in Madagascar under a 2°C warming scenario. On the other hand, Colwell et al. (2008) predicts an almost negligible rate of mountaintop extinctions for 1900 species of plants and insects distributed along a 2900 m elevational gradient in Costa Rica under a 3.2°C warming scenario, whereas about 50% of species were predicted to contribute to lowland biotic attrition or face spatial gaps between their current and predicted range.

The reconstruction and prediction of the species‘ response to changing land-use and climate is complicated by the fact that taxa in different regions and at different elevations respond in different ways depending on their ecology, environment, and evolutionary traits (Daniels and Veblen, 2004). High elevation species may more easily tolerate climate change than low elevation species because they are adapted to an environment experiencing greater natural temperature variation (McCain, 2009). Contrariwise, high elevation species may be less capable of adapting to climate change because they have less upslope habitat available to migrate to than low elevation species. Our understanding of past, present and future changes in biodiversity in response to climate change is severely limited by a lack of data.

However, due to the rapid land-use change in the Tropics it may well be that this will have much stronger impact on the vegetation that climate change might have.

The Global Observation Research Initiative in Alpine Environments (GLORIA: Grabherr, 2012) has begun a coordinated, strategic program to monitor global biodiversity and climate in alpine ecological zones, with a focus on high elevation plants. Expansion of networks such as GLORIA is urgently needed, particularly multi-taxa monitoring along broad latitudinal and altitudinal gradients in the tropical East African Mountains, especially in areas where high diversity and endemism coincide with high vulnerability to climate change.

Concluding remarks, uncertainties and perspective

Each palaeoecological topic covered in the chapters of this dissertation contributes to the understanding of how tropical ecosystems and climate vary naturally and respond to changes in environmental forcing. However, at the same time, key uncertainties remain.

Even though the body of knowledge about glacial-interglacial variations in climate is large, a comprehensive explanation of these variations remains to be clarified. Similarly, the mechanisms of abrupt climate change are not well enough understood, nor are the key climate thresholds that trigger acceleration in sea level rise or regional climate change.

Our knowledge of ecosystem dynamics and climate variability in the southern hemisphere tropics during the late Quaternary is still severely limited by the lack of palaeoecological records. Differing amplitudes and variability observed in the available southern-hemisphere reconstructions, and the extent to which these differences relate to choice of proxy data and statistical calibration methods, need to be reconciled. Similarly, the understanding of how climatic extremes varied in the past and how that impacted the ecosystems is incomplete. Eventually, this assessment would be improved with extensive interdisciplinary networks of high-resolution multiproxy data. Further high resolution records of Mt Kilimanjaro are needed, in particular for the Holocene. The results will surely allow a more elaborate comparison with other East African palaeo-archives and they will provide more elaborate and applicable knowledge for conservation and management issues.

For the coming years, several palaeoecological investigations in the Mt Kilimanjaro area will be carried out. A palaeoecological comparison between the drier northern slope and the wetter southern slope of Mt Kilimanjaro will give insight into differences in vegetation and climate dynamics mainly caused by variations in precipitation. Further such studies may unravel more detailed information on north-eastern and south-eastern African monsoon patterns during the late Glacial which are assumed to be the main driver for changes rainfall pattern.

Moreover, palynological and sedimentological studies in the surrounding mountain systems of Mt Kilimanjaro, e.g. Mt Meru and Pare Mountains, will allow the reconstruction of past biogeographical patterns, and hence, shed light on the origin and evolution of the tropical East African mountain ecosystems, their past connections and disjunctions and their role for the development of the biodiversity hot spots in East Africa. The results will contribute to a better understanding of modern and future ecosystem dynamics and will help maintain and manage the high biodiversity in the East African biodiversity hot spots.

Our current focus on global warming incites us to highlight the relevance of palaeoclimate for predictions of future climate change. However, we should not lose sight of the inherent value of palaeoclimate and palaeoecological research which enables us to gain valuable insight into the ability of our ecosystems and climate systems to change. Further, in unearthing new scientific evidence we gain a deeper understanding of today’s ecosystem and climate dynamics. Above all, palaeoecological and palaeoclimate research captivates and inspires. – Presumably in the same way as watching the dark sky on a clear night inspires current and future astronomers. Doesn’t our knowledge of the intricate, yet forceful patterns in the past, such as climate change events and glacial-interglacial cycles, enrich our conceptual view?!

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Appendix A

Identified pollen and spores of the Maundi Crater and the WeruWeru records – complete list and photos

Appendix A1: Table of identified pollen and spore types

Appendix A2: Plates of identified pollen and spore types

Remarks:

- Morphological descriptions of pollen and spore types are given in case own observations differ from those described by the African Pollen Data Base (Lézine, 2001)[1] and Assemien *et al.* (1974)[2]

- All pollen and spore photos were taken by Barbara Kurz and by myself

- Abbreviations for the pollen records:
  MD – Maundi Crater
  WW – WeruWeru at 2650 m asl
  WW-MPR – Modern pollen-rain from the WeruWeru transect

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[1] L ézine, A. M. (2001) African Pollen Database - Late Quaternary Pollen Flora. Centre National de la Recherche Scientifique, France.

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Appendix A1: Table of identified pollen and spore types

Family	Pollen Type	Photo N°	Morphology Note	Record
Acanthaceae	*Blepharis*	1		MD
Acanthaceae	*Justicia*	2		WW-MPR
Acanthaceae	*Monechma*	3		MD
Acanthaceae	*Thunbergia*	4		WW-MPR
Acanthaceae	Type I			WW-MPR
Acanthaceae	Type II			WW
Amaranthaceae	*Amaranthus*	5	periporate	MD, WW-MPR
Amaranthaceae	*Achyranthes aspera*	6	periporate	WW
Amaranthaceae / Chenopodiaceae	Type I			WW
Amaranthaceae / Chenopodiaceae	Type II			WW-MPR
Anacardiaceae	*Rhus longipes*		3 colporate / 3 colporidate, striate	WW, WW-MPR
Apiaceae	*Oenanthe*	7		WW, MD
Apiaceae	Type			MD
Apocynaceae	*Tabernaemontana*	8		MD, WW, WW-MPR
Apocynaceae	Type I			WW, WW-MPR
Aquifoliaceae	*Ilex mitis*	9		MD, WW, WW-MPR
Araliaceae	*Polyscias*	10		WW, MD
Araliaceae	*Schefflera*	11	3 colporate / 3 colporidate, 25 x 21 µm, irregular Reticulum, heterobrochate, rounded poles, thick exine at pole, butterfly pore	MD
Araliaceae	Type			MD, WW-MPR, WW
Arecaceae	Type		echinulate	WW, MD
Asteraceae	*Artemisia*	12	3 colporate / 3 colporidate, reticulate, <25 µm, pores round, colpes evenly narrow / slightly opened, lobate	WW, MD, WW-MPR
Asteraceae	*Centaurea*	13		WW-MPR, WW, MD
Asteraceae	cf *Achyrothalamus*			WW
Asteraceae	cf *Blepharisperum*			MD
Asteraceae	cf *Carthamus*			MD

Asteraceae	cf *Centaurea*			MD
Asteraceae	*Conyza*	14		MD
Asteraceae	*Crassocephalum*	15		WW-MPR
Asteraceae	*Dicoma tomentosa*	16		WW
Asteraceae	*Emilia*	17		WW, MD
Asteraceae	*Helichrysum*	18		MD
Asteraceae	*Schkuhria pinnata*	19		MD
Asteraceae	*Senecio hadiense*	20		MD
Asteraceae	*Senecio johnstonii*			MD
Asteraceae	Subf. *Asteroidea*			MD
Asteraceae	Type I		psilate, 17µm	MD
Asteraceae	Type II		psilate	WW
Asteraceae	Type III			WW
Asteraceae	Type IV			MD
Asteraceae	Type V			WW-MPR
Balsaminaceae	*Impatiens*	21		MD, WW
Begoniaceae	*Begonia*	23		WW-MPR, WW, MD
Begoniaceae	Type			WW, MD
Bignoniaceae	*Jacaranda mimosifolia*	24	3 colpate, psilate, smooth exine, syncolpate, hyaline exine, wide colpi, mostly >25-30 µm	WW-MPR
Bignoniaceae	*Markhamia lutea*	25	3 colpate, reticulate, 45 x 45 µm, round, wide colpi, fissured aperture membrane	WW-MPR
Bignoniaceae	*Tecoma stans*	27	3 colpate, reticulate, 37 µm, wide and long colpi	MD
Boraginaceae	*Ehretia*	28		WW-MPR, WW
Boraginaceae	*Heliotropium*	29		WW-MPR, WW, MD
Boraginaceae	*Lithospermum afromontanum*	30		WW, MD
Boraginaceae	*Trichodesma*			WW-MPR
Brassicaceae	Type			MD, WW, WW-MPR
Caesalpinaceae	Type		roughly reticulate	MD
Caesalpinaceae	*Pterolobium stellatum*	31		MD, WW-MPR
Capparaceae	Type		3 colporate / 3 colporidate, reticulate / striate, prolate / subprolate, mostly thick exine, long colpes	WW
Capparaceae	*Capparis*			WW-MPR, WW
Capparaceae	*Cleome*	32		WW, WW-MPR, MD
Capparaceae	*Gynandropsis gyandra*	33		MD

Capparaceae	Type I			MD
Capparaceae	Type II			WW-MPR
Caprifoliaceae	*Sambucus nigra*	34	3 colporate / 3 colporidate, reticulate, 13 x 17-25 µm, high and thin Reticulum, homobrochate, long and deeply sunken colpes, small polar fields, intercolpate edges curved - here exine thicker 1.2 µm, elsewhere 1 µm at colpus	WW-MPR
Caryophyllaceae	*Drymaria cordata*			
Caryophyllaceae	*Polycarpa eriantha*	36		MD
Caryophyllaceae	Type I		relatively thick-walled, clear annulus: at least 0.7-1.0 µm, operculum with corns/thorns, perforate, partially net-like columella, most times less and bigger pores	MD
Caryophyllaceae	Type II			WW
Caryophyllaceae	*Ubellinia rotundifolia*	37		MD
Casuarinaceae	*Casuarina*	38	triangular	WW, MD
Celastraceae	*Maytenus*	39		MD, WW-MPR
Chenopodiaceae	*Chenopodium*		periporate	WW
Combretaceae	Type			MD
Combretaceae	*Combretum*	40	6 colporate, heterocolporate, 18-35 µm, rugulate / psilate / scabrate, long colpi	WW-MPR, WW, MD
Combretaceae	*Terminalia*		6 colporate, heterocolporate, 18 µm, rugulate / psilate / scabrate, long colpi	MD
Commelinaceae	*Aneilema*	41	monosulcate, echinate, long sulcus, 50 µm	MD, WW, WW-MPR
Commelinaceae	*Commelina*	42	monosulcate, verrucate, wide sulcus 30 x 21 µm, edge of colpi rough	WW-MPR, WW
Commelinaceae	Type			WW
Connaraceae	cf *Connarus*		3 colporidate, reticulate, 25 µm, lolongate poroide region, ± rectangular grain - actually just *Rourea* and *Agelea*	MD
Connaraceae	Type			MD
Convolvulaceae	Type			MD
Convolvulaceae	cf *Ipomoea*			WW-MPR
Convolvulaceae	*Convolvulus*	44	3 colporidate, echinate, big, round	WW-MPR, WW
Convolvulaceae	*Meremmia*	45	3 colporidate, echinate, 50 µm, high columella, echinulate, thick exine, perforate, short colpi with irregular edge, Echini unremarkable, big, round	WW-MPR, WW
Cupressaceae	*Juniperus procera*	46		MD

Cyperaceae	*Carex*	47	tectate, columellate, but thin exine, scabrate, verrucate, granulate, perforate, long and round aperture, 30-60 µm	WW-MPR
Cyperaceae	Type I			MD
Cyperaceae	Type II			WW-MPR, WW
Dracaenaceae	*Dracaena afromontana*	49		WW, WW-MPR
Ebenaceae	*Diospyros mesipiliformis*			WW-MPR, WW
Ebenaceae	*Euclea*	50		WW-MPR, WW
Ericaceae	cf *Agarista salicifolia*		42µm	WW-MPR, WW
Ericaceae	*Erica*	51		MD, WW-MPR, WW
Euphorbiaceae	*Acalypha*		3 colporate / 3 colporidate, also 4 colporate, psilate / scabrate, prolate / subprolate, 12 µm, tectate, round pores, short colpi	WW-MPR, WW
Euphorbiaceae	*cf Alchornea*		3 colporate / 3 colporidate, psilate / scabrate, prolate / subprolate, 20 µm, short and wide colpi, costae, butterfly spores	WW
Euphorbiaceae	cf *Dalechampia*			WW-MPR
Euphorbiaceae	cf *Margaritaria*			MD
Euphorbiaceae	*Croton*			MD
Euphorbiaceae	*Drypetes*	52		WW-MPR, WW
Euphorbiaceae	*Euphorbia*	53	3 colporate / 3 colporidate, reticulate, >25 µm, colpes equatorially tied (E. engleri) / widely open (E. schimp.), pores thick and clearly lolongate, *E. engleri*: thick exine, *E. schimperiana*: thin exine	WW-MPR, WW, MD
Euphorbiaceae	*Macaranga*	54		WW-MPR, WW, MD
Euphorbiaceae	*Phyllantus*			MD
Euphorbiaceae	Type			WW-MPR, WW, MD
Fabaceae	*Abrus*	55	3 colporate / 3 colporidate, reticulate, prolate, 25 µm, lang and narrow colpes, pores lolongate, short and narrow, thin Reticulum, but relatively high	MD
Fabaceae	*Aschynomene*	56		MD
Fabaceae	*Calpurnia aurea*	57	3 colporate / 3 colporidate, reticulate, 17 x 21 µm, equatorially tied, pores unremarkable, but long lalongate, narrow reticulum	MD
Fabaceae	cf *Hedysarum*			WW
Fabaceae	*Dalbergia*	58		WW-MPR, MD

Fabaceae	*Desmodium*	59	3 colporate / 3 colporidate, scabrate, round, 25 µm	MD
Fabaceae	*Eriosema*	60	3 colporate / 3 colporidate, verrucate	WW
Fabaceae	*Lonchocarpus eriocalyx*			MD
Fabaceae	Type			MD, WW
Flacourtiaceae	*Dasylepis integra*	61		WW-MPR
Flacourtiaceae	Type			MD
Geraniaceae	*Geranium*	63	3 colporidate, echinate, 90 µm, clavate, reticulate, short colpi	WW-MPR, WW, MD
Hammamelidaceae	*Trichocladus ellipticus*	66	3 colpate, reticulate, 15 µm, colpi with unclean edges, round in polar and equatorial view, lobate in polar view, long and wide colpi, very rough reticulum	MD
Hypericaceae	*Garcinia*	67		WW-MPR, WW, MD
Hypericaceae	*Hypericum*			MD, WW
Hypericaceae	*Hypericum keniense*	68	3 colporate / 3 colporidate, scabrate / reticulate, subprolate / prolate, 23 µm, pore tied, open and long colpi, type exine	WW-MPR, WW
Hypericaceae	*Hypericum kiboense*	69	3 colporate / 3 colporidate, reticulate, rather subprolate, nice egg-shaped, 20-23 µm	WW-MPR, WW
Hypericaceae	*Hypericum revolutum*	70	3 colporate / 3 colporidate, reticulate, annulate pore	WW
Icacinaceae	*Apodytes dimidiata*			MD
Iridaceae	*Gladiolus watsonii*	71	monosulcate, >20 µm	MD
Iridaceae	Type I		24µm	MD
Iridaceae	Type II			MD
Lamiaceae	*Basilicum polystachyon*			MD
Lamiaceae	*Hoslundia opposita*		6 colpate, striate, reticulate	WW
Lamiaceae	*Hyptis brevipes*			MD
Lamiaceae	cf *Ibozoa*	72	6 colpate, striate / reticulate, tectate, columellate, long colpi, 24 µm	WW, WW-MPR
Lamiaceae	*Leonotis*	73	3 colpate, reticulate, 24-32 µm, thick exine, wide colpi, narrow Reticulum, Margo, round in polar and equatorial view	WW, MD
Lamiaceae	*Leucas*	74	3 colpate, reticulate, 23 µm, long colpi, exine thicker than *Leonotis*, no margo, colpi more narrow than *Leonotis*	WW, MD
Lamiaceae	*Ocimum*		6 colpate, striate, reticulate	WW
Lamiaceae	*Plectranthus*	75	6 colpate, striate, reticulate	WW, WW-MPR
Lamiaceae	Type I		3 colpate, rough reticulate, 30µm	WW
Lamiaceae	Type II		6 colpate, thin reticulate	WW
Lamiaceae	Type IV			MD

Lamiaceae	*Vitex strickeri*		3 colpate, reticulate, 20 µm, thick reticulum, long and wide colpi, circular - subprolate	MD
Lauraceae	*Ocotea usambarensis*			WW
Liliaceae / Iridaceae	Type I			WW-MPR
Liliaceae / Iridaceae	Type II			WW, WW-MPR
Lobeliaceae	*Lobelia*	76	3 colporidate, very thin reticulate, reticulum similar to *Mallotus*, 28 x 24 µm, long and narrow colpi, equatorially tied, Margo	WW-MPR
Loganiaceae	*Nuxia*	77		WW-MPR
Loganiaceae	*Strychnos*	78		WW-MPR, MD
Lythraceae	cf *Lythrum*	79		WW-MPR
Malvaceae	*Sida*			MD
Malvaceae	Type		3 colpate	WW
Melastomataceae	Type		6 colpate, heterocolpate, more thin-walled than Combretaceae, psilate / granulate, colpori longer than pseudocolpi, equatorially tied, often heterosyncolpate	MD
Meliaceae	Type I	80		MD
Meliaceae	Type II		3 colporate, 20µm, psilate	WW-MPR
Meliaceae	*cf Cedrela*			WW-MPR
Menispermaceae	*Cissampelos pareirea*	81	3 colporate / 3 colporidate, reticulate, high and rough reticulum, small grain, 20 µm, intectate, thin exine	MD
Menispermaceae	*Cocculus hirsutus*	82	3 colporate/ 3 colporidate, reticulate, high and thin Reticulum, small grain, 15 µm, long and deep colpi, oval pores	MD
Menispermaceae	*Stephania abyssincia*	83		WW-MPR
Menispermaceae	*Tiliacora funifera*	84	3 colporate / 3 colporidate, reticulate, high and thin reticulum, small grain	MD
Menispermaceae	Type I			MD
Menispermaceae	Type II			WW
Mimosaceae	*Acacia / Albizia*	85 / 86		MD
Mimosaceae	*Mimosa invisa*	87		MD
Mimosaceae	Type		polyade (8 pollen grains)	WW-MPR, WW, MD
Moraceae/Urticaceae	Type I		2 porate	WW-MPR, WW, MD
Moraceae/Urticaceae	Type II		2 porate, echinulate, 12µm	WW-MPR, WW, MD
Moraceae/Urticaceae	Type III		3 porate	WW-MPR, WW, MD

Moraceae/Urticaceae	Type IV		3 porate, annulate	WW-MPR, WW, MD
Moraceae/Urticaceae	Type V		3 porate, annulate, 25µm	WW-MPR, MD
Moraceae/Urticaceae	Type VI		4 porate	WW-MPR, WW, MD
Musaceae	*Ensete edule*			WW-MPR
Myricaceae	*Myrica salicifolia*		3 porate, scabrate / psilate, triangular	WW-MPR, WW, MD
Myrsinaceae	*Embelia*			WW-MPR
Myrsinaceae	*Maesa*			WW-MPR
Myrsinaceae	*Myrsine*	88		MD, WW-MPR, WW
Myrtaceae	*Eucalyptus saligna*	89	triangular	WW-MPR
Myrtaceae	*Syzygium*	90	triangular	WW-MPR, WW
Olacaceae	*Strombosia scheffleri*		3 colpate, psilate, 20 µm, aperture membrane granulate - 3 porate, scabrate / psilate	WW-MPR, MD
Oleaceae	*Jasminum*	91		MD
Oleaceae	*Olea*	92	3 colpate, reticulate, 20 µm, colporoideate, circular, thick exine, in polar view pores sunken, round in polar and equatorial view, short colpi	WW-MPR, WW, MD
Oxalidaceae	*Oxalis*	93		WW, MD
Piperaceae	*Peperomia* I		inaperturate, 8µm	WW-MPR
Piperaceae	*Peperomia* II		inaperturate, 15µm	MD
Piperaceae	*Piper*	95	monosulcate / monocolpate, <20 µm	WW-MPR, WW, MD
Piperaceae	Type		verrucate, 8 µm	WW
Plantaginaceae	*Plantago*	96	periporate, granulate / verrucate, 25 µm, round	WW-MPR, WW, MD
Plumbaginaceae	*Plumbago*	97		WW-MPR
Poaceae	Type I		<10 µm, large anulus	MD, WW-MPR, WW
Poaceae	Type II		<10 µm, small anulus	MD, WW-MPR, WW
Poaceae	Type IV		10-20 µm, large anulus	MD, WW-MPR, WW
Poaceae	Type V		10-20 µm, small anulus	MD, WW-MPR, WW
Poaceae	Type VI		20-30 µm, large anulus	MD, WW-MPR, WW
Poaceae	Type VII		20-30 µm, small anulus	MD, WW-MPR, WW
Poaceae	*Zea mays*		100µm	WW-MPR
Podocarpaceae	*Podocarpus*	98		WW-MPR, WW, MD
Polygonaceae	Type			MD
Polygonaceae	*Rumex*	99		MD, WW, WW-MPR
Polypodiaceae	Type			MD
Primulaceae	*Anagallis serpens*	100		WW

Proteaceae	*Protea caffra*	101		WW-MPR, WW, MD
Ranunculaceae	*Clematis*	103	3 colporidate, echinate, 25 µm, perforate, tectate, thick columella, colpi, Echini unremarkable, exine regular, big, round	WW-MPR, WW, MD
Ranunculaceae	*Ranunculus*	104	pericolpate, spheroidal, 6-12 colpi, irregular edge, exine 1.5-2.5 µm, 40-50 µm, appears dotted from above, columellate, except at colpi exine rather regular	WW-MPR, WW, MD
Ranunculaceae	*Thalictrum rhynchocarpus*	105		WW-MPR, WW, MD
Resedaceae	*Caylusea abyssinica*	106		WW, MD
Rhamnaceae	*Scutia myrtina*	107		MD
Rosaceae	*Alchemilla*	108	3 colporidate, reticulate, 23 x 17 µm, lalongate clearly poroide region, thick exine with auricles, clearly columellate, triangular at polar view, exine equatorial 2-4 µm thick, intercolpate exine max. 2 µm	WW-MPR, WW, MD
Rosaceae	*Hagenia abyssinica*	109 / 110		WW-MPR, WW, MD
Rosaceae	*Prunus / Rubus*	111	3 colporate, s-shaped pore, striate / reticulate, subprolate, 23 µm, short colpi, rather spheroidal	WW-MPR, WW
Rubiaceae	*Canthium*			WW
Rubiaceae	cf *Coffea*			WW-MPR
Rubiaceae	cf *Cremaspora*			WW-MPR
Rubiaceae	cf *Parapentas*			WW-MPR
Rubiaceae	*Chassalia*	112		WW
Rubiaceae	cf *Gaertnera*		roughly reticulate	WW-MPR
Rubiaceae	*Kohautia*	113		WW-MPR
Rubiaceae	*Lasianthus kilimandscharicus*	114		WW-MPR
Rubiaceae	*Mussaenda*	115		WW-MPR
Rubiaceae	*Oldenlandia*			MD
Rubiaceae	cf *Parapentas*	116	3 colporate / 3 colporidate, reticulate	WW
Rubiaceae	cf *Pauridiantha*	117	3 colporate / 3 colporidate, reticulate	MD, WW-MPR
Rubiaceae	*Pavetta*		3 colporate / 3 colporidate, reticulate	WW-MPR
Rubiaceae	*Pentas*	118	3 colporate / 3 colporidate, reticulate	WW-MPR, WW
Rubiaceae	*Pentodon pentandrus*	119		WW-MPR
Rubiaceae	cf *Polysphaeria*	120		WW-MPR
Rubiaceae	*Psychotria*	121		WW-MPR, MD
Rubiaceae	*Psychotria capense*	122		WW-MPR, WW

Rubiaceae	*Psychotria fractinervata*	123		WW-MPR, WW
Rubiaceae	Type I		Tetrade, 45µm, thin reticulate	WW, MD
Rubiaceae	Type II			WW-MPR, WW
Rutaceae	*Teclea*	124	3 colporate / 3 colporidate, striate	WW-MPR
Rutaceae	Type			WW-MPR, WW
Santalaceae	*Osyris lanceolata*	125		MD
Sapindaceae	*Allophylus*	126		MD, WW, WW-MPR
Sapindaceae	*Blighia unijugata*			MD
Sapindaceae	*Dodonaea viscosa*	127		WW-MPR, WW, MD
Sapindaceae	*Filicium decipiens*	128		WW-MPR, MD
Sapindaceae	*Paullinia pinnata*	129		MD
Sapotaceae	*Aningeria adolfi-friderici*	130		MD
Scrophulariaceae	*Striga*	131	3-4 colpate, psilate, 15-23 µm, tectate, granulate,	MD
Solanaceae	*Discopodium penninervum*			MD
Solanaceae	*Solanum*	132		MD
Solanaceae	*Solanum seaforthianum*	133		WW-MPR
Sterculiaceae	*Dombeya*	134		WW-MPR, WW
Sterculiaceae	Type			MD
Thymeliaceae	*Peddiea fischeri*			WW-MPR
Tiliaceae	*Triumfetta brachyceras*	135		MD, WW, WW-MPR
Typhaceae	*Typha domingensis*			WW-MPR
Ulmaceae	*Celtis*	136		WW-MPR, WW, MD
Ulmaceae	*Chaetacme aristata*		20 x 30 µm, circular, 3 porate, round annulate pores	WW-MPR
Ulmaceae	*Trema orientalis*	137	2 porate, annulate, 15 x 19 µm, psilate / scabrate,	WW-MPR, WW
Urticaceae	*Laportea*		4poorate, periporate, 12 µm, round, psilate / scabrate, round pores, small	WW, WW-MPR
Urticaceae	*Pilea*	138	15 µm, 2 porate, clearly granulate, round pores	WW-MPR
Valerianaceae	*Valeriana*	140		WW-MPR, WW
Verbenaceae	*Clerodendron*	141	3 colpate, also 3 colporate, psilate,	MD
Verbenaceae	*Vitex strickeri*			MD
Violaceae	*Rinorea*		3 colporate / 3 colporidate, psilate / scabrate, prolate / subprolate, 20 x 23 µm, columellate	WW
Violaceae	*Viola*		3 colporate / 3 colporidate, scabrate, prolate / subprolate	WW-MPR
Vitaceae	*Cyphostemma*	142		WW-MPR

Appendix A1: Table of identified pollen and spore types

Family	Spore Type	Photo N°	Morphology Note	Record
Adiantaceae	*Adiantum*			WW-MPR
Aspleniaceae	*Asplenium*	1		MD, WW, WW-MRP
Athyriaceae	*Cystopteris*	2		WW-MPR, WW
Athyriaceae	Type			WW-MPR
Cyatheaceae	*Cyathea*	3		WW-MPR, WW
Dennstaedtiaceae	Type			WW-MPR
Dryopteridaceae	*Arachnoides*			WW-MPR
Hymenophyllaceae	*Trichomanes*			WW-MPR
Lomariopsidaceae	*Elaphoglossum*			WW-MPR
Lycopodiaceae	*Huperzia*	4		WW-MPR, WW
Lycopodiaceae	*Lycopodium*			MD
Marattiaceae	*Marattia*			WW-MPR
Ophioglossaceae	*Ophioglossum*			WW-MPR
Polypodiaceae	cf *Loxogramme*			WW-MPR
Polypodiaceae	cf *Polypodium*			WW-MPR
Polypodiaceae	*Pleopeltis macrocarpa*	5		WW-MPR, WW
Tectariaceae	*Tectaria*			WW-MPR
Thelypteridaceae	Type			WW-MPR
Woodsiaceae	Type			WW-MPR

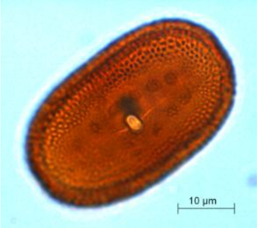
Appendix A2: Identified Pollen Types

ACANTHACEAE

A

1) *Blepharis*

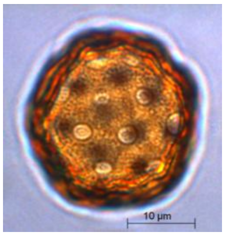
2) *Justicia*



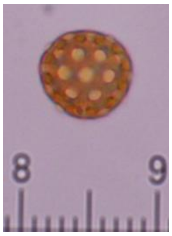
3) *Monechma*

4) *Thunbergia*

AMARANTHACEAE

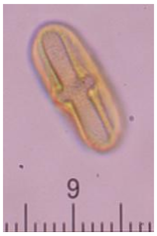


5) *Amaranthus*



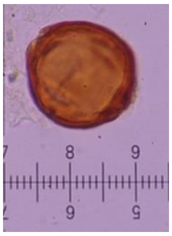
6) *Achyranthes aspera*

APIACEAE



7) *Oenanthe*

APOCYNACEAE



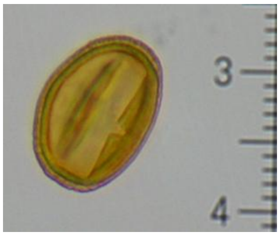
8) *Tabernaemontana*

AQUIFOLIACEAE

9) *Ilex mitis*

ARALIACEAE

10) *Polyscias*

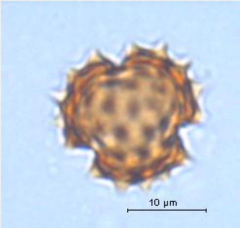


11) *Schefflera*

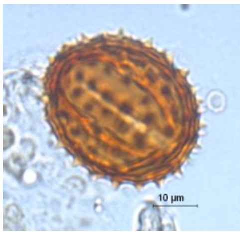
ASTERACEAE

12) *Artemisia*

13) *Centaurea*

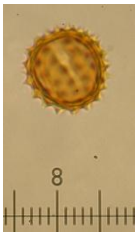


14) *Conyza*

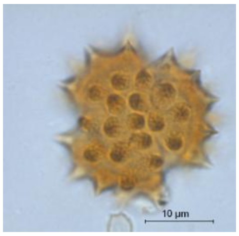


15) *Crassocephalum*

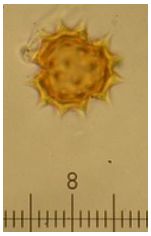
16) *Dicoma tomentosa*



17) *Emilia*



18) *Helichrysum*



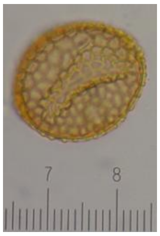
19) *Schkuhria pinnata*

20) *Senecio*

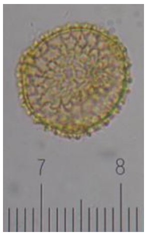
Appendix A2: Identified Pollen Types

B

BALSAMINACEAE

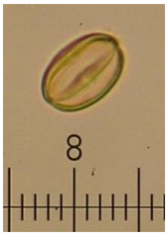


21) *Impatiens*



22) *Impatiens pseudoviola*

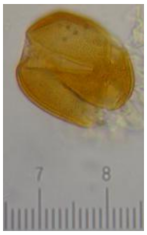
BEGONIACEAE



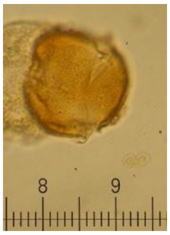
23) *Begonia*

BIGONIACEAE

24) *Jacaranda mimosifolia*



25) *Markhamia lutea*



26) *Stereospermum kunthianum*

27) *Tecoma stans*

C

BORAGINACEAE

28) *Ehretia*

29) *Heliotropium*

30) *Lithospermum afromonatnum*

CAESALPINACEAE

31) *Pterolobium stellatum*

CAPPARACEAE

32) *Cleome*

33) *Gynandropsis gyandra*

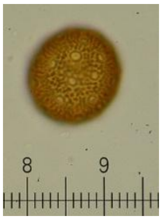
CAPRIFOLIACEAE

34) *Sambucus nigra*

CARYOPHYLLACEAE

35) *Cerastium*

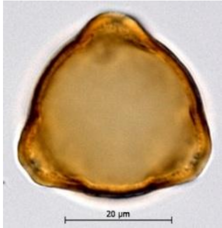
36) *Polycarpa eriantha*



37) *Ubellinia rotundofolia*

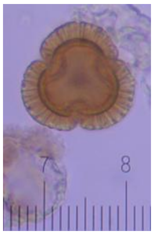
Appendix A2: Identified Pollen Types

CASUARINACEAE



38) *Casuarina*

CELASTRACEAE

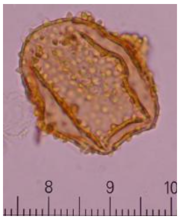


39) *Maytenus*

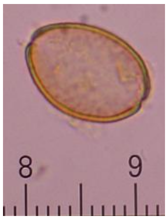
COMBRETACEAE

40) *Combretum*

COMMELINACEAE



41) *Aneilema*

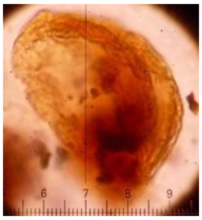


42) *Commelina*

CONVOLVULACEAE

43) *Astripomoea*

44) *Convolvulus*



45) *Meremmia*

D

CUPRESSACEAE

46) *Juniperus procera*

CYPERACEAE

47) *Carex*

48) *Cyperus*

DRACAENACEAE

49) *Dracaena afromontana*

E

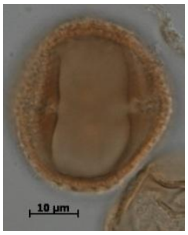
EBENACEAE

50) *Euclea*

ERICACEAE

51) *Erica*

EUPHORBIACEAE



52) *Drypetes*

53) *Euphorbia*

54) *Macaranga*

F

FABACEAE

55) *Abrus*

56) *Aschynomene*

57) *Calpurnia*

58) *Dalbergia*

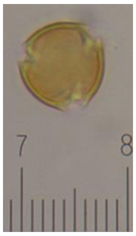
59) *Desmodium*

60) *Eriosema*

Appendix A2: Identified Pollen Types

G

FLACOURTIACEAE

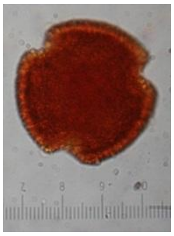


61) *Dasylepis integra*

FUMARIACEAE

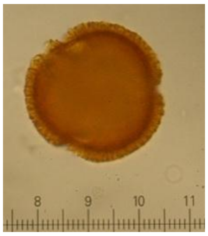
62) *Corydalis mildebraedii*

GERANIACEAE



63) *Geranium*

64) *Monsonia*



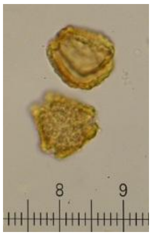
65) *Pelargonium*

H

HAMMAMELIDACEAE

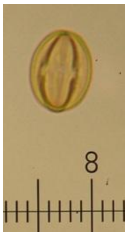
66) *Trichocladus ellipticus*

HYPERICACEAE

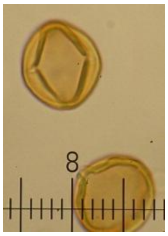


67) *Garcinia*

68) *Hypericum keniense*



69) *Hypericum kiboense*



70) *Hypericum revolutum*

IL

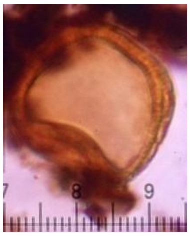
IRIDACEAE

71) *Gladiolus watsonii*

LAMIACEAE

72) Cf *Ibozoa*

73) *Leonotis*



74) *Leucas*

75) *Plectranthus*

M

LOBELIACEAE

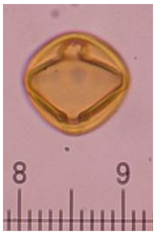
76) *Lobelia*

LOGANIACEAE

77) *Nuxia*

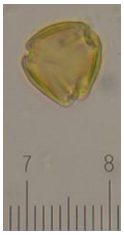
78) *Strychnos*

LYTHRACEAE



79) Cf *Lythrum*

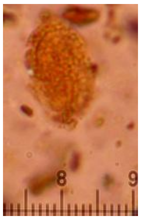
MELIACEAE



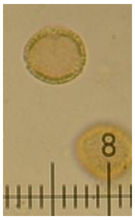
80) Meliaceae Type I

MENISPERMACEAE

81) *Cissampelos pareira*



82) *Cocculus hirsutus*

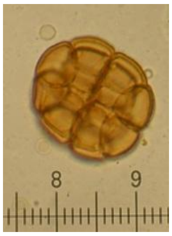


83) *Stephania abyssinica*

84) *Tiliacora funifera*

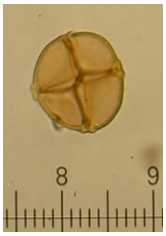
Appendix A2: Identified Pollen Types

MIMOSACEAE



85) *Acacia*

86) *Albizia*



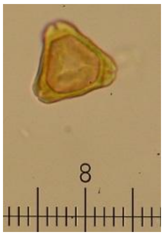
87) *Mimosa invisa*

MYRSINACEAE

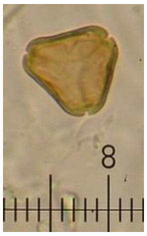
88) *Myrsine*

O

MYRTACEAE

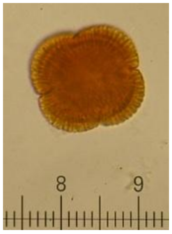


89) *Eucalyptus saligna*

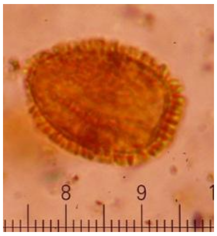


90) Syzygium

OLEACEAE



91) *Jasminum*



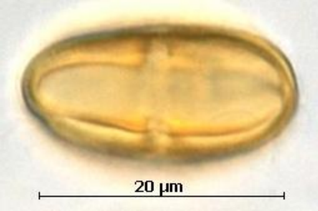
92) *Olea*

P

OXALIDACEAE

93) *Oxalis*

PHYLLANTACEAE

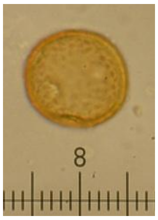


94) *Antidesma*

PIPERACEAE

95) *Piper*

PLANTAGINACEAE

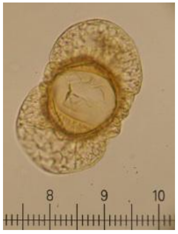


96) *Plantago*

PLUMBAGINACEAE

97) *Plumbago*

PODOCARPACEAE



98) *Podocarpus latifolius*

POLYGONACEAE

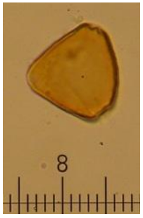
99) *Rumex*

PRIMULACEAE

100) *Anagallis serpens*

R

PROTEACEAE

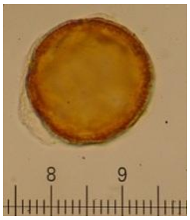


101) *Protea caffra*

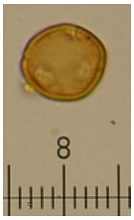
RANUNCULACEAE

102) *Anemona*

103) *Clematis*



104) *Ranunculus*



105) *Thalictrum rhynchocarpus*

Appendix A2: Identified Pollen Types

RESEDACEAE

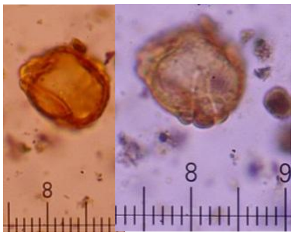
106) *Caylusea abyssinica*

RHAMNACEAE

107) *Scutia myrtina*

ROSACEAE

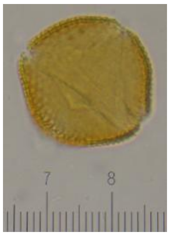
108) *Alchemilla*



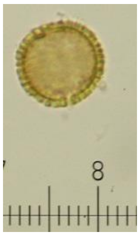
109/110) *Hagenia abyssinica*

111) Prunus/*Rubus*

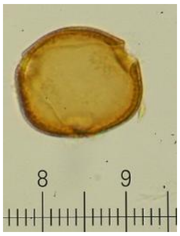
RUBIACEAE



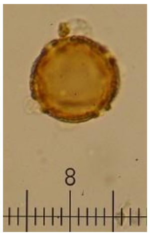
112) *Chassalia*



113) *Kohautia*

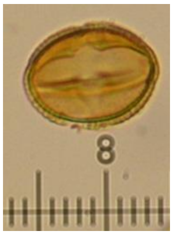


114) *Lasianthus kilimandscharicus*



115) *Mussarenda*

116) Cf *Parapentas*

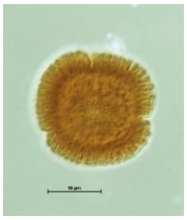


117) Cf *Pauridiantha*

118) *Pentas*

119) *Pentodon pentandrus*

120) Cf *Polysphaeria*



121) *Psychotria*

122) *Psychotria capense*

123) *Psychotria fractinervata*

S

RUTACEAE

124) *Teclea*

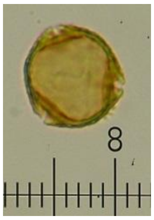
SANTALACEAE

125) *Osyris lanceolata*

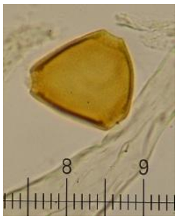
SAPINDACEAE

126) *Allophylus*

127) *Dodonaea viscosa*



128) *Filicium decipiens*



129) *Paullinia pinnata*

Sapotaceae

130) *Aningeria adolfi- friderici*

Scrophulariaceae

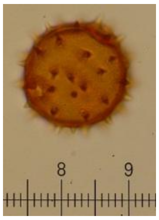
131) *Striga*

Solanaceae

132) *Solanum*

133) *Solanum seaforthianum*

Sterculariaceae



134) *Dombeya Type*

Appendix A2: Identified Pollen Types

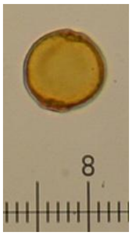
TU

TILIACEAE

135) *Triumfetta brachyceras*

ULMACEAE

136) *Celtis*



137) *Trema domingensis*

URTICACEAE

138) *Pilea*

V

VALERIANACEAE

140) *Valeriana*

VERBENACEAE

141) *Clerodendron*

VITACEAE

142) *CyphostemmA*

Appendix A2: Identified Spore Types

A-L

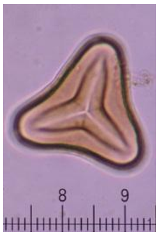
ASPLENIACEAE

1) *Asplenium*

ATHYRIACEAE

2) *Cystopteris*

CYATHEACEAE



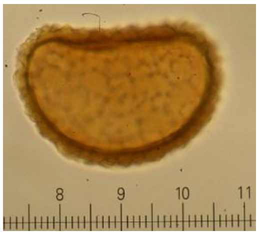
3) *Cyathea*

LYCOPODIACEAE

4) *Huperzia*

M-Z

POLYPODIACEAE



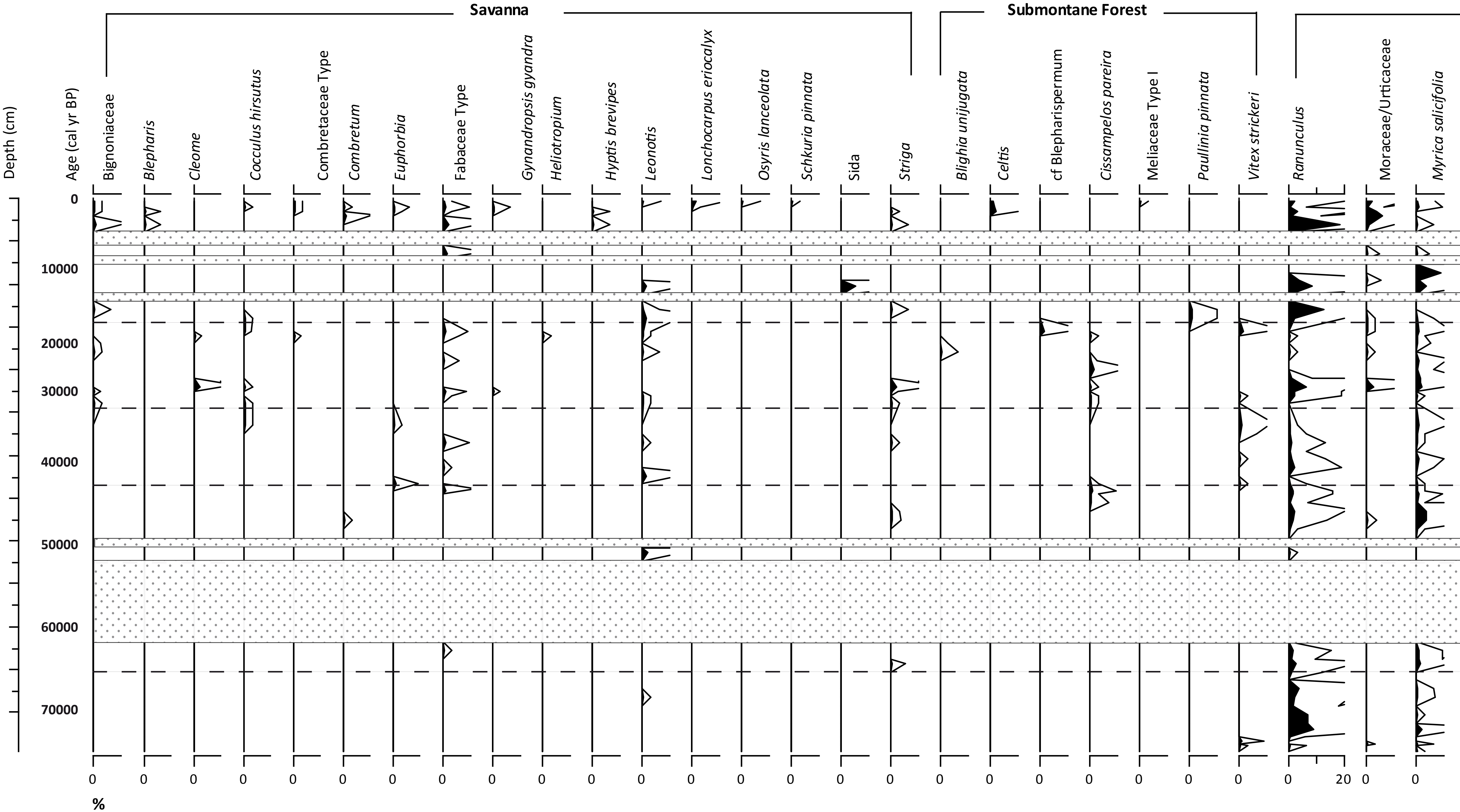
5) *Pleopeltis macrocarpa*

Appendix B

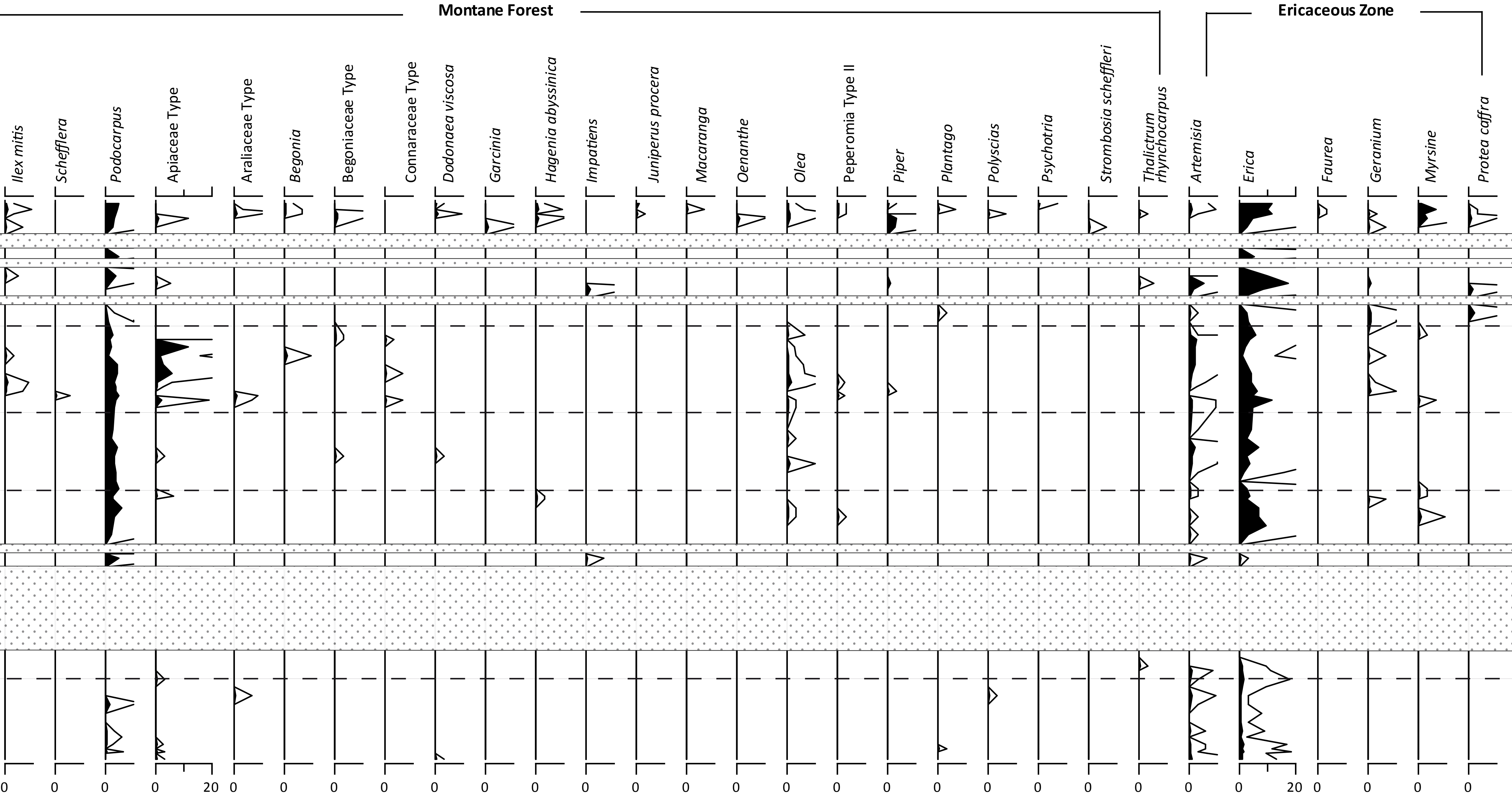
Complete Pollen Records

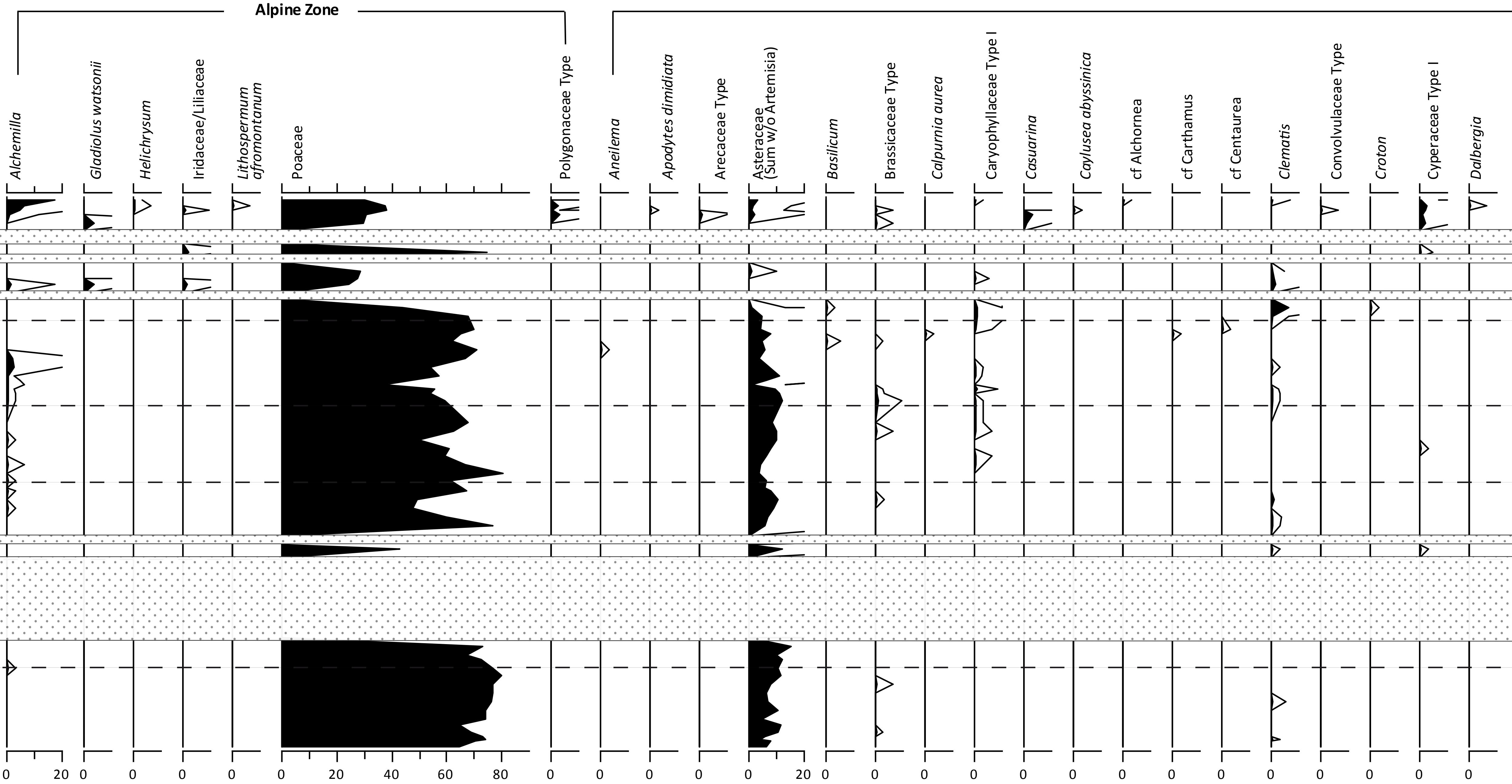
Maundi Pollen Record

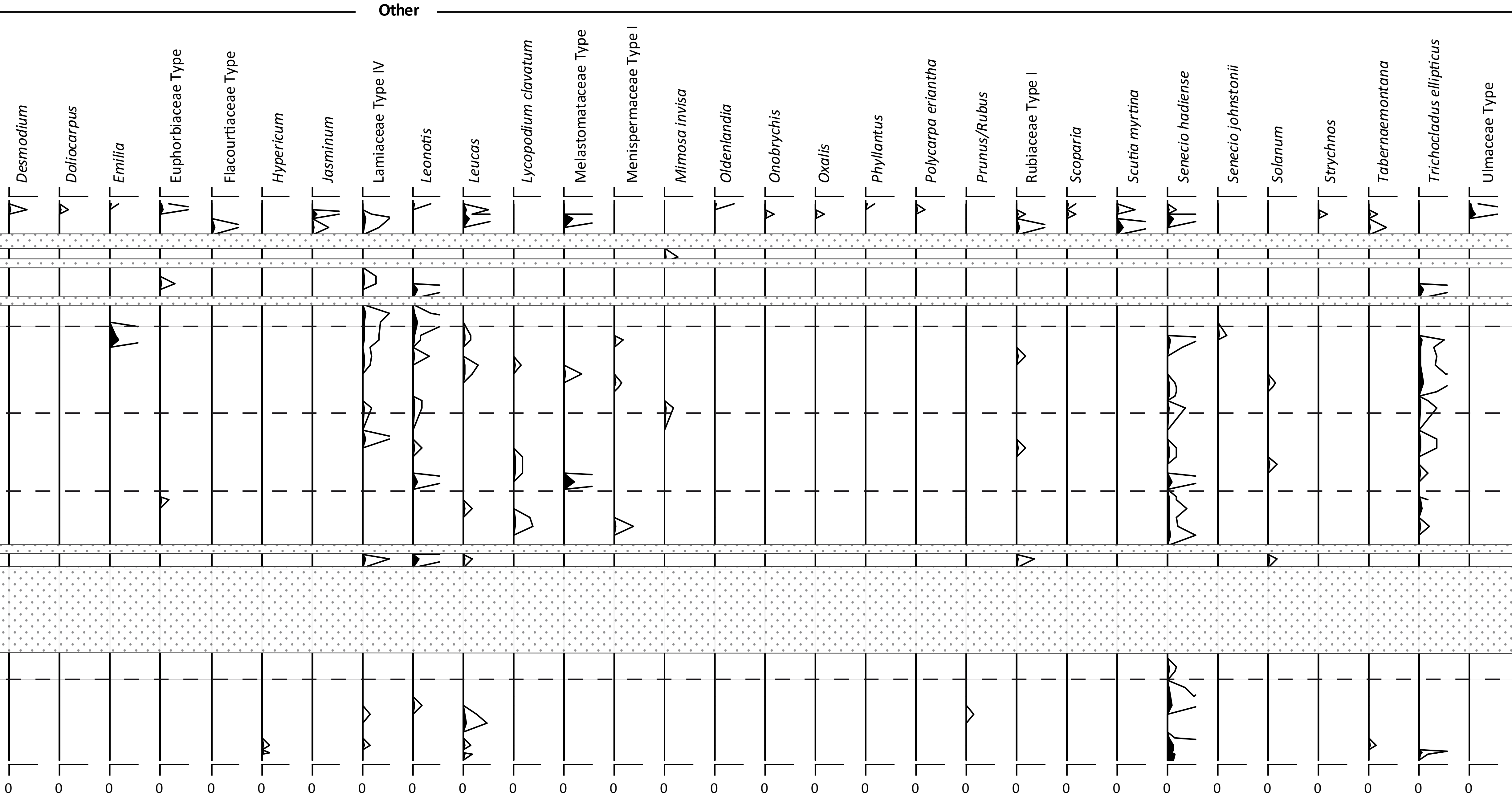
Maundi Crater, Kilimanjaro



▨ no pollen preservation


Montane Forest
Ericaceous Zone
Ilex mitis
Scheffera
Podocarpus
Apiaceae Type
Araliaceae Type
Begonia
Begoniaceae Type
Connaraceae Type
Dodonaea viscosa
Garcinia
Hagenia abyssinica
Impatiens
Juniperus procera
Macaranga
Oenanthe
Olea
Peperomia Type II
Piper
Plantago
Polyscias
Psychotria
Strombosia scheffleri
Thalictrum rhynchocarpus
Artemisia
Erica
Faurea
Geranium
Myrsine
Protea caffra
0
0
0
0
20
0
0
0
0
0
0
0
0
0
0
0
0
0
0
0
0
0
0
0
0
20
0
0
0
0


Alpine Zone
Alchemilla
Gladiolus watsonii
Helichrysum
Iridaceae/Liliaceae
Lithospermum afromontanum
Poaceae
Polygonaceae Type
Aneilema
Apodytes dimidiata
Arecaceae Type
Asteraceae (Sum w/o Artemisia)
Basilicum
Brassicaceae Type
Calpurnia aurea
Caryophyllaceae Type I
Casuarina
Caylusea abyssinica
cf Alchornea
cf Carthamus
cf Centaurea
Clematis
Convolvulaceae Type
Croton
Cyperaceae Type I
Dalbergia
0
20
0
0
0
0
0
20
40
60
80
0
0
0
0
0
20
0
0
0
0
0
0
0
0
0
0
0
0
0
0


Other
Desmodium
Doliocarpus
Emilia
Euphorbiaceae Type
Flacourtiaceae Type
Hypericum
Jasminum
Lamiaceae Type IV
Leonotis
Leucas
Lycopodium clavatum
Melastomataceae Type
Menispermaceae Type I
Mimosa invisa
Oldenlandia
Onobrychis
Oxalis
Phyllantus
Polycarpa eriantha
Prunus/Rubus
Rubiaceae Type I
Scoparia
Scutia myrtina
Senecio hadiense
Senecio johnstonii
Solanum
Strychnos
Tabernaemontana
Trichocladus ellipticus
Ulmaceae Type
0
0
0
0
0
0
0
0
0
0
0
0
0
0
0
0
0
0
0
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0
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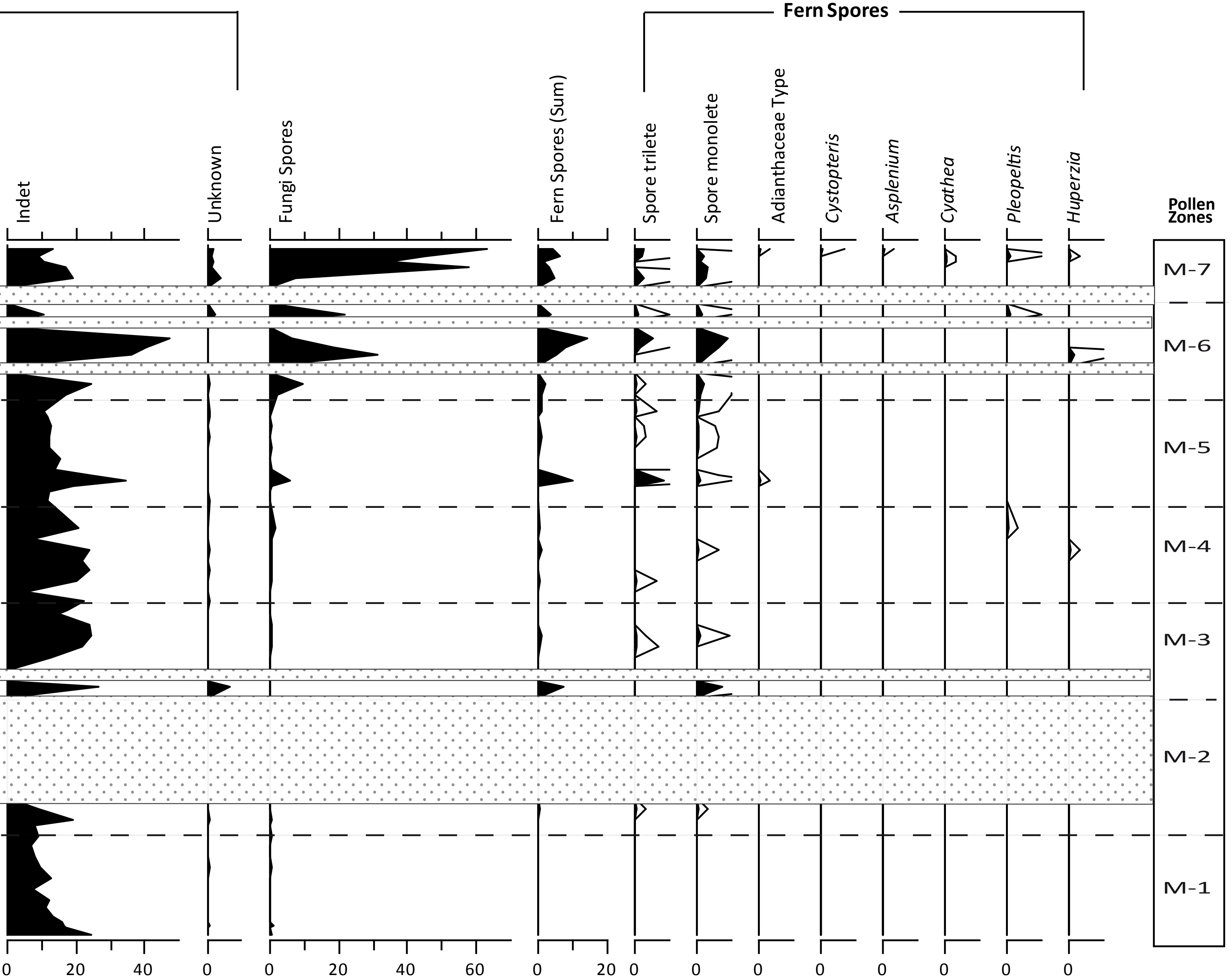
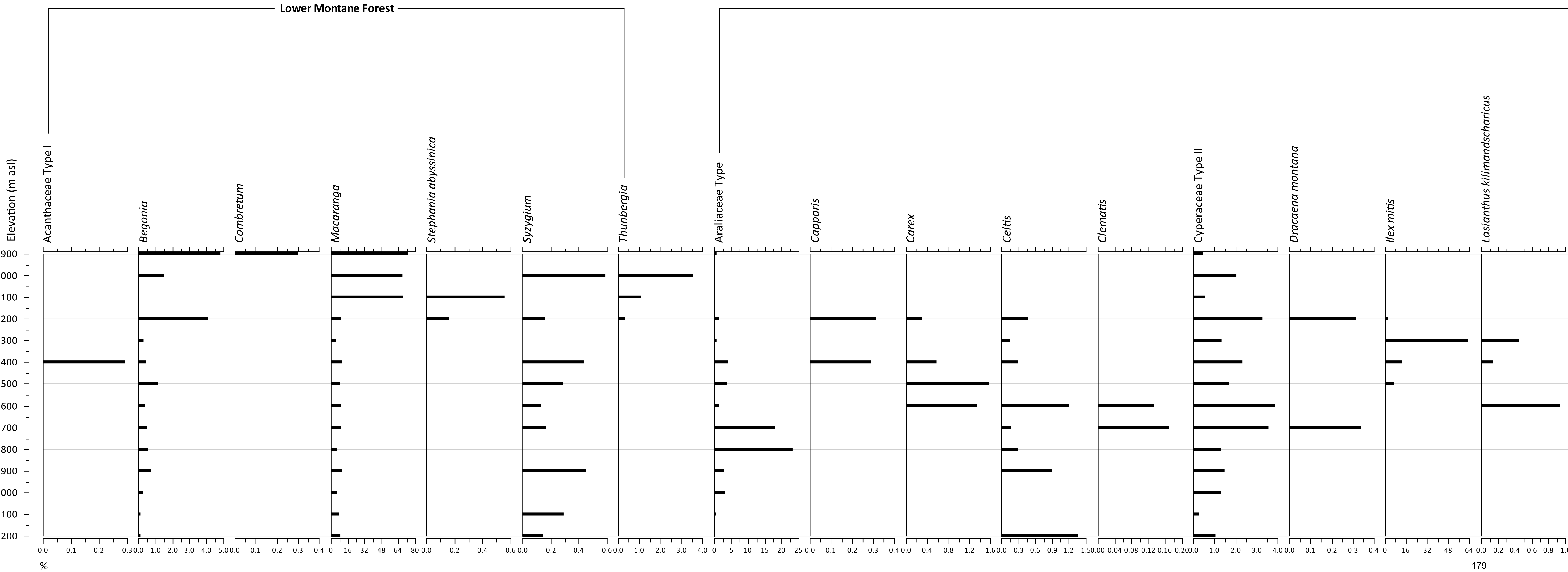
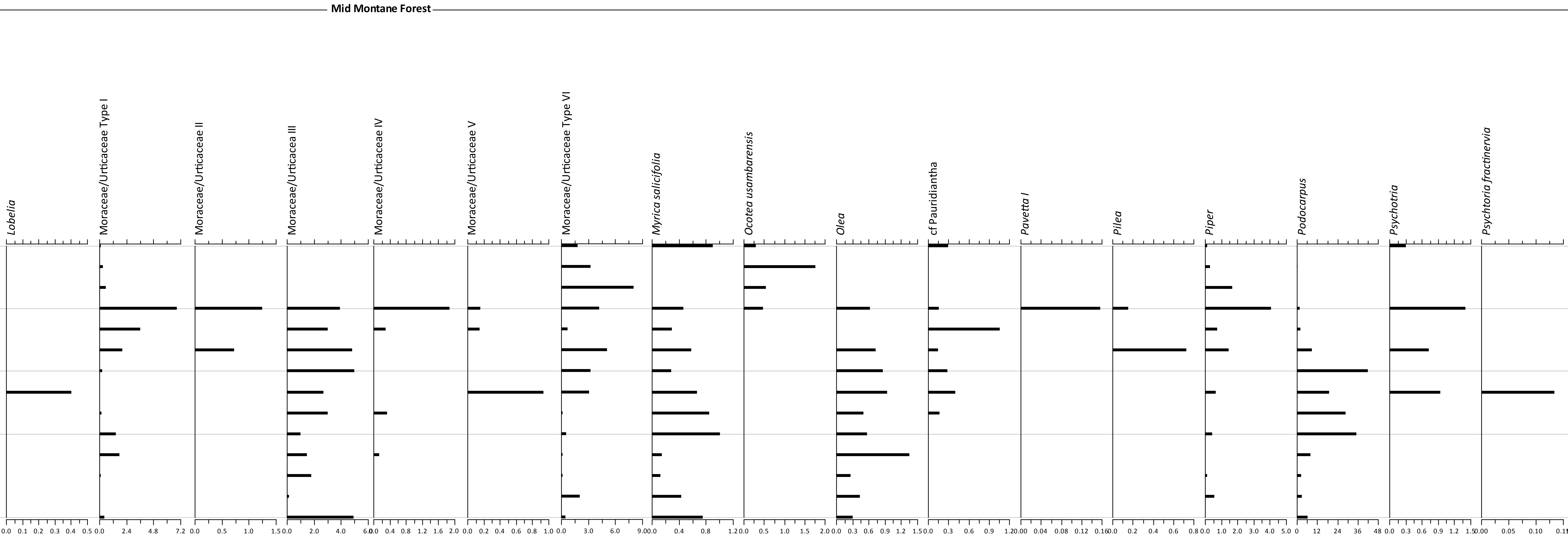
0
0
0


Fern Spores
Indet
Unknown
Fungi Spores
Fern Spores (Sum)
Spore trilete
Spore monolete
Adianthaceae Type
Cystopteris
Asplenium
Cyathea
Pleopeltis
Huperzia
Pollen Zones
M-7
M-6
M-5
M-4
M-3
M-2
M-1
0
20
40
0
0
20
40
60
0
20
0
0
0
0
0
0
0
0

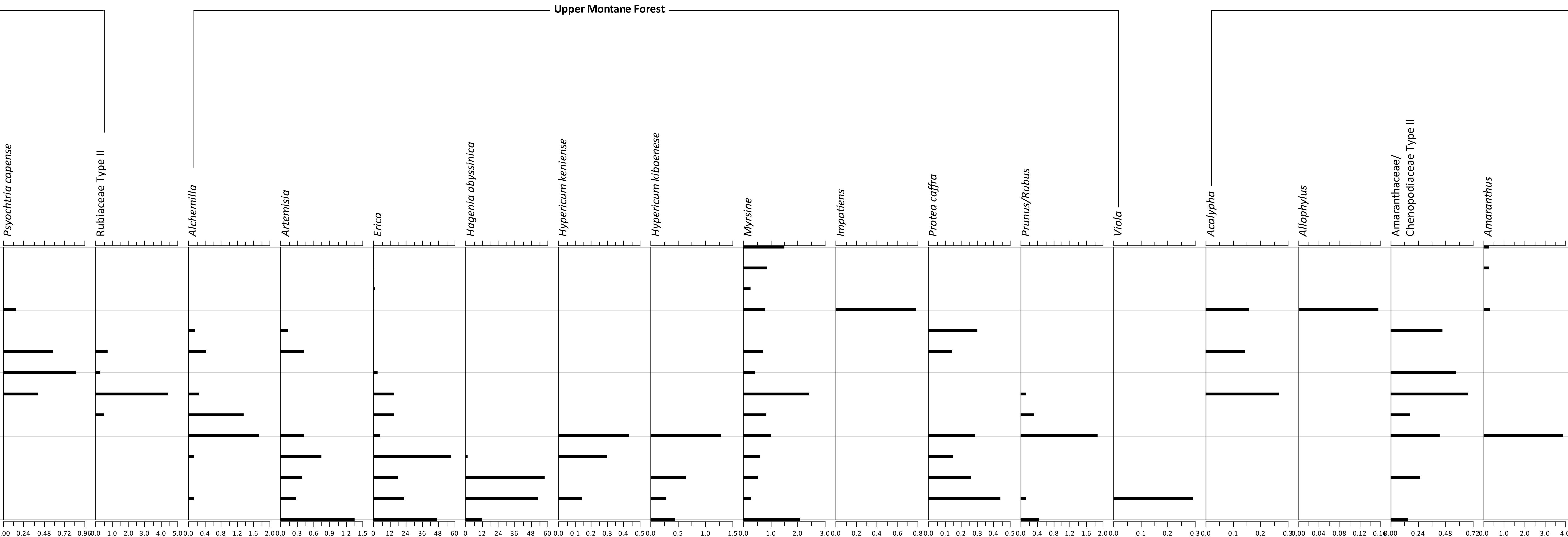
Modern Pollen Rain Record WeruWeru

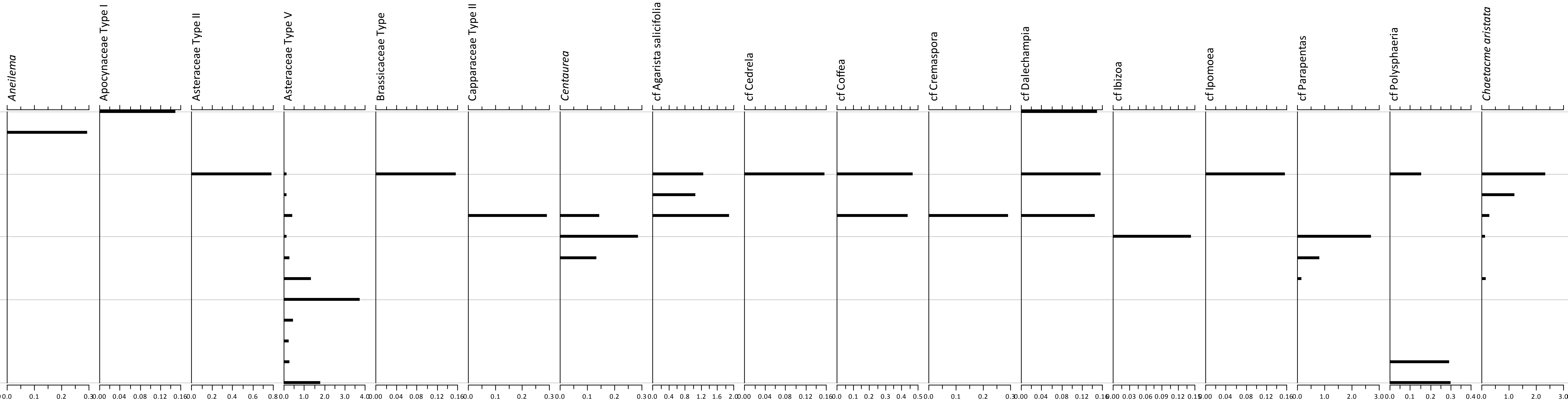
Weru Weru Modern Pollen Rain, Kilimanjaro



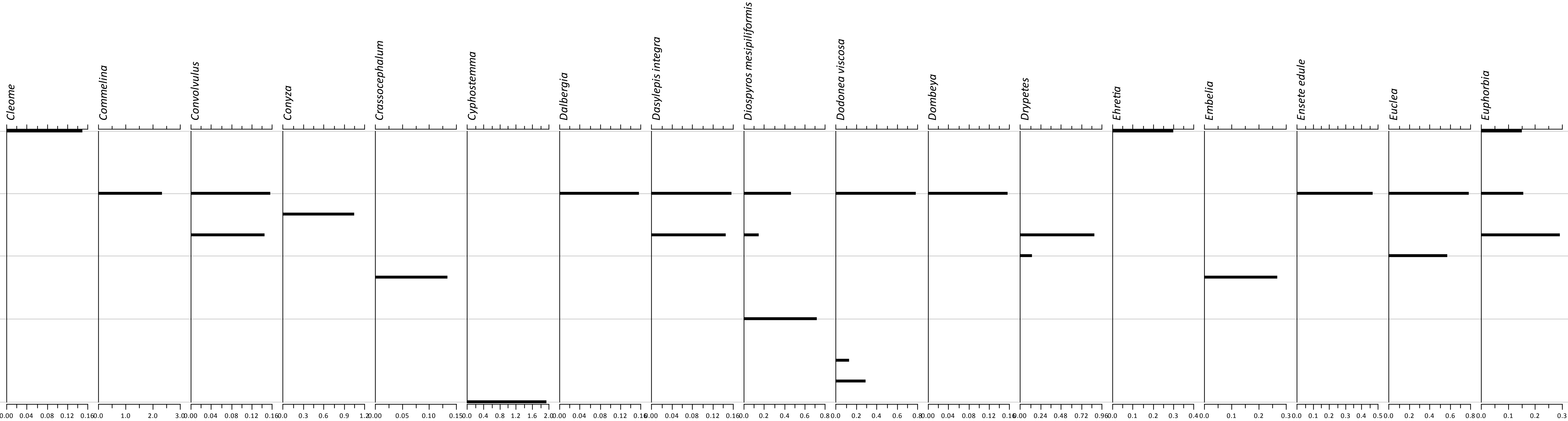


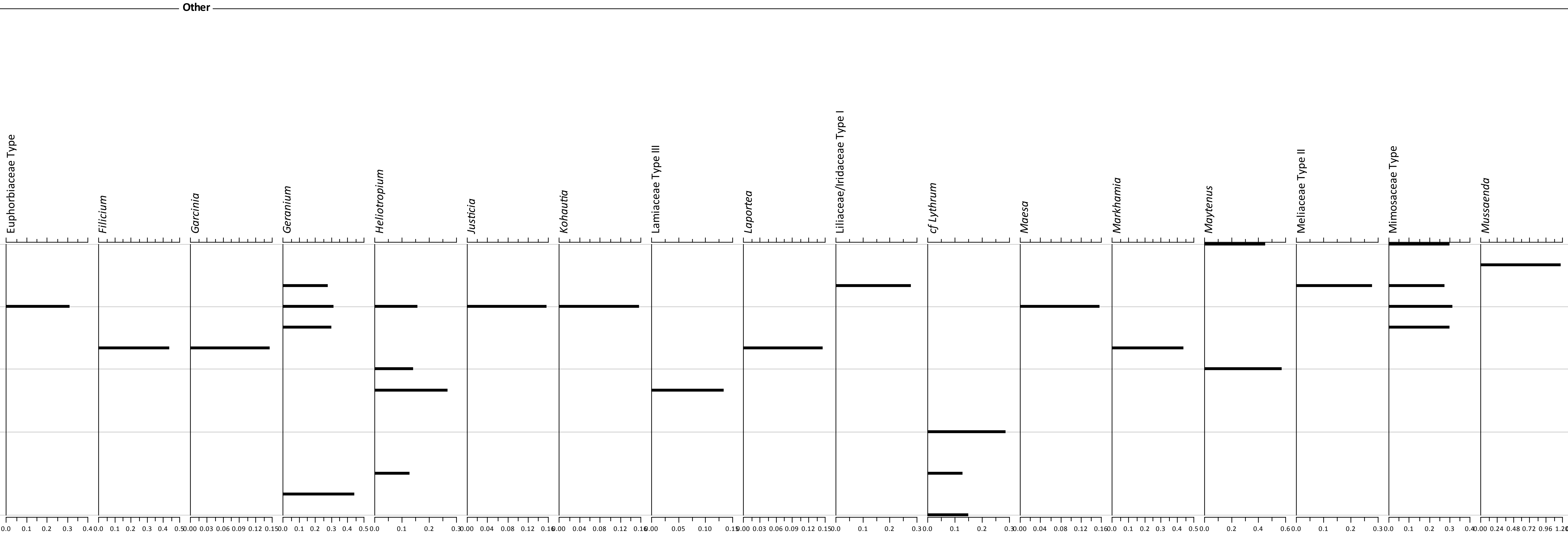
Mid Montane Forest
Lobelia
Moraceae/Urticaceae Type I
Moraceae/Urticaceae II
Moraceae/Urticacea III
Moraceae/Urticaceae IV
Moraceae/Urticaceae V
Moraceae/Urticaceae Type VI
Myrica salicifolia
Ocotea usambarensis
Olea
cf Pauridiantha
Pavetta I
Pilea
Piper
Podocarpus
Psychotria
Psychtoria fractinervia
0.0 0.1 0.2 0.3 0.4 0.5
0.0 2.4 4.8 7.2
0.0 0.5 1.0 1.5
0.0 2.0 4.0 6.0
0.0 0.4 0.8 1.2 1.6 2.0
0.0 0.2 0.4 0.6 0.8 1.0
0.0 3.0 6.0 9.0
0.0 0.4 0.8 1.2
0.0 0.5 1.0 1.5 2.0
0.0 0.3 0.6 0.9 1.2 1.5
0.0 0.3 0.6 0.9 1.2
0.00 0.04 0.08 0.12 0.16
0.0 0.2 0.4 0.6 0.8
0.0 1.0 2.0 3.0 4.0 5.0
0 12 24 36 48
0.0 0.3 0.6 0.9 1.2 1.5
0.00 0.05 0.10 0.15

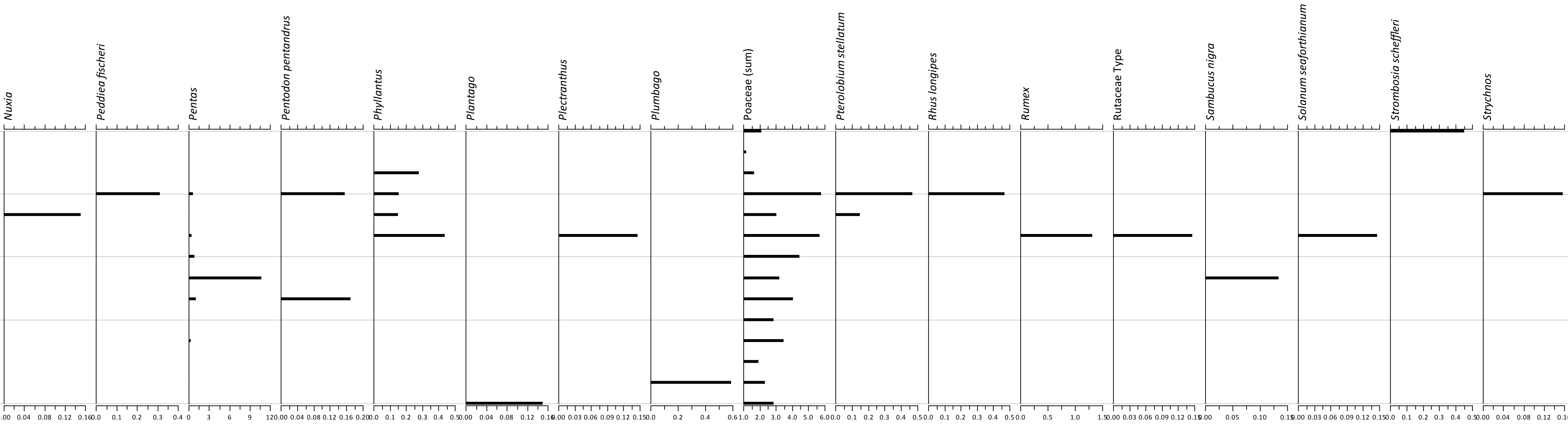

Upper Montane Forest
Psyochtria capense
Rubiaceae Type II
Alchemilla
Artemisia
Erica
Hagenia abyssinica
Hypericum keniense
Hypericum kiboenese
Myrsine
Impatiens
Protea caffra
Prunus/Rubus
Viola
Acalypha
Allophylus
Amaranthaceae/
Chenopodiaceae Type II
Amaranthus
.00 0.24 0.48 0.72 0.96
0.0 1.0 2.0 3.0 4.0 5.0
0.0 0.4 0.8 1.2 1.6 2.0
0.0 0.3 0.6 0.9 1.2 1.5
0 12 24 36 48 60
0 12 24 36 48 60
0.0 0.1 0.2 0.3 0.4 0.5
0.0 0.5 1.0 1.5
0.0 1.0 2.0 3.0
0.0 0.2 0.4 0.6 0.8
0.0 0.1 0.2 0.3 0.4 0.5
0.0 0.4 0.8 1.2 1.6 2.0
0.0 0.1 0.2 0.3
0.0 0.1 0.2 0.3
0.00 0.04 0.08 0.12 0.16
0.00 0.24 0.48 0.72
0.0 1.0 2.0 3.0 4.0

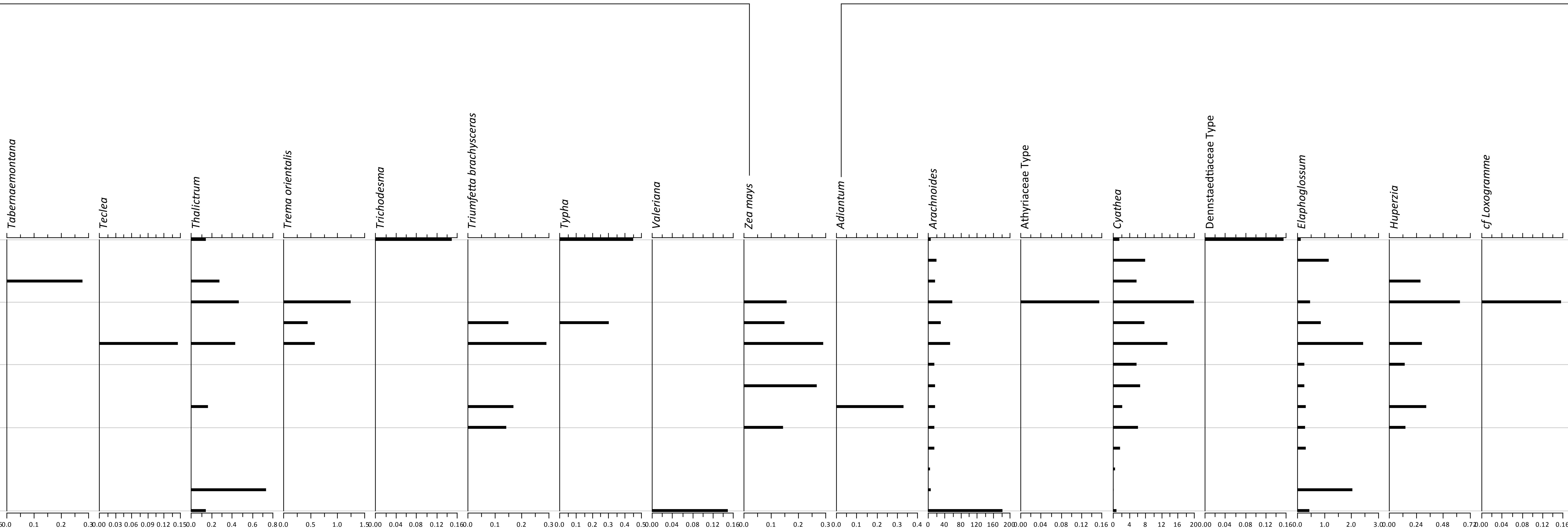


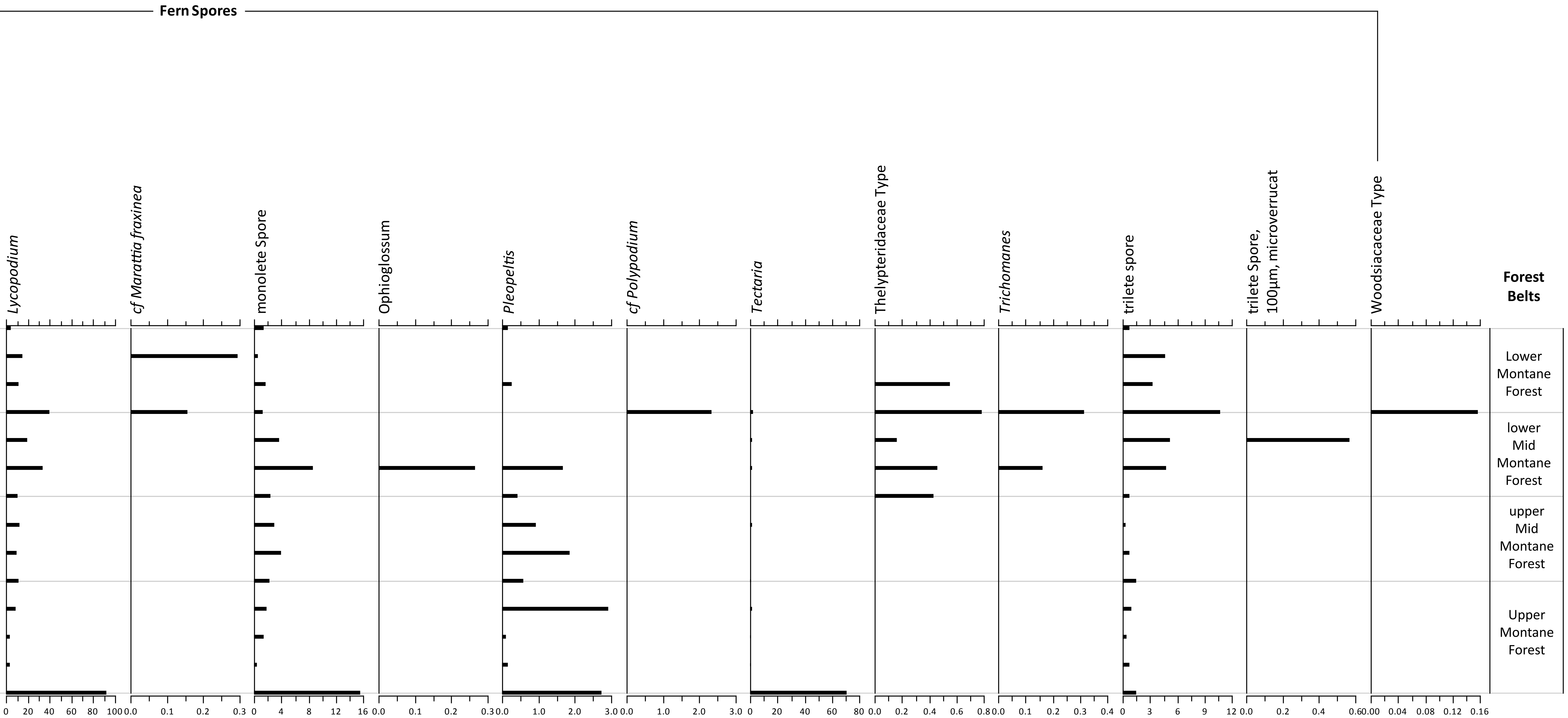
Aneilema
Apocynaceae Type I
Asteraceae Type II
Asteraceae Type V
Brassicaceae Type
Capparaceae Type II
Centaurea
cf Agarista salicifolia
cf Cedrela
cf Coffea
cf Cremaspora
cf Dalechampia
cf Ibizoa
cf Ipomoea
cf Parapentas
cf Polysphaeria
Chaetacme aristata
0.0 0.1 0.2 0.3
0.00 0.04 0.08 0.12 0.16
0.0 0.2 0.4 0.6 0.8
0.0 1.0 2.0 3.0 4.0
0.00 0.04 0.08 0.12 0.16
0.0 0.1 0.2 0.3
0.0 0.1 0.2 0.3
0.0 0.4 0.8 1.2 1.6 2.0
0.00 0.04 0.08 0.12 0.16
0.0 0.1 0.2 0.3 0.4 0.5
0.0 0.1 0.2 0.3
0.00 0.04 0.08 0.12 0.16
0.00 0.03 0.06 0.09 0.12 0.15
0.00 0.04 0.08 0.12 0.16
0.0 1.0 2.0 3.0
0.0 0.1 0.2 0.3 0.4
0.0 1.0 2.0 3.0


Cleome
Commelina
Convolvulus
Conyza
Crassocephalum
Cyphostemma
Dalbergia
Dasylepis integra
Diospyros mesipiliformis
Dodonea viscosa
Dombeya
Drypetes
Ehretia
Embelia
Ensete edule
Euclea
Euphorbia
0.00 0.04 0.08 0.12 0.16
0.0 1.0 2.0 3.0
0.00 0.04 0.08 0.12 0.16
0.0 0.3 0.6 0.9 1.2
0.00 0.05 0.10 0.15
0.0 0.4 0.8 1.2 1.6 2.0
0.00 0.04 0.08 0.12 0.16
0.00 0.04 0.08 0.12 0.16
0.0 0.2 0.4 0.6 0.8
0.0 0.2 0.4 0.6 0.8
0.00 0.04 0.08 0.12 0.16
0.00 0.24 0.48 0.72 0.96
0.0 0.1 0.2 0.3 0.4
0.0 0.1 0.2 0.3
0.0 0.1 0.2 0.3 0.4 0.5
0.0 0.2 0.4 0.6 0.8
0.0 0.1 0.2 0.3


Other
Euphorbiaceae Type
Filicium
Garcinia
Geranium
Heliotropium
Justicia
Kohautia
Lamiaceae Type III
Laportea
Liliaceae/Iridaceae Type I
cf Lythrum
Maesa
Markhamia
Maytenus
Meliaceae Type II
Mimosaceae Type
Mussaenda
0.0 0.1 0.2 0.3 0.4
0.0 0.1 0.2 0.3 0.4 0.5
0.00 0.03 0.06 0.09 0.12 0.15
0.0 0.1 0.2 0.3 0.4 0.5
0.0 0.1 0.2 0.3
0.00 0.04 0.08 0.12 0.16
0.00 0.04 0.08 0.12 0.16
0.00 0.05 0.10 0.15
0.00 0.03 0.06 0.09 0.12 0.15
0.0 0.1 0.2 0.3
0.0 0.1 0.2 0.3
0.00 0.04 0.08 0.12 0.16
0.0 0.1 0.2 0.3 0.4 0.5
0.0 0.2 0.4 0.6
0.0 0.1 0.2 0.3
0.0 0.1 0.2 0.3 0.4
0.00 0.24 0.48 0.72 0.96 1.2

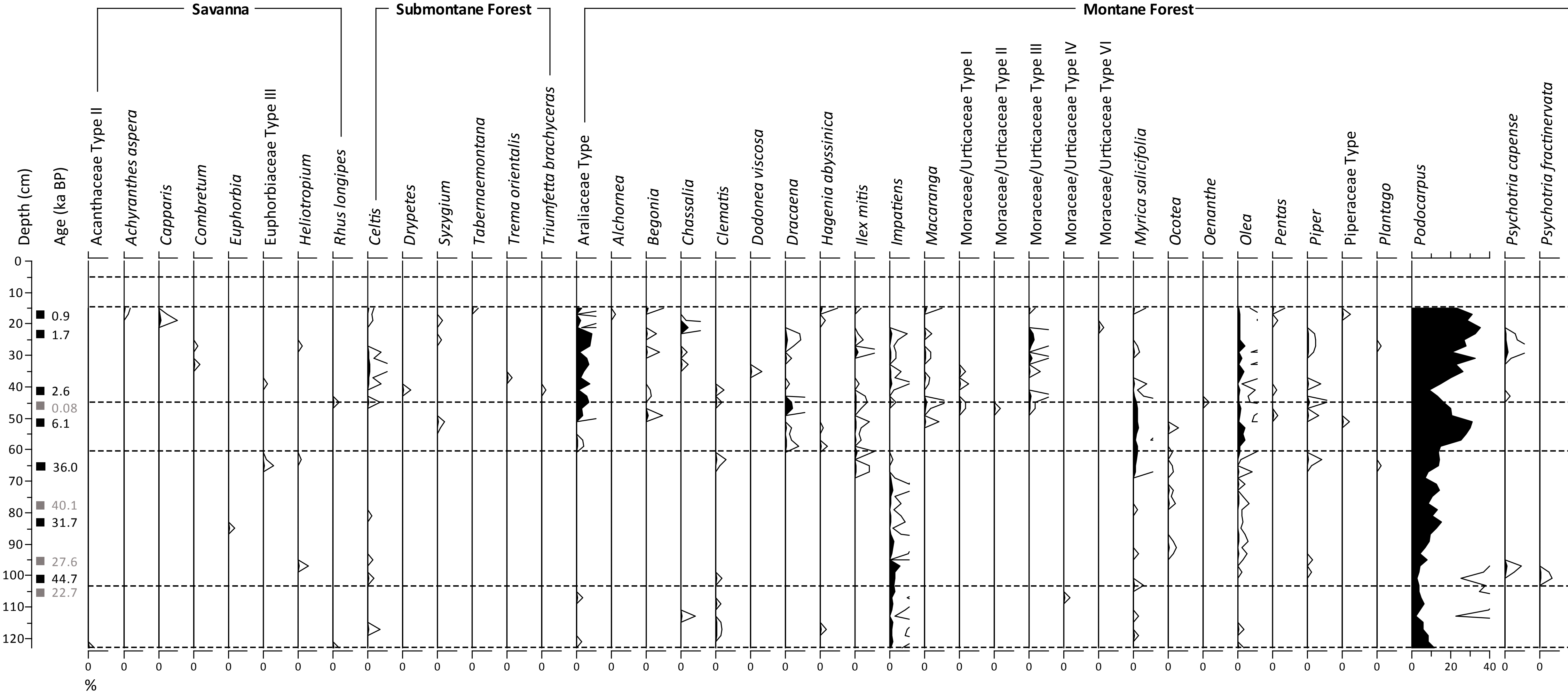

Nuxia
Peddiea fischeri
Pentas
Pentodon pentandrus
Phyllantus
Plantago
Plectranthus
Plumbago
Poaceae (sum)
Pterolobium stellatum
Rhus longipes
Rumex
Rutaceae Type
Sambucus nigra
Solanum seaforthianum
Strombosia scheffleri
Strychnos
0.00 0.04 0.08 0.12 0.16
0.0 0.1 0.2 0.3 0.4
0 3 6 9 12
0.00 0.04 0.08 0.12 0.16 0.20
0.0 0.1 0.2 0.3 0.4 0.5
0.00 0.04 0.08 0.12 0.16
0.00 0.03 0.06 0.09 0.12 0.15
0.0 0.2 0.4 0.6
1.0 2.0 3.0 4.0 5.0 6.0
0.0 0.1 0.2 0.3 0.4 0.5
0.0 0.1 0.2 0.3 0.4 0.5
0.0 0.5 1.0 1.5
0.00 0.03 0.06 0.09 0.12 0.15
0.00 0.05 0.10 0.15
0.00 0.03 0.06 0.09 0.12 0.15
0.0 0.1 0.2 0.3 0.4 0.5
0.00 0.04 0.08 0.12 0.16

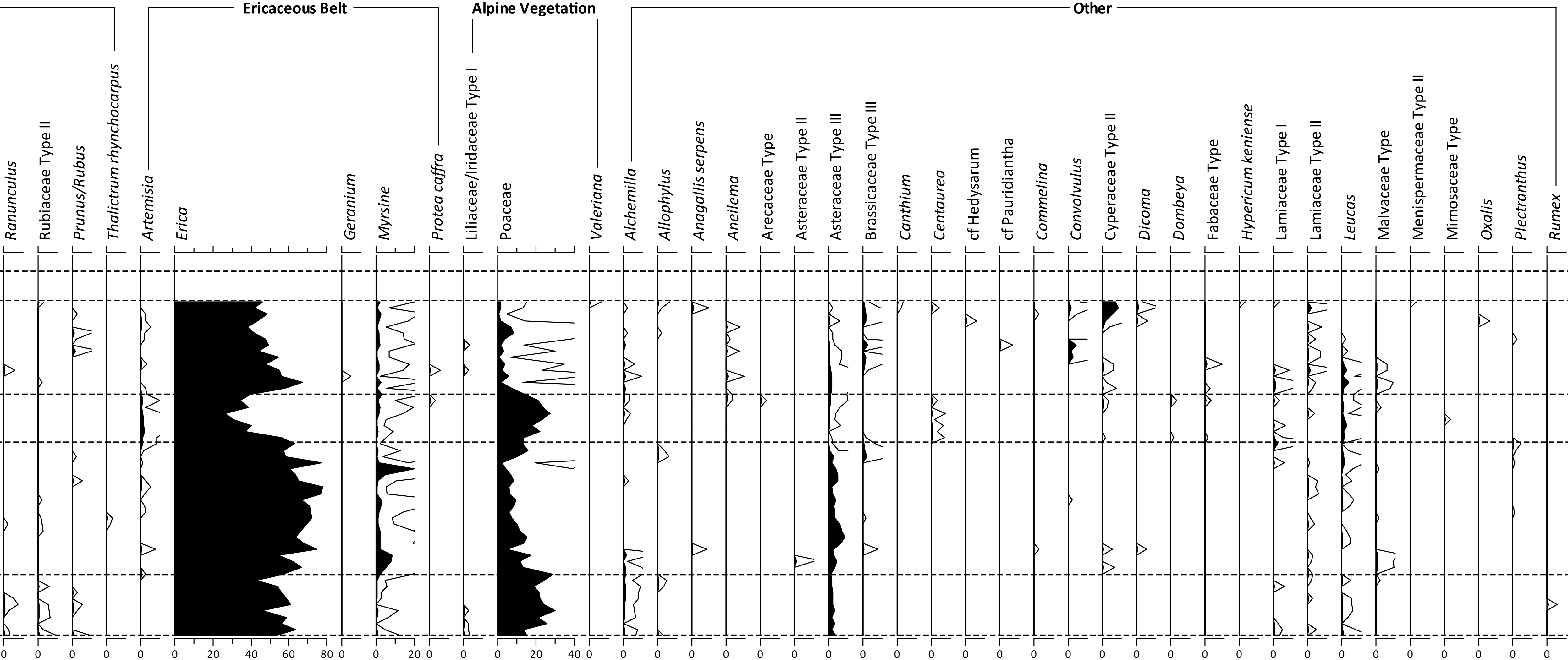

Tabernaemontana
0.0 0.1 0.2 0.3
Teclea
0.00 0.03 0.06 0.09 0.12 0.15
Thalictrum
0.0 0.2 0.4 0.6 0.8
Trema orientalis
0.0 0.5 1.0 1.5
Trichodesma
0.00 0.04 0.08 0.12 0.16
Triumfetta brachysceras
0.0 0.1 0.2 0.3
Typha
0.0 0.1 0.2 0.3 0.4 0.5
Valeriana
0.00 0.04 0.08 0.12 0.16
Zea mays
0.0 0.1 0.2 0.3
Adiantum
0.0 0.1 0.2 0.3 0.4
Arachnoides
0 40 80 120 160 200
Athyriaceae Type
0.00 0.04 0.08 0.12 0.16
Cyathea
0 4 8 12 16 20
Dennstaedtiaceae Type
0.00 0.04 0.08 0.12 0.16
Elaphoglossum
0.0 1.0 2.0 3.0
Huperzia
0.00 0.24 0.48 0.72
cf Loxogramme
0.00 0.04 0.08 0.12 0.16


Fern Spores
Lycopodium
cf Marattia fraxinea
monolete Spore
Ophioglossum
Pleopeltis
cf Polypodium
Tectaria
Thelypteridaceae Type
Trichomanes
trilete spore
trilete Spore, 100µm, microverrucat
Woodsiacaeae Type
Forest Belts
Lower Montane Forest
lower Mid Montane Forest
upper Mid Montane Forest
Upper Montane Forest
0 20 40 60 80 100
0.0 0.1 0.2 0.3
0 4 8 12 16
0.0 0.1 0.2 0.3
0.0 1.0 2.0 3.0
0.0 1.0 2.0 3.0
0 20 40 60 80
0.0 0.2 0.4 0.6 0.8
0.0 0.1 0.2 0.3 0.4
0 3 6 9 12
0.0 0.2 0.4 0.6
0.00 0.04 0.08 0.12 0.16

WeruWeru 26 Pollen Record

Weru Weru 2600 m asl, Kilimanjaro




Ericaceous Belt
Alpine Vegetation
Other
Ranunculus
Rubiaceae Type II
Prunus/Rubus
Thalictrum rhynchocarpus
Artemisia
Erica
Geranium
Myrsine
Protea caffra
Liliaceae/Iridaceae Type I
Poaceae
Valeriana
Alchemilla
Allophylus
Anagallis serpens
Aneilema
Arecaceae Type
Asteraceae Type II
Asteraceae Type III
Brassicaceae Type III
Canthium
Centaurea
cf Hedysarum
cf Pauridiantha
Commelina
Convolvulus
Cyperaceae Type II
Dicoma
Dombeya
Fabaceae Type
Hypericum keniense
Lamiaceae Type I
Lamiaceae Type II
Leucas
Malvaceae Type
Menispermaceae Type II
Mimosaceae Type
Oxalis
Plectranthus
Rumex
0
0
0
0
0
0
20
40
60
80
0
0
20
0
0
0
20
40
0
0
0
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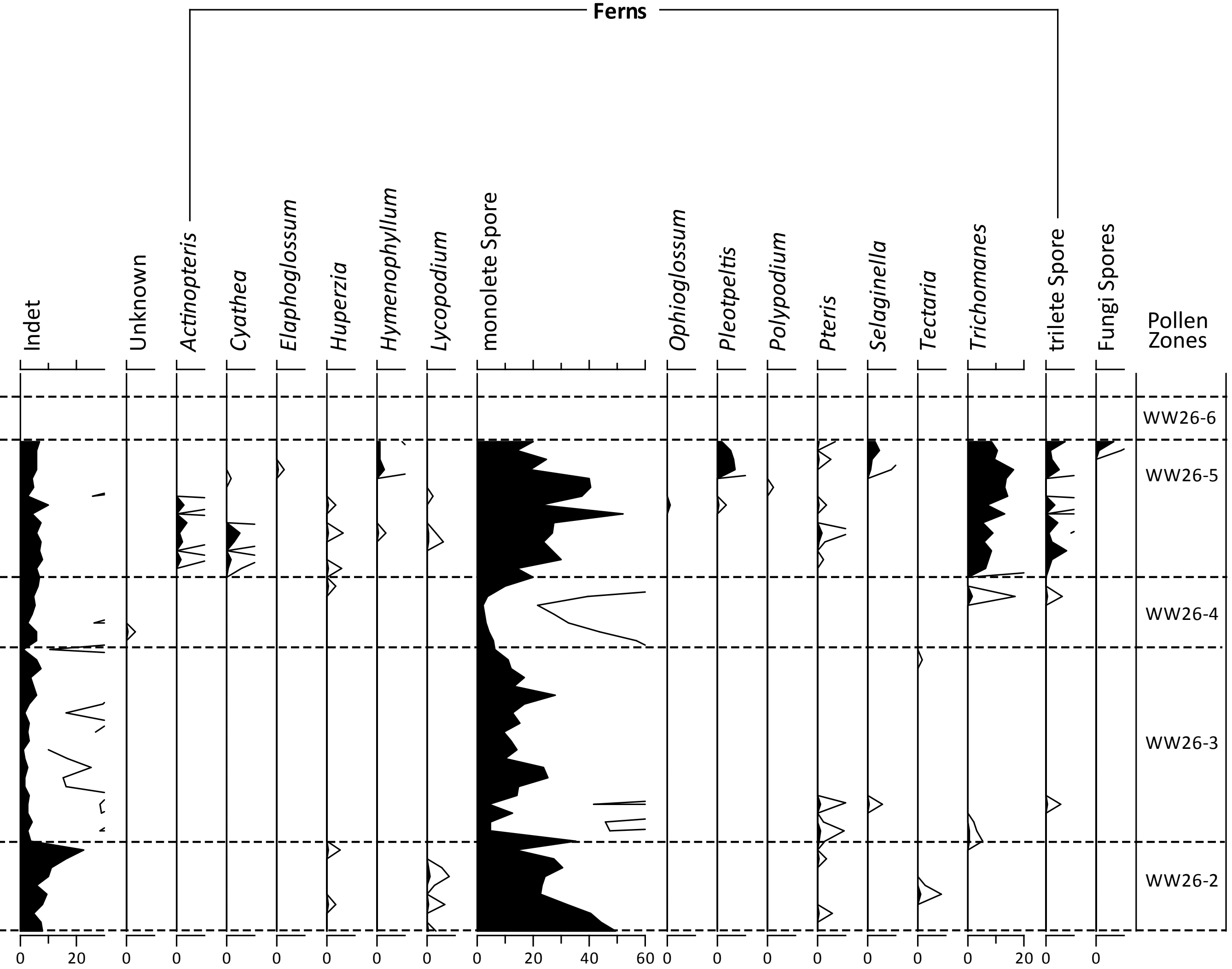
Ferns
Indet
Unknown
Actinopteris
Cyathea
Elaphoglossum
Huperzia
Hymenophyllum
Lycopodium
monolete Spore
Ophioglossum
Pleotpeltis
Polypodium
Pteris
Selaginella
Tectaria
Trichomanes
trilete Spore
Fungi Spores
Pollen Zones
WW26-6
WW26-5
WW26-4
WW26-3
WW26-2
0
20
0
0
0
0
0
0
0
0
20
40
60
0
0
0
0
0
0
0
20
0
0

Statement

Herewith I confirm that this thesis is my own work and that I have documented all sources used.

Lisa Schüler

Göttingen, November 22th, 2012