Treeline dynamics in the tropical African highlands - identifying drivers and dynamics

Miro Jacob, Sofie Annys, Amaury Frankl, Maaike De Ridder, Hans Beeckman, Etefa Guyassa & Jan Nyssen

Jacob, M. (corresponding author, Miro.Jacob@ugent.be), **Annys, S.** (Sofie.Annys@ugent.be), **Frankl, A.** (Amaury.Frankl@ugent.be), **Guyassa, E.** (etefag@yahoo.com) & **Nyssen, J.** (Jan.Nyssen@ugent.be): Department of Geography, Ghent University, Krijgslaan 281 S8, 9000, Gent, Belgium

Beeckman H. (hans.beeckman@africamuseum.be): Royal Museum for Central Africa, Laboratory for Wood Biology and Xylarium, Leuvensesteenweg 13, 8030, Tervuren, Belgium

Guyassa, E.: Department of Land Resource and Environmental Protection, Mekelle University, Mekelle, Ethiopia

Abstract

Questions: What are the potential drivers of treeline change in the tropical African highlands? Are the temperature sensitive treelines in these highlands shifting as a result of climate change?

Significance: The high altitude forests provide important ecosystem services for the vulnerable environment of the tropical highlands. Climate change is expected to have pronounced effects on the treeline limit of these forests. Afro-alpine tropical treelines are therefore potentially valuable as a proxy of climate change and the related response of ecosystems in the tropical highlands.

Location: Tropical African highlands

Results: The influence of the climatic factors in the African tropical highlands is significantly different compared to other regions. The potentially determining factors for treeline distribution in tropical Africa are temperature, precipitation and cloudiness, carbon balance, fire and anthropo-zoogenic impacts. Despite recent temperature increase, treelines have not risen to higher altitudes in the tropical African highlands. Instead, high human pressure has caused stabilization and even recession of the treelines below their natural climatic limit, particularly through livestock herding. But, even neglecting human pressure, there might be a lag in response time between temperature and treeline change.

Conclusions: The actual drivers of treeline change in the African tropical highlands are mainly fire and anthropogenic pressure rather than climate change. But, long-term drought periods can be a trigger for fire induced deforestation of the treeline vegetation. Additionally, in volcanic active mountains, is volcanic activity also a potentially limiting factor for the treeline distribution. Treeline dynamics can thus not be used as a proxy of climate change for the African tropical highlands.

Keywords: Anthropogenic impact; tropical afroalpine highlands; ericaceous belt; climate change

1. Introduction

Alpine treelines mark the transition between mountain and alpine environments on high mountain slopes (Berdanier 2010) and are one of the most apparent vegetation boundaries worldwide (Körner & Paulsen 2004; Berdanier 2010). According to Callaghan et al. (2002) and Holtmeier (2009), the shift from dense montane forests to treeless alpine grasses and shrubs is characterized by increasing stand fragmentation and stuntedness. This transition is called the treeline ecotone (Fig. 1a). There are three frequently used terminologies which refer to the transition from forest to non-forest stages (Fig. 1b) (Körner & Paulsen 2004; Van Bogaert et al. 2011): (i) the 'timberline', i.e. the boundary of the closed forest, (ii) the 'tree species limit', i.e. the boundary formed by the upper individuals of tree species, regardless of the growth form, and (iii) the 'treeline', i.e. the upper limit of forest patches characterized by a growth height of more than 3 m, or 2 m in absence of snow accumulation as is the case in the tropics (Holtmeier 2009). Trees from the *Ericoideae* subfamily form the upper treeline forest in the tropical African mountains (Wesche et al. 2000).

The first systematic treeline studies occurred approximately 150 years ago, as reviewed in Marek (1910). At present, knowledge on the ecophysical situation of treelines in the tropics is still fragmental (Bader 2007; Holtmeier 2009). Tree growth is constrained by changing environmental conditions with increasing altitude (Körner 2012). This makes the altitudinal tree-limit potentially responsive to climate change (Körner & Paulsen 2004). This is illustrated by a lowering of the treelines in tropical Africa during the dry and cold Last Glacial Maximum (LGM) and by rising treelines in the Holocene as a result of temperature increase (Wu et al. 2007). Atmospheric CO_2 concentrations are higher since the start of the Holocene, which caused a switch from rainfall limited treelines in the LGM to temperature limited treelines in the Holocene (Wu et al. 2007).

There are few continuous long-term climate reconstructions available that focus on the African tropics. Among the first, Thompson et al. (2002) reconstructed the Holocene climatic history in Africa from an ice core of the Kilimanjaro ice fields. Evidence was given for three periods of abrupt climatic shifts and predicted complete melting of the Kilimanjaro ice fields by 2015-2020 (Thompson et al. 2002). The IPCC (2007) stated that 'warming of the climate system is unequivocal, as is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice and rising global average sea level'. The temperature rise of the past century is most prominent and rapid at high altitudes and latitudes IPCC (2007).

The tropical African mountains are hotspots in biodiversity, comprising a high amount of endemic species that have their habitat in these mountains. A substantial reduction, shift and extinction of African flora and fauna species is expected in diverse African ecosystems (IPCC 2007). Species that reproduce slowly, disperse poorly, and are isolated are most vulnerable to climate warming (McNeely et al. 1990). The mountain-restricted species of the African highlands are good examples of such isolated species, which are highly sensitive to environmental stress (IPCC 2007). The value of forests on mountain slopes is much wider than only for biodiversity. High mountain forests are important for slope stability and regionally important as a hygric buffer providing water for downstream sources and for agriculture in the surrounding lowlands (Miehe & Miehe 1994; Price 2003). The climate controlled tree limit of these mountain forests forms a clearly visible ecotone worldwide. Afro-alpine tropical treelines are therefore considered to be a potential proxy of climate change (Bader 2007). Evidence for this is given by LGM treeline oscillations due to past climate change in the afro-alpine mountains (Wu et al. 2007). The associated counterpart of treeline shifts are shifts in the altitudinal range of grass- and shrubland. Such shifts increase the risk of species extinctions and can impede the provision of important non-forest ecosystem services. Understanding the drivers of treeline dynamics in the tropics is important to understand dynamics and spatial patterns of vegetation at the treeline (Bader 2007). It is important to understand the dynamics that are taking place, in order to develop sustainable conservation strategies (Burgess et al. 2007).

The aim of this paper is to identify the potential drivers of treeline change in the tropical African highlands mountains and to answer the question whether temperature sensitive treelines in these mountains are shifting as a result of climate change. This will also allow to evaluate if treeline shifts can serve as a proxy of climate change in tropical Africa.

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1.1 Study Area

Previously studied African tropical mountains with summits ranging above the present tropical treeline elevation (3300 - 4000 m) were selected for this paper (Fig. 2). These mountains are: Rwenzori Mountains (5109 m), Virguna Mountains (4507 m), Simen Mountains (4550 m), Bale Mountains (4377 m), Mount Elgon (4321 m), Mount Kilimanjaro (5896 m), Mount Kenya (5199 m), and Mount Cameroon (4095 m). For all these mountains, the upper treeline ecotone is formed by trees from the *Ericoideae* subfamily dominated by the genus *Erica L.* (Miehe & Miehe 1994; Wesche et al. 2000). Treeline forests are prominent above 3000 m in most tropical African mountains and grow over an elevation range of up to 1000 m (Miehe & Miehe 1994); described by Hedberg (1951) as the 'ericaceous belt'. Beyond this elevation, tree growth is not possible and afroalpine scrubs dominate in the landscape. *Erica L.* trees are small (ca. 8 m) and have needle-like scleromorphic leaves. Afroalpine scrubs are dominated by species of *Alchemilla* and *Helichrysum* (Bussmann 2006). Anthropo-zoogenic impact strongly modified the vertical extent of the ericaceous belt by woodcutting, fire and grazing. But despite the limited area still covered by ericaceous forest at the high altitude tree limit, this forest type remains vital for the regional environment of the tropical African highlands (Miehe & Miehe 1994).

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2 Biophysical and anthropo-zoogenic constraints for tree growth in the tropical African highlands

The elevation of the treeline is limited by local and global environmental and anthropo-zoogenic constraints, which cause trees to reach their limit at a certain elevation and prevent tree growth above that limit (Wieser & Tausz 2007; Körner 2012). The biological limit is caused by severe habitat stress, which is limiting metabolism, development and reproduction of the trees. At a global scale there are evident differences in the impact of these constrains between the tropical highlands and the boreal and temperate environments (table 1).

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The elevation of the treeline in the tropics is determined by a combination of biophysical factors. Of which, low ambient temperature is a key factor regulating growth, regeneration and survival of trees at the treeline (Körner 1998; Holtmeier 2009; Harsch et al. 2009). The seasonal mean temperature at the treeline varies from 6 to 8°C outside the tropics and around 5°C in the tropics (Körner 2012).

The limiting factor of growth in the tropics is mainly caused by the permanent stress resulting from the pronounced temperature fluctuation between day and night (Wardle & Coleman 1992; Miehe & Miehe 1994; Bader 2007). This is because high intensities of solar radiation can be reached at tropical alpine treelines during the day, due to the low latitude and high altitude, while night frost can occur during every night (Bader 2007). Because of the tropical diurnal climate variability, it is important to differentiate the soil temperature regime in the tropics from that outside the tropics (Holtmeier 2009). In the tropics, mean temperature should be considered a rough indicator only, since there is a large variation in site-specific temperature cycles (Miehe & Miehe 1994). An annual mean soil temperature of 6.1 ± 0.7°C was found to correspond with the upper tree limit all year round in the tropics (Hoch & Körner 2003).

While snowfall and snow accumulation at treeline elevations is common outside the tropics, this is rare in the tropics (Sarmiento 1986; Smith & Young 1987). High seasonal rainfall variability with cold, cloudy and wet seasons alternating with long droughts at the treeline are common in the African tropical highlands, both having a negative impact on tree growth at the treeline (Smith & Young 1987). Increasing precipitation and cloudiness at the treeline elevation reduces solar radiation for photosynthesis and reduces temperatures and thus limits tree growth (Wieser & Tausz 2007). On the other hand, water stress due to long term drought impedes seedling establishment during the growing season and reduces the resilience of the vegetation against fire (Körner 2012). Outside the tropics, winter desiccation caused by long-term frost drought is one of the main constraints for tree growth in high mountains (Wieser & Tausz 2007). Hygric and thermal differences caused by differences in cloudiness are considered more important as controlling factors than exposure effects for the treeline elevation in the tropics (Sarmiento 1986).

Freezing is generally less severe and frost damage can occur all year round at the tropical treeline (Smith 1974; Goldstein et al. 1994). Diurnal differences are especially high in the dry season, when clear skies prevail (Sarmiento 1986). Physiological adaptations for frost resistance must therefore be permanent in tropical highlands (Sarmiento 1986).

The partial CO_2 pressure is lower at high elevations at all latitudes. Treeline vegetation is therefore potentially responsive to increased atmospheric CO_2 pressure (Smith et al. 2009). However, Hoch and Körner (2012) studied carbon reserves of treeline trees worldwide and did not find evidence of carbon shortage. Similar results were found in single mountain ranges by Piper et al. (2006) and Shi et al. (2008). This increasingly favours the growth limit hypothesis over the traditional carbon balance hypothesis (Hoch & Körner 2012; Simard et al. 2013). However, there is another potential effect of elevated CO_2 in the tropics, caused by the different response of C4 tropical grasses and C3 woody vegetation to elevated CO_2 pressure; C3 vegetation is competitively favoured (Ziska 2008).

Wind speed and direction are controlled by the local topography. In general, wind speeds at treeline elevation in the tropics are lower than in extratropical mountains (Holtmeier 2009). Evidence is given by giant groundsels and lobelias of several meters high above the treeline in the tropics (Hedberg 1964). The influence of wind is very important to site conditions of temperate and boreal treeline ecotones; especially in the winter season when the treeline is affected by wind-driven snow relocation and abrasion by ice particles (Holtmeier 2009). In addition there exist many local constraining factors, such as the mass elevation effect of mountain ranges or topography effects or differences caused by the soil properties.

Beside these environmental constraints, the treeline elevation is also limited by anthropo-zoogenic influences. Human induced land use and land cover changes are the main drivers of forest cover loss (Kidane et al. 2012), controlled by the continuous pressure for new farmland and firewood (Burgess et al. 2007). Based upon research in Ethiopia (Simen and Bale Mountains) and Uganda (Rwenzori Range and Mount Elgon), Wesche et al. (2000) concluded that fire is an important factor influencing the treeline in East Africa. Natural fires are caused by lightening, but the majority of fires in tropical mountains are human-caused (Hedberg 1964). Multiple reasons exist for human ignited fires. For example, in the Bale Mountains, fire is used to improve the grazing conditions.

Effects of herbivores on the treeline structure and position are globally observed (Cairns & Moen 2004). The negative effects of herbivores on the treeline are primarily caused by livestock. In the agricultural system of the tropical highlands, livestock plays a key role as provider of energy, food, fertilizer and status (Nyssen et al. 2004). Livestock browsing impedes regeneration of Erica and other trees of the sub-alpine zone through foliage consumption, trampling and seed predation (Castro et al. 2004).

3. The potential drivers of treeline change

The potential drivers of treeline change are the biophysical and anthropo-zoogenic constraints, outlined above, which have recently significantly changed and thus had a potential impact on the elevation of the treeline limit.

3.1 Temperature increase

Hulme et al. (2001) studied air temperature patterns in Africa over the last 100 years and found that temperature in the African continent rose with 0.5°C. In the mountains of East Africa, temperature increased with 0.3°C since 1980 (Fig. 3a). According to the A1B-scenario of the Intergovernmental Panel on Climate Change (IPCC) the temperature in the tropics will increase with 3.3°C by 2100 (IPCC 2007). The A1B model takes into account a rapid economic growth, a global population peak in the mid-century followed by a decline, a rapid introduction of new more sustainable technologies and a switch to balanced fossil and non-fossil energy sources (IPCC 2007). The scenarios neglecting mitigating policy actions, even project an increase of up to 4.9°C (IPCC 2007). Vegetation belts have to adapt to these increasing temperatures, as a result temperature sensitive species may disperse to new habitats (Wright et al. 2009). In the high altitude tropical mountains, these new temperature refuges are relatively nearby and can be accessed by migration upwards the mountain until the growth limit is again reached (Wright et al. 2009).

Körner (2012) has calculated that an increase of 1°C would correspond with an increase in elevation of the treeline with 186 meter. This is a general prediction on a worldwide scale, taking only temperature into account. Other factors such as the tree species sensitivity or site specific conditions (e.g. topography, inter-specific competition, moisture availability, etc.) are not included (Chambers et al. 1998; Holtmeier 2009). The altitudinal temperature lapse rate of East Africa is 0.6°C per 100 meter elevation (Peyron et al. 2000). A marked temperature increase of 0.3°C since 1980 (Hulme et al. 2001) would thus theoretically correspond with an upwards treeline shift of 50 meter; and the IPCC projection of 3.3°C by 2100 with an upwards shift of 550 meter (taking only temperature in account).

3.2 Rainfall variability

On a global scale, an average temperature rise of 5°C by 2100, would result in a drastic decrease in annual precipitation and soil moisture by 20% (Schiermeier 2008). However, the high interannual rainfall variability makes it difficult to identify rainfall trends for Africa. According to Hulme et al. (2001), there is a relatively stable regime in East Africa with some evidence of long-term wetting. In contrast, for West Africa and the Gulf of Guinea there has been a pronounced decrease in rainfall. The scenarios of de Wit & Stankiewicz (2006) predict an increase of rainfall up to 10% and even 20% by 2100 for all tropical mountains (Fig. 3b). Climatic wetter conditions for East Africa under global warming are predicted by most climatic models (Lanckriet et al. 2012). Hulme et al. (2001) predict a spreading trend for the equatorial zone of East Africa, where rainfall is expected to increase by 5 to 30% in December-February, but to decrease by 5 to 10% in June-August

The impact of these changes on the treeline limit is difficult to predict. Increased rainfall and a better spread of rainfall throughout the year decreases water stress and thus enhances tree growth at the treeline. But, this will at the same time increase cloudiness and indirectly decreases the air temperature.

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3.3 Change in carbon balance

The atmospheric CO_2 level rose from pre-industrial 285 µmol l^{-1} (600 gigatonnes (Gt)) to the current level of 384 µmol l^{-1} (800 Gt) and is predicted to rise to 1000 Gt by 2050 (IPCC 2007). The main focus of increased CO_2 concentrations, due to anthropogenic intensification, is on the likely effect on global mean surface temperature rise. But there are also direct effects on plant growth and physiology, independent of the climatic effect (Ziska 2008). This effect of elevated CO_2 concentrations is different for C_3, C_4 and Crassulacean Acid Metabolism (CAM) plant species. The widespread C_3 plants and CAM plants show a significant positive response, while C_4 plants exhibit a negative response (Reddy et al. 2010). The negative effect on C_4 plants of increased CO_2 concentrations is by reduced stomatal conductance and transpiration, which causes higher leaf temperatures and increased drought stress (Bernacchi et al. 2007).

At treeline elevation in the tropics, the vegetation boundary between afroalpine woodland and grasses correspond with the boundary between C_4 and C_3 plants, respectively. Elevated CO_2 concentrations in the tropics would thus potentially support the advance of the C_3 woody vegetation to higher elevations in competition to C_4 tropical grasses (Leakey et al. 2009). But more research is necessary for a better understanding of this different CO_2 response and the linkage with other environmental factors (Leakey et al. 2009).

3.4 Anthropo-zoogenic impact

The global population will grow annually with on average 1% over the period 2010-2025, which correspond to a population increase of 1.2 billion people in 15 years (UNdata 2013). A growing proportion of the global population will be living in Africa, as the population in Africa is growing very fast (up to 3% annually) (Fig. 4, FAO 2007). The associated growing population and livestock pressure will further increase environmental pressure in the tropical highlands (Burgess et al. 2007). The impact is already visible through increased, wood cutting and uprooting of Erica stumps, inhibiting tree regeneration (Bishaw 2001).

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4. Current position and dynamics of the treeline in the African tropical highlands

The potential response of treelines to climate warming is currently studied worldwide (Holtmeier & Broll 2007). Harsch et al. (2009) analysed a global dataset of 166 treeline sites; advancing treelines were recorded in 52% of the sites and in only 1% there was a recession of the treeline. There is an association between treeline advance and temperature increase, although the mechanisms are not always straightforward. However, the analysis of Harsch et al. (2009) almost completely lacks study sites in the tropics; there are only four tropical sites included of which none are in Africa. This is because little is known about treeline dynamics in the tropical highlands of Africa (Körner 2012). A global representation of the latitudinal position of treelines is given by Körner (1998), showing a strong relation between treeline altitude and latitude in the temperate zone and a maximum in the subtropics. But no significant changes of the treeline position with altitude over a 50° range around the equator (Körner 1998). This graph again illustrates that treeline data is limited in the tropical and southern regions. The treeline elevation of the tropical African mountain ranges studied in this paper are therefore included in the Körner (1998) graph in figure 5b; the tropical African treeline elevation is, although scattered, following the general trendline found by Körner (1998). The current understanding of treeline dynamics in Africa are compiled in an overview below and summarized in Table 2.

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4.1 Shoulders of the Ethiopian Rift Valley

The Simen Mountains (4543 m) are situated in the northern highlands of Ethiopia and are protected under national legislation since 1969. The Simen Mountains have a unimodal precipitation regime, which is relatively dry compared to the bimodal precipitation regime of the more southern tropical African mountains (Hurni & Stähli 1982). The treeline formed by *Erica arborea* lies at an average altitude of 3715 m (Hurni & Stähli 1982). Shifting of this treeline has been observed by repeat photography at Nebir Mekemacha, which shows an increase of the treeline of approximately 120 m from 4000 to 4120 m between 1967 and 1997 (Fig. 5) (Nievergelt et al. 1998; Wesche et al. 2000). There are two possible explanations for this treeline shift: recent climate change and reduced human and livestock pressure. Evidence against the climatic change hypothesis is given by individual Erica trees high above the treeline already in 1968 (Nievergelt et al. 1998). The impact of cattle grazing, woodcutting and burning reduced since the National Park was installed (Wesche et al. 2000).

The treeline in the Bale Mountains (4400 m) in southern Ethiopia is formed by *Erica trimera*, which is the dominant species from 3400 up to 4000 m (Fig. 5). Outliers of individual Erica species are even observed up to 4200 m (Miehe & Miehe 1994). These individuals have a mat-like structure as a result of strong eastern winds (Holtmeier 2009). Although that the Bale Mountains are also protected since 1969, the upper treeline of the Bale Mountains is lowered by recurrent fires at many places, to maintain or extend the grazing area (Wesche et al. 2000). As a result, mosaics of forests scrubs and afroalpine grasslands prevail at the treeline in the Bale highlands (Bussmann 2006).

In both mountain ranges is the treeline located at 4000 m, ca. 400-500 meters below the highest summit (Fig. 5). There is thus a potential impact of the summit syndrome described by Körner (2012). But, observations of recent treeline increase in the Simen

Mountains give evidence against the influence of the summit effect at the current treeline elevation.

4.2 West Africa

The climate of Mount Cameroon (4095 m) is extremely moist with up to 10 000 mm annual rainfall at lower elevations and 2000 mm at the summit (Bussmann 2006). Although the western slopes receive more rainfall, this is not reflected in the vegetation profile. The ericaceous specie *Erica mannii*, *Agauria salicifolia* and *Myrica arborea* form the patchy high altitude treeline ecotone (Bussmann 2006). The abrupt treeline at 3500 m (Fig. 5) is controlled by periodic volcanic activity, which influences the tree limit directly by destroying existing forest through lava flows and fire and indirectly by unequal deposition of fertile volcanic ashes (Proctor et al. 2007). As a result, the treeline is depressed below its climatic limit (Bussmann 2006). In addition, there is also a high anthropo-zoogenic pressure through woodcutting, fire and livestock browsing, since the population density is almost twice the average of that in sub-Saharan Africa (Burgess et al. 2007).

4.3 Mountain ranges along the Eastern Rift Valley

The *Erica excelsa* treeline at Mount Elgon (4321 m) lies on average at 3300 m and rises up to 3450 m in the humid valleys (Wesche 2003; Holtmeier 2009). Despite the negative effects of waterlogging and cold air accumulation, trees grow better in the valleys due to protection from frequent fires. The highest stands in the valleys even occur at 3950 m (Hamilton & Perrot 1981; Wesche 2003). The vegetation is, on average every 7-10 year, exposed to high-altitude droughts and thus severe desiccation stress. The impact of drought stress is striking, with up to 50% of the leaves dying, but the plant phenology is little affected (Wesche 2003). However, the striking consequence of these drought conditions is fire. More than half of the Erica and afro-alpine vegetation was burned during the extremely dry conditions of 1997 (Wesche et al. 2000). Extensive burning caused large scale replacement of woody vegetation by grasslands, which recover much faster. As a result of fire and anthropogenic impact by pastoralists the present treeline is depressed below the climatic tree limit (Fig. 5) (Hamilton & Perrot 1981; Wesche 2003).

On Mount Kenya (5199 m), the current boundary between the lower alpine zone and upper Erica forest is situated at ca. 3400 m (Fig. 5) (Bussmann 2006). The poorly developed

Ericaceous forest belt is formed by remnant stands of *Erica excelsa*, *Erica trimera* and *Erica arborea* (Bussmann 2006). The warmer moister climate of the Holocene enabled the treeline to rise in comparison to LGM levels (Rucina et al. 2009). However, the position of the treeline is currently under high anthropogenic pressure, which is marked by increased fire frequency. This has locally resulted in a transition to open vegetation (Bussmann 2006; Rucina et al. 2009). The presence of the plant species *Asteraceae Stoebe kilimandscharica* and *Protea kilimascharicaoften* at the treeline, indicate this regular disturbance by high altitude fires. As a result of this disturbances the boundary between the ericaceous belt and the afroalpine grasses is formed by a patchy mosaic rather than a clear altitudinal boundary (Bussmann 2006).

The ericaceous belt of Mount Kilimanjaro (5895 m) is formed by *Erica excelsa* forest prevailing above 3000 m, with remnants of *Erica trimera* growing above 3700 m (Hemp 2009). The treeline is situated at ca. 3800 m, which is below its natural limit (Fig. 5) (Hemp 2005; Körner 2012). In 1976 the treeline reached the 4100 m elevation limit (Hemp 2009). The cause of the treeline lowering with several hundred meters since 1976 is a drier climate, which caused an increased frequency and intensity of fires on the slopes of the Kilimanjaro (Hemp 2005). Precipitation has decreased over 30% in the recent years, in particular over the last three decades. More frequent and intensive fires have not only lowered the treeline position, but even caused a deforestation of one third of the Kilimanjaro forest in the last 70 years (Hemp 2005).

4.4 Albertine Western Rift and Congo Nile Crestline

Because of the political instability in this region, scientific studies about treeline dynamics are lacking. The research presented therefore only gives an overview about the current vegetation zonation.

The Rwenzori Mountains (5109 m) are well preserved from anthropogenic influences. There are fires, but these are comparatively small (Wesche et al. 2000). This makes the Rwenzori Mountains one of the most intact Ericaceous vegetation belts of the African tropical highlands (Wesche et al. 2000). The Erica forest dominated by *Erica arborea* follows immediately after the bamboo belt (at 3000 m) and marks the treeline at 3900 m (Fig. 5) (Livingstone 1967; Bussmann 2006). Although the eastern slopes are drier, this is not reflected in the vegetation profile (Bussmann 2006).

The Virunga Mountains (4507 m) are formed by eight adjacent volcanoes. On the highest peak of Mount Karisimbi the treeline is situated at by average 3800 m. On the drier Mount Muhabura (4127 m) trees are only growing up to 3600 m (Fig. 5). In the Virguna volcanoes the treeline is formed by *Erica arborea* forest, growing above the *Hagenia abyssinica* and *Hypericum revolutum* forest (Bussmann 2006).

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5. Discussion and conclusion

The discussion is structured according to the two main questions of this paper: (i) understanding the driving factors determining treeline elevation limits and (ii) identifying treeline dynamics in the African tropical highlands.

(i) What are the driving factors determining the treeline elevation in the African tropical highlands?

At present climate change is unequivocal and caused global warming and changing rainfall patterns. These changes have the potential to influence the altitudinal tree growth limit. Unlike in temperate and boreal regions, wind, frost damage and snow accumulation are less important in controlling the treeline position. Treeline species in the tropical highlands must be particularly adapted to high diurnal temperature variation. A temperature increase of 3.3°C by 2100 would correspond with an increase of the tropical African treeline by 550 meter, using the vertical temperature lapse rate of East Africa from Peyron et al. (2000) (only taking temperature in account). But, past increases in population pressure in the tropical highlands have depressed the treeline elevation below its climatic limit. Anthropo-zoogenic influences disturb the treeline, mainly by man-made fire to clear the forest for grazing land. The impact of these fires is locally intensified as a result of long term drought, which decreases the resilience of the environment to fire disturbances. Beside this is volcanic activity also a locally important constraint of high altitude tree growth.

(i) Are treelines in the African tropical highlands subjected to change?

Hedberg (1951) presented a general classification of the vegetation belts of the Eastern African Mountains. He recognized three belts on each mountain: the alpine, the ericaceous and the montane forest belts. The treeline is situated in between the alpine and ericaceous belt with an elevation limit between 3550 and 4100 m (Hedberg 1951). This 4100m-limit corresponds with the treeline in the Simen Mountains at present. The Simen Mountains are the only mountain range in this study of which the treeline rose locally. This indicates that here, the tropical treeline lies below its potential climatic limit (Miehe & Miehe 1994; Kessler 1995; Bader 2007). A tentative explanation is that the Simen Mountains are located most northern and thus closer to the subtropics and as a result receive less rainfall and cloudiness, which can cause the treeline to rise higher (Körner 2012). But this explanation is too simplistic, because decreasing human impact after national park establishment should also be taken into account.

However, the general trend is that treelines were moved down due to high anthropo-zoogenic pressure and especially fire (Miehe & Miehe 1994; Kessler 1995; Ellenberg 1996; Wesche et al. 2000; Hemp & Beck 2001; Bader 2007). This is the case for most of the mountain ranges studied. In the Bale Mountains, Mount Elgon, Mount Cameroon and Mount Kenya, the treeline is lowered due to high anthropogenic pressure. In addition, on Mount Cameroon volcanic activities have also had a negative effect on the treeline elevation. Disturbance by human and livestock is controlling the treeline elevation at elevations below their natural climatic limit in many African tropical mountain ranges. In the Rwenzori and Virguna Mountains the human pressure is lower because of the politic instability in this region. As a result is the treeline elevation potentially more stable. Yet, little is known about potential vegetation shift in this region. When neglecting human interference, treelines in the tropical African highlands might rise to higher elevations. This is witnessed in the Simen Mountains, although decreasing pasture and wood cutting also played a major role here. A hypothetical upper treeline limit at 4100m is suggested by Hedberg (1951). The 4100m-limit as suggested by Hedberg (1951) used to be also corresponding with the limit at the Kilimanjaro in 1976. But due to climatic drier conditions in combination with growing anthropogenic pressure is the treeline of the Kilimanjaro also lowered. The effect of decreasing rainfall conditions is thus opposite between the Simen Mountains and the Kilimanjaro.

Overall, treelines in the African tropics are strongly disturbed by human and livestock pressure, which makes it not possible to use them as a proxy of climate change in the tropics. The general trend of a depressed treeline below the climatic limit in the tropical

African highlands favours the hypothesis that treelines are still moving upwards from lower positions due to a slow response time to climate change (Wardle & Coleman 1992; Holtmeier 1994). Because shifts in species distributions may lag behind climate changes (Dullinger et al. 2012). But evidence against this hypothesis is given by past higher treeline elevations and by evidence of a rising treeline in the Simen Mountains.

(iii) Outline for future work

Overall, more treeline research in the African tropical highlands is vital to improve the scientific understanding of the response of high altitude tropical treelines to environmental changes. In the global treeline research of Harsch et al. (2009), continental Africa is a blank spot on the map. The IPCC has recognized this need to understand the ecosystem dynamics and climate variability in Africa. Climate change may have important effects on the functioning of the ecosystems of the African tropical highland. A better understanding of this can help to make realistic predictions, which are important as an input to land management scenarios.

Acknowledgments

This research was financially supported by the Belgian Special Research Fund (BOF fund, Ghent University). We sincerely thank Gebrekidan Mesfin and Silke Broidioi for their assistance. We also express our thanks for the valuable inputs of the editor and the anonymous reviewers.

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Table 1: A comparison of potential environmental constraints for tree growth at the treeline between the tropical and the boreal and temperate zones[a]

Factor	Tropics	Boreal and temperate zone
Air temperature	Mean seasonal temperature: 5°C Diurnal fluctuation Strong solar radiation	Mean seasonal temperature: 6-8°C Length of the growing season Less strong solar radiation
Soil temperature	Diurnal variation Mean temperature: 6.1 ± 0.7°C	Seasonal variation Permafrost
Precipitation and cloudiness	High seasonal rainfall variability Cloudiness differences	Snowfall accumulation Winter desiccation
Frost damage	Lower influence: permanent adaptations	Critical factor: high influence
Carbon balance	C_3/C_4 balance	C_3 vegetation
Wind	Gentle wind: low influence	Stronger wind: high influence Snow relocation; wind-driven abrasion
Local factors	Site specific	Site specific
Anthropo-zoogenic pressure	Very high influence	Lower influence
Fire	Very high influence	Lower influence

[a] The factors are described and fully referenced in the text.

Table 2: Treeline dynamics and driving processes in the Tropical Highlands of Africa

Mountain range	Latitude	Elevation	Treeline[a]	Trend	Cause	Source
Simen Mountains	13°14'N	4543	4000	Upward	Decrease in anthropogenic pressure	Hurni & Stähli (1982); Wesche et al. (2000)
Bale Mountains	06°49'N	4377	4000	Downward	Anthropogenic pressure: fire	Miehe & Miehe (1994); Wesche et al. (2000)
Mount Cameroon	04°13'N	4095	3500	Downward	Volcanic activity and anthropogenic pressure	Proctor et al. (2007)
Mount Elgon	01°09'N	4321	3300	Downward	Drought pressure: fire Anthropogenic pressure	Wesche (2003); Holtmeier (2009)
Mount Kenya	00°08'N	5199	3400	Downward	Anthropogenic pressure: fire	Bussmann (2006); Rucina et al. (2009)
Mount Kilimanjaro	03°04'S	5895	3800	Downward	Drought pressure: fire	Hemp (2005); Körner (2012)
Rwenzori Mountains	00°27'N	5109	3900	?	Preserved from anthropogenic pressure	Wesche et al. (2000); Bussmann (2006)
Virunga Mountains[b]	01°14'S	4507	3800 3600	?	Mount Muhabura: Rainfall limited?	Bussmann (2006)

[a] Average treeline elevation

[b] The Virunga Mountains: Mount Karisimbi and Mount Muhabura

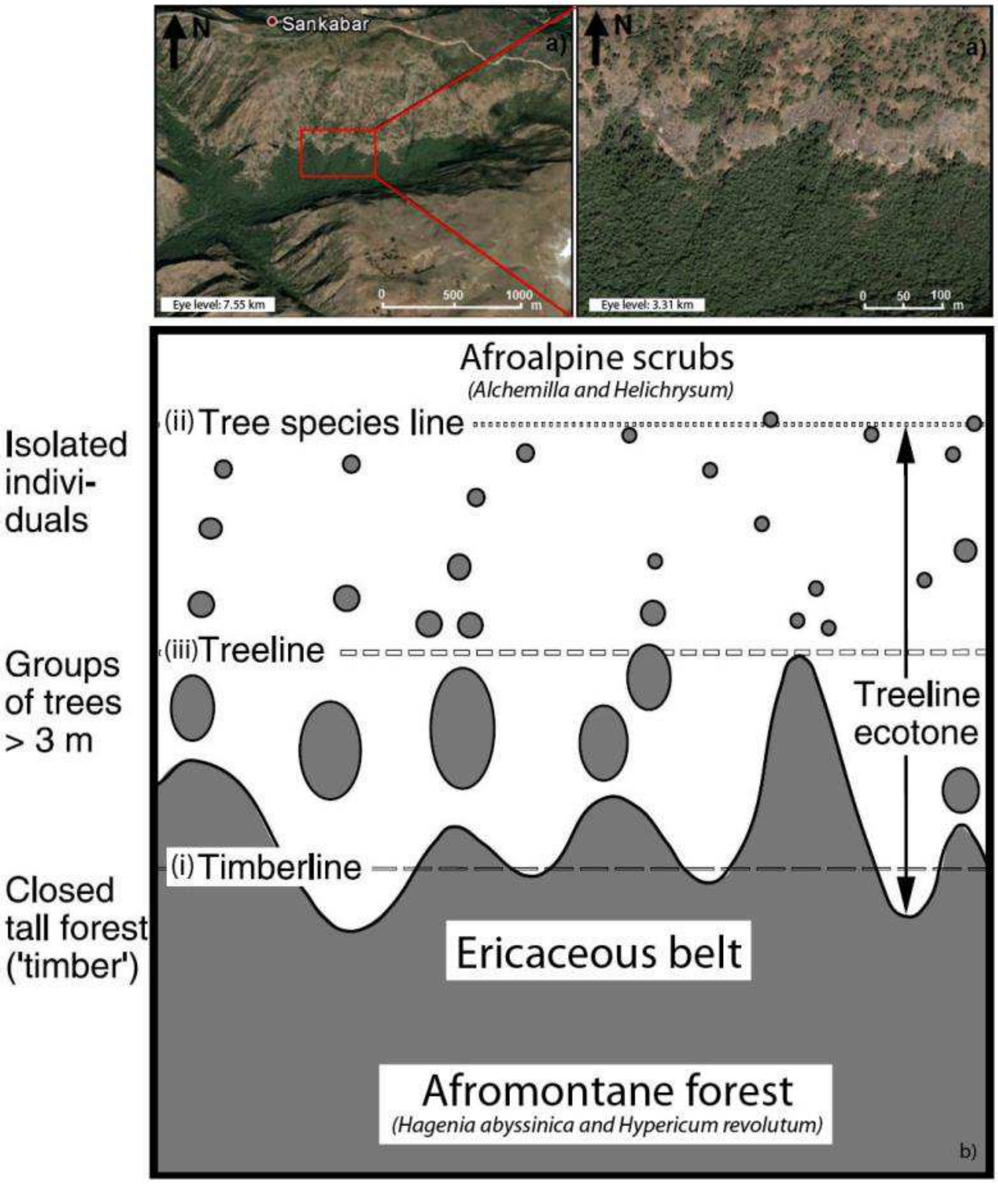

***Figure 1*: Complexity of the treeline (a) Google Earth Image of the treeline at the Simen Mountains, Sankabar camp (13°14’N, 38°3’E), visualized at two different scales to emphasize the treeline gradient. (b) The treeline ecotone modified after Körner & Paulsen (2004) with distinction between timberline, treeline and tree species line.

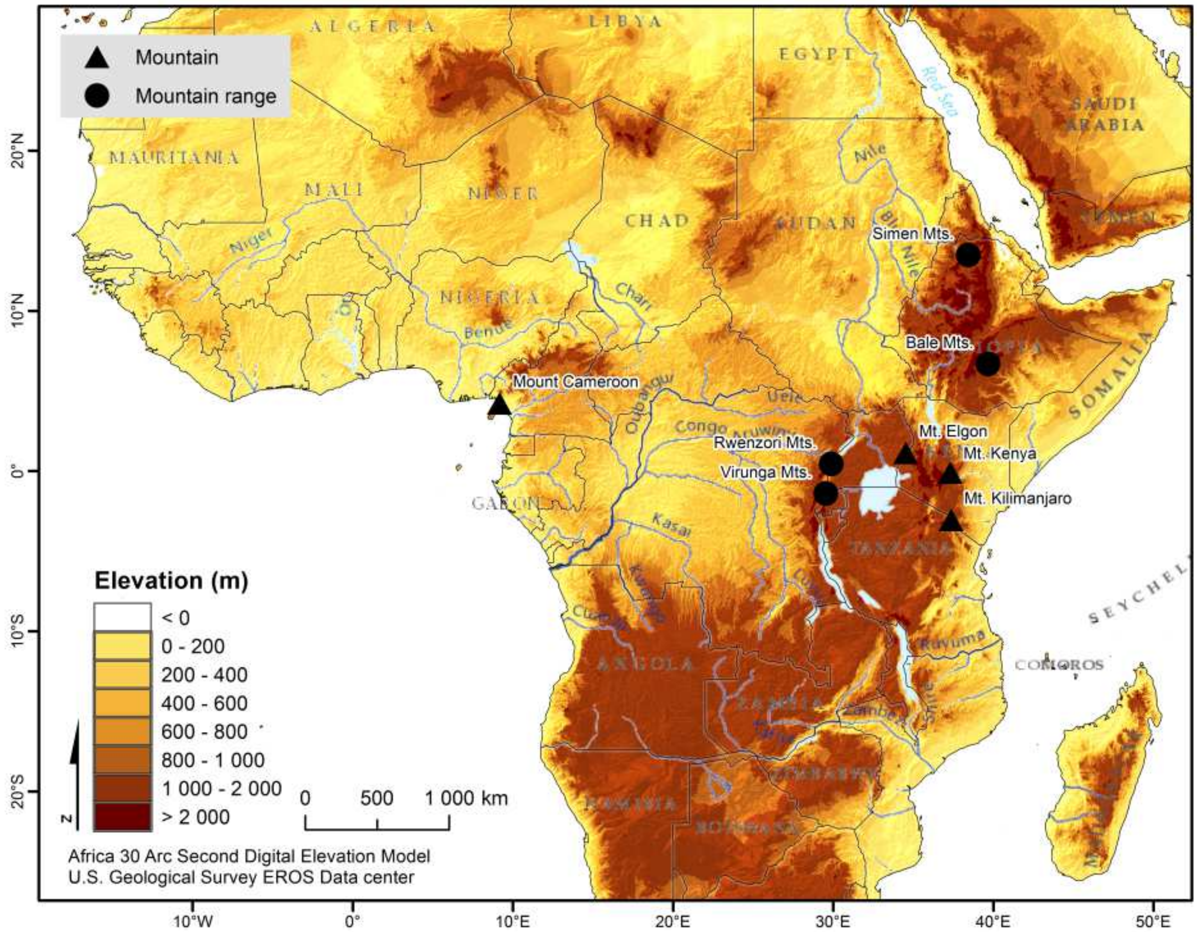

Figure 2**:** The studied tropical mountains of Africa that range above the treeline elevation.

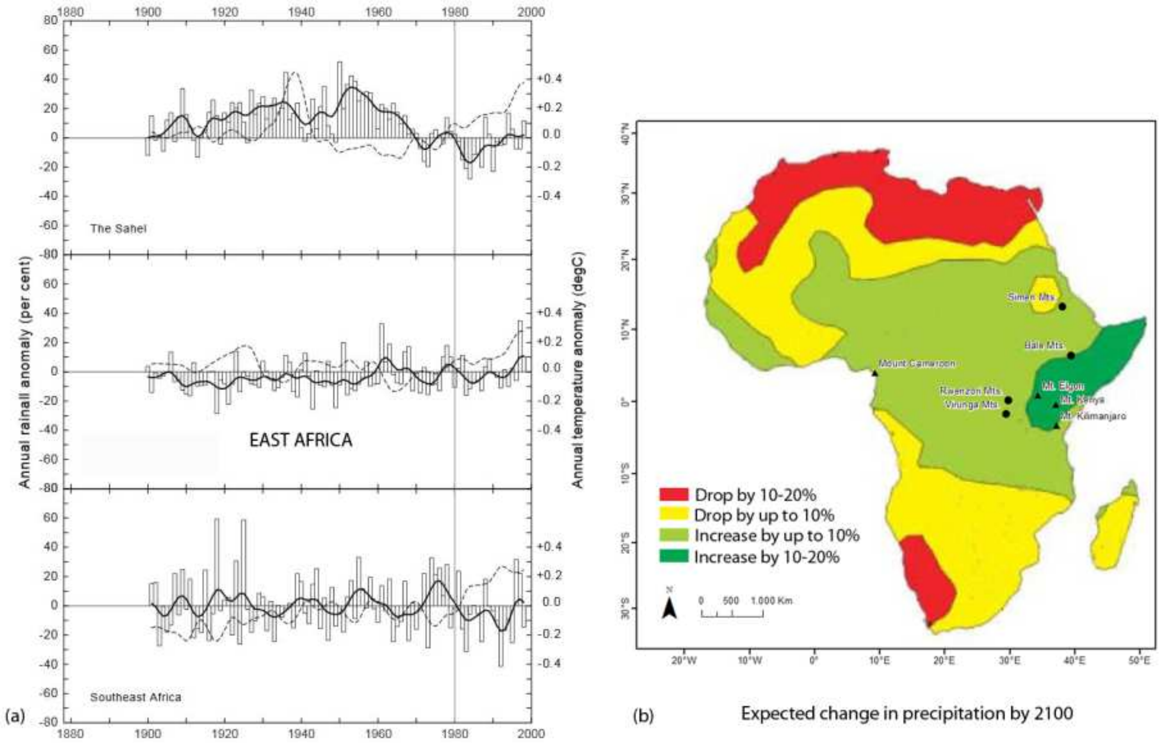

***Figure 3*:** Temperature and rainfall trends in Africa since 1900 (modified after Hulme et al. (2001) and de Wit & Stankiewicz (2006)): (a) Annual rainfall (histogram and bold line) and mean temperature (dashed line) anomalies for the period 1900-1998, with the 1961-1990 average as reference. The trend is given for three African regions, of which East Africa is best corresponding with the tropical African mountain regions. Note, the temperature increase after 1980 (indicated by a vertical line); (b) expected change in precipitation by the end of the 21st century for Africa. Note, the long term wetting trend in East Africa.

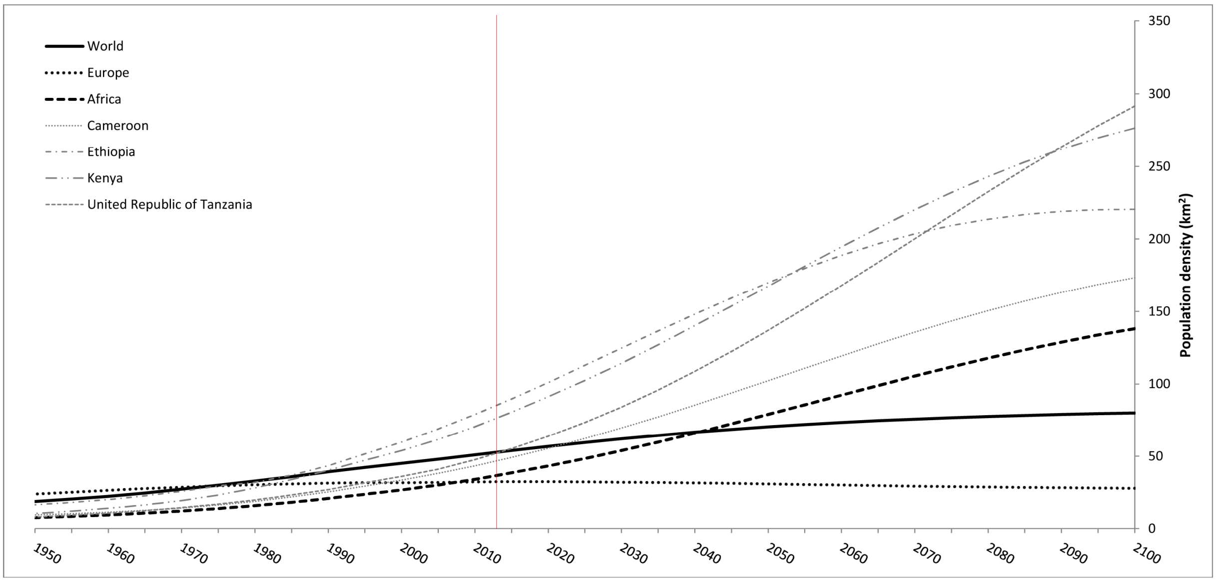

Figure 4: Population dynamics in the tropical African highlands: (a) Population density, (b) growth rate. The situation of 2013 is indicated with a red vertical line.

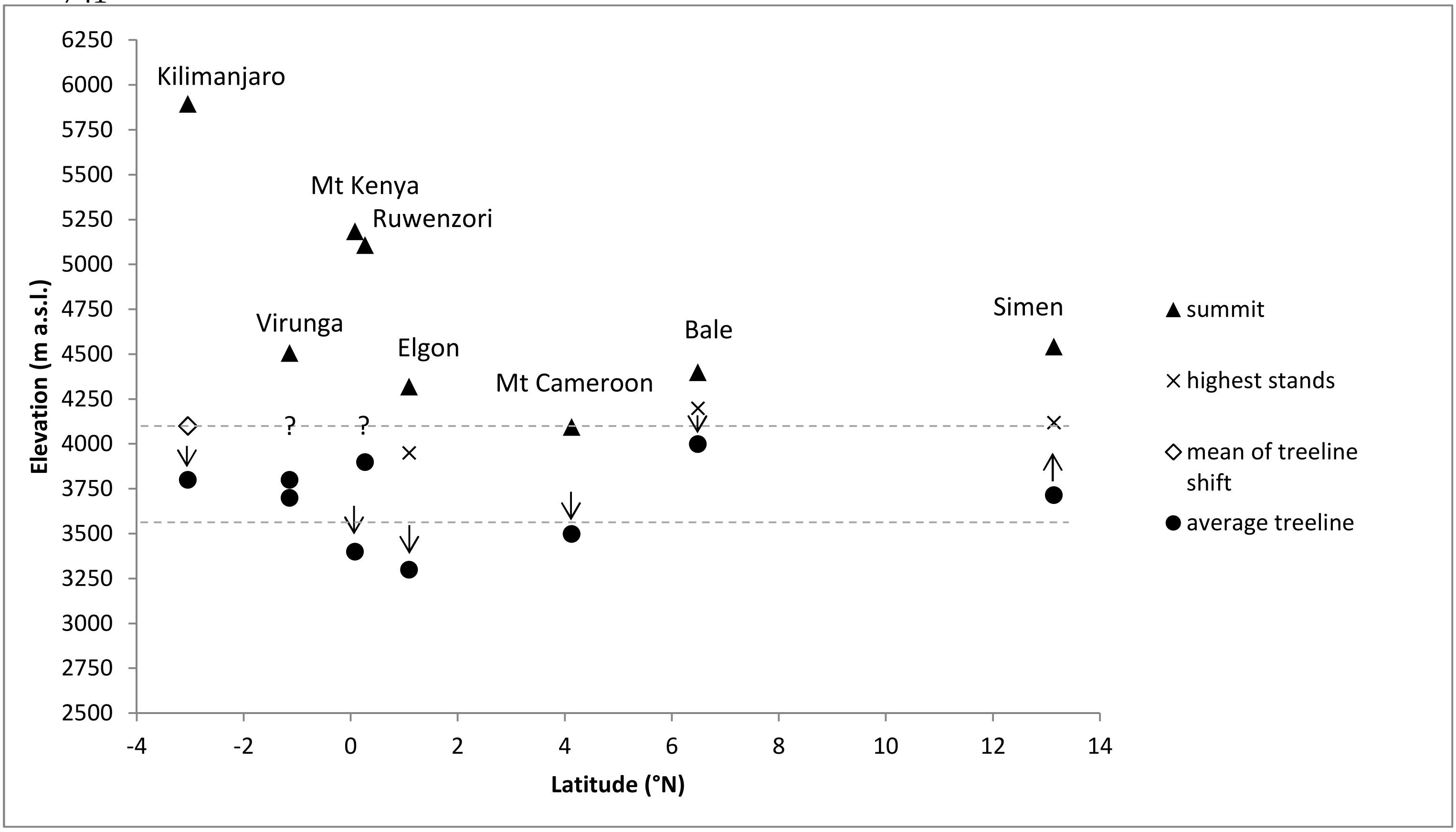

Figure 5: Synthesis of treeline dynamics in the tropical African highlands (see table 2 for references). Arrows indicate the treeline trend. The zone between the dashed lines refers to the upper treeline limit zone described by Hedberg (1951).