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SYNTHESIS

Tree line dynamics in the tropical African highlands – identifying drivers and dynamics

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Abstract

Questions: What are the potential drivers of tree line change in the tropical African highlands? Are the temperature-sensitive tree lines 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 tree line limit of these forests. Afro-alpine tropical tree lines 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 climatic factors in the African tropical highlands is significantly different compared to other regions. The potentially determining factors for tree line distribution in tropical Africa are temperature, precipitation and cloudiness, carbon balance, fire and anthropo-zoogenic impacts. Despite recent temperature increase, tree lines have not risen to higher altitudes in the tropical African highlands. Instead, high human pressure has caused stabilization and even recession of the tree lines 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 tree line change.

Conclusions: The actual drivers of tree line 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 tree line vegetation. Additionally, in volcanic active mountains, volcanic activity is also a potentially limiting factor for the tree line distribution. Tree line dynamics can thus not be used as a proxy of climate change for the African tropical highlands.

Introduction

Alpine tree lines 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 tree line 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): (1) the 'timberline', i.e. the boundary of the closed forest; (2) the 'tree species limit', i.e. the boundary formed by the upper individuals of tree species, regardless of the growth form; and (3) the 'tree line', i.e. the upper limit of forest patches characterized by a growth height of >3 m, or 2 m in the absence of snow accumulation, as is the case in the tropics (Holtmeier 2009). Trees from the *Ericoideae* subfamily form the upper tree line forest in the tropical African mountains (Wesche et al. 2000).

The first systematic tree line studies occurred approximately 150 yr ago, as reviewed in Marek (1910). At present, knowledge on the ecophysiological situation of

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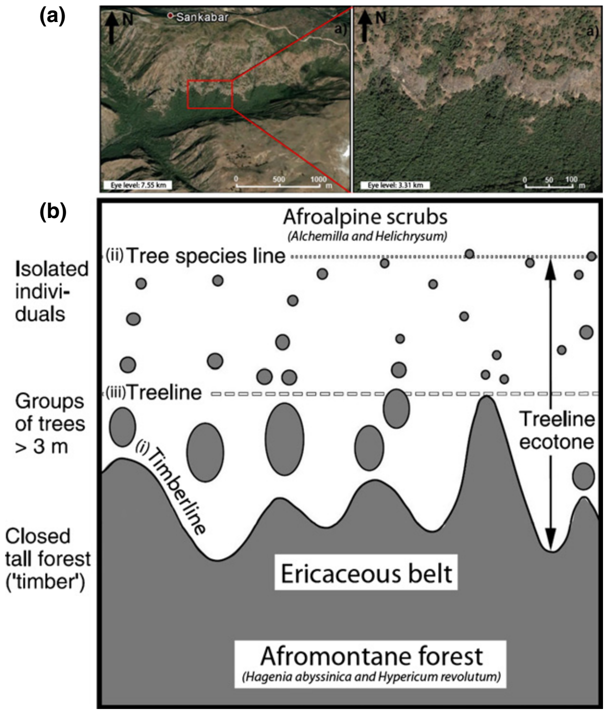

Fig. 1. Complexity of the treeline (**a**) Google Earth Image of the tree line at the Simen Mountains, Sankabar camp (13° 14′N, 38° 3′E), visualized at two different scales to emphasize the treeline gradient. (**b**) The tree line ecotone modified after Körner & Paulsen (2004) with distinction between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

tree lines in the tropics is still fragmentary (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 tree lines in tropical Africa during the dry and cold Last Glacial Maximum (LGM) and by rising tree lines in the Holocene as a result of temperature increase (Wu et al. 2007). Atmospheric CO_2 concentrations have become higher since the start of the Holocene, which has caused a switch from rainfall-limited tree lines in the LGM to temperature-limited tree lines 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 of 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 tree lines are therefore considered to be a potential proxy of climate change (Bader 2007). Evidence for this is given by LGM tree line oscillations due to past climate change in the afro-alpine mountains (Wu et al. 2007). The associated counterparts of tree line 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 tree line dynamics in the tropics is important to understand dynamics and spatial patterns of vegetation at the tree line (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 tree line change in the tropical African highlands mountains and to answer the question whether temperature-sensitive tree lines in these mountains are shifting as a result of climate change. This will also evaluate whether tree line shifts can serve as a proxy for climate change in tropical Africa.

Study area

Previously studied African tropical mountains with summits ranging above the present tropical tree-line elevation (3300–4000 m·a.s.l.) 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

Journal of Vegetation Science
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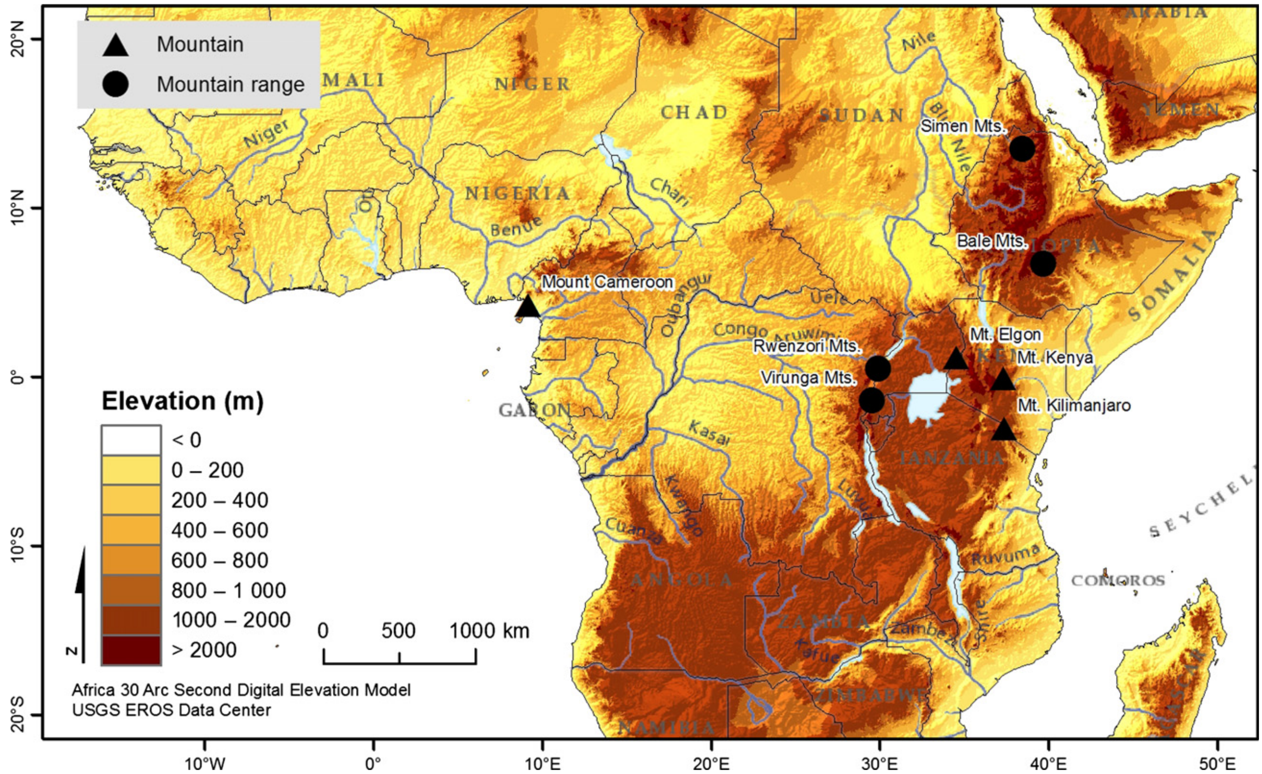

Fig. 2. The studied tropical mountains of Africa that range above the tree line elevation.

upper tree line ecotone is formed by trees from the *Ericoideae* subfamily, dominated by the genus *Erica L.* (Miehe & Miehe 1994; Wesche et al. 2000). Tree line 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); which is described by Hedberg (1951) as the 'ericaceous belt'. Beyond this elevation, tree growth is not possible and afro-alpine scrub dominates the landscape. *Erica L.* trees are small (ca. 8 m) and have needle-like scleromorphic leaves. Afro-alpine scrub is dominated by species of *Alchemilla* and *Helichrysum* (Bussmann 2006). Anthropo-zoogenic impact has strongly modified the vertical extent of the ericaceous belt through 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).

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

The elevation of the tree line 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 limits metabolism, development and reproduction of the trees. At a global scale, there are evident differences in the impact of these constraints between the tropical highlands and the boreal and temperate environments (Table 1).

The elevation of the tree line 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 tree line (Körner 1998; Harsch et al. 2009; Holtmeier 2009). The seasonal mean temperature at the tree line varies from 6 to 8 °C outside the tropics and around 5 °C in the tropics (Körner 2012).

The limiting factor for growth in the tropics is mainly caused by permanent stress resulting from the pronounced temperature fluctuations 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 tree lines during the day, due to the low latitude and high altitude, while night frost can occur during almost 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

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Table 1. A comparison of potential environmental constraints for tree growth at the tree line between the tropical and the boreal and temperate zones*.

Factor	Tropics	Boreal and Temperate Zone
Air Temperature	Mean seasonal temperature: 5 °C	Mean seasonal temperature: 6–8 °C
	Diurnal fluctuation	Length of the growing season
	Strong solar radiation	Less strong solar radiation
Soil Temperature	Diurnal variation	Seasonal variation
	Mean temperature: 6.1 ± 0.7 °C	Permafrost
Precipitation and Cloudiness	High seasonal rainfall variability	Snowfall accumulation
	Cloudiness differences	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

*The factors are described and fully referenced in the text.

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 tree line 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 tree line are common in the African tropical highlands, both having a negative impact on tree growth at the tree line (Smith & Young 1987). Increasing precipitation and cloudiness at the tree line elevation reduces solar radiation for photosynthesis and thus reduces temperatures and 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 tree line elevation in the tropics (Sarmiento 1986).

Freezing is generally less severe, and frost damage can occur throughout the year at the tropical tree line (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. Tree line vegetation is therefore potentially responsive to increased atmospheric CO_2 pressure (Smith et al. 2009). However, Hoch & Körner (2012) studied carbon reserves of tree line 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 C_4 tropical grasses and C_3 woody vegetation to elevated CO_2 pressure; where C_3 vegetation is competitively favoured (Ziska 2008).

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

Beside these environmental constraints, the tree line 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 on 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 tree line 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 grazing conditions.

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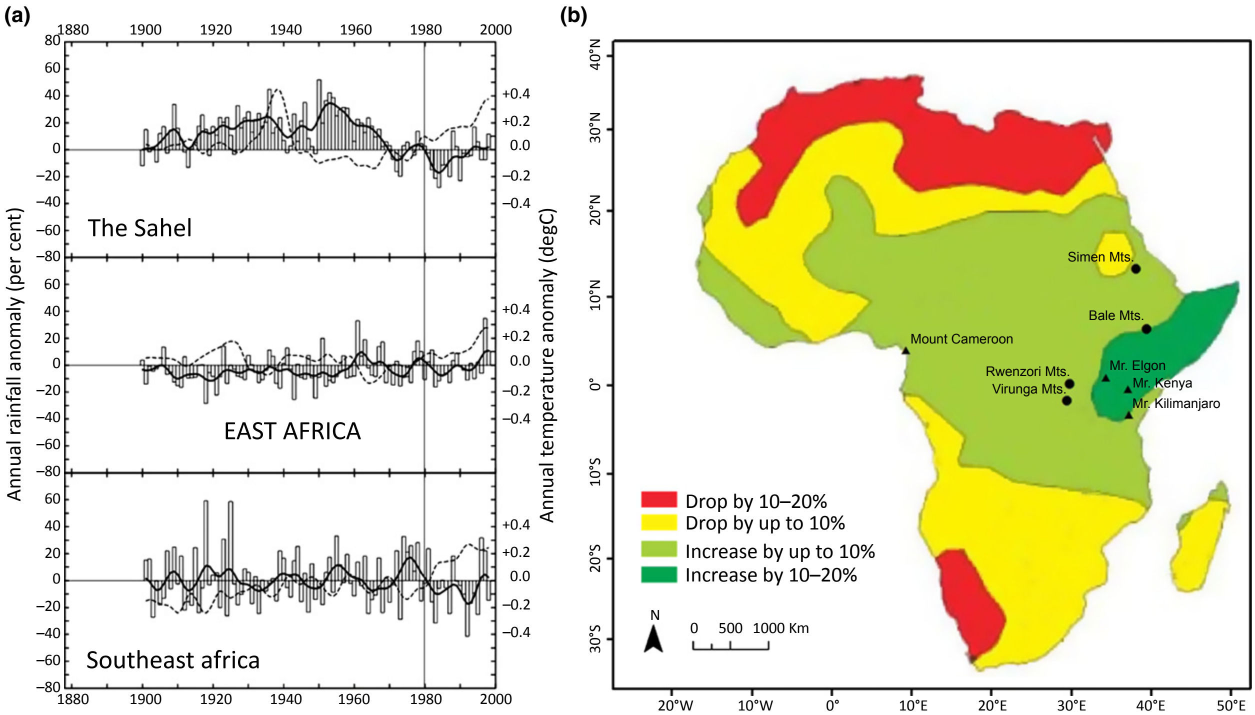

Fig. 3. Temperature and rainfall trends in Africa since 1900 (modified after Hulme et al. (2001) and De Wit & Stankiewicz (2006)): (**a**) Annual rainfall (histogram and bold line) and mean temperature (dashed line) anomalies for the period 1900–1998, with the 1961–1990 average as reference. The trend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

Effects of herbivores on the tree line structure and position are globally observed (Cairns & Moen 2004). The negative effects of herbivores on the tree line 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).

The potential drivers of tree line change

The potential drivers of tree line 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 tree line limit.

Temperature increase

Hulme et al. (2001) studied air temperature patterns in Africa over the last 100 yr and found that temperature in the African continent rose 0.5 °C. In the mountains of East Africa, temperature increased 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 by 3.3 °C by 2100 (IPCC 2007). The A1B model takes into account rapid economic growth, a global population peak in the mid-century followed by a decline, rapid introduction of new more sustainable technologies and a switch to balanced fossil and non-fossil energy sources (IPCC 2007). The scenarios neglect mitigating policy actions, and 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 close and can be accessed through migration higher into 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 to an increase in elevation of the tree line of 186 m. 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 m elevation (Peyron et al. 2000). A marked temperature increase of 0.3 °C since 1980 (Hulme et al. 2001) would thus theoretically correspond to an upwards tree line shift of 50 m; and the IPCC projection of 3.3 °C by 2100 with an upwards shift of 550 m (taking only temperature in account).

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 of 20% (Schiermeier 2008). However, the high inter-annual 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 climate 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%–30% in December–February, but to decrease by 5%–10% in June–August.

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

Change in carbon balance

The atmospheric CO_2 level rose from pre-industrial 285 $\mu mol \cdot l^{-1}$ (600 Gt) to the current level of 384 $\mu mol \cdot l^{-1}$ (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 through reduced stomatal conductance and transpiration, which cause higher leaf temperatures and increased drought stress (Bernacchi et al. 2007).

At tree line elevation in the tropics, the vegetation boundary between afro-alpine woodland and grasses corresponds 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 with 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).

Anthropo-zoogenic impact

The global population will grow annually at, on average, 1% over the period 2010–2025, which corresponds to a population increase of 1.2 billion people in 15 yr (UN data 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).

Current position and dynamics of the tree line in the African tropical highlands

The potential response of tree lines to climate warming is currently studied worldwide (Holtmeier & Broll 2007). Harsch et al. (2009) analysed a global data set of 166 tree line sites; advancing tree lines were recorded in 52% of the sites, and in only 1% was there a recession of the tree line. There is an association between tree line 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 tree line dynamics in the tropical highlands of Africa (Körner 2012). A global representation of the latitudinal position of tree lines is given in Körner (1998), showing a strong relation between tree line altitude and latitude in the temperate zone and a maximum in the subtropics. But there are no significant changes of the tree line position with altitude over a 50° range around the equator (Körner 1998). This graph again illustrates that tree line data are limited in the tropical and southern regions. The tree line elevation of the tropical African mountain ranges studied in this paper are therefore included in the Körner (1998) graph in Fig. 5b; the tropical African tree line elevation is, although scattered, following the general trend line found by Körner (1998). The current understanding of tree line dynamics in Africa is compiled in an overview below and summarized in Table 2.

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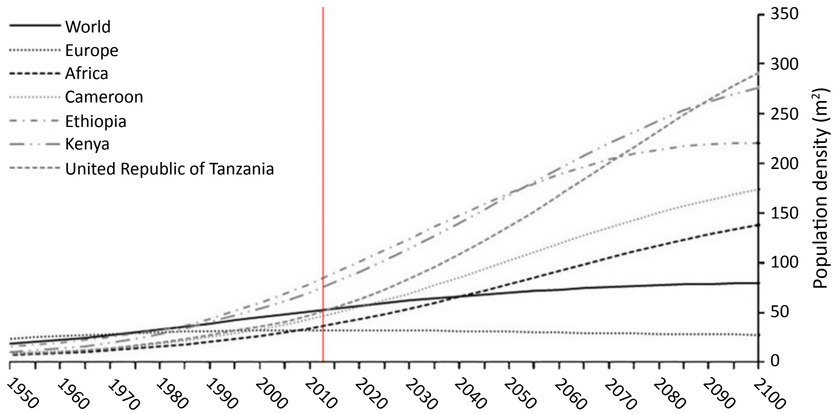

Fig. 4. Past and future population density in the tropical African highlands based on UN data (2013). The situation of 2013 is indicated with a red vertical line.

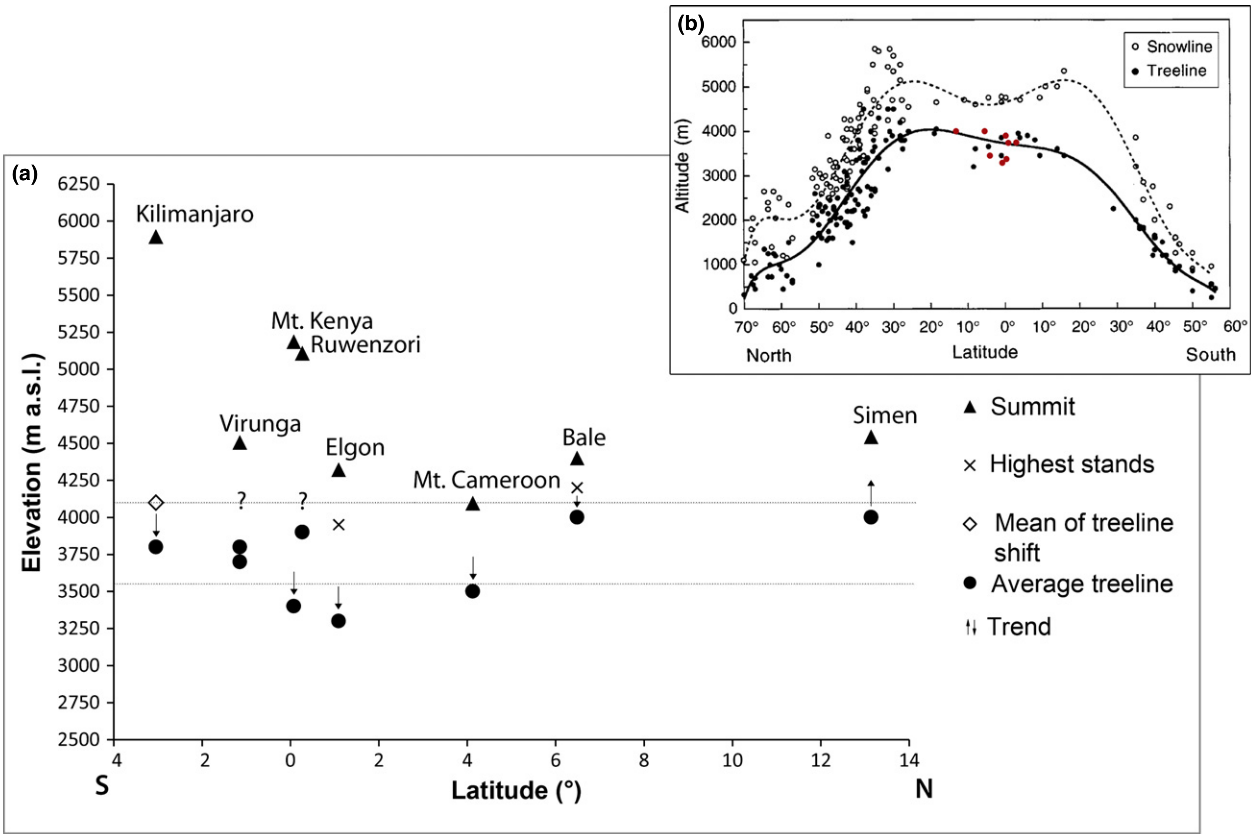

Fig. 5. Synthesis of tree line dynamics in the tropical African highlands (see Table 2 for references): (**a**) tree line dynamics in the African tropical highlands, arrows indicate the tree line trend. The zone between the dashed lines refers to the upper tree line limit zone described by Hedberg (1951); (**b**) Körner (1998) adjusted with tree line elevations from the tropical African highlands in red.

Shoulders of the Ethiopian Rift Valley

The Simen Mountains (4543 m) are situated in the northern highlands of Ethiopia and have been 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 tree line formed by *Erica arborea* lies at an average altitude of 3715 m (Hurni & Stähli 1982). Shifting of this tree line has been observed by repeat photography at Nebir Mekemacha, which shows an increase of the tree

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Table 2. Tree line dynamics and driving processes in the Tropical Highlands of Africa.

Mountain range	Latitude	Elevation	Tree line*	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†	01° 14′S	4507	3800 3600	?	Mount Muhabura: Rainfall limited?	Bussmann (2006)

*Average tree line elevation.
†The Virunga Mountains: Mount Karisimbi and Mount Muhabura.

line of ca. 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 tree line shift: recent climate change and reduced human and livestock pressure. Evidence against the climatic change hypothesis was provided for individual *Erica* trees high above the tree line already in 1968 (Nievergelt et al. 1998). The impact of cattle grazing, woodcutting and burning has reduced since the National Park was installed (Wesche et al. 2000).

The tree line 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 easterly winds (Holtmeier 2009). Although the Bale Mountains have also been protected since 1969, the upper tree line of the Bale Mountains is lowered by recurrent fires in many places to maintain or extend the grazing area (Wesche et al. 2000). As a result, mosaics of forests scrub and afro-alpine grasslands prevail at the tree line in the Bale highlands (Bussmann 2006).

In both mountain ranges the tree line is located at 4000 m, ca. 400–500 m below the highest summit (Fig. 5). There is thus a potential impact of the summit syndrome described by Körner (2012). But observations of recent tree line increase in the Simen Mountains provide evidence against the influence of the summit effect at the current tree line elevation.

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 tree line ecotone (Bussmann 2006). The abrupt tree line 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 ash (Proctor et al. 2007). As a result, the tree line is depressed below its climatic limit (Bussmann 2006). In addition, there is also 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).

Mountain ranges along the Eastern Rift Valley

The *Erica excelsa* tree line 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 yr exposed to high-altitude droughts and thus severe desiccation stress. The impact of drought stress is striking, with up to 50% of 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 tree line is depressed below the climatic tree limit (Fig. 5; Hamilton & Perrot 1981; Wesche 2003).

Journal of Vegetation Science
Doi: 10.1111/jvs.12215

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*, *E. trimera* and *E. arborea* (Bussmann 2006). The warmer moister climate of the Holocene enabled the tree line to rise in comparison to LGM levels (Rucina et al. 2009). However, the position of the tree line 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 plant species in the *Asteraceae*, *Stoebe kilimandscharica* and *Protea kilimascharica*, often at the tree line, indicates this regular disturbance by high-altitude fires. As a result of this disturbances, the boundary between the ericaceous belt and the afro-alpine 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 above 3000 m, with remnants of *Erica trimera* growing above 3700 m (Hemp 2009). The tree line is situated at ca. 3800 m, which is below its natural limit (Fig. 5; Hemp 2005; Körner 2012). In 1976 the tree line reached the 4100 m elevation limit (Hemp 2009). The cause of the tree line lowering several hundred meters since 1976 is a drier climate, which has caused an increased frequency and intensity of fires on the slopes of Kilimanjaro (Hemp 2005). Precipitation has decreased over 30% in recent years, in particular over the last three decades. More frequent and intense fires have not only lowered the tree line position, but even caused deforestation of one third of the Kilimanjaro forest in the last 70 yr (Hemp 2005).

Albertine Western Rift and Congo Nile Crestline

Because of political instability in this region, scientific studies on tree line dynamics are lacking. The research presented therefore only provides an overview on 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 *E. arborea*, which follows immediately after the bamboo belt (at 3000 m) and marks the tree line 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 five adjacent volcanoes. On the highest peak of Mount Karisimbi the tree line is situated at an average of 3800 m. On the drier Mount Muhabura (4127 m) trees only grow up to 3600 m (Fig. 5). In the Virguna volcanoes the tree line is formed by *E. arborea* forest, growing above the *Hagenia abyssinica* and *Hypericum revolutum* forest (Bussmann 2006).

Discussion and conclusion

The discussion is structured according to the two main questions of this paper: (1) understanding the driving factors determining tree line elevation limits, and (2) identifying tree line dynamics in the African tropical highlands.

What are the driving factors determining tree line elevation in African tropical highlands?

At present, climate change is unequivocal and has 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 tree line position. Tree line species in the tropical highlands must be specifically adapted to high diurnal temperature variations. A temperature increase of 3.3 °C by 2100 would correspond to an increase of the tropical African tree line by 550 m, 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 tree line elevation below its climatic limit. Anthropo-zoogenic influences disturb the tree line, mainly through 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. Moreover, volcanic activity is also a locally important constraint on high-altitude tree growth.

Are tree lines in the African tropical highlands subject 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 tree line is situated in between the alpine and ericaceous belt, with an elevation limit between 3550 and 4100 m (Hedberg 1951). This 4100 m limit currently corresponds with the tree line in the Simen Mountains. The Simen Mountains are the only mountain range in this study in which the tree line has risen locally. This indicates that, here, the tropical tree line lies below its potential climatic limit (Miehe & Miehe 1994; Kessler 1995; Bader 2007). A tentative explanation is that the Simen Mountains are at the most northerly location and thus closer to the subtropics, and as a result receive less rainfall and cloudiness, which can cause the tree line to increase in height (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 tree lines have moved downwards 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 tree line has lowered due to high anthropogenic pressure. In addition, on Mount Cameroon, volcanic activity has also had a negative effect on the tree line elevation. Disturbance by humans and livestock is controlling the tree line 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 political instability in this region. As a result, the tree line elevation is potentially more stable. Yet little is known about potential vegetation shift in this region. When neglecting human interference, tree lines in the tropical African highlands might rise to higher elevations. This is witnessed in the Simen Mountains, although reducing pasture and wood-cutting have also played a major role here. A hypothetical upper tree line limit at 4100 m is suggested by Hedberg (1951). This 4100 m limit used to also correspond to the limit at Kilimanjaro in 1976, but due to climatic drier conditions, in combination with growing anthropogenic pressure, the tree line of Kilimanjaro has also been lowered. The effect of decreasing rainfall conditions is thus opposite between the Simen Mountains and Kilimanjaro.

Overall, tree lines in the African tropics are strongly disturbed by human and livestock pressure, which makes it impossible to use them as a proxy for climate change in the tropics. The general trend of a depressed tree line below the climatic limit in the tropical African highlands favours the hypothesis that tree lines 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 provided by past higher tree line elevations and by evidence of a rising tree line in the Simen Mountains.

Outline for future work

Overall, more tree line research in the African tropical highlands is vital to improve scientific understanding of the response of high-altitude tropical tree lines to environmental changes. In the global tree line 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 functioning of the ecosystems of the African tropical highlands. A better understanding of this can help to make realistic predictions, which are important as an input to land management scenarios.

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