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

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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.

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

40

41 **1. Introduction**

42

43 Alpine treelines mark the transition between mountain and alpine environments on
44 high mountain slopes (Berdanier 2010) and are one of the most apparent vegetation
45 boundaries worldwide (Körner & Paulsen 2004; Berdanier 2010). According to Callaghan et
46 al. (2002) and Holtmeier (2009), the shift from dense montane forests to treeless alpine
47 grasses and shrubs is characterized by increasing stand fragmentation and stuntedness. This
48 transition is called the treeline ecotone (Fig. 1a). There are three frequently used
49 terminologies which refer to the transition from forest to non-forest stages (Fig. 1b) (Körner
50 & Paulsen 2004; Van Bogaert et al. 2011): (i) the 'timberline', i.e. the boundary of the closed
51 forest, (ii) the 'tree species limit', i.e. the boundary formed by the upper individuals of tree
52 species, regardless of the growth form, and (iii) the 'treeline', i.e. the upper limit of forest
53 patches characterized by a growth height of more than 3 m, or 2 m in absence of snow
54 accumulation as is the case in the tropics (Holtmeier 2009). Trees from the *Ericoideae*
55 subfamily form the upper treeline forest in the tropical African mountains (Wesche et al.
56 2000).

57 The first systematic treeline studies occurred approximately 150 years ago, as
58 reviewed in Marek (1910). At present, knowledge on the ecophysical situation of treelines in
59 the tropics is still fragmental (Bader 2007; Holtmeier 2009). Tree growth is constrained by
60 changing environmental conditions with increasing altitude (Körner 2012). This makes the
61 altitudinal tree-limit potentially responsive to climate change (Körner & Paulsen 2004). This
62 is illustrated by a lowering of the treelines in tropical Africa during the dry and cold Last
63 Glacial Maximum (LGM) and by rising treelines in the Holocene as a result of temperature
64 increase (Wu et al. 2007). Atmospheric CO₂ concentrations are higher since the start of the
65 Holocene, which caused a switch from rainfall limited treelines in the LGM to temperature
66 limited treelines in the Holocene (Wu et al. 2007).

67 There are few continuous long-term climate reconstructions available that focus on
68 the African tropics. Among the first, Thompson et al. (2002) reconstructed the Holocene
69 climatic history in Africa from an ice core of the Kilimanjaro ice fields. Evidence was given for
70 three periods of abrupt climatic shifts and predicted complete melting of the Kilimanjaro ice

71 fields by 2015-2020 (Thompson et al. 2002). The IPCC (2007) stated that ‘warming of the
72 climate system is unequivocal, as is now evident from observations of increases in global
73 average air and ocean temperatures, widespread melting of snow and ice and rising global
74 average sea level’. The temperature rise of the past century is most prominent and rapid at
75 high altitudes and latitudes IPCC (2007).

76 The tropical African mountains are hotspots in biodiversity, comprising a high amount
77 of endemic species that have their habitat in these mountains. A substantial reduction, shift
78 and extinction of African flora and fauna species is expected in diverse African ecosystems
79 (IPCC 2007). Species that reproduce slowly, disperse poorly, and are isolated are most
80 vulnerable to climate warming (McNeely et al. 1990). The mountain-restricted species of the
81 African highlands are good examples of such isolated species, which are highly sensitive to
82 environmental stress (IPCC 2007). The value of forests on mountain slopes is much wider
83 than only for biodiversity. High mountain forests are important for slope stability and
84 regionally important as a hygric buffer providing water for downstream sources and for
85 agriculture in the surrounding lowlands (Miehe & Miehe 1994; Price 2003). The climate
86 controlled tree limit of these mountain forests forms a clearly visible ecotone worldwide.
87 Afro-alpine tropical treelines are therefore considered to be a potential proxy of climate
88 change (Bader 2007). Evidence for this is given by LGM treeline oscillations due to past
89 climate change in the afro-alpine mountains (Wu et al. 2007). The associated counterpart of
90 treeline shifts are shifts in the altitudinal range of grass- and shrubland. Such shifts increase
91 the risk of species extinctions and can impede the provision of important non-forest
92 ecosystem services. Understanding the drivers of treeline dynamics in the tropics is
93 important to understand dynamics and spatial patterns of vegetation at the treeline (Bader
94 2007). It is important to understand the dynamics that are taking place, in order to develop
95 sustainable conservation strategies (Burgess et al. 2007).

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

100

101 ***INSERT FIGURE 1

102

103 **1.1 Study Area**

104 Previously studied African tropical mountains with summits ranging above the present
105 tropical treeline elevation (3300 - 4000 m) were selected for this paper (Fig. 2). These
106 mountains are: Rwenzori Mountains (5109 m), Virguna Mountains (4507 m), Simen
107 Mountains (4550 m), Bale Mountains (4377 m), Mount Elgon (4321 m), Mount Kilimanjaro
108 (5896 m), Mount Kenya (5199 m), and Mount Cameroon (4095 m). For all these mountains,
109 the upper treeline ecotone is formed by trees from the *Ericoideae* subfamily dominated by
110 the genus *Erica L.* (Miehe & Miehe 1994; Wesche et al. 2000). Treeline forests are prominent
111 above 3000 m in most tropical African mountains and grow over an elevation range of up to
112 1000 m (Miehe & Miehe 1994); described by Hedberg (1951) as the 'ericaceous belt'.
113 Beyond this elevation, tree growth is not possible and afroalpine scrubs dominate in the
114 landscape. *Erica L.* trees are small (ca. 8 m) and have needle-like scleromorphic leaves.
115 Afroalpine scrubs are dominated by species of *Alchemilla* and *Helichrysum* (Busmann 2006).
116 Anthro-zoogenic impact strongly modified the vertical extent of the ericaceous belt by
117 woodcutting, fire and grazing. But despite the limited area still covered by ericaceous forest
118 at the high altitude tree limit, this forest type remains vital for the regional environment of
119 the tropical African highlands (Miehe & Miehe 1994).

120

121 ***INSERT FIGURE 2

122

123 **2 Biophysical and anthro-zoogenic constraints for tree growth in the tropical African**
124 **highlands**

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

132

133 ***INSERT TABLE 1

134

135 The elevation of the treeline in the tropics is determined by a combination of
136 biophysical factors. Of which, low ambient temperature is a key factor regulating growth,
137 regeneration and survival of trees at the treeline (Körner 1998; Holtmeier 2009; Harsch et al.
138 2009). The seasonal mean temperature at the treeline varies from 6 to 8°C outside the
139 tropics and around 5°C in the tropics (Körner 2012).

140 The limiting factor of growth in the tropics is mainly caused by the permanent stress
141 resulting from the pronounced temperature fluctuation between day and night (Wardle &
142 Coleman 1992; Miehe & Miehe 1994; Bader 2007). This is because high intensities of solar
143 radiation can be reached at tropical alpine treelines during the day, due to the low latitude
144 and high altitude, while night frost can occur during every night (Bader 2007). Because of the
145 tropical diurnal climate variability, it is important to differentiate the soil temperature
146 regime in the tropics from that outside the tropics (Holtmeier 2009). In the tropics, mean
147 temperature should be considered a rough indicator only, since there is a large variation in
148 site-specific temperature cycles (Miehe & Miehe 1994). An annual mean soil temperature of
149 $6.1 \pm 0.7^\circ\text{C}$ was found to correspond with the upper tree limit all year round in the tropics
150 (Hoch & Körner 2003).

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

164 Freezing is generally less severe and frost damage can occur all year round at the
165 tropical treeline (Smith 1974; Goldstein et al. 1994). Diurnal differences are especially high in

166 the dry season, when clear skies prevail (Sarmiento 1986). Physiological adaptations for frost
167 resistance must therefore be permanent in tropical highlands (Sarmiento 1986).

168 The partial CO₂ pressure is lower at high elevations at all latitudes. Treeline vegetation
169 is therefore potentially responsive to increased atmospheric CO₂ pressure (Smith et al.
170 2009). However, Hoch and Körner (2012) studied carbon reserves of treeline trees
171 worldwide and did not find evidence of carbon shortage. Similar results were found in single
172 mountain ranges by Piper et al. (2006) and Shi et al. (2008). This increasingly favours the
173 growth limit hypothesis over the traditional carbon balance hypothesis (Hoch & Körner
174 2012; Simard et al. 2013). However, there is another potential effect of elevated CO₂ in the
175 tropics, caused by the different response of C₄ tropical grasses and C₃ woody vegetation to
176 elevated CO₂ pressure; C₃ vegetation is competitively favoured (Ziska 2008).

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

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

195 Effects of herbivores on the treeline structure and position are globally observed
196 (Cairns & Moen 2004). The negative effects of herbivores on the treeline are primarily
197 caused by livestock. In the agricultural system of the tropical highlands, livestock plays a key

198 role as provider of energy, food, fertilizer and status (Nyssen et al. 2004). Livestock browsing
199 impedes regeneration of Erica and other trees of the sub-alpine zone through foliage
200 consumption, trampling and seed predation (Castro et al. 2004).

201

202 **3. The potential drivers of treeline change**

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

206

207 *3.1 Temperature increase*

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

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

230

231 *3.2 Rainfall variability*

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

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

247

248 ***INSERT FIGURE 3

249

250 *3.3 Change in carbon balance*

251 The atmospheric CO₂ level rose from pre-industrial 285 μmol l⁻¹ (600 gigatonnes (Gt))
252 to the current level of 384 μmol l⁻¹ (800 Gt) and is predicted to rise to 1000 Gt by 2050 (IPCC
253 2007). The main focus of increased CO₂ concentrations, due to anthropogenic intensification,
254 is on the likely effect on global mean surface temperature rise. But there are also direct
255 effects on plant growth and physiology, independent of the climatic effect (Ziska 2008). This
256 effect of elevated CO₂ concentrations is different for C₃, C₄ and Crassulacean Acid
257 Metabolism (CAM) plant species. The widespread C₃ plants and CAM plants show a
258 significant positive response, while C₄ plants exhibit a negative response (Reddy et al. 2010).
259 The negative effect on C₄ plants of increased CO₂ concentrations is by reduced stomatal
260 conductance and transpiration, which causes higher leaf temperatures and increased
261 drought stress (Bernacchi et al. 2007).

262 At treeline elevation in the tropics, the vegetation boundary between afroalpine
263 woodland and grasses correspond with the boundary between C₄ and C₃ plants, respectively.
264 Elevated CO₂ concentrations in the tropics would thus potentially support the advance of the
265 C₃ woody vegetation to higher elevations in competition to C₄ tropical grasses (Leahey et al.
266 2009). But more research is necessary for a better understanding of this different CO₂
267 response and the linkage with other environmental factors (Leahey et al. 2009).

268

269 *3.4 Anthropo-zoogenic impact*

270 The global population will grow annually with on average 1% over the period 2010-
271 2025, which correspond to a population increase of 1.2 billion people in 15 years (UNdata
272 2013). A growing proportion of the global population will be living in Africa, as the
273 population in Africa is growing very fast (up to 3% annually) (Fig. 4, FAO 2007). The
274 associated growing population and livestock pressure will further increase environmental
275 pressure in the tropical highlands (Burgess et al. 2007). The impact is already visible through
276 increased, wood cutting and uprooting of Erica stumps, inhibiting tree regeneration (Bishaw
277 2001).

278

279 ***INSERT FIGURE 4

280

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

282 The potential response of treelines to climate warming is currently studied worldwide
283 (Holtmeier & Broll 2007). Harsch et al. (2009) analysed a global dataset of 166 treeline sites;
284 advancing treelines were recorded in 52% of the sites and in only 1% there was a recession
285 of the treeline. There is an association between treeline advance and temperature increase,
286 although the mechanisms are not always straightforward. However, the analysis of Harsch et
287 al. (2009) almost completely lacks study sites in the tropics; there are only four tropical sites
288 included of which none are in Africa. This is because little is known about treeline dynamics
289 in the tropical highlands of Africa (Körner 2012). A global representation of the latitudinal
290 position of treelines is given by Körner (1998), showing a strong relation between treeline
291 altitude and latitude in the temperate zone and a maximum in the subtropics. But no
292 significant changes of the treeline position with altitude over a 50° range around the equator
293 (Körner 1998). This graph again illustrates that treeline data is limited in the tropical and

294 southern regions. The treeline elevation of the tropical African mountain ranges studied in
295 this paper are therefore included in the Körner (1998) graph in figure 5b; the tropical African
296 treeline elevation is, although scattered, following the general trendline found by Körner
297 (1998). The current understanding of treeline dynamics in Africa are compiled in an overview
298 below and summarized in Table 2.

299

300 *** INSERT TABLE 2

301

302 4.1 Shoulders of the Ethiopian Rift Valley

303 The Simen Mountains (4543 m) are situated in the northern highlands of Ethiopia and
304 are protected under national legislation since 1969. The Simen Mountains have a unimodal
305 precipitation regime, which is relatively dry compared to the bimodal precipitation regime of
306 the more southern tropical African mountains (Hurni & Stähli 1982). The treeline formed by
307 *Erica arborea* lies at an average altitude of 3715 m (Hurni & Stähli 1982). Shifting of this
308 treeline has been observed by repeat photography at Nebir Mekemacha, which shows an
309 increase of the treeline of approximately 120 m from 4000 to 4120 m between 1967 and
310 1997 (Fig. 5) (Nievergelt et al. 1998; Wesche et al. 2000). There are two possible
311 explanations for this treeline shift: recent climate change and reduced human and livestock
312 pressure. Evidence against the climatic change hypothesis is given by individual *Erica* trees
313 high above the treeline already in 1968 (Nievergelt et al. 1998). The impact of cattle grazing,
314 woodcutting and burning reduced since the National Park was installed (Wesche et al. 2000).

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

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

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

328

329 4.2 West Africa

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

341

342 4.3 Mountain ranges along the Eastern Rift Valley

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

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

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

368 The ericaceous belt of Mount Kilimanjaro (5895 m) is formed by *Erica excelsa* forest
369 prevailing above 3000 m, with remnants of *Erica trimera* growing above 3700 m (Hemp
370 2009). The treeline is situated at ca. 3800 m, which is below its natural limit (Fig. 5) (Hemp
371 2005; Körner 2012). In 1976 the treeline reached the 4100 m elevation limit (Hemp 2009).
372 The cause of the treeline lowering with several hundred meters since 1976 is a drier climate,
373 which caused an increased frequency and intensity of fires on the slopes of the Kilimanjaro
374 (Hemp 2005). Precipitation has decreased over 30% in the recent years, in particular over
375 the last three decades. More frequent and intensive fires have not only lowered the treeline
376 position, but even caused a deforestation of one third of the Kilimanjaro forest in the last 70
377 years (Hemp 2005).

378

379 4.4 Albertine Western Rift and Congo Nile Crestline

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

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

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

395

396 *** INSERT FIGURE 5

397

398 **5. Discussion and conclusion**

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

402

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

405 At present climate change is unequivocal and caused global warming and changing
406 rainfall patterns. These changes have the potential to influence the altitudinal tree growth
407 limit. Unlike in temperate and boreal regions, wind, frost damage and snow accumulation
408 are less important in controlling the treeline position. Treeline species in the tropical
409 highlands must be particularly adapted to high diurnal temperature variation. A temperature
410 increase of 3.3°C by 2100 would correspond with an increase of the tropical African treeline
411 by 550 meter, using the vertical temperature lapse rate of East Africa from Peyron et al.
412 (2000) (only taking temperature in account). But, past increases in population pressure in
413 the tropical highlands have depressed the treeline elevation below its climatic limit.
414 Anthro-po-zoogenic influences disturb the treeline, mainly by man-made fire to clear the
415 forest for grazing land. The impact of these fires is locally intensified as a result of long term
416 drought, which decreases the resilience of the environment to fire disturbances. Beside this
417 is volcanic activity also a locally important constraint of high altitude tree growth.

418

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

420 Hedberg (1951) presented a general classification of the vegetation belts of the
421 Eastern African Mountains. He recognized three belts on each mountain: the alpine, the

422 ericaceous and the montane forest belts. The treeline is situated in between the alpine and
423 ericaceous belt with an elevation limit between 3550 and 4100 m (Hedberg 1951). This
424 4100m-limit corresponds with the treeline in the Simen Mountains at present. The Simen
425 Mountains are the only mountain range in this study of which the treeline rose locally. This
426 indicates that here, the tropical treeline lies below its potential climatic limit (Miehe &
427 Miehe 1994; Kessler 1995; Bader 2007). A tentative explanation is that the Simen Mountains
428 are located most northern and thus closer to the subtropics and as a result receive less
429 rainfall and cloudiness, which can cause the treeline to rise higher (Körner 2012). But this
430 explanation is too simplistic, because decreasing human impact after national park
431 establishment should also be taken into account.

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

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

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

459

460 *(iii) Outline for future work*

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

469

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475

476 **References**

- 477 Bader, M.Y. 2007. *Tropical alpine treelines: how ecological processes control vegetation*
478 *patterning and dynamics*. Wageningen University, Wageningen.
- 479 Berdanier, A. 2010. Global Treeline Position. *Nature Education Knowledge* 3: 11–19.
- 480 Bernacchi, C.J., Kimball, B. a, Quarles, D.R., Long, S.P., & Ort, D.R. 2007. Decreases in
481 stomatal conductance of soybean under open-air elevation of CO₂ are closely coupled
482 with decreases in ecosystem evapotranspiration. *Plant physiology* 143: 134–44.
- 483 Bishaw, B. 2001. Deforestation and Land Degredation in the Ethiopian Highlands: A Strategy
484 for Physical Recovery. *Northeast African Studies* 8: 7–25.
- 485 Van Bogaert, R., Haneca, K., Hoogesteger, J., Jonasson, C., De Dapper, M., & Callaghan, T.V.
486 2011. A century of tree line changes in sub-Arctic Sweden shows local and regional
487 variability and only a minor influence of 20th century climate warming. *Journal of*
488 *Biogeography* 38: 907–921.
- 489 Burgess, N., Balmford, a, Cordeiro, N., Fjeldsa, J., Kuper, W., Rahbek, C., Sanderson, E.,
490 Scharlemann, J., Sommer, J., & Williams, P. 2007. Correlations among species
491 distributions, human density and human infrastructure across the high biodiversity
492 tropical mountains of Africa. *Biological Conservation* 134: 164–177.
- 493 Bussmann, R.W. 2006. Vegetation zonation and nomenclature of African Mountains - An
494 overview. *Lyonia* 11: 41–66.
- 495 Cairns, D.M., & Moen, J. 2004. Herbivory influences tree lines. *Journal of Ecology* 92: 1019–
496 1024.
- 497 Callaghan, T.V., Werkman, B.R., & Crawford, R.M. 2002. The Tundra-Taiga interface and its
498 dynamics: concepts and applications. *Ambio* 12: 6–14.
- 499 Castro, J., Zamora, R., Hódar, J.A., & Gómez, J.M. 2004. Seedling establishment of a boreal
500 tree species (*Pinus sylvestris*) at its southernmost distribution limit : *Journal of Ecology*
501 92: 266–277.
- 502 Chambers, J.Q., Higuchi, N., & Schimel, J.P. 1998. Ancient trees in Amazonia. *Nature* 391:
503 135–136.
- 504 Dullinger, S., Willner, W., Plutzer, C., Englisch, T., Schrott-Ehrendorfer, L., Moser, D., Ertl, S.,
505 Essl, F., & Niklfeld, H. 2012. Post-glacial migration lag restricts range filling of plants in
506 the European Alps. *Global Ecology and Biogeography* 21: 829–840.
- 507 Ellenberg, H. 1996. Páramos und Punas der hochanden Südamerikas, heure größenteils als
508 potentielle Wälder anerkannt. *Verhandlungen der Gesellschaft für ökologie* 25: 17–23.

- 509 FAO. 2007. *State of the world's forest*. Rome.
- 510 Gehrig-Fasel, J., Guisan, A., & Zimmermann, N.E. 2008. Evaluating thermal treeline indicators
511 based on air and soil temperature using an air-to-soil temperature transfer model.
512 *Ecological Modelling* 213: 345–355.
- 513 Gehrig-Fasel, J., Guisan, A., & Zimmermann, N. 2007. Tree line shifts in the Swiss Alps :
514 Climate change or land abandonment ? *Journal of Vegetation Science* 18: 571–582.
- 515 Goldstein, G., Meinzer, F.C., & Rada, F. 1994. Environmental biology of a tropical treeline
516 specie, *Polylepis sericea*. In Rundel, P.W., Smith, A.P., & Meinzer, F.P. (eds.), *Tropical*
517 *Alpine Environments: plant form and function*, Cambridge University Press, Cambridge.
- 518 Hamilton, A.C., & Perrot, R.A. 1981. A study of altitudinal zonation in the montane forest belt
519 of Mt. Elgon, Kenya/Uganda. *Vegetatio* 45: 107–125.
- 520 Harsch, M. a, Hulme, P.E., McGlone, M.S., & Duncan, R.P. 2009. Are treelines advancing? A
521 global meta-analysis of treeline response to climate warming. *Ecology letters* 12: 1040–
522 9.
- 523 Hedberg, O. 1964. *Features of afroalpine plant ecology*. Svenska växtgeografiska sällsk,
524 Uppsala.
- 525 Hedberg, O. 1951. Vegetation belts of the east African mountains. *Svensk Botanisk Tidskrift*
526 45: 140–202.
- 527 Hemp, A. 2009. Climate change and its impact on the forests of Kilimanjaro. *African Journal*
528 *of Ecology* 47: 3–10.
- 529 Hemp, A. 2005. Climate change-driven forest fires marginalize the impact of ice cap wasting
530 on Kilimanjaro. *Global Change Biology* 11: 1013–1023.
- 531 Hemp, A., & Beck, E. 2001. *Erica excelsa* as a fire-tolerating component of Mt. Kilimanjaro's
532 forests. *Phytocoenologia* 47: 3–10.
- 533 Hoch, G., & Körner, C. 2012. Global patterns of mobile carbon stores in trees at the high-
534 elevation tree line. *Global Ecology and Biogeography* 21: 861–871.
- 535 Hoch, G., & Körner, C. 2003. The carbon charging of pines at the climatic treeline: a global
536 comparison. *Oecologia* 135: 10–21.
- 537 Holtmeier, F.K. 1994. Ecological aspects of climatically caused timberlines fluctuations -
538 review and outlook. In Beniston, M. (ed.), *Mountain environment in changing climates*,
539 pp. 220–232. Routledge, London and New York.
- 540 Holtmeier, F.K. 2009. *Mountain timberlines: Ecology, Patchiness and Dynamics* (M. Beniston,
541 Ed.). Springer, Havixbeck, Germany.

- 542 Holtmeier, F.K., & Broll, G. 2007. Treeline advance - driving processes and adverse factors.
543 *Landscape Online* 1: 1–32.
- 544 Hulme, M., Doherty, R., Ngara, T., New, M., & Lister, D. 2001. African climate change : 1900 –
545 2100. 17: 145–168.
- 546 Hurni, H., & Stähli, P. 1982. *Simen mountains, Ethiopia: climate and dynamics of altitudinal*
547 *belts from the last cold period to the present day*. Geographisches Institut der
548 Universität Bern, Bern, Switzerland.
- 549 IPCC. 2007. *Climate Change, the physical science basis. Contribution of working group I to the*
550 *fourth assessment report of the Intergovernmental Panel on Climate Change*.
- 551 Kessler, M. 1995. Present and potential distribution of *Polylepis* (Rosaceae) forests in Bolivia.
552 In Churchill, S.P., Baslev, H., Forero, E., & Luteyn, J.L. (eds.), *Biodiversity and*
553 *conservation of Neotropical montane forests*, pp. 281–294. Proceedings of the
554 neotropical montane forest biodiversity and conservation symposium, New York.
- 555 Kidane, Y., Stahlmann, R., & Beierkuhnlein, C. 2012. Vegetation dynamics, and land use and
556 land cover change in the Bale Mountains, Ethiopia. *Environmental monitoring and*
557 *assessment* 184: 7473–89.
- 558 Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation.
559 *Oecologia* 115: 445–459.
- 560 Körner, C. 2012. *Alpine treelines - Functional ecology of the global high elevation tree limits*.
561 Springer, Basel.
- 562 Körner, C., & Paulsen, J. 2004. A world-wide study of high altitude treeline temperatures.
563 *Journal of Biogeography* 31: 713–732.
- 564 Lanckriet, S., Araya, T., Cornelis, W., Verfaillie, E., Poesen, J., Govaerts, B., Bauer, H., Deckers,
565 J., Haile, M., & Nyssen, J. 2012. Impact of conservation agriculture on catchment runoff
566 and soil loss under changing climate conditions in May Zeg-zeg (Ethiopia). *Journal of*
567 *Hydrology* 475: 336–349.
- 568 Leakey, A.D.B., Ainsworth, E. a, Bernacchi, C.J., Rogers, A., Long, S.P., & Ort, D.R. 2009.
569 Elevated CO₂ effects on plant carbon, nitrogen, and water relations: six important
570 lessons from FACE. *Journal of experimental botany* 60: 2859–76.
- 571 Livingstone, D.A. 1967. Postglacial vegetation of the Ruwenzori Mountains in Equatorial
572 Africa. *Journal of experimental botany* 37: 25–52.
- 573 Marek, R. 1910. Waldgrenzstudien in den österreichischen Alpen. *Petermanns*
574 *Geographische Mitteilungen, Ergänzungsheft*
- 575 McNeely, J.A., Miller, K.R., Reid, W. V., Mittermeier, R.A., & Werner, T.B. 1990. *Conserving*
576 *the world's biological diversity*.

- 577 Miede, G., & Miede, S. 1994. *Ericaceous Forests and Heathlands in the Bale Mountains of*
578 *South Ethiopia - Ecology and man's Impact*. Stiftung Walderhaltung in Afrika, Hamburg.
- 579 Nievergelt, B., Good, T., & Güttinger, R. 1998. *A survey of the flora and fauna of the Simen*
580 *Mountains National Park*. *Walia* (special issue), Zürich.
- 581 Nyssen, J., Poesen, J., Moeyersons, J., Deckers, J., Haile, M., & Lang, A. 2004. Human impact
582 on the environment in the Ethiopian and Eritrean highlands—a state of the art. *Earth-*
583 *Science Reviews* 64: 273–320.
- 584 Peyron, O., Jolly, D., Bonnefille, R., Vincens, A., Guiot, J. 2000. Climate of East Africa 6000 ¹⁴C
585 Yr B.P. as inferred from Pollen Data. *Quaternary Research* 54: 90–101.
- 586 Piper, F.I., Cavieres, L. a., Reyes-Díaz, M., & Corcuera, L.J. 2006. Carbon sink limitation and
587 frost tolerance control performance of the tree *Kageneckia angustifolia* D. Don
588 (Rosaceae) at the treeline in central Chile. *Plant Ecology* 185: 29–39.
- 589 Price, M.F. 2003. Why mountain forests are important. *The forestry chronicle* 79: 1998–2001.
- 590 Proctor, J., Edwards, I.D., Payton, R.W., & Nagy, L. 2007. Zonation of forest vegetation and
591 soils of Mount Cameroon, West Africa. *Plant Ecology* 192: 251–269.
- 592 Reddy, A.R., Rasineni, G.K., & Raghavendra, A.S. 2010. The impact of global elevated CO₂
593 concentration on photosynthesis and plant. *Current Science* 99: 46–57.
- 594 Rucina, S.M., Muiruri, V.M., Kinyanjui, R.N., McGuinness, K., & Marchant, R. 2009. Late
595 Quaternary vegetation and fire dynamics on Mount Kenya. *Palaeoecology* 283: 1–14.
- 596 Sarmiento, G. 1986. *Ecological features of climate in high tropical mountains*. Oxford
597 University press, Oxford.
- 598 Schiermeier, Q. 2008. The long summer begins. *Nature* 454: 266–269.
- 599 Shi, P., Körner, C., & Hoch, G. 2008. A test of the growth-limitation theory for alpine tree line
600 formation in evergreen and deciduous taxa of the eastern Himalayas. *Functional*
601 *Ecology* 22: 213–220.
- 602 Simard, S., Giovannelli, A., Treydte, K., Traversi, M.L., King, G.M., Frank, D., & Fonti, P. 2013.
603 Intra-annual dynamics of non-structural carbohydrates in the cambium of mature
604 conifer trees reflects radial growth demands. *Tree physiology* 33: 913–23.
- 605 Smith, A.P. 1974. Bud temperature in relation to Nyctinastic leaf movement in an Andean
606 Giant Rosette plant. *Biotropica* 6: 263–265.
- 607 Smith, W.K., Germino, M.J., Johnson, D.M., & Reinhardt, K. 2009. The Altitude of Alpine
608 Treeline: A Bellwether of Climate Change Effects. *The Botanical Review* 75: 163–190.

- 609 Smith, A.P., & Young, T.P. 1987. Tropical alpine ecology. *Annual Review of Ecology and*
610 *Systematics* 18: 137–158.
- 611 Thompson, L.G., Mosley-Thompson, E., Davis, M.E., Henderson, K. a, Brecher, H.H.,
612 Zagorodnov, V.S., Mashiotta, T. a, Lin, P.-N., Mikhalenko, V.N., Hardy, D.R., & Beer, J.
613 2002. Kilimanjaro ice core records: evidence of holocene climate change in tropical
614 Africa. *Science* 298: 589–93.
- 615 UNdata. 2013. United Nations Statistics Division of the Department of Economics and Social
616 Affairs.
- 617 Wardle, P., & Coleman, M.C. 1992. Evidence for rising upper limits of four native New
618 Zealand forest trees. *New Zealand Journal of Botanica* 30: 303–314.
- 619 Wesche, K. 2003. The importance of occasional droughts for afroalpine landscape ecology.
620 *Journal of Tropical Ecology* 19: 197–208.
- 621 Wesche, K., Miehe, G., & Kaeppli, M. 2000. The Significance of Fire for Afroalpine
622 Ericaceous Vegetation. *Mountain Research and Development* 20: 340–347.
- 623 Wieser, G., & Tausz, M. 2007. Current Concepts for Treelife Limitation at the Upper
624 Timberline. In *Trees at their upper limit: treelife limitation at the Alpine Timberline*, pp.
625 1–18. Springer, Dordrecht.
- 626 De Wit, M., & Stankiewicz, J. 2006. Changes in surface water supply across Africa with
627 predicted climate change. *Science* 311: 1917–21.
- 628 Wright, S.J., Muller-Landau, H.C., & Schipper, J. 2009. The future of tropical species on a
629 warmer planet. *Conservation Biology* 23: 1418–26.
- 630 Wu, H., Guiot, J., Brewer, S., Guo, Z., & Peng, C. 2007. Dominant factors controlling glacial
631 and interglacial variations in the treeline elevation in tropical Africa. *Proceedings of the*
632 *National Academy of Sciences of the United States of America* 104: 9720–4.
- 633 Ziska, L.H. 2008. Controversies in Science Rising Atmospheric Carbon Dioxide and Plant
634 Biology : The Overlooked Paradigm. *DNA and Cell Biology* 27: 165–172.
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637 *Table 1: A comparison of potential environmental constraints for tree growth at the treeline*
 638 *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.

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

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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

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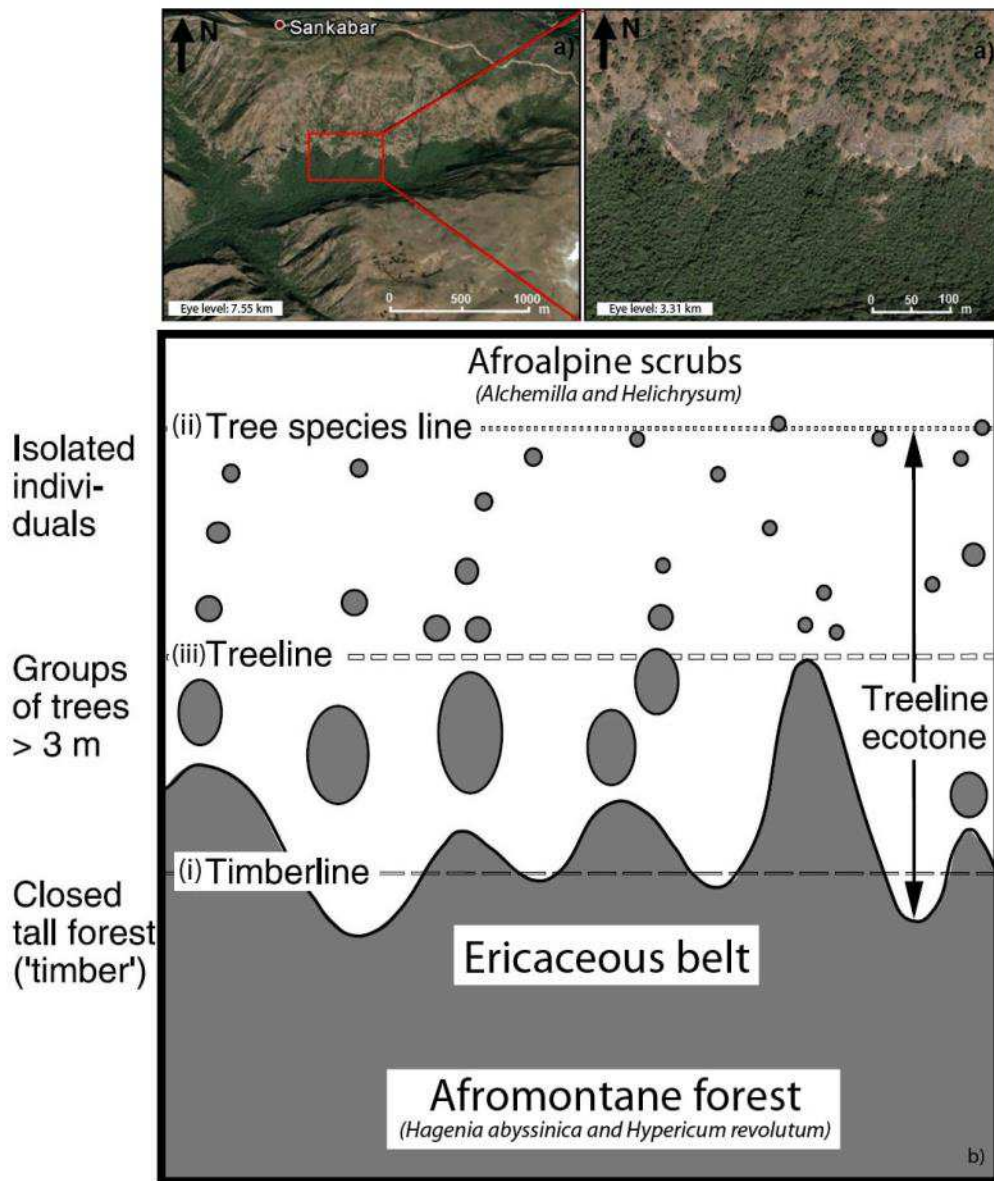
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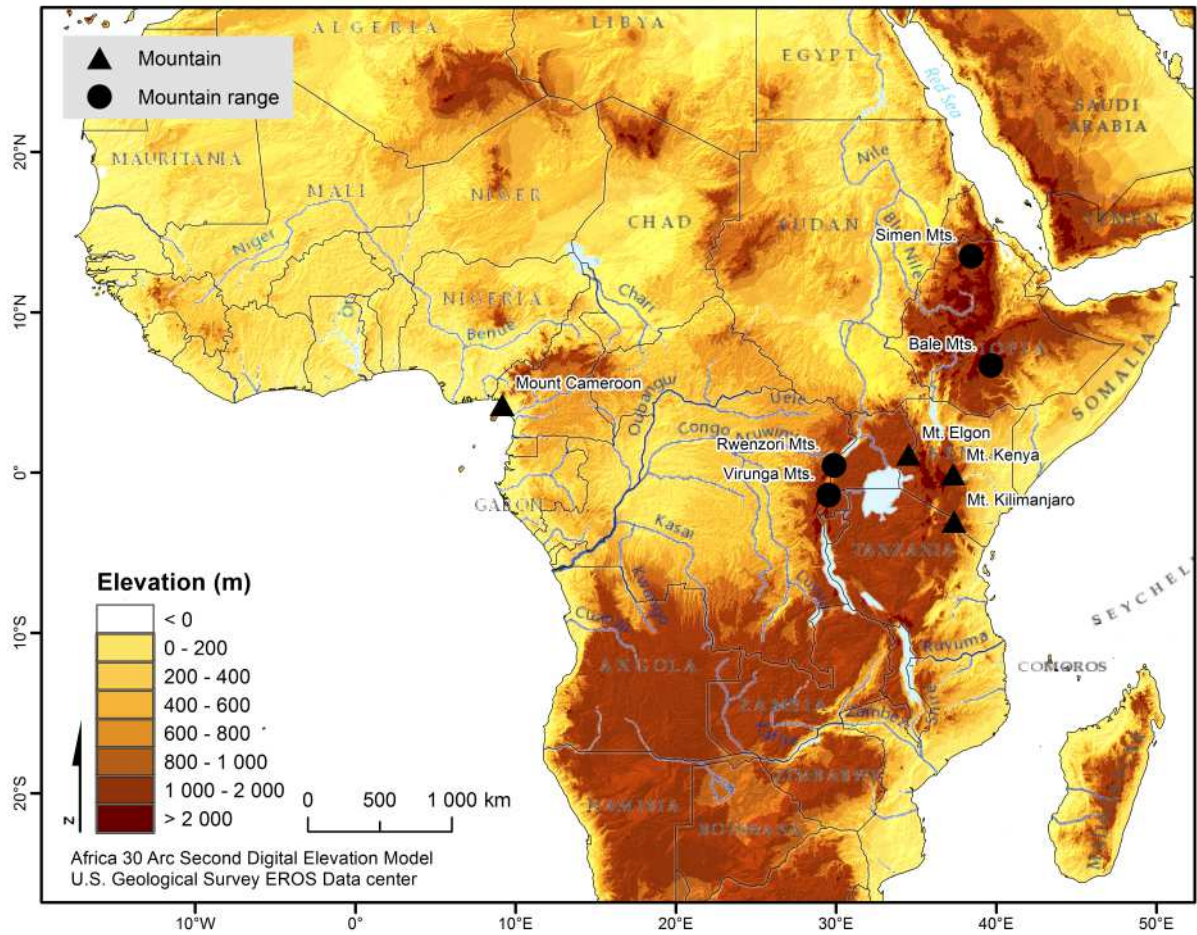
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Figure 1: Complexity of the treeline (a) Google Earth Image of the treeline at the Simen Mountains, Sankabar camp (13°14'N, 38°3'E), visualized at two different scales to emphasize the treeline gradient. (b) The treeline ecotone modified after Körner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

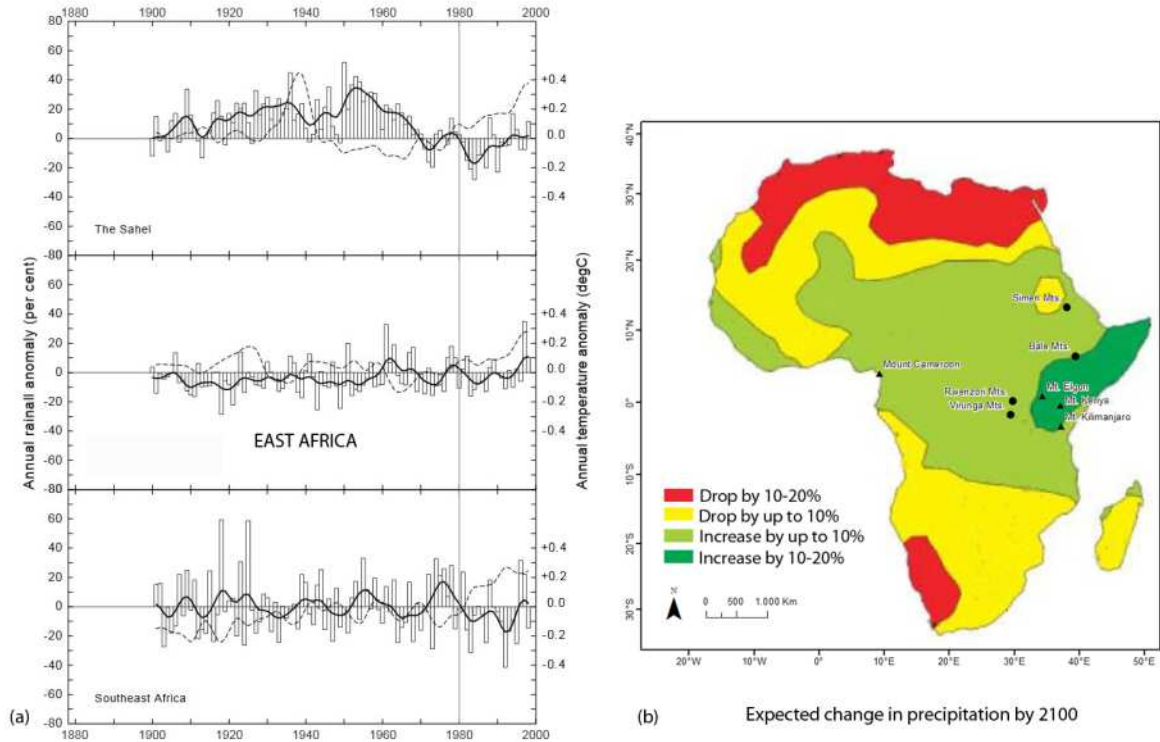
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Figure 2: The studied tropical mountains of Africa that range above the treeline elevation.

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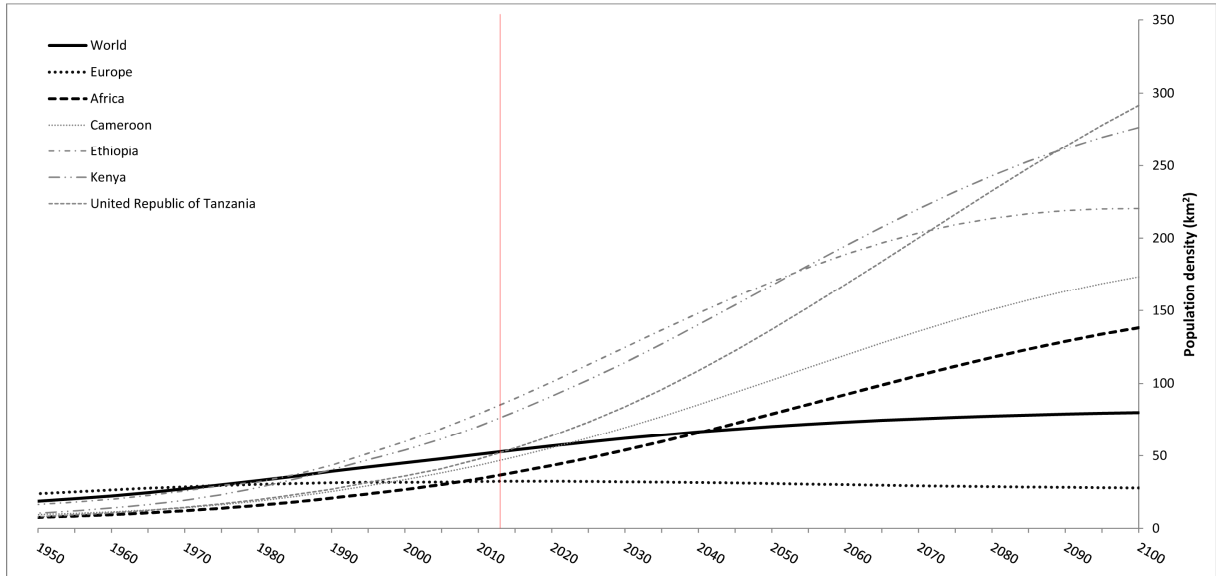


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688 **Figure 3:** Temperature and rainfall trends in Africa since 1900 (modified after Hulme et al.
689 (2001) and de Wit & Stankiewicz (2006)): (a) Annual rainfall (histogram and bold line) and
690 mean temperature (dashed line) anomalies for the period 1900-1998, with the 1961-1990
691 average as reference. The trend is given for three African regions, of which East Africa is best
692 corresponding with the tropical African mountain regions. Note, the temperature increase
693 after 1980 (indicated by a vertical line); (b) expected change in precipitation by the end of
694 the 21st century for Africa. Note, the long term wetting trend in East Africa.

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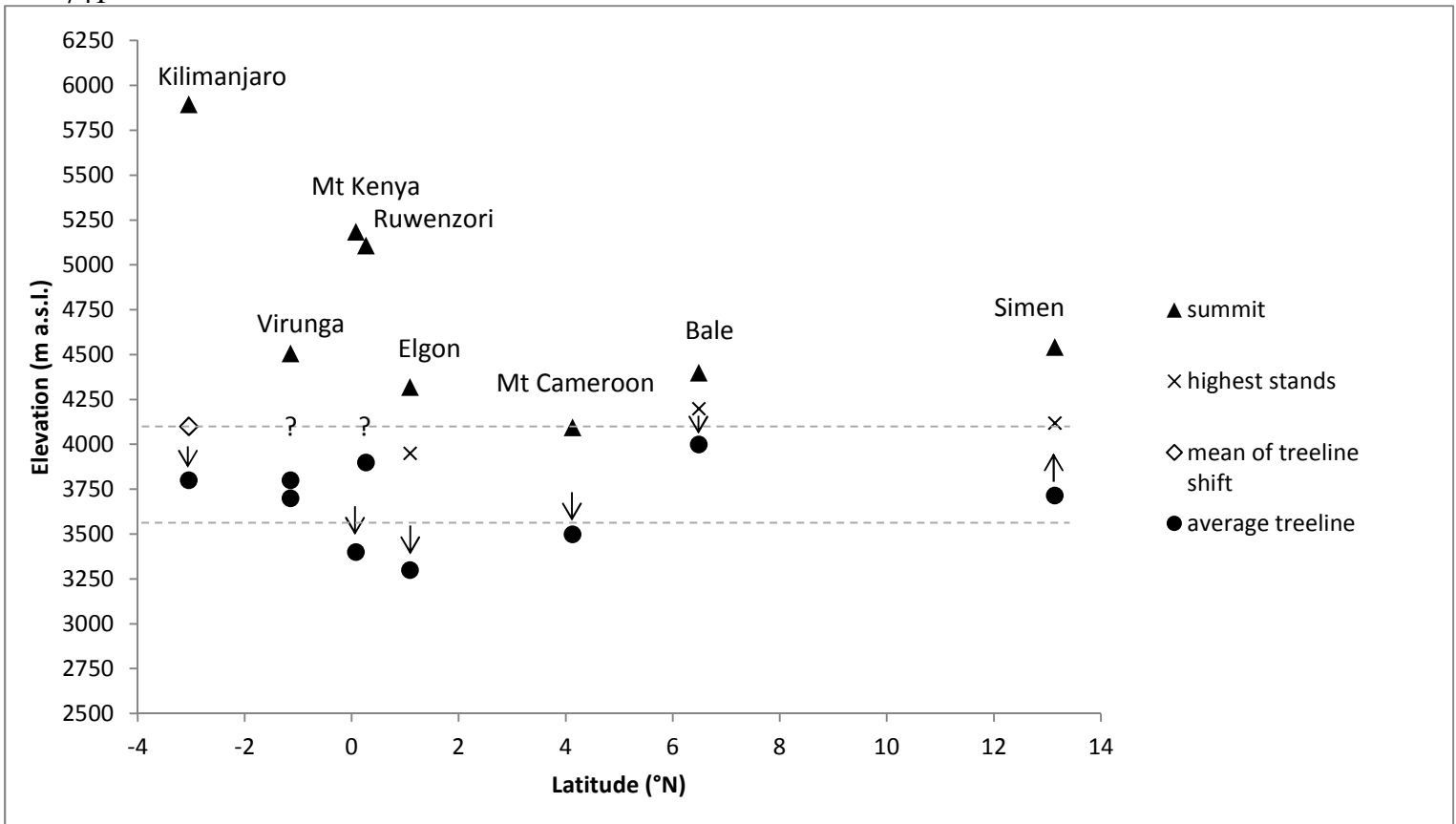
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Figure 4: Population dynamics in the tropical African highlands: (a) Population density, (b) growth rate. The situation of 2013 is indicated with a red vertical line.

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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).

