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1  **New insights on above ground biomass and forest attributes in tropical montane forests**

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23  **Abstract**

24  Despite the potential of tropical montane forests to store and sequester substantial amounts of

25  carbon, little is known about the above ground biomass (AGB) and the factors affecting it in

26  these ecosystems, especially in Africa. We investigated the height-diameter allometry, AGB,

27  and related differences in AGB to taxonomic and structural forest attributes in three distinct

28  forest types (dry, mixed species and elfin) in three mountains of northern Kenya. We

29  established 24 permanent plots (20m x 100m) and sampled all trees $\geq$ 10 cm diameter

30  following standard Rainfor protocols.

31

32  We identified that different height-diameter allometric models could be used for different

33  forests types, with the exception of the Michaelis–Menten model. In our study area, model

34  choice had little effects on AGB estimates.

35

36    In general, mixed forests had greater AGB than other forest types: in Mt Nyiro AGB

37    estimates were 611, 408 and 241 Mg ha$^{-1}$ for mixed, elfin and dry forests respectively.

38    Forests in Mt Nyiro, the highest mountain had greater AGB than in the other mountains. In

39    our study area, differences in AGB were related to forest structure attributes, with little

40    influence of taxonomic attributes. The mixed and elfin forests in Mt Nyiro, dominated by

41    Podocarpus latifolius and Faurea saligna contained comparable AGB to lowland rainforests,

42    highlighting the importance of tropical montane forests as large carbon stock, which could be

43    released if converted to another land cover type.

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1. **Introduction**

A considerable amount of data on above-ground biomass (AGB) stored in live trees in lowland tropical forests, and the factors affecting it, have become available in the past few years (e.g. Malhi et al., 2006; Slik et al., 2010; Quesada et al., 2012; Lewis et al., 2013; Poorter et al., 2015; Fayolle et al., 2016). Far less information is available on patterns of AGB in tropical montane forests, although their potential to store and sequester substantial amounts of carbon has been emphasised (Spracklen and Righelato, 2014). Tropical montane forests (TMFs), defined here as forests between 23.5°N and 23.5°S above 1000 m.a.s.l., make up 8% of the world's tropical forests (Spracklen and Righelato, 2014). They are of importance, not only because they have high levels of biodiversity and endemism, but also because they provide water to tens of millions of people (Mittermeier et al., 2004; Bruijnzeel et al., 2011).

Most studies of AGB along elevational transects have found a declining relationship with elevation (e.g. Girardin et al., 2010, 2014; Leuschner et al., 2013), which has been linked to associated declines in tree height (reviewed in Girardin et al., 2014). Individual tree height does not correlate with diameter in a simple manner (Nagendra, 2012) but instead the height-diameter allometry is related to species, precipitation, temperature and region (Feldpausch et al., 2011; Banin et al., 2012, Fayolle et al. 2016), and usually decreases with elevation (Girardin et al., 2014).

In fact, there has been a historical debate on the shape of the height-diameter allometry for tropical trees. Some authors argued in favour of a truly asymptotic model (Lewis et al., 2009; Rutishauser et al., 2013), or a second order polynomial of the log-log data (Chave et al., 2014) mimicking the saturation of tree height with tree diameter, while others argued in favour of the power law model (Djomo et al., 2010; Feldpausch et al., 2011) such as predicted by the metabolic theory of ecology (West et al., 1997; 1999)(see Fayolle et al. 2016 for further details). It has been highlighted that the power law model is unrealistic biologically because of the basic assumption of factors limiting tree growth in height but not in diameters (Molto et al., 2014), and most recent studies have chosen a truly asymptotic model. Among the asymptotic models, Feldpausch et al. (2012) found that the Weibull model was the most appropriate for biomass prediction, as it reduces error in small-diameter trees. This is important because of the skewed distribution of stand-level biomass found in smaller-

83    diameter trees in many forests (Feldpausch et al. 2012). However, Banin et al. (2012) and

84    Kearsley et al. (2013) found that a nonlinear 3-parameter exponential model was the most

85    appropriate for biomass prediction. Two recent studies, which considered an asymptotic

86    model Michaelis-Menten (Molto et al. 2014; Fayolle et al. 2016), not included in previous

87    studies, preferred this later one, arguing that not only it outperformed Weibull but also that it

88    was easier to manipulate than Weibull and its exponential function. All these studies focused

89    on lowland rainforest types, and to our knowledge, the shape of the height-diameter allometry

90    for tropical has not been studied in depth for TMFs, which tend to have shorter trees for a

91    given diameter.

92

93    Declining AGB with increasing elevation has also been related to changes in other

94    characteristics of forest structure affecting AGB, such as stem density and stand basal area.

95    In general, stem density and stand basal area have been shown to increase with altitude in

96    Hawaii (US), Mt Kinabalu (Malaysia), Udzungwa Mountains (Tanzania) and the Andes

97    (Herbert and Fownes, 1990; Takyu, 2002; Lovett et al., 2006; Girardin et al., 2014).

98    However, some studies demonstrate a decrease in stem density with increasing altitude (e.g.

99    Mt Elgon in Kenya-Uganda, Hamilton and Perrott, 1981) or no trend between stand basal

100   area and altitude (e.g. Andes: Girardin et al., 2014). Because biomass increases exponentially

101   with tree diameter, average tree diameter, large tree density and stand basal area tend to be

102   better predictors of AGB than overall tree density (Slik et al., 2010; Lewis et al., 2013;

103   Poorter et al., 2015).

104

105   Changes in AGB with increasing elevation have also been related to changes in tree species

106   richness. Higher species richness enhances the variation in species traits found in the

107   community, leading to niche complementarity, a higher resource capture, more efficient

108   resource use and higher productivity (Poorter et al., 2015). Higher species richness may also

109   enhance facilitation (e.g. a nitrogen-fixing species enhances soil fertility, and therefore the

110   productivity of the other species); and it might also increase the chance of a selection effect

111   (selecting highly productive or large species). Generally, there is a decline in tree species

112   richness with increasing altitude (e.g. Dossa et al., 2013; Sassen and Sheil, 2013; Girardin et

113   al., 2014), because of a greater role of environmental filtering at higher elevations (e.g. cooler

114   temperatures, fog, reduced light incidence and higher relative humidity). Nevertheless, this

115   was not observed on, for example, the Udzungwa Mountains in Tanzania (Lovett et al.,

116   2006). In the Andes, several elevation gradients showed mid-elevational peaks in numbers of

4

families, genera and species, at the base or below the cloud base, highlighting the importance of the cloud formation as a driver of species composition (Girardin et al., 2014). Apart from tree species richness, tree species evenness can also affects AGB. A recent study on TMFs in Tanzania described a unimodal relationship between AGB and tree species evenness (Shirima et al., 2016). These authors suggested that forests at higher altitudes with a high number of multi-stemmed individuals may contribute to the unimodal pattern in the AGB-richness relationship, because multi-stem dominated plots comprise less biomass than plots dominated by large single-stem trees and low tree species richness.

In this study, we estimated AGB in different TMFs located at different altitudes and mountains and we investigated the relationship between AGB and forest structural and taxonomic attributes, including height-diameter allometry. We address three major questions: are there significant differences in height-diameter allometry between different types of TMFs? Does AGB differ significantly between different types of TMFs? And, are differences in AGB related to differences in forest structure, tree species composition or both?


**2. Materials and methods**

2.1 Study Area

This study focused on the forests present on three prominent mountains in northern Kenya: Mt Nyiro (2752m), Mt Kulal (2285m) and Mt Marsabit (1707m) (see Appendix A). While Mt Nyiro consists of old crystalline Precambrian basement rocks, mainly extremely durable gneisses and granites, Mt Kulal and Mt Marsabit are Quaternary volcanic peaks. Soils are generally attributed to Regosols and Cambisols in Mt Nyiro (higher to lower altitudes respectively), Andosols and Cambisols in Mt Kulal (higher to lower altitudes respectively) and Andosols and Nitisols in Mt Marsabit (higher to lower altitudes respectively) (Sombroek and Pauw, 1980). Annual rainfall ranges between 800-1400 mm (semi-humid area, zone III Somboerk et al., 1982). Rainfall is concentrated in two wet seasons, from March to May and from October to December, but great inter-annual variation occurs, with some years having one or no rainy season. Fog presence is common at higher altitudes and is known to be an important source of water for these montane forests (Bussmann, 2002).

151 These mountains support similar vegetation types (Bussmann, 2002). From low to high

152 altitudes, these comprise: (i) dense thorny bushland (Commiphora, Grewia and partly

153 Acacia), (ii) 'dry montane forest' (Croton megalocarpus-Olea europaea subsp. africana

154 forest association in Mt Marsabit or O. europaea-Juniperus procera forest association in Mt

155 Kulal and Mt Nyiro), (iii) 'mixed species forest' (with abundant Cassipourea malosana and

156 Olea capensis in all mountains), and (iv) 'elfin-like forest' (with similar composition to

157 mixed species forest but at least 15% shorter trees with twisted stems and many epiphytes on

158 their branches) (see Bussmann, 2002). This study focuses on the last three types thereafter

159 called dry, mixed and elfin. These forest types occur at different altitudes in the mountains

160 studied (see Fig. 1), because of (i) mountain distance to the ocean (the further, the drier, see

161 Fig. A1 in Appendix A) and (ii) the mass-elevation or telescopic effect (larger mountains are

162 better at warming the atmosphere above them and are warmer at a given altitude, Jarvis and

163 Mulligan, 2011).

164

165 The forests studied provide key services to surrounding communities, including water,

166 firewood, medicine resources and fodder (Cuni-Sanchez et al., 2016). Mt Marsabit is an

167 important elephant habitat in northern Kenya (Ngene et al., 2009), but there are no elephants

168 on Mt Kulal or Mt Nyiro. While commercial logging never occurred on Mt Kulal or Mt

169 Nyiro, because of the steep terrain and remoteness of the area, local communities around Mt

170 Marsabit reported small-scale 'illegal' selective logging in some parts of the forest during the

171 1960s (Cuni-Sanchez 2015, pers. obs.). For the purpose of this study, we assume that the

172 forests are largely pristine and that currently observed forests' structure and species

173 composition is unaffected by potential historical disturbance events.

174

175

176 2.2 Study design and field measurements

177

178 In each forest type per mountain (dry, mixed and elfin), three permanent plots of 20 x 100m

179 were established at least 1km apart from each other, >100m from footpaths, signs of plant

180 harvesting and cliffs (total number of plots = 24, Fig. 1). We selected our plots depending

181 upon forest type rather than elevation, because of the abovementioned differences in altitude

182 between mountains where the same forest type is found (see Fig 1). Elfin forest in Mt

183 Marsabit was found to be very small and fragmented and could not be sampled. Although

184 larger plots (1-ha) are often preferred for these type of studies (Poorter et al., 2015), larger

185 plots were not viable due to the steep terrain (mean plot slope ranged from 10 to 30 degrees).

186 Within each plot, we recorded tree diameter at 1.3 m along the stem from the ground (or

187 above buttresses if present) of each tree ≥ 10 cm diameter and tree height (measured using a

188 handheld laser Nikon Forestry Pro) for some trees, following RAINFOR/AfriTRON

189 protocols (www.rainfor.org;  www.afritron.org). In total, 1010 stems were sampled for

190 height in all plots. These included 35-50% of the trees present in each plot, comprising

191 several individuals from each diameter class. Only trees whose crown top was clearly visible

192 from the ground were measured. Thick fog, common at higher altitudes, hampered height

193 measurements; which are known to be difficult in tropical forests (Larjavaara and Muller-

194 Landau, 2013). No lianas or bamboo were sampled in this study as these were not found

195 inside our study plots.

196

197 Stems were identified to species where possible and samples of unidentified trees were

198 collected for identification and deposited at the Herbarium of the University of Nairobi. The

199 vernacular name (in Samburu language) of all the unidentified trees collected was also

200 recorded. Eight of the unidentified morphospecies could not be identified to species level due

201 to the poor quality of the samples collected and their vernacular name was used for tree

202 diversity calculations. Unidentified trees represented 0.8% of the trees sampled in Mt Nyiro

203 (8/987 individuals), 0.3% in Mt Kulal (3/1164 individuals) and 1% in Mt Marsabit (8/736

204 individuals). Taxonomy followed the plant list (www.theplantlist.org). Species presence in

205 each mountain was checked with the literature (e.g. Beentje, 1995). The most abundant

206 species in Mt Nyiro were found to be: Juniperus procera, Ochna holstii, Olea capensis (dry

207 forests) and Faurea saligna, Xymalos monospora, Podocarpus latifolius (mixed and elfin

208 forests). The most abundant species in Mt Kulal were: Vepris nobilis, Apodytes dimidiata,

209 Olea capensis (dry forests) and Vepris nobilis, Cassipourea malosana, Xymalos monospora

210 (mixed and elfin forests). The most abundant species in Mt Marsabit were: Croton

211 megalocarpus, Drypetes gerrardii, Coptosperma graveolens (dry forests) and Croton

212 megalocarpus, Drypetes gerrardii, Rinorea convallarioides (mixed forests). For more details

213 see Appendix B.

214

215

216 2.3 Height-diameter allometric models

217

218   A total of six different height-diameter allometric models were fitted for each forest type and

219   mountain, and to all sites combined (Table 1). These included a monotonic model (the power

220   law model or **m1**, Feldpausch et al., 2011; King, 1996; Niklas, 1994); a second order

221   polynomial model (of a log-linear model or **m2,** see Chave et al., 2014; Niklas, 1995 for a

222   log–log transformation); and four asymptotic models: the monomolecular (or three-

223   parameters exponential) model (**m3**, Banin et al., 2012; Feldpausch et al., 2012), the

224   Gompertz model (**m4**), the Weibull model (**m5**, Bailey, 1980; Feldpausch et al., 2012) and

225   the Michaelis–Menten model (**m6**, Molto et al., 2014; Fayolle et al. 2016) (see Appendix C

226   for model equations). The best model for each forest type and mountain was selected

227   according to the Akaike Information Criterion (AIC) and the Root Mean Squared Error

228   (RMSE), following Fayolle et al. (2016). We also computed ΔAIC (the difference in AIC for

229   each model compared to the best one for that forest type and mountain) and the relative

230   likelihood of each model, expressed as exp(-ΔAIC/2).

231

232

233   2.4 Estimating AGB

234

235   The Chave et al. (2014) equation including tree diameter, wood mass density (WMD) and

236   tree height was used to estimate the AGB of each tree in the plot. The best taxonomic match

237   WMD of each stem was extracted from a global database (Chave et al., 2009; Zanne et al.,

238   2009) following Lewis et al. (2013). For the trees whose height was not measured in the field,

239   their height was estimated using the second order polynomial model (m2), which performed

240   well for all forest types and mountains (see results section). In four plots on Mt Nyiro, a

241   number of Xymalos monospora trees had been partially pruned to feed the animals during

242   drought events. We also estimated the height of these trees using m2, as if they had not been

243   disturbed, following preliminary findings on the effects of X. monospora pruning on AGB

244   (these are discussed in detail in Cuni-Sanchez et al. in prep). AGB was then summed across

245   all trees in a plot to obtain plot AGB (in Mg ha$^{-1}$). In order to assess if the choice of height-

246   diameter allometric model affected AGB estimates, we also computed AGB using the six

247   different models for each forest type and mountain, and the m3 model developed for 'all

248   sites' combined.

249

250

251   2.5 Assessing forest structure and tree diversity

For each plot, we calculated six structural attributes: stem density, density of large trees (≥50cm diameter, named $SD_{50}$), basal area (BA), BA-weighted wood mass density ($WMD_{BA}$) and mean tree diameter ($D_{mean}$) and mean tree height ($H_{mean}$). BA and $WMD_{BA}$ were calculated following Lewis et al. (2013). At tree level, AGB scales closely with the basal area of the individual tree, but at stand level, high stand basal area can be caused by many small trees (each containing low amounts of biomass) or by few trees each featuring a large basal area (each containing a disproportionately large biomass) (Poorter et al., 2015)

Four indicators of tree diversity where calculated for each plot: species richness (number of species per plot), rarefied species richness per 50 individuals (named Rsp), the Shannon index ($H'$) and the Pielou's evenness index ($J'$). The Rsp removes the confounding effect of tree density on species richness. With regard to the indexes calculated, a value of $J' = 1$ indicates little variation in communities between species, while $J' = 0$ indicates high variation between species. For each plot we also computed species dominance in terms of % of BA and % of stem density (see Appendix B). Apart from these four indicators, in order to assess similarities between forest types, the Bray-Curtis Index of dissimilarity (BC) was calculated for each forest type per mountain.

2.5 Data analysis

R statistical software R v3.2.1 was used for all statistical analyses (R Development Core Team, 2013). The nlsLM function in minpack.lm_1.2-0 was used to fit the non-linear models of the height-diameter models assessed. We used multiple regression analysis (lm method in R) to determine important predictor variables of AGB. We first considered mountain, distance to ocean, mountain maximum altitude (related to mass effect), forest type and altitude. We then re-ran the multiple regressions replacing altitude with relative altitude (altitude of the plot with regard to the top of the mountain). We only used the predictors that were poorly correlated with each other to avoid problems of collinearity. The vegan package was used to calculate the BC index and the distances between groups. Significant differences between AGB estimates calculated using different height-diameter allometric models were tested using paired t-tests.

285 MANOVA was used to determine significant differences between forest types and
286 mountains. Post-hoc pair wise multiple comparisons were performed using Tukey's-b test.
287 Pearson correlations were used to evaluate whether there was an association between AGB
288 and each of the measures of taxonomic and structural attributes calculated. All significant
289 differences reported refer to p<0.01 if not stated otherwise.
290
291

### 3.  Results

293
294 3.1 Height-diameter allometric models
295
296 Most models gave similar values of AIC and RMSE for the different forest types and
297 mountains (Table 1, Table C1 in Appendix C). The curves were also very close (Fig. 2).
298 Overall, the polynomial (m2) was found to be suitable for all the different forest types and
299 mountains (Table 1). The Gompertz model (m4) also seems suitable for all the different
300 forest types and mountains except for Mt Nyiro mixed forest (see Table 1). When 'all sites'
301 were combined, m2, m3 and m4 outperformed the other models (Table 1, Table C1 in
302 Appendix C). The Michaelis–Menten model (m6) was the model performing the worst for
303 most forest types and 'all sites' model (Table 1, Table C1 in Appendix C).
304
305 Model parameters varied considerably among and within forest types, and with the models
306 build with 'all sites' combined (Table 1). For some models, the parameters were more similar
307 among the same forest type across mountains than among forest types within a mountain (e.g.
308 see m2 and m5, see Table 1).
309
310
311  3.2 AGB estimates
312
313 The choice of height-diameter allometric model did not significantly affect AGB estimates if
314 a height-diameter allometric model was developed for each forest type and mountain
315 separately (Table not included). The use of the m3 model developed for 'all sites' combined
316 changed AGB estimates up to 11%, with mixed forests having less AGB, and dry and elfin
317 forests having more AGB (Table 2). However, these differences were not significant (Table
318 2).

10

AGB showed significant differences between forest types and mountains. In Mt Nyiro mixed forests had greater AGB than elfin and dry forests (611, 408 and 241 Mg ha$^{-1}$ respectively, see Table 3). Forests in Mt Nyiro, the highest mountain, had greater biomass than in the other mountains (Table 3). AGB ranged between 157 and 310 Mg ha$^{-1}$ in Mt Kulal and between 117 and 203 Mg ha$^{-1}$ in Mt Marsabit (Table 3). If the different forest types are considered separately, AGB tended to increase with altitude, but the increase was not significantly different, see Fig. 3). The p-values of the multiple regression analysis indicated that distance to ocean was the most important predictor of AGB ($p<0.01$). The interaction between distance to ocean and relative altitude (or altitude, depending on the choice of model) was significant.

3.3 Forest attributes and their relationship with AGB

Overall, mixed and elfin forests in Mt Nyiro had greater density of large trees, greater BA and $D_{mean}$ than the other forests (Table 3), while mixed forests in Mt Kulal had the greatest $H_{mean}$, and mixed forests in Mt Marsabit the greatest stem density (Table 3). No significant differences in $WMD_{BA}$, tree species richness, rarefied species richness, Shannon diversity or evenness were observed between forest types (Table 3). In total, 20 tree species were recorded on Mt Marsabit, 31 on Mt Kulal and 30 on Mt Nyiro. The rarefied species richness was found to be similar to species richness as few species were observed in each forest type.

The Bray-Curtis index showed that species were more similar between different forest types of one mountain than between the same forest type across mountains (Fig. 4). When data from all plots was combined, AGB was found to be significantly positively correlated with BA, $SD_{50}$, $D_{mean}$ and $H_{mean}$ but not with stem density or any taxonomic attribute (Table 4, Fig. 5).

**4. Discussion**

4.1 Choosing one height-diameter allometric model

353  Most models performed similarly for the different forest types and mountains studied, with

354  the exception of the Michaelis–Menten model (m6). This is different from previous studies

355  on lowland rainforests where m6 was the preferred model (e.g. Fayolle et al. 2016). This

356  finding might be related to the fact that very large trees are not abundant in montane forests

357  (except for mixed species forests), as models mainly differed in large diameter classes (see

358  Fig. 2).

359

360  In our study area, site specific model choice did not affect AGB estimates for a give forest

361  type and the use of a 'all sites' model produced small changes in AGB estimates. Most

362  authors choose the same model for the different forest types they study (e.g. Kearsley et al.,

363  2013; Molto et al., 2014), and discuss the different values of the parameters in the selected

364  model. Our results support this approach.

365

366

367  4.2 The variable AGB per forest type

368

369  AGB showed significant differences between forest types and mountains: in general, greater

370  AGB in mixed forests and greater in Mt Nyiro, the highest mountain. If all forest types and

371  mountains are considered, our AGB estimates ranged from 117 Mg ha$^{-1}$ to 612 Mg ha$^{-1}$,

372  which is in line with estimates reported by Spracklen and Righelato (2014) for the world's

373  TMFs (77-785 Mg ha$^{-1}$). The observed differences in AGB between mountains (especially for

374  mixed species forest) may be related to soils and substrate. In general, soils with higher levels

375  of limiting nutrients increase productivity, which increases AGB. For example, in the

376  Amazon, AGB has been positively linked with total soil phosphorus (Quesada et al., 2012).

377  Mixed forests in Mt Kulal and Mt Marsabit growing on andosols have higher fertility than the

378  regosols found in Mt Nyiro, and so should be expected to have higher AGB. However, it has

379  also been reported that faster-growing forest stands may become dominated by low wood

380  density species with shorter lifespans and hence lower AGB (see Baker et al., 2004; Lewis et

381  al., 2013). That is the carbon residence time in more nutrient rich forests is shorter, which

382  may explain lower AGB in Mt Kulal and Mt Marsabit, compared with Mt Nyiro. Future

383  repeat censuses of plots will allow us to assess this hypothesis. Another factor which should

384  also be considered is that other nutrient-cycling mechanisms apart from direct nutrient

385  absorption from soil, such as nutrient uptake from litter, or the storage of nutrients in the

386  biomass might control forest biomass (see Grau et al. 2017).

387

388   Another factor which should also be considered is precipitation. Mt Marsabit is located closer

389   to the Indian Ocean and it is considered wetter than the other two mountains studied

390   (Bussmann, 2002; AFRICLIM data from Platts et al., 2015). However, preliminary findings

391   for the area indicate that mixed species forests in Mt Nyiro, the highest mountain, receive

392   more precipitation than those of Mt Marsabit (unpublished data). In this study we did not

393   correlate AGB with climate or soil variables, as other authors have done (Girardin et al.,

394   2013; Marshall et al., 2012; Ensslin et al., 2015), because WorldClim data, which has been

395   used in some studies (e.g. Marshall et al., 2012), is of limited accuracy in small mountains

396   with complex terrains (Platts et al., 2013; 2015) as preliminary findings for the area also

397   indicate (unpublished data).

398

399   Available studies from other montane forests in East Africa also report significant variation

400   between and within locations, with values ranging from 25 Mg ha$^{-1}$ in high altitude forests in

401   Hanang to >800 Mg ha$^{-1}$ on the West Usambara Mountains (Table 5). Although the different

402   methods used to estimate AGB (minimum tree diameter sampled and the biomass allometric

403   equation selected, see Table 5), can explain some of these differences; environmental

404   conditions (e.g. rainfall), soil type and human disturbance history might play an important

405   role too.

406

407   The distribution of AGB along elevational gradients observed in Mt Nyiro agrees with

408   patterns observed in TMFs elsewhere in Tanzania, e.g. Mt Kilimanjaro (Ensslin et al., 2015),

409   Udzungwa and Usambara Mountains (Marshall et al., 2012). Montane forests at mid altitudes

410   (mixed forest) had greater biomass than both forests at higher altitudes (elfin) and forests at

411   lower altitudes (dry forest). Lower AGB in elfin forests is expected as cloud cover, common

412   at highest altitudes, is known to limit net $CO_2$ uptake and growth of trees (Graham et al.,

413   2003). Wind exposure, greater in elfin forests, also limits tree height (Thomas et al., 2015).

414   With regard to forests at lower altitudes, most studies report more AGB at lower altitudes

415   than at middle ones (e.g. Girardin et al., 2010, 2014; Leuschner et al., 2013). As highlighted

416   by Ensslin et al. (2015), rainfall might not have been the limiting factor at lower altitudes in

417   most of these studies, contrary to many TMFs in East Africa, including Mt Nyiro.

418

419   Compared with TMF outside Africa, our AGB estimates (which range from 117 to 612 Mg

420   ha$^{-1}$, mean of all plots studied 276 Mg ha$^{-1}$) seem high, particularly in Mt Nyiro. For example,

421 AGB ranged between 100 and 200 Mg ha$^{-1}$ (1500-2500m) in Andean TMF (Girardin et al.,

422 2014), between 100 and 300 Mg ha$^{-1}$ (1000 and 2200m) at Mt Rinjani in Indonesia (Dossa et

423 al., 2013), while it was estimated at 247 Mg ha$^{-1}$ and 271 Mg ha$^{-1}$ for submontane and

424 montane Atlantic forest in Brazil (Alves et al., 2010). Interestingly, it has been reported that

425 Asian and Neotropical TMFs have similar mean AGB (257 and 247 Mg ha$^{-1}$, n = 31 and 56,

426 respectively) while that of African TMF is higher (527 Mg ha$^{-1}$ n = 7) (Spracklen and

427 Righelato, 2014). Although few African plots were included in Spracklen and Righelato

428 (2014), other studies seem to support this finding. For example, Ensslin et al. (2015)

429 emphasised the high AGB found in Podocarpus-dominated forest on Mt Kilimanjaro (364

430 Mg ha$^{-1}$). We observed that mixed and elfin forests in Mt Nyiro, dominated by large

431 specimens of not only Podocarpus latifolius but also Faurea saligna, have even greater AGB

432 than that reported on Mt Kilimanjaro. Faurea saligna was also a dominant species

433 contributing to great AGB in Nyungwe National Park in Rwanda (Nyirambangutse et al.

434 (2016). Interestingly, mixed and elfin forests in Mt Nyiro contain comparable biomass to

435 African lowland rainforests (mean 395.7 Mg ha$^{-1}$, see Lewis et al. 2013). Our results support

436 the idea that the African Podocarpus-dominated forest has particularly high biomass.

437

438

439 4.3 The effects of forest structure and tree diversity on AGB

440

441 Results indicate that the observed variation in AGB in the different forest types was related to

442 differences in forest structure, but not tree species composition or a combination of both

443 structure and tree species composition. This was a rather unexpected finding considering the

444 decline in tree species richness generally observed with increasing altitude and its effects on

445 AGB.

446

447 In this study, despite considerable variation observed in stem density (from 441 to 785

448 individuals ha$^{-1}$), high AGB was more related to (a) few trees with a large basal area (each

449 containing a disproportionately large biomass) than to (b) many small trees (each containing

450 little biomass) (see correlation AGB~SD$_{50}$). With regard to the range of values observed,

451 values of stem density are within those from other studies (Table 5), although most of these

452 other studies included trees ≥5cm diameter. Our values of basal area are also within the range

453 reported from other studies (Table 5).

454

We did not find any significant relationship between AGB and taxonomic attributes, for our 0.2-ha plots. Interestingly, Poorter et al. (2015) showed that there was a consistent significant positive relationship between AGB and taxonomic attributes at the 0.1-ha scale, whereas this relationship disappeared at the 1-ha scale (study focused on the Amazon lowland rainforest). Chisholm et al. (2013) also found that diversity–biomass relationships were strong and positive at very small spatial scales (20 m × 20 m), whereas at larger spatial scales (0.25 and 1 ha) there was no consistent relationship. A recent pan-tropical study of intact old-growth closed-canopy forest by Sullivan et al. (2017) also show that diversity effects in tropical forests carbon stocks are scale dependent.

It should be noted that the similarities in species composition between different forest types within one mountain agrees with the theory of island biogeography which explains the species richness of an ecosystem isolated due to being surrounded by unlike ecosystems (Lomolino 2000). Shirima et al. (2016) studying another small dry montane forest in Tanzania (Hanang) reported similar species richness, tree diversity and evenness (species richness= 8.8, $H'$= 1.54, $J'$=0.67) to that observed in our study area.

**5. Conclusion**

The objectives of this study were to investigate the height-diameter allometry in different TMFs, to estimate AGB and to relate differences in AGB to taxonomic and structural forest attributes. We found that different height-diameter allometry models could be used for a given forest type and mountain (with the exception of the Michaelis–Menten model), and that the use of different models had little effects on AGB estimates. We also reported important differences in AGB, which tended to be greater in mixed forests and in Mt Nyiro, the highest mountain. These differences in AGB were related to differences in forest structure attributes, with little influence of taxonomic attributes. Moreover, mixed and elfin forests in Mt Nyiro, dominated by Podocarpus latifolius and Faurea saligna contain comparable AGB to lowland rainforests, highlighting the importance of African TMFs as large carbon stock, which could be released if converted to another land cover type.

15

**References**

Alves, L.F., Vieira, S.A., Scaranello, M.A., Camargo, P.B., Santos, F.A.M., Joly, C.A., Martinelli, L.A., 2010. Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). Forest Ecol. Manag. 260, 679-691.

Bailey, R.L., 1980. The potential of Weibull-type functions as flexible growth curves: discussion. Can. J. For. Res. 10, 117-118.

Banin, L., Feldpausch, T.R., Phillips, O.L., Baker, T.R., Lloyd, J., Affum-Baffoe, K., Arets, E.J.M.M., Berry, N.J., Bradford, M., Breinen, R.J.W., Davies, S., Drescher, M.,Higuchi, N., Hilbert, D., Hladik, A., Iida, Y., Silam, K.A., Kassim, A.R., King, D.A., Lopez-Gonzalez, G., Metcalfe, D., Nilus, R., Peh, K.S.-H., Reitsma, J.M., Sonké, B., Taedoumg, H., Tan, S., White, L., Wöll, H., Lewis, S.L., 2012. What controls forest architecture? Testing environmental, structural and floristic drivers, Global Ecol. Biogeogr. 21, 1179-1190.

Beentje, H.J., 1995. Kenya Trees, Shrubs and Lianas. National Museums of Kenya, Nairobi, Kenya.

521 Bruijnzeel, L.A., Mulligan, M., Scatena, F.N., 2011. Hydrometeorology of tropical montane

522 cloud forests: emerging patterns. Hydrolol. Process 25, 465-498.

523

524 Bussmann, R.W., 2002. Islands in the desert-a synopsis of the forest vegetation of Kenya's

525 northern, central and southern mountains and highlands. Journal of East African Natural

526 History 91, 27-79.

527

528 Chave, J., Coomes, D., Jansen, S., Lewis, S., Swenson, N.G., Zanne, A.E., 2009. Towards a

529 worldwide wood economics spectrum, Ecol. Lett. 12, 351-366.

530

531 Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.C., Eamus, D., Fîlster, H.,

532 Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riéra,

533 B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and

534 balance in tropical forests. Oecologia 145, 87-99.

535

536 Chave, J., et al., 2014. Improved allometric models to estimate the aboveground biomass of

537 tropical trees. Glob. Change Biol. 20, 3177-3190.

538

539 Chisholm, R.A., Muller-Landau, H.C., Abdul Rahman, K. et al., 2013. Scale-dependent

540 relationships between tree species richness and ecosystem function in forests. J. Ecol., 101,

541 1214-1224.

542

543 Cuni-Sanchez, A., Pfeifer, M., Marchant, R., Burgess, N.D., 2016. Ethnic and locational

544 differences in ecosystem service values: insights from the communities in forest islands in the

545 desert. Ecosystem services 19, 42-50.

546

547 Djomo, A.N., Ibrahima, A., Saborowski, J., Gravenhorst, G., 2010. Allometric equations for

548 biomass estimations in Cameroon and pan moist tropical equations including biomass data

549 from Africa. For. Ecol. Manage. 260, 1873-1885.

550

551 Dossa, G.G.O., Paudel, E., Fujinuma, J., Yu, H., Chutipong, W., Zhang, Y., Paz, S., Harrison,

552 R.D., 2013. Factors determining forest diversity and biomass on a tropical volcano, Mt.

553 Rinjani, Lombok, Indonesia, PLoS ONE 8, e67720.

554

555   Ensslin, A., Rutten, G., Pommer, U., Zimmermann, R., Hemp, A., Fischer, M., 2015. Effects

556   of elevation and land use on the biomass of trees, shrubs and herbs at Mount Kilimanjaro.

557   Ecosphere 6, 1-15.

558

559   Fayolle, A., Panzou, G.J.L., Drouet, T., Swaine, M.D., Bauwens, S., Vleminckx, J., Biwole,

560   A., Lejeune, P., Doucet, J-L. 2016. Taller trees, denser stands and greater biomass in semi-

561   deciduous than in evergreen lowland central African forests. For. Ecol. Manage. 374, 42-50.

562

563   Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A.,

564   AffumBaffoe, K., Arets, E., Berry, N.J., Bird, M., 2011. Height-diameter allometry of

565   tropical forest trees. Biogeosciences 8, 1081-1106.

566

567   Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, E., Monteagudo Mendoza,

568   A., Lopez-Gonzalez, G., Banin, L., Abu Salim, K., Affum-Baffoe, K., 2012. Tree height

569   integrated into pan-tropical forest biomass estimates. Biogeosci. Discuss. 9, 2567-2622.

570

571   Girardin, C.A.J., Malhi, Y., Aragão, L.E.O.C., Mamani-Solórzano, M., Huaraca Huasco, W.,

572   Durand, L., Feeley, K.J., Rapp, J., Silva-Espejo, J.E., Silman, M.R., Salinas, N., Whittaker

573   R.J., 2010. Net primary productivity allocation and cycling of carbon along a tropical forest

574   elevational transect in the Peruvian Andes. Glob. Change Biol. 16, 3176-3192.

575

576   Girardin, C.A.J., Farfan-Rios, W., Garcia, K., Feeley, K.J., Jørgensen, P.M., Murakami, A.A.,

577   Pérez, L.C., Seidel, R., Paniagua, N., Claros, A.F.F., Maldonado, C., Silman, M., Salinas, N.,

578   Reynel, C., Neill, D.A., Serrano, M., Caballero, C.J., La Torre-Cuadros, M.D.L.A., Macìa,

579   M.J., Killeen, T.J., Malhi, Y., 2014. Spatial patterns of above-ground structure, biomass and

580   composition in a network of six Andean elevation transects. Plant Ecol. Divers. 1-11.

581

582   Graham, A.E., Mulkey, S.S., Kitajima, K., Phillips, N.G., Wright, S.J., 2003. Cloud cover

583   limits net CO2 uptake and growth of a rainforest tree during tropical rainy seasons. PNAS

584   100, 572-576.

585

586   Grau, O. et al., 2017. Nutrient-cycling mechanisms other than the direct absorption from soil

587   may control forest structure and dynamics in poor Amazonian soils. Sci. Rep. 7, 45017.

588

589    Hamilton, A.C., Perrott, R.A., 1981. A study of altitudinal zonation in the montane forest belt

590    of Mt Elgon, Kenya–Uganda. Vegetation 45, 107-125.

591

592    Hansen, E.H., Gobakken, T., Bollandsås, O.M., Zahabu E., Næsset, E., 2015. Modeling

593    aboveground biomass in dense tropical submontane rainforest using airborne laser scanner

594    data. Remote Sens. 7, 788-807.

595

596    Herbert, D.A., Fownes, J.H., 1999. Forest productivity and efficiency of resource use across a

597    chronosequence of tropical montane soils. Ecosyst. 2, 242-254.

598

599    Jarvis, A., Mulligan, M., 2001. The climate of cloud forests. Hydrol. Process. 25, 327-343.

600

601    Kearsley, E., de Haulleville, T., Hufkens, K., Kidimbu, A., Toirambe, B., Baert, G., Huygens,

602    D., Kebede, Y., Defourny, P., Bogaert, J., Beeckman, H., Steppe, K., Boeckx, P., Verbeeck,

603    H., 2013. Conventional tree height–diameter relationships significantly overestimate

604    aboveground carbon stocks in the Central Congo Basin. Nat. Commun. 4.

605    http://dx.doi.org/10.1038/ncomms3269.

606

607    King, D.A., 1996. Allometry and life history of tropical trees. J. Trop. Ecol. 12, 25-44.

608

609    Kinyanjui, M.J., Latva-Käyrä, P., Bhuwneshwar, P.S., Kariuki, P., Gichu, A., Wamichwe, K.,

610    2014. An Inventory of the Above Ground Biomass in the Mau Forest Ecosystem, Kenya.

611    Open Journal of Ecology 4, 619-627.

612

613    Larjavaara, M., Muller-Landau, H.C., 2013. Measuring tree height: a quantitative comparison

614    of two common field methods in a moist tropical forest. Method Ecol. Evol. 4, 793-801.

615

616    Leuschner, C., Zach, A., Moser, G., Homeier, J., Graefe, S., Hertel, D., Wittich, B., Soethe,

617    N., Iost, S., Röpderstein, M., Horna, V., Wolf, K., 2013. The carbon balance of tropical

618    mountain forests along an altitudinal transect. Ecological Studies 221, 117-139.

619

620    Lewis, S.L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O.,

621    Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., K, M.-N.D., Ewango, C.E.N.,

622    Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J. C.,

623     Makana, J.-R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K.S.-H., Sheil,

624     D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R., Wöll, H.,

625     2009. Increasing carbon storage in intact African tropical forests. Nature 457, 1003-1006.

626

627     Lewis, S.L., Sonke, B., Sunderland, T., Begne, S.K., Lopez-Gonzalez, G., van der Heijden,

628     G.M.F., Phillips, O.L., Affum-Baffoe, K., Banin, L., Bastin, J.-F., 2013. Aboveground

629     biomass and structure of 260 African tropical forests. Philos. Trans. R. Soc. Lond. Ser. B

630     Contain. Pap. Biol. Character, 1896-1934.

631

632     Lomolino, M. V. 2000. A species-based theory of insular zoogeography. Global Ecology and

633     Biogeography 9:39-58.

634

635     Lovett, J.C., Marshall, A.R., Carr, J., 2006. Changes in tropical forest vegetation along an

636     altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. Afr. J. Ecol. 44,

637     478-490.

638

639     Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochranek, T., Meir, P., Chave,

640     J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F.,

641     Lewis, S.L., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Pitman, N.C.A., Quesada, C.A.,

642     Salomão, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., Vásquez Martínez, R., Vincet, B.,

643     2006. The regional variation of aboveground live biomass in old-growth Amazonian forests.

644     Glob. Change Biol. 12, 1107-1138.

645

646     Marshall, A. R., Willcock, S., Platts, P. J., Lovett, J. C., Balmford, A., Burgess, N. D., et al.,

647     2012. Measuring and modelling above-ground carbon and tree allometry along a tropical

648     elevation gradient. Biol. Conserv. 154, 20-33.

649

650     Mittermeier, R. A., Robles G.P., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G.,

651     Lamoreux, J., da Fonseca G.A.B., 2004. Hotspots Revisited. Garza Garcia N.L. Mexico:

652     CEMEX.

653

654     Molto, Q., Hérault, B., Boreux, J.-J., Daullet, M., Rousteau, A., Rossi, V., 2014. Predicting

655     tree heights for biomass estimates in tropical forests–a test from French Guiana.

656     Biogeosciences 11, 3121-3130.

657

658 Munishi P.K.T., Shear T.H. 2004. Carbon storage in Afromontane rain forests of the Eastern

659 Arc mountains of Tanzania: their net contribution to atmospheric carbon. Journal of Tropical

660 Forest Science 16, 78-93.

661

662 Nagendra, H., 2012. Assessing relatedness and redundancy of forest monitoring and change

663 indicators. J. Environ. Manage. 95, 108-133.

664

665 Ngene, S.M., Van Gils, H., Van Wieren, S.E., Rasmussen, H., Skidmore, A.K., Prins, H.H.T.,

666 Toxopeus, A.G., Omondi, P., Douglas-Hamilton, I., 2009. The ranging patterns of elephants

667 in Marsabit protected area, Kenya: the use of satellite-linked GPS collars. Afr. J. Ecol., 48,

668 386-400.

669

670 Niklas, K.J., 1995. Size-dependent allometry of tree height, diameter and trunktaper. Ann.

671 Bot. 75, 217-227.

672

673 Niklas, K.J., 1994. Plant Allometry: The Scaling of Form and Process. University of Chicago

674 Press.

675

676 Nyirambangutse, B., Zibera, E., Uwizeye, F.K., Nsabimana D., Bizuru, E., Pleijel H.,

677 Uddling, J., Wallin, G., 2016. Carbon stocks and dynamics at different successional stages in

678 an Afromontane tropical forest. Biogeosciences Discuss., doi:10.5194/bg-2016-353.

679

680 Omoro, L.M.A., Starr, M., Pellikka, P.K.E., 2013. Tree biomass and soil carbon stocks in

681 indigenous forests in comparison to plantations of exotic species in the Taita Hills of Kenya.

682 Silva Fenn. 47, 1-18.

683

684 Platts, J.P, Peter A. Omeny, P.A., Marchant, R., 2015. AFRICLIM: high-resolution climate

685 projections for ecological applications in Africa. Afr. J. Ecol. 53, 103-108.

686

687 Platts, P.J., Gereau, R.E., Burgess, N.D., Marchant, R., 2013. Spatial heterogeneity of climate

688 change in an Afromontane centre of endemism. Ecography 36, 518-530.

689

690 Poorter, L., et al. 2015. Diversity enhances carbon storage in tropical forests. Global Ecology
691 and Biogeography 24, 1314-1328.

692

693 Quesada, C.A. et al., 2012 Basin-wide variations in Amazon forest structure and function are
694 mediated by both soils and climate. Biogeosciences 9, 2203-2246.

695

696 R Development Core Team, 2013. R Development Core Team. R: A Language and
697 Environment for Statistical Computing.

698

699 Rutishauser, E., Noor'an, F., Laumonier, Y., Halperin, J., Hergoualch, K., Verchot, L., 2013.
700 Generic allometric models including height best estimate forest biomass and carbon stocks in
701 Indonesia. For. Ecol. Manage. 307, 219-225.

702

703 Sassen, M., Sheil, D., 2013. Human impacts on forest structure and species richness on the
704 edges of a protected mountain forest in Uganda. Forest Ecol. Manag. 307, 206-218.

705

706 Shirima, D., Munishi, P.K.T., Lewis, S.L., Burgess, N.D., Marshall, A.R., Balmford, A., et
707 al., 2011. Carbon storage, structure and composition of miombo woodlands in Tanzania's
708 Eastern Arc Mountains. Afr. J. Ecol. 49, 332-342.

709

710 Shirima, D.D., Totlanda, Ø., Munishi, P.K.T., Moea, S.R., 2016. Relationships between tree
711 species richness, evenness and aboveground carbon storage in montane forests and miombo
712 woodlands of Tanzania. Basic and Applied Ecology 16, 239-249.

713

714 Slik, J.W.F., Aiba, S.I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., Nagamasu,
715 H., Nilus, R., Payne, J., Paoli, G., Poulsen, A.D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E.,
716 van Valkenburg, J.C.L.H., 2010. Environmental correlates of tree biomass, basal area, wood
717 specific gravity and stem density gradients in Borneo's tropical forests. Glob. Ecol. Biogeogr.
718 19, 50-60.

719

720 Sombroek, W.G., Pauw, B.J.A. van der , 1980. Exploratory Soil Map of Kenya. Appendix 1
721 to Report no. E1. Republic of Kenya. Ministry of Agriculture. Kenya Soil Survey, Nairobi.

722

723  Sombroek, W.G., Braun, H.M.H., van der Pauw, B.J.A., 1982.Exploratory Soil Map and

724  AgroClimatic Zone Map of Kenya, 1980. Scale: 1:1'000'000. Exploratory Soil Survey Report

725  No. E1. Kenya Soil Survey Ministry of Agriculture - National Agricultural Laboratories,

726  Nairobi, Kenya.

727

728  Spracklen, D.V., Righelato, R., 2014. Tropical montane forests are a larger than expected

729  global carbon store. Biogeosciences 11, 2741-2754.

730

731  Sullivan, JM.J.P., et al., 2017. Diversity and carbon storage across the tropical forest biome.

732  Scientific Reports 6:39102 | DOI: 10.1038/srep39102.

733

734  Swai, G., Ndangalasi, H.J., Munishi, P.K.T., Shirima, D.D., 2014. Carbon stocks of Hanang

735  forest, Tanzania: An implication for climate mitigation. Journal of Ecology and the Natural

736  Environment 6, 90-98.

737

738  Takyu, M., Aiba, S.I., Kitayama, K., 2002. Effects of topography on tropical lower montane

739  forests under different geological conditions on Mount Kinabalu, Borneo. Plant Ecol.

740  159, 35-49.

741

742  Thomas, S.C., Martin, A.R., Mycroft, E.E., 2015. Tropical trees in a wind-exposed island

743  ecosystem: height-diameter allometry and size at onset of maturity. J. Ecol. 103, 594-605.

744

745  West, G.B., Brown, J.H., Enquist, B.J., 1999. The fourth dimension of life: fractal geometry

746  and allometric scaling of organisms. Science 284, 1677-1679.

747

748  West, G.B., Brown, J.H., Enquist, B.J., 1997. A general model for the origin of allometric

749  scaling laws in biology. Science 276, 122-126.

750

751  Zanne, A., Lopez-Gonzalez, G., Coomes D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B.,

752  Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Towards a Worldwide Wood Economics,

753  Spectrum. 10.5061/dryad.234.

754

755

756

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758

# Appendix A: Plot locations

**Fig. A1.** Location of the montane forests studied. Black lines refer to major roads, dark grey areas to forests. Note that Mt Marsabit, Mt Nyiro and Mt Kulal are located 570km, 630 and 680 km from the Indian Ocean, respectively. Mt Marsabit is 125km from Mt Kulal and Mt Nyiro, and Mt Nyiro and Mt Kulal are located about 70km apart.
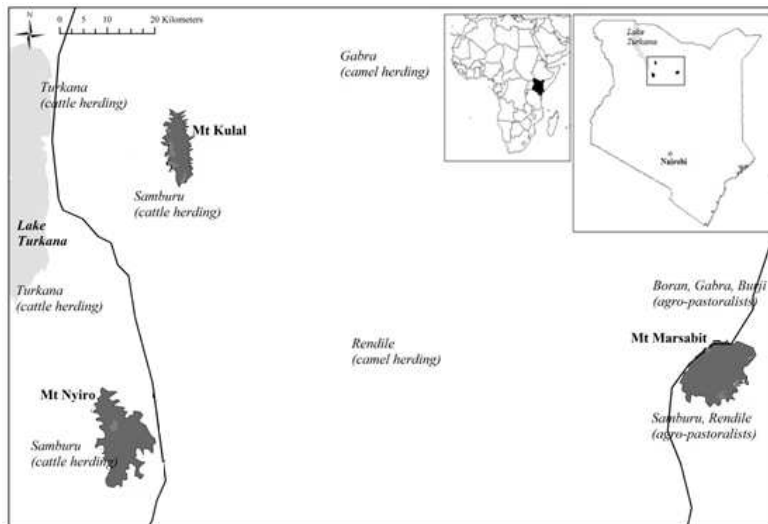


**Table A1** Location of the plots studied.

| Location | Forest type | Latitude (N) | Longitude (E ) |
|---|---|---|---|
| Mt Marsabit | dry | 2.261447 | 38.003735 |
| Mt Marsabit | dry | 2.245083 | 37.985573 |
| Mt Marsabit | dry | 2.270944 | 38.010338 |
| Mt Marsabit | mixed | 2.262975 | 37.970977 |
| Mt Marsabit | mixed | 2.26976 | 37.977254 |
| Mt Marsabit | mixed | 2.285276 | 37.972309 |
| Mt Kulal | dry | 2.673575 | 36.956503 |
| Mt Kulal | dry | 2.685428 | 36.953454 |
| Mt Kulal | dry | 2.655145 | 36.953305 |
| Mt Kulal | mixed | 2.670021 | 36.948298 |
| Mt Kulal | mixed | 2.684323 | 36.944241 |
| Mt Kulal | mixed | 2.691129 | 36.948334 |
| Mt Kulal | elfin | 2.6746 | 36.942031 |
| Mt Kulal | elfin | 2.686477 | 36.941752 |
| Mt Kulal | elfin | 2.692789 | 36.942945 |
| Mt Nyiro | dry | 2.077588 | 36.868687 |
| Mt Nyiro | dry | 2.143501 | 36.874662 |
| Mt Nyiro | dry | 2.148761 | 36.871055 |
| Mt Nyiro | mixed | 2.142402 | 36.865697 |
| Mt Nyiro | mixed | 2.128205 | 36.859785 |
| Mt Nyiro | mixed | 2.103207 | 36.840689 |

| Mt Nyiro | elfin | 2.147158 | 36.83802 |
| Mt Nyiro | elfin | 2.121039 | 36.833272 |
| Mt Nyiro | elfin | 2.158162 | 36.825684 |

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**Appendix B: Species dominance**

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For each plot we computed species dominance in terms of % of basal area (BA) and % of stem density. Stem density (number trees ha$^{-1}$) included all trees ≥10 cm diameter while BA (sum of the cross-sectional area at 1.3 m, or above buttresses) was calculated in m$^2$ ha$^{-1}$. Dominant species were found to be more similar between forest types of one mountain than between the same forest type across mountains, with mixed and elfin forests on Mt Nyiro having exactly the same dominant species (Table B1). Most species dominant in terms of stem density were also dominant in terms of BA (Table B1). Two dominant species on Mt Marsabit (Drypetes gerrardii and Rinorea convallarioides) do not occur in the other mountains studied and Faurea saligna, dominant on Mt Nyiro, does not occur on the other mountains (Beentje, 1995; Bussmann, 2002). Although it has been reported that Podocarpus latifolius does occur on Mt Kulal (Bussmann 2002), we could not find it in any plot sampled in this forest, or during exploratory surveys.

785

**Table B1** The most important dominant species ranked by stem density (SD) and basal area (BA) in each forest type per mountain. * refers to a species only found in one mountain of the three studied.

788

| Forest type | Mountain | Dominance % SD | Dominance % BA |
|---|---|---|---|
| Dry | Mt Marsabit | Croton megalocarpus, Drypetes gerrardii*, Coptosperma graveolens, Strychnos henningsii | Croton megalocarpus, Psydrax schimperiana, Olea europaea |
| | Mt Kulal | Vepris nobilis, Apodytes dimidiata, Olea capensis, indet1 | Vepris nobilis, Apodytes dimidiata, Olea capensis, Diospyros abyssinica, Psydrax schimperiana |
| | Mt Nyiro | Juniperus procera, Ochna holstii, Olea europaea, Olea capensis, Faurea saligna* | Juniperus procera, Olea europaea, Olea capensis, Faurea saligna* |
| Mixed | Mt Marsabit | Drypetes gerrardii*, Croton megalocarpus, Olea capensis, Rinorea convallarioides* | Drypetes gerrardii*, Croton megalocarpus, Olea capensis, Strombosia scheffleri |
| | Mt Kulal | Cassipourea malosana, Xymalos monospora, Pavetta gardeniifolia, indet1 | Cassipourea malosana, Nuxia congesta, Xymalos monospora, indet1 |
| | Mt Nyiro | Faurea saligna*, Xymalos monospora, Podocarpus latifolius | Faurea saligna*, Podocarpus latifolius |
| Elfin | Mt Kulal | Vepris nobilis, Cassipourea malosana, Xymalos monospora | Vepris nobilis, Prunus africana, Cassipourea malosana, Nuxia congesta |
| | Mt Nyiro | Faurea saligna*, Xymalos monospora, Podocarpus latifolius | Faurea saligna*, Xymalos monospora, Podocarpus latifolius |

**Appendix C: Height-diameter allometric models used in this study and AIC values**

792

793 Monotonic models

794 (**m1**) Power model, $H = a \times D^b$

795

796 Second-order polynomial models

797 (**m2**) $H = a + b \times \log(D) + c \, (\times \log(D^2))$

798

799 Asymptotic models

800 (**m3**) Monomolecular model, $H = a - b \times \exp(-c \times D)$

801 (**m4**) Gompertz model, $H = a \times \exp(-b \times \exp(-c \times D))$

802 (**m5**) Weibull model, $H = a \times (1 - \exp(-b \times D^c))$

803 (**m6**) Michaelis–Menten model, $H = a \times D/(b + D)$

804

805 **Table C1** The difference in Akaike Information Criteria (AIC) for each model compared to the best one for that forest type and mountain, and 'all sites' (ΔAIC) and the
806 relative likelihood of each model.

| | $\Delta AIC_{m1}$ | $\Delta AIC_{m2}$ | $\Delta AIC_{m3}$ | $\Delta AIC_{m4}$ | $\Delta AIC_{m5}$ | $\Delta AIC_{m6}$ | Likelihood m1 | Likelihood m2 | Likelihood m3 | Likelihood m4 | Likelihood m5 | Likelihood m6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Marsabit.dry** | 0.00 | 0.58 | 0.33 | 0.38 | 2.01 | 6.22 | 1.000 | 0.749 | 0.848 | 0.828 | 0.365 | 0.045 |
| **Kulal.dry** | 6.02 | 1.58 | 10.74 | 0.00 | 7.98 | 3.14 | 0.049 | 0.454 | 0.005 | 1.000 | 0.018 | 0.208 |
| **Nyiro.dry** | 6.57 | 0.74 | 1.45 | 0.00 | 8.61 | 17.93 | 0.037 | 0.690 | 0.483 | 1.000 | 0.013 | 0.000 |
| **Marsabit.mixed** | 0.37 | 1.39 | 1.45 | 1.54 | 2.18 | 0.00 | 0.832 | 0.498 | 0.484 | 0.463 | 0.337 | 1.000 |
| **Kulal.mixed** | 2.35 | 2.49 | 1.58 | 1.27 | 1.78 | 0.00 | 0.308 | 0.288 | 0.453 | 0.530 | 0.410 | 1.002 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Nyiro.mixed** | 0.31 | 0.00 | 2.31 | 3.78 | 0.64 | 0.23 | 0.855 | 1.000 | 0.315 | 0.151 | 0.728 | 0.891 |
| **Kulal.elfin** | 2.81 | 1.52 | 1.92 | 2.02 | 4.75 | 0.00 | 0.245 | 0.467 | 0.383 | 0.365 | 0.093 | 1.001 |
| **Nyiro.elfin** | 0.00 | 1.74 | 1.40 | 1.81 | 2.02 | 8.84 | 1.001 | 0.418 | 0.497 | 0.404 | 0.365 | 0.012 |
| **all sites** | 2.82 | 0.66 | 0.00 | 1.49 | 4.90 | 52.48 | 0.245 | 0.720 | 1.000 | 0.474 | 0.086 | 0.000 |

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