

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 ≥ 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.

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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47 **Keywords:** Africa, forest structure, tree diversity, height-diameter allometry

48

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

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

125

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

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133

134 **2. Materials and methods**

135

136 **2.1 Study Area**

137

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

150

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 $\exp(-\Delta\text{AIC}/2)$.

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

252

253 For each plot, we calculated six structural attributes: stem density, density of large trees
254 (≥ 50 cm diameter, named SD_{50}), basal area (BA), BA-weighted wood mass density (WMD_{BA})
255 and mean tree diameter (D_{mean}) and mean tree height (H_{mean}). BA and WMD_{BA} were
256 calculated following Lewis et al. (2013). At tree level, AGB scales closely with the basal area
257 of the individual tree, but at stand level, high stand basal area can be caused by many small
258 trees (each containing low amounts of biomass) or by few trees each featuring a large basal
259 area (each containing a disproportionately large biomass) (Poorter et al., 2015)

260

261 Four indicators of tree diversity were calculated for each plot: species richness (number of
262 species per plot), rarefied species richness per 50 individuals (named R_{sp}), the Shannon
263 index (H') and the Pielou's evenness index (J'). The R_{sp} removes the confounding effect of
264 tree density on species richness. With regard to the indexes calculated, a value of $J' = 1$
265 indicates little variation in communities between species, while $J' = 0$ indicates high variation
266 between species. For each plot we also computed species dominance in terms of % of BA and
267 % of stem density (see Appendix B). Apart from these four indicators, in order to assess
268 similarities between forest types, the Bray-Curtis Index of dissimilarity (BC) was calculated
269 for each forest type per mountain.

270

271

272 2.5 Data analysis

273

274 R statistical software R v3.2.1 was used for all statistical analyses (R Development Core
275 Team, 2013). The `nlsLM` function in `minpack.lm_1.2-0` was used to fit the non-linear models
276 of the height-diameter models assessed. We used multiple regression analysis (`lm` method in
277 R) to determine important predictor variables of AGB. We first considered mountain,
278 distance to ocean, mountain maximum altitude (related to mass effect), forest type and
279 altitude. We then re-ran the multiple regressions replacing altitude with relative altitude
280 (altitude of the plot with regard to the top of the mountain). We only used the predictors that
281 were poorly correlated with each other to avoid problems of collinearity. The `vegan` package
282 was used to calculate the BC index and the distances between groups. Significant differences
283 between AGB estimates calculated using different height-diameter allometric models were
284 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

292 **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).

319

320 AGB showed significant differences between forest types and mountains. In Mt Nyiro mixed
321 forests had greater AGB than elfin and dry forests (611, 408 and 241 Mg ha⁻¹ respectively,
322 see Table 3). Forests in Mt Nyiro, the highest mountain, had greater biomass than in the other
323 mountains (Table 3). AGB ranged between 157 and 310 Mg ha⁻¹ in Mt Kulal and between
324 117 and 203 Mg ha⁻¹ in Mt Marsabit (Table 3). If the different forest types are considered
325 separately, AGB tended to increase with altitude, but the increase was not significantly
326 different, see Fig. 3). The p-values of the multiple regression analysis indicated that distance
327 to ocean was the most important predictor of AGB (p<0.01). The interaction between
328 distance to ocean and relative altitude (or altitude, depending on the choice of model) was
329 significant.

330

331 3.3 Forest attributes and their relationship with AGB

332

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

340

341 The Bray-Curtis index showed that species were more similar between different forest types
342 of one mountain than between the same forest type across mountains (Fig. 4). When data
343 from all plots was combined, AGB was found to be significantly positively correlated with
344 BA, SD₅₀, D_{mean} and H_{mean} but not with stem density or any taxonomic attribute (Table 4, Fig.
345 5).

346

347

348

349 4. Discussion

350

351 4.1 Choosing one height-diameter allometric model

352

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 CO₂ 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~SD₅₀). 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

455 We did not find any significant relationship between AGB and taxonomic attributes, for our
456 0.2-ha plots. Interestingly, Poorter et al. (2015) showed that there was a consistent significant
457 positive relationship between AGB and taxonomic attributes at the 0.1-ha scale, whereas this
458 relationship disappeared at the 1-ha scale (study focused on the Amazon lowland rainforest).
459 Chisholm et al. (2013) also found that diversity–biomass relationships were strong and
460 positive at very small spatial scales (20 m × 20 m), whereas at larger spatial scales (0.25 and
461 1 ha) there was no consistent relationship. A recent pan-tropical study of intact old-growth
462 closed-canopy forest by Sullivan et al. (2017) also show that diversity effects in tropical
463 forests carbon stocks are scale dependent.

464

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

471

472

473 **5. Conclusion**

474

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

486

487

488 **Acknowledgements**

489

490 We are deeply grateful to our field assistants and translators A.M. Aide, H. Lerapo, J.
491 Harugura, R.A. Wamuro, J. Lekatap and L. Lemooli for making this research possible, and to
492 P.Ch. Mutiso at the School of Biological Sciences, University of Nairobi, for helping with
493 plant identification. We also thank the kind support given by M. Kirimama, L. Olaka, B.
494 Mamo and NEMA Marsabit Office, T. Kinyua and WARMA Marsabit Office, S. Rucina and
495 NMK, A-S. Delbanco and the British Institute in Eastern Africa (BIEA). This research was
496 funded by Marie Curie Actions Intra-European Fellowships (IEF), number 328075, and by
497 the Percy Sladen Fund (the Linnaean Society of London). M.P. is supported by European
498 Research Council Project number 281986.

499

500

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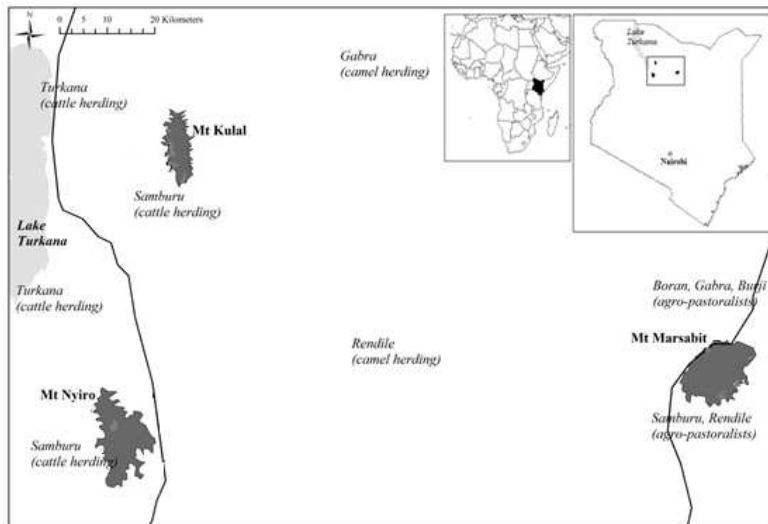
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759 **Appendix A: Plot locations**

760

761 **Fig. A1.** Location of the montane forests studied. Black lines refer to major roads, dark grey areas to forests.
 762 Note that Mt Marsabit, Mt Nyiro and Mt Kulal are located 570km, 630 and 680 km from the Indian Ocean,
 763 respectively. Mt Marsabit is 125km from Mt Kulal and Mt Nyiro, and Mt Nyiro and Mt Kulal are located about
 764 70km apart.



765

766

767

768 **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

769

770

771 **Appendix B: Species dominance**

772

773 For each plot we computed species dominance in terms of % of basal area (BA) and % of
 774 stem density. Stem density (number trees ha⁻¹) included all trees ≥ 10 cm diameter while BA
 775 (sum of the cross-sectional area at 1.3 m, or above buttresses) was calculated in m² ha⁻¹.

776 Dominant species were found to be more similar between forest types of one mountain than
 777 between the same forest type across mountains, with mixed and elfin forests on Mt Nyiro
 778 having exactly the same dominant species (Table B1). Most species dominant in terms of
 779 stem density were also dominant in terms of BA (Table B1). Two dominant species on Mt
 780 Marsabit (*Drypetes gerrardii* and *Rinorea convallarioides*) do not occur in the other
 781 mountains studied and *Faurea saligna*, dominant on Mt Nyiro, does not occur on the other
 782 mountains (Beentje, 1995; Bussmann, 2002). Although it has been reported that *Podocarpus*
 783 *latifolius* does occur on Mt Kulal (Bussmann 2002), we could not find it in any plot sampled
 784 in this forest, or during exploratory surveys.

785

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

788

789

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

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

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793 Monotonic models

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

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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.

	ΔAIC_{m1}	ΔAIC_{m2}	ΔAIC_{m3}	ΔAIC_{m4}	ΔAIC_{m5}	ΔAIC_{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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