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

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Abstract

Despite the potential of tropical montane forests to store and sequester substantial amounts of carbon, little is known about the above ground biomass (AGB) and the factors affecting it in these ecosystems, especially in Africa. We investigated the height-diameter allometry, AGB, and related differences in AGB to taxonomic and structural forest attributes in three distinct forest types (dry, mixed species and elfin) in three mountains of northern Kenya. We established 24 permanent plots (20m x 100m) and sampled all trees ≥ 10 cm diameter following standard Rainfor protocols.

We identified that different height-diameter allometric models could be used for different forests types, with the exception of the Michaelis–Menten model. In our study area, model choice had little effects on AGB estimates.

In general, mixed forests had greater AGB than other forest types: in Mt Nyiro AGB estimates were 611, 408 and 241 Mg ha^{-1} for mixed, elfin and dry forests respectively. Forests in Mt Nyiro, the highest mountain had greater AGB than in the other mountains. In our study area, differences in AGB were related to forest structure attributes, with little influence of taxonomic attributes. The mixed and elfin forests in Mt Nyiro, dominated by Podocarpus latifolius and Faurea saligna contained comparable AGB to lowland rainforests, highlighting the importance of tropical montane forests as large carbon stock, which could be released if converted to another land cover type.

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

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 23.5ºN and 23.5ºS 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 smallerdiameter trees in many forests (Feldpausch et al. 2012). However, Banin et al. (2012) and Kearsley et al. (2013) found that a nonlinear 3-parameter exponential model was the most appropriate for biomass prediction. Two recent studies, which considered an asymptotic model Michaelis-Menten (Molto et al. 2014; Fayolle et al. 2016), not included in previous studies, preferred this later one, arguing that not only it outperformed Weibull but also that it was easier to manipulate than Weibull and its exponential function. All these studies focused on lowland rainforest types, and to our knowledge, the shape of the height-diameter allometry for tropical has not been studied in depth for TMFs, which tend to have shorter trees for a given diameter.

Declining AGB with increasing elevation has also been related to changes in other characteristics of forest structure affecting AGB, such as stem density and stand basal area. In general, stem density and stand basal area have been shown to increase with altitude in Hawaii (US), Mt Kinabalu (Malaysia), Udzungwa Mountains (Tanzania) and the Andes (Herbert and Fownes, 1990; Takyu, 2002; Lovett et al., 2006; Girardin et al., 2014). However, some studies demonstrate a decrease in stem density with increasing altitude (e.g. Mt Elgon in Kenya-Uganda, Hamilton and Perrott, 1981) or no trend between stand basal area and altitude (e.g. Andes: Girardin et al., 2014). Because biomass increases exponentially with tree diameter, average tree diameter, large tree density and stand basal area tend to be better predictors of AGB than overall tree density (Slik et al., 2010; Lewis et al., 2013; Poorter et al., 2015).

Changes in AGB with increasing elevation have also been related to changes in tree species richness. Higher species richness enhances the variation in species traits found in the community, leading to niche complementarity, a higher resource capture, more efficient resource use and higher productivity (Poorter et al., 2015). Higher species richness may also enhance facilitation (e.g. a nitrogen-fixing species enhances soil fertility, and therefore the productivity of the other species); and it might also increase the chance of a selection effect (selecting highly productive or large species). Generally, there is a decline in tree species richness with increasing altitude (e.g. Dossa et al., 2013; Sassen and Sheil, 2013; Girardin et al., 2014), because of a greater role of environmental filtering at higher elevations (e.g. cooler temperatures, fog, reduced light incidence and higher relative humidity). Nevertheless, this was not observed on, for example, the Udzungwa Mountains in Tanzania (Lovett et al., 2006). In the Andes, several elevation gradients showed mid-elevational peaks in numbers of 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).

These mountains support similar vegetation types (Bussmann, 2002). From low to high altitudes, these comprise: (i) dense thorny bushland (Commiphora, Grewia and partly Acacia), (ii) 'dry montane forest' (Croton megalocarpus-Olea europaea subsp. africana forest association in Mt Marsabit or O. europaea-Juniperus procera forest association in Mt Kulal and Mt Nyiro), (iii) 'mixed species forest' (with abundant Cassipourea malosana and Olea capensis in all mountains), and (iv) 'elfin-like forest' (with similar composition to mixed species forest but at least 15% shorter trees with twisted stems and many epiphytes on their branches) (see Bussmann, 2002). This study focuses on the last three types thereafter called dry, mixed and elfin. These forest types occur at different altitudes in the mountains studied (see Fig. 1), because of (i) mountain distance to the ocean (the further, the drier, see Fig. A1 in Appendix A) and (ii) the mass-elevation or telescopic effect (larger mountains are better at warming the atmosphere above them and are warmer at a given altitude, Jarvis and Mulligan, 2011).

The forests studied provide key services to surrounding communities, including water, firewood, medicine resources and fodder (Cuni-Sanchez et al., 2016). Mt Marsabit is an important elephant habitat in northern Kenya (Ngene et al., 2009), but there are no elephants on Mt Kulal or Mt Nyiro. While commercial logging never occurred on Mt Kulal or Mt Nyiro, because of the steep terrain and remoteness of the area, local communities around Mt Marsabit reported small-scale 'illegal' selective logging in some parts of the forest during the 1960s (Cuni-Sanchez 2015, pers. obs.). For the purpose of this study, we assume that the forests are largely pristine and that currently observed forests' structure and species composition is unaffected by potential historical disturbance events.

2.2 Study design and field measurements

In each forest type per mountain (dry, mixed and elfin), three permanent plots of 20 x 100m were established at least 1km apart from each other, >100m from footpaths, signs of plant harvesting and cliffs (total number of plots = 24, Fig. 1). We selected our plots depending upon forest type rather than elevation, because of the abovementioned differences in altitude between mountains where the same forest type is found (see Fig 1). Elfin forest in Mt Marsabit was found to be very small and fragmented and could not be sampled. Although larger plots (1-ha) are often preferred for these type of studies (Poorter et al., 2015), larger plots were not viable due to the steep terrain (mean plot slope ranged from 10 to 30 degrees). Within each plot, we recorded tree diameter at 1.3 m along the stem from the ground (or above buttresses if present) of each tree ≥ 10 cm diameter and tree height (measured using a handheld laser Nikon Forestry Pro) for some trees, following RAINFOR/AfriTRON protocols (www.rainfor.org; www.afritron.org). In total, 1010 stems were sampled for height in all plots. These included 35-50% of the trees present in each plot, comprising several individuals from each diameter class. Only trees whose crown top was clearly visible from the ground were measured. Thick fog, common at higher altitudes, hampered height measurements; which are known to be difficult in tropical forests (Larjavaara and Muller-Landau, 2013). No lianas or bamboo were sampled in this study as these were not found inside our study plots.

Stems were identified to species where possible and samples of unidentified trees were collected for identification and deposited at the Herbarium of the University of Nairobi. The vernacular name (in Samburu language) of all the unidentified trees collected was also recorded. Eight of the unidentified morphospecies could not be identified to species level due to the poor quality of the samples collected and their vernacular name was used for tree diversity calculations. Unidentified trees represented 0.8% of the trees sampled in Mt Nyiro (8/987 individuals), 0.3% in Mt Kulal (3/1164 individuals) and 1% in Mt Marsabit (8/736 individuals). Taxonomy followed the plant list (www.theplantlist.org). Species presence in each mountain was checked with the literature (e.g. Beentje, 1995). The most abundant species in Mt Nyiro were found to be: Juniperus procera, Ochna holstii, Olea capensis (dry forests) and Faurea saligna, Xymalos monospora, Podocarpus latifolius (mixed and elfin forests). The most abundant species in Mt Kulal were: Vepris nobilis, Apodytes dimidiata, Olea capensis (dry forests) and Vepris nobilis, Cassipourea malosana, Xymalos monospora (mixed and elfin forests). The most abundant species in Mt Marsabit were: Croton megalocarpus, Drypetes gerrardii, Coptosperma graveolens (dry forests) and Croton megalocarpus, Drypetes gerrardii, Rinorea convallarioides (mixed forests). For more details see Appendix B.

2.3 Height-diameter allometric models

A total of six different height-diameter allometric models were fitted for each forest type and mountain, and to all sites combined (Table 1). These included a monotonic model (the power law model or **m1**, Feldpausch et al., 2011; King, 1996; Niklas, 1994); a second order polynomial model (of a log-linear model or **m2,** see Chave et al., 2014; Niklas, 1995 for a log–log transformation); and four asymptotic models: the monomolecular (or three-parameters exponential) model (**m3**, Banin et al., 2012; Feldpausch et al., 2012), the Gompertz model (**m4**), the Weibull model (**m5**, Bailey, 1980; Feldpausch et al., 2012) and the Michaelis–Menten model (**m6**, Molto et al., 2014; Fayolle et al. 2016) (see Appendix C for model equations). The best model for each forest type and mountain was selected according to the Akaike Information Criterion (AIC) and the Root Mean Squared Error (RMSE), following Fayolle et al. (2016). We also computed ΔAIC (the difference in AIC for each model compared to the best one for that forest type and mountain) and the relative likelihood of each model, expressed as exp(-ΔAIC/2).

2.4 Estimating AGB

The Chave et al. (2014) equation including tree diameter, wood mass density (WMD) and tree height was used to estimate the AGB of each tree in the plot. The best taxonomic match WMD of each stem was extracted from a global database (Chave et al., 2009; Zanne et al., 2009) following Lewis et al. (2013). For the trees whose height was not measured in the field, their height was estimated using the second order polynomial model (m2), which performed well for all forest types and mountains (see results section). In four plots on Mt Nyiro, a number of Xymalos monospora trees had been partially pruned to feed the animals during drought events. We also estimated the height of these trees using m2, as if they had not been disturbed, following preliminary findings on the effects of X. monospora pruning on AGB (these are discussed in detail in Cuni-Sanchez et al. in prep). AGB was then summed across all trees in a plot to obtain plot AGB (in Mg ha^{-1}). In order to assess if the choice of height-diameter allometric model affected AGB estimates, we also computed AGB using the six different models for each forest type and mountain, and the m3 model developed for ‘all sites’ combined.

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.

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

3. Results

3.1 Height-diameter allometric models

Most models gave similar values of AIC and RMSE for the different forest types and mountains (Table 1, Table C1 in Appendix C). The curves were also very close (Fig. 2). Overall, the polynomial (m2) was found to be suitable for all the different forest types and mountains (Table 1). The Gompertz model (m4) also seems suitable for all the different forest types and mountains except for Mt Nyiro mixed forest (see Table 1). When 'all sites' were combined, m2, m3 and m4 outperformed the other models (Table 1, Table C1 in Appendix C). The Michaelis–Menten model (m6) was the model performing the worst for most forest types and 'all sites' model (Table 1, Table C1 in Appendix C).

Model parameters varied considerably among and within forest types, and with the models build with 'all sites' combined (Table 1). For some models, the parameters were more similar among the same forest type across mountains than among forest types within a mountain (e.g. see m2 and m5, see Table 1).

3.2 AGB estimates

The choice of height-diameter allometric model did not significantly affect AGB estimates if a height-diameter allometric model was developed for each forest type and mountain separately (Table not included). The use of the m3 model developed for 'all sites' combined changed AGB estimates up to 11%, with mixed forests having less AGB, and dry and elfin forests having more AGB (Table 2). However, these differences were not significant (Table 2).

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

Most models performed similarly for the different forest types and mountains studied, with the exception of the Michaelis–Menten model (m6). This is different from previous studies on lowland rainforests where m6 was the preferred model (e.g. Fayolle et al. 2016). This finding might be related to the fact that very large trees are not abundant in montane forests (except for mixed species forests), as models mainly differed in large diameter classes (see Fig. 2).

In our study area, site specific model choice did not affect AGB estimates for a give forest type and the use of a 'all sites' model produced small changes in AGB estimates. Most authors choose the same model for the different forest types they study (e.g. Kearsley et al., 2013; Molto et al., 2014), and discuss the different values of the parameters in the selected model. Our results support this approach.

4.2 The variable AGB per forest type

AGB showed significant differences between forest types and mountains: in general, greater AGB in mixed forests and greater in Mt Nyiro, the highest mountain. If all forest types and mountains are considered, our AGB estimates ranged from 117 Mg ha^{-1} to 612 Mg ha^{-1}, which is in line with estimates reported by Spracklen and Righelato (2014) for the world's TMFs (77-785 Mg ha^{-1}). The observed differences in AGB between mountains (especially for mixed species forest) may be related to soils and substrate. In general, soils with higher levels of limiting nutrients increase productivity, which increases AGB. For example, in the Amazon, AGB has been positively linked with total soil phosphorus (Quesada et al., 2012). Mixed forests in Mt Kulal and Mt Marsabit growing on andosols have higher fertility than the regosols found in Mt Nyiro, and so should be expected to have higher AGB. However, it has also been reported that faster-growing forest stands may become dominated by low wood density species with shorter lifespans and hence lower AGB (see Baker et al., 2004; Lewis et al., 2013). That is the carbon residence time in more nutrient rich forests is shorter, which may explain lower AGB in Mt Kulal and Mt Marsabit, compared with Mt Nyiro. Future repeat censuses of plots will allow us to assess this hypothesis. Another factor which should also be considered is that other nutrient-cycling mechanisms apart from direct nutrient absorption from soil, such as nutrient uptake from litter, or the storage of nutrients in the biomass might control forest biomass (see Grau et al. 2017).

Another factor which should also be considered is precipitation. Mt Marsabit is located closer to the Indian Ocean and it is considered wetter than the other two mountains studied (Bussmann, 2002; AFRICLIM data from Platts et al., 2015). However, preliminary findings for the area indicate that mixed species forests in Mt Nyiro, the highest mountain, receive more precipitation than those of Mt Marsabit (unpublished data). In this study we did not correlate AGB with climate or soil variables, as other authors have done (Girardin et al., 2013; Marshall et al., 2012; Ensslin et al., 2015), because WorldClim data, which has been used in some studies (e.g. Marshall et al., 2012), is of limited accuracy in small mountains with complex terrains (Platts et al., 2013; 2015) as preliminary findings for the area also indicate (unpublished data).

Available studies from other montane forests in East Africa also report significant variation between and within locations, with values ranging from 25 Mg ha^{-1} in high altitude forests in Hanang to >800 Mg ha^{-1} on the West Usambara Mountains (Table 5). Although the different methods used to estimate AGB (minimum tree diameter sampled and the biomass allometric equation selected, see Table 5), can explain some of these differences; environmental conditions (e.g. rainfall), soil type and human disturbance history might play an important role too.

The distribution of AGB along elevational gradients observed in Mt Nyiro agrees with patterns observed in TMFs elsewhere in Tanzania, e.g. Mt Kilimanjaro (Ensslin et al., 2015), Udzungwa and Usambara Mountains (Marshall et al., 2012). Montane forests at mid altitudes (mixed forest) had greater biomass than both forests at higher altitudes (elfin) and forests at lower altitudes (dry forest). Lower AGB in elfin forests is expected as cloud cover, common at highest altitudes, is known to limit net CO_2 uptake and growth of trees (Graham et al., 2003). Wind exposure, greater in elfin forests, also limits tree height (Thomas et al., 2015). With regard to forests at lower altitudes, most studies report more AGB at lower altitudes than at middle ones (e.g. Girardin et al., 2010, 2014; Leuschner et al., 2013). As highlighted by Ensslin et al. (2015), rainfall might not have been the limiting factor at lower altitudes in most of these studies, contrary to many TMFs in East Africa, including Mt Nyiro.

Compared with TMF outside Africa, our AGB estimates (which range from 117 to 612 Mg ha^{-1}, mean of all plots studied 276 Mg ha^{-1}) seem high, particularly in Mt Nyiro. For example, AGB ranged between 100 and 200 Mg ha^{-1} (1500-2500m) in Andean TMF (Girardin et al., 2014), between 100 and 300 Mg ha^{-1} (1000 and 2200m) at Mt Rinjani in Indonesia (Dossa et al., 2013), while it was estimated at 247 Mg ha^{-1} and 271 Mg ha^{-1} for submontane and montane Atlantic forest in Brazil (Alves et al., 2010). Interestingly, it has been reported that Asian and Neotropical TMFs have similar mean AGB (257 and 247 Mg ha^{-1}, n = 31 and 56, respectively) while that of African TMF is higher (527 Mg ha^{-1} n = 7) (Spracklen and Righelato, 2014). Although few African plots were included in Spracklen and Righelato (2014), other studies seem to support this finding. For example, Ensslin et al. (2015) emphasised the high AGB found in Podocarpus-dominated forest on Mt Kilimanjaro (364 Mg ha^{-1}). We observed that mixed and elfin forests in Mt Nyiro, dominated by large specimens of not only Podocarpus latifolius but also Faurea saligna, have even greater AGB than that reported on Mt Kilimanjaro. Faurea saligna was also a dominant species contributing to great AGB in Nyungwe National Park in Rwanda (Nyirambangutse et al. (2016). Interestingly, mixed and elfin forests in Mt Nyiro contain comparable biomass to African lowland rainforests (mean 395.7 Mg ha^{-1}, see Lewis et al. 2013). Our results support the idea that the African Podocarpus-dominated forest has particularly high biomass.

4.3 The effects of forest structure and tree diversity on AGB

Results indicate that the observed variation in AGB in the different forest types was related to differences in forest structure, but not tree species composition or a combination of both structure and tree species composition. This was a rather unexpected finding considering the decline in tree species richness generally observed with increasing altitude and its effects on AGB.

In this study, despite considerable variation observed in stem density (from 441 to 785 individuals ha^{-1}), high AGB was more related to (a) few trees with a large basal area (each containing a disproportionately large biomass) than to (b) many small trees (each containing little biomass) (see correlation $AGB \sim SD_{50}$). With regard to the range of values observed, values of stem density are within those from other studies (Table 5), although most of these other studies included trees ≥5cm diameter. Our values of basal area are also within the range reported from other studies (Table 5).

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.

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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.

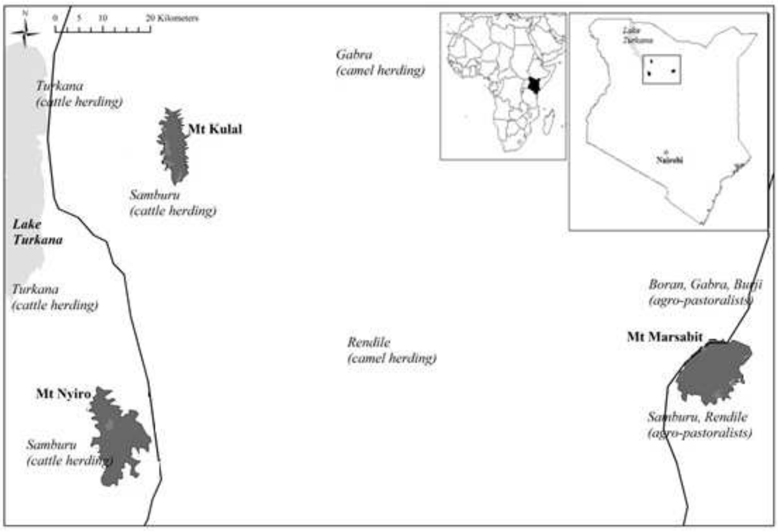

Table A1 Location of the plots studied.

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

Appendix B: Species dominance

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.

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.

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

Monotonic models

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

Second-order polynomial models

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

Asymptotic models

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

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

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

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

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 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