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Investigating above ground biomass in old-growth and secondary montane forests of the Cameroon Highlands

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Data Availability Statement

Forest plot inventory data will be deposited at Forestplots (<https://www.forestplots.net/>), a publicly requestable/accessible repository which provides data upon request for research purposes.

Additionally, all data that support the findings of this study are available from the corresponding author upon reasonable request.

Abstract

Tropical montane forests can store and sequester substantial amounts of carbon in above ground biomass (AGB), but variations in this storage related to location or degradation have not been quantified in the Cameroon Highlands. We established 25 permanent plots (20m x 40m) and sampled all trees ≥ 10 cm diameter following standard RAINFOR protocols. We estimated AGB, and investigated variations related to taxonomic and structural forest attributes, including the height-diameter allometry in five forest types (four old-growth dominated by different species and one secondary forest).

Secondary forests had significantly lower AGB than old-growth forests (49.4 ± 2.5 vs $> 476.3 \pm 168.7$ Mg ha⁻¹, respectively), mostly related to lower basal area and tree height. Significant differences in species composition but not in forest structure or AGB were found between the four types of old-growth forests studied, located at different altitudes and mountains. We discuss the importance of these montane forests for carbon storage and, considering their high diversity and current threats, their potential for carbon finance mechanisms related to both avoided deforestation and forest restoration.

Keywords: African Mountains, forest structure, tree diversity, height-diameter allometry

1. Introduction

Tropical montane forests are important for the provision of numerous ecosystem services, such as biodiversity, water and, as recently highlighted, carbon storage (Bruijnzeel et al., 2011; Mittermeier et al., 2004; Spracklen & Righelato, 2014). Remarkably in Africa, while a considerable amount of data on above-ground biomass (AGB) and carbon storage in tropical lowland forests have become available in the past few years (e.g. in Cameroon Fayolle et al., 2016, 2018; in DR Congo Kearsley et al., 2013, 2017; across Africa Lewis et al., 2013; in Cameroon Peh et al., 2011; 2014;), less information is available on patterns of AGB and carbon storage in montane forests, especially outside Tanzania (Cuni-Sanchez et al., 2017).

The montane forests of the Cameroon Highlands are known internationally for their rich flora and high levels of endemism, combined with high degrees of threat, making them a conservation

priority (Myers et al., 2000; Onana and Cheek, 2011). While several studies on plant diversity in the Cameroon Highlands have been recently published (see Sainge et al., 2017 and references therein), none has assessed AGB. If Cameroon Highland forests are also shown to have high biomass, carbon projects could help conserve these threatened forests, with the added benefit of conserving high plant diversity.

Most studies have shown that AGB decreases with increasing elevation (e.g. Girardin et al., 2014; Marshall et al., 2012). At higher altitudes, trees tend to be shorter for a given diameter (Girardin et al., 2014), related to greater cloud cover limiting net CO₂ uptake and growth of trees (Graham et al., 2003) and wind exposure (Thomas et al., 2015). While stem density tends to increase with increasing altitude (there are often more multi-stemmed trees at higher altitudes), basal area generally decreases (Girardin et al., 2014; Lovett et al., 2006; Shirima et al., 2016). With regard to species' composition, tree species richness generally declines with increasing altitude, because of a greater role of environmental filtering at higher elevations e.g. cooler temperatures, fog, reduced light incidence and higher relative humidity (Girardin et al., 2014; Sassen & Sheil, 2013). Nevertheless, this was not observed on, for example, the Udzungwa Mountains in Tanzania (Lovett et al., 2006).

Pantropical equations are often used to estimate AGB from a number of tree structural measurements, including tree diameter, wood density, and preferably tree height which gives more accurate estimates (Chave et al., 2005; 2014; Feldpausch et al., 2011). However, sampling tree height is particularly difficult in tropical montane forests due to steep slopes and the challenges of seeing tree crowns (Mugasha et al., 2013). Consequently, tree heights are often only measured for a few individuals, and a height-diameter model is applied to estimate the height for the remaining unmeasured trees (e.g. Sullivan et al., 2018). Therefore, one important issue to consider when studying montane forests is which height-diameter model to use, as (i) with increasing altitude trees tend to be shorter for a diameter class and (ii) height-diameter models built for lowland rainforests might not be applicable to montane areas (Imani et al., 2017). Apart from altitude, species composition, precipitation, temperature, edaphic factors and geographical region also affect the height-diameter allometry (Banin et al., 2012; Fayolle et al., 2016; Feldpausch et al., 2011).

Available data indicate that different functional forms of allometric height-diameter models might be preferred in different geographic mountain regions. For example a three-parameter Weibull function was the preferred height-diameter model in the wet montane forests of Peru (Ledo et al., 2016), while the Gompertz and the Richards Asymptotic models were preferred for wet montane forests at middle and higher altitudes, respectively, in eastern DR Congo (Imani et al., 2017). However, results from the drier montane forests of northern Kenya show that several height-diameter models perform similarly (Cuni-Sanchez et al., 2017). To our knowledge, height-diameter allometry has not been investigated for montane forests in the Cameroon Highlands, and local height-diameter allometries are needed to improve AGB estimates (Chave et al., 2014).

In this study, focused on the Cameroon Highlands, we estimated AGB in five different montane forest types (one secondary and four old-growth dominated by different species) and we investigated the relationship between AGB and forest structural and taxonomic attributes, including height-diameter allometry. We address three major research questions: (1) does AGB differ significantly between different forest types? (2) Are differences in AGB related to differences in structural attributes, taxonomic diversity, or both? And, (3) are there significant differences in height-diameter allometry between the different types of montane forests? We then compare our findings with other montane forests in Africa, and discuss the implications of our findings for the conservation of these highly diverse and threatened forests.

2. Methods

2.1 Study area

This study focused on the montane forests present on Mt. Oku (3011 m), and Mt. Mbam (2335 m) (Fig. 1). These mountains receive more rainfall than the surrounding lowlands and are commonly covered in mist/fog during the rainy season, which supports the existence of montane forests. Annual rainfall is over 2400 mm yr⁻¹ on Mt. Oku (Forboseh et al., 2003). There are two main seasons; the rainy season (April-October), and the dry season (November-March). The dry season is characterized by the influence of the Harmattan (a dry wind that blows from the south from the Sahara) (Innocent et al. 2016).

While the forest on Mt. Oku extends to about 9500 ha, that of Mt. Mbam is only 2000 ha (Momo-Solefack et al., 2012; Njabo & Languy, 2000). Two types of montane forests can be found on Mt. Mbam: riverine (at riverine valleys, 1700-1900 m, with larger and taller trees), and ridge forest, often dominated by *Nuxia congesta* (>1900 m, with smaller and shorter trees) (unpublished data, see Table 1). In Mt. Oku there are *Carapa grandiflora* dominated forest (<2400 m, old-growth), *Nuxia congesta-Podocarpus latifolius* forest (>2400 m, old-growth) and *Gnidia glauca* (secondary) forest, see Table 1. Secondary forests have grown in the last decades on fallow lands previously cultivated and are mainly characterised by light-demanding and fire-resistant trees and shrubs (such as *G. glauca*).

Several rare species endemic to Mt. Oku or the Bamenda Highlands can be found in these two forests, including the Lake Oku Clawed Frog (*Xenopus longipes*) (critically endangered, only known from Lake Oku), and notable populations of Bannerman's Turaco (*Tauraco bannermani*, endangered, see <<http://www.iucnredlist.org/>>), a secretive bird restricted to montane forest habitats, renowned for its highly prized red flight feathers that adorn men's black hats as status symbol throughout western Cameroon (Forboseh et al., 2003, Ngute et al., 2019).

Both forests are community forests in which extraction activities are regulated using customary laws (e.g. firewood collection of dead sticks only). Two conservation projects organised by BirdLife International operated in Mt. Oku between 1987 and 2004, which helped delimit forest boundaries, grazing areas, plant trees and promote forest conservation (Abbot et al., 2001). Despite the success of these two conservation projects, illegal grazing, fire and unsustainable exploitation of *Prunus africana*'s bark remain major threats degrading Mt. Oku forest (Stewart, 2009; Sunjo, 2015). No conservation project has ever taken place in Mt. Mbam. Fire (set up by pastoralists to promote grass growth or by hunters) is a major threat to Mt. Mbam forest (Njabo and Languy, 2000; Ngute et al., 2019). Note that traditional authorities in both mountains, who are in charge of forest conservation, hold considerable power and command local respect (Hakizumwami and Fuchi, 2000).

2.2 Study design and field measurements

We established 25 permanent plots of 20 x 40 m (0.08 ha), at least 800 m apart from each other within one mountain (Table 1, Fig. 1). We initially planned to have seven plots per forest type (*Carapa*, *Nuxia*, *Gnidia*, riverine and ridge, see Table 1), but this was not possible during the field campaign and we ended with an unbalanced plot design (Table 1). Although larger plots (1-ha) are sometimes preferred (Poorter et al., 2015), larger plots are not always viable in montane areas due to the steep terrain (mean plot slope ranged from 10 to 30 degrees in our study area). 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 protocols (<<http://www.rainfor.org/>>). In total, 49.5% of the stems were sampled for height, comprising several individuals from each diameter class within each plot, as recommended by Sullivan et al. (2018). Only trees whose crown top was clearly visible from the ground were measured. No lianas were sampled in this study as our study plots did not contain any liana ≥ 10 cm diameter.

Stems were identified to species where possible and samples of unidentified trees were collected for identification and verification of their local name at the Limbe Botanical & Zoological Gardens and at the National Herbarium of Cameroon in Yaoundé (acronyms: SCA and YA respectively, according to Thiers, 2018), and Tropical Plant Exploration Group (TroPEG). The common name (in Oku or Bansa language) of all the unidentified trees collected was also recorded. Twenty 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. These represented 1% of the individuals on Mt. Oku, and 12% of the individuals on Mt. Mbam (for the latter forest, this research is its first comprehensive botanical survey). Taxonomy followed the plant list (<http://www.theplantlist.org/>). Species presence in each mountain was checked with the literature (e.g. Cheek et al., 2000; Sainge, 2017; Vivien & Fare, 1985).

2.3 Height-diameter allometric models

A total of six different height-diameter allometric models were fitted for each forest type, except *Gnidia* forests for which most trees were < 10 m height and could not be sampled with the laser. These included a monotonic model (the power law model or m1, Feldpausch et al., 2011; 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, Fayolle et al. 2016; Molto et al., 2014). The best model for each forest type was selected according to the Akaike Information Criterion (AIC) and the Root Mean Squared Error (RMSE).

Monotonic model

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

Second-order polynomial model

(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, $H=a \times D / (b+D)$

2.4 Estimating AGB

The most recent pantropical biomass allometric equation (Chave et al. 2014) 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 Gompertz model (m4) (see results section). AGB was then summed across all trees in a plot to obtain plot AGB (in Mg ha⁻¹). As we wanted to investigate the effects of not sampling tree height in the field, we also a) computed tree height using the Feldpausch et al. (2012) height-diameter allometric model for Central Africa and estimated AGB using Chave et al. (2014); and b) we estimated AGB using the recently published Fayolle et al. (2018) AGB equation for the Congo Basin, based on tree diameter and WMD (but not height).

2.5 Assessing forest structure and tree diversity

For each plot, we calculated six structural attributes: stem density (SD), density of large trees (≥ 50 cm diameter, named SD₅₀), basal area (BA), BA-weighted wood mass density (WMD_{BA}), 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 and species' proportions were calculated for each plot: species richness (number of species per plot), rarefied species richness per 15 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). Apart from these four indicators, in order to assess similarities between forest types, the Bray-Curtis Index of dissimilarity (BC) was calculated and used to cluster the plots sampled.

2.6 Data analysis

R statistical software R v3.1 was used for all statistical analyses (R Development Core Team, 2013). The nlsLM function in minpack.lm_1.2-0 (Elzhov et al., 2016) was used to fit the non-linear models of the height-diameter models assessed. The vegan package of R (Oksanen et al., 2018) was used to calculate the BC dissimilarity index of all plots in different forest types. Significant differences between AGB estimates calculated using different height-diameter allometric models were tested using paired t-tests.

Given the unbalanced plot design, Kruskal-Wallis 1-way ANOVA for k samples was used to determine significant differences between forest types. Post-hoc pair wise comparisons were performed using Mann-Whitney U 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 $p < 0.05$ if not stated otherwise.

3. Results

In total we sampled 1005 individuals comprising 68 species within 29 Families. Notably, four species found in the plots sampled are of conservation concern: *Allophylus bullatus* (VU), *Embelia mildbraedii* (NT), *Prunus africana* (VU) and *Schefflera mannii* (VU) (VU: Vulnerable, NT: Nearly threatened, see <<http://www.iucnredlist.org/>>).. Moreover, several species of *Cuviera*, *Psychotria* and *Rinorea* found in the Bamenda Highlands are of conservation concern, but we could not identify our samples of these three genera to species level.

3.1 Height-diameter allometric models and AGB estimates

Most models gave similar values of AIC and RMSE for each forest type studied (see Tables A1 & A2 in Appendix), so we used the Gompertz model (m4), which was the one with lowest AIC and RMSE in two of the four montane forest types studied. On Mt. Oku, mean AGB was 49.4 Mg ha⁻¹ in *Gnidia* forest, 399.9 Mg ha⁻¹ in *Carapa* forest and 506.3 in *Nuxia* forest Mg ha⁻¹. On Mt. Mbam it was 559.2 Mg ha⁻¹ in riverine forests and 495 Mg ha⁻¹ in ridge forests. *Gnidia* forests AGB estimates were significantly lower than the other forest types, but there were no significant differences between the other forest types studied (Table 1). The use of tree height estimated using Feldpausch Central Africa height-diameter allometric model overestimated AGB, as also did the use of Fayolle AGB equation (Table 2). Overestimations ranged from 36 % per riverine forests to 78 % in *Nuxia* forests.

3.2 Forest attributes and their relationship with AGB

In terms of forest structure and taxonomic attributes, *Gnidia* forests were significantly different from the other forest types: they had significantly higher SD but lower D_{mean} , H_{mean} , WMD_{BA} , R_{sp} , H' and J' (Table 1), as expected of secondary forests. The other forest types were not significantly different from one another, except for riverine and ridge forests on Mt. Mbam which had higher species richness than all forests on Mt. Oku (Table 1). Considerable variation in some forest structural attributes was noted within one forest type (see standard deviations in SD and BA in Table 1).

We found some similarities in dominant species across forest types: e.g. *Nuxia congesta* was amongst the top three dominant species in *Carapa*, *Nuxia* and ridge forests; *Syzygium staudtii* was amongst the top three dominant species in *Nuxia*, riverine and ridge forests (Table A3, Appendix). However, some dominant species were only present in one forest type (Table A3, Appendix). With regard to clustering of plots, in general, plots from a given forest type were grouped together, except for one riverine plot which was more similar to ridge plots than to the other two riverine plots (Fig. 2). *Gnidia* plots were the most different plots from other forest types, followed by riverine plots (Fig. 2). AGB in old-growth forests was found to be positively correlated with BA, SD_{50} , H_{mean} , and D_{mean} , but not with SD, WMD_{BA} , or tree species attributes (Fig. 3).

4. Discussion

4.1 Height-diameter allometric models

We found that in our study area most height-diameter allometric models gave similar values of AIC and RMSE. It has been argued that the lack of large differences between height-diameter allometric model functional forms in montane forests, compared to tropical lowland forests, occurs because allometric models' estimates mainly differ at large diameter classes, and montane forests tend to have few large stems (Cuni-Sanchez et al., 2017). However, most of the forest types we studied (except the secondary *Gnidia* forest) have high density of large (> 50 cm diameter) trees (> 60 individuals ha^{-1}), which is unusual in montane forests (about 30 individuals ha^{-1} were reported from Kenya and DRC, see Cuni-Sanchez et al., 2017; Imani et al., 2017). Large individuals of *Schefflera* spp., a characteristic genus of montane forests in the Cameroon Highlands, have also been reported from Mt. Cameroon and Rumpi Hills (Forboseh et al., 2011; Sainge, 2017). However, despite their large diameters, this genus does not reach great heights in our study area (pers. Obs. 2018), which might explain why most height-diameter allometric models gave similar estimates, even for large diameter classes.

Our results indicate that the use of height-diameter models parameterized with data from lowland forests (Feldpausch et al. 2012) overestimate AGB in montane areas, as shown by Imani et al. (2017) for montane forests in DRC. We also show that the Fayolle et al. (2018) AGB equation, the most comprehensive equation for the Congo basin (numerous destructive sampling), also overestimates AGB in montane areas. These findings highlight the inherent structural differences between lowland and montane tropical forests, and by extension the importance of sampling tree height in the field when working in montane forests.

4.2 AGB estimates

Significant differences in AGB were observed between old-growth (> 400 Mg ha^{-1}) and secondary *Gnidia* forests (50 Mg ha^{-1}), but not between the four types of old-growth forests we studied, despite the range of values observed (400 to 560 Mg ha^{-1}). This might be related to the small number of plots we sampled or the unbalanced plot design, but future studies including more plots could provide further insights. Estimates from old-growth forests in our study area were higher than those from submontane forests in Ngovayang Massif, 900m a.s.l. (257-269 Mg ha^{-1} in southern Cameroon: Gonmadje et al., 2017) and montane forests in Rumpi Hills, 1700m a.s.l. (354-362 Mg ha^{-1} in western Cameroon: Sainge, 2017). Compared with other montane forests in Africa, our

estimates are slightly higher than Udzungwa and Usambara in Tanzania (360-400 Mg ha⁻¹, Marshall et al., 2012), Kilimanjaro (274-355 Mg ha⁻¹, Ensslin et al., 2015), or Kahuzi in eastern DRC (252-290 Mg ha⁻¹, Imani et al. 2017); but they are similar to *Podocarpus* forests in northern Kenya (400-600 Mg ha⁻¹, Cuni-Sanchez et al., 2017). While some differences in AGB might be related to the methodology used (the AGB or the height-diameter allometric equation selected), other differences could also be explained by environmental characteristics (e.g. climatic regime including effects related to altitude, soil fertility, nutrient content). It is possible that the volcanic soils of Mt. Oku and Mt. Mbam, rich in organic matter content (humic soils), are less limiting to productivity and AGB than soils in other mountains in Africa. Future studies should investigate the relationship between soil characteristics and AGB in montane regions in Africa.

On Mt. Oku, secondary *Gnidia* forests had much less biomass than *Carapa* and *Nuxia* old-growth forests, as has been reported from other studies comparing nearby secondary and old-growth forests. For instance, Njomgang et al. (2011) studying lowland forests in southern Cameroon, reported 440 Mg ha⁻¹ versus 300 Mg ha⁻¹ for AGB in old-growth and secondary forests, respectively. Although we were unable to obtain estimates on secondary *Gnidia* forests age, several studies have shown that AGB recovers faster than plant species richness after slash-and-burn agriculture (see Martin et al., 2013). In the lowland rainforests of Ivory Coast, AGB recovered to 50% in about 50 years (N'Guessan et al., 2018) while in Sierra Leone it recovered in 10 years (as some trees were left during land clearing)(Cuni-Sanchez et al., 2016). Montane forests often have very low growth rates and productivity (Fahey et al., 2016) and recovery from disturbance is likely to be very slow (Ewel, 1980). Crausbay and Martin (2016) recently highlighted the importance of investigating the role of natural disturbance in forest dynamics in tropical montane forests. We also recommend more studies on the role of human disturbance, including recovery of forest after slash-and-burn agriculture.

Even if AGB also recovers faster than plant species richness in montane areas, on Mt. Oku, AGB and plant species richness in secondary *Gnidia* forests had not recovered to the average values of old-growth forests. About 80% of the trees on Mt. Oku are dispersed by animals, and of these, most are dispersed by birds or monkeys (Maisels & Forboseh, 1997). Unfortunately, most large mammals have already been hunted out on Mt. Oku, which is likely to affect the future tree species' composition and structure of old-growth forests (Maisels et al., 2001), and also, the recovery potential of secondary *Gnidia* forests.

4.3 Forest attributes and their relationship with AGB

With regard to the old-growth forest types studied, no differences were observed on forest structure between forest types, but we observed considerable variation in SD and BA within one forest type. Although we set up our plots in areas which did not have signs of recent human disturbance (e.g. timber collection or debarking), it seems that some might have been located in areas with past human disturbance. Unsustainable exploitation of *Prunus africana* bark (traded internationally for its medicinal properties) can lead to the death of individuals, as has been reported from Mt. Oku (Stewart, 2009). Past harvesting of *Prunus africana* (found in both *Carapa* and *Nuxia* forests) could explain why some plots had lower stem density or basal area than others.

In these old-growth forests, our mean estimates of SD are similar to submontane forests in Rumpi Hills (500 individuals ha⁻¹), but higher than those of Mt. Cameroon (380 individuals ha⁻¹) (Forboseh et al., 2011; Sainge, 2017). Our estimates of BA are much higher than for submontane forests in Rumpi Hills and Mt. Cameroon (35 and 36 m²ha⁻¹, respectively); but similar to montane forests on Mt. Cameroon (88.9 m²ha⁻¹) (Forboseh et al., 2011; Sainge, 2017). On Mt. Cameroon, the differences in BA between submontane and montane forests were attributed to the presence of large individuals of *Schefflera* spp., found in montane forests not in submontane forests (Forboseh et al., 2011). In our study *Schefflera* spp. were found in *Carapa*, *Nuxia* and ridge forests, but not in

riverine forests. Possibly, the presence of large *Carapa grandiflora* and *Parkia* spp. in riverine forests compensated the absence of large individuals of *Schefflera* spp., as there were no differences in BA between these forest types. With regard to the secondary *Gnidia* forests, they had higher SD, lower BA and fewer species than old-growth forests, which has also been reported from other studies (e.g. Njomgang et al., 2011).

, Riverine and ridge forests in Mt. Mbam had higher species richness than all forests in Mt. Oku, which could be explained by the fact that there is lower human pressure in Mt. Mbam (the forest is located farther from villages, see Cuni-Sanchez et al. 2019), or that large mammals (seed dispersers) such as Preuss's monkey (*Allochrocebus preussi*), Olive baboons (*Papio anubis*) and bushbucks (*Tragelaphus scriptus*) can still be found in Mt. Mbam (Njabo & Languy, 2000). Thia et al. (2016), studying Ngel Nyaki Forest (a montane forest located in Nigeria, with similar species' composition to the forests we studied), showed how *Cordia millennii* is disproportionately dependent on large-bodied vertebrates for dispersal. Further plant and animal diversity studies on Mt. Mbam could help provide further insights into the factors explaining its greater tree diversity.

In this study AGB was more related to structural attributes than to taxonomic attributes; the same was reported from montane forests in northern Kenya and DRC (Cuni-Sanchez et al., 2017; Imani et al., 2017) and for lowland rainforests (e.g. Loubota Panzou et al., 2018; Poorter et al., 2015). AGB was related to H_{mean} , highlighting the importance of sampling tree height in the field to obtain accurate AGB estimates. A study from Tanzania showed that when excluding tree height in the calculations of AGB in montane forests over-valued the carbon resource by 24% (Marshall et al., 2012).

4.4 Implications of the findings and conclusions

Our findings show that the old-growth montane forests of the Cameroon Highlands (*Carapa*, *Nuxia*, ridge or riverine) store notable quantities of carbon in their AGB, indicating that carbon finance mechanisms related to avoiding deforestation could help protect these forests. Despite the limited extent of the remaining montane forests, biomass per unit area is high, and the degree of current threat and potential loss of the carbon store is high. Given the number of endemic and threatened species present (e.g. the Bannerman's Turaco), and the presence of Mbororo or Fulani pastoralists (considered indigenous, see <<https://www.theredddesk.org/>>), one option could be to consider the Carbon Communities & Biodiversity Alliance (CCBA) Standards to enter into the voluntary carbon market, which help provide extra livelihood income in the form of traded carbon units. Considering that montane forests store important quantities of carbon in their soils, due to slow decomposition rates at high altitudes (Girardin et al., 2010), soil carbon stocks could also be investigated and incorporated into such a mechanism. For instance, a recent study reported that soil organic carbon ranged between 86 and 302 Mg ha⁻¹ in Bambouto Mountains (also in the Cameroon Highlands) (Tsozué et al., 2019).

Another option to be considered is carbon finance mechanisms related to reforestation with a focus on taxa that allow additional income streams, in either a) the degraded parts of the old-growth forests or b) in the secondary *Gnidia* forests. One option could be to practice enrichment planting of indigenous trees which are useful to local communities (e.g. *Prunus africana* used for medicine or *Schefflera mannii* used for honey production). As highlighted by Greve et al. (2014), for reforestation projects to succeed in Africa, surrounding communities must obtain benefits from forests. Among these additional potential co-benefits which can improve the success of carbon-stocking projects there is improved market access of non-timber forest products harvested from within the reforested patch (Le et al., 2012), which would be possible if appropriate species (i.e. providing non-timber forest products) are chosen for enrichment planting projects.

In summary, we quantified AGB in four old-growth forest types and one secondary montane forest in the Cameroon Highlands. We documented that the old-growth forests store large quantities of AGB (about eight times more than secondary). We also showed that several height-diameter allometric models can be used in our study area, and that AGB was more affected by structural than taxonomic attributes. We recommend more research on the relationships between soil fertility, nutrient content and carbon stocks. There is great potential of these forests, both for avoided deforestation and reforestation carbon finance mechanisms, which could lead to stronger conservation through livelihood diversification for the communities living around these forests.

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Figures

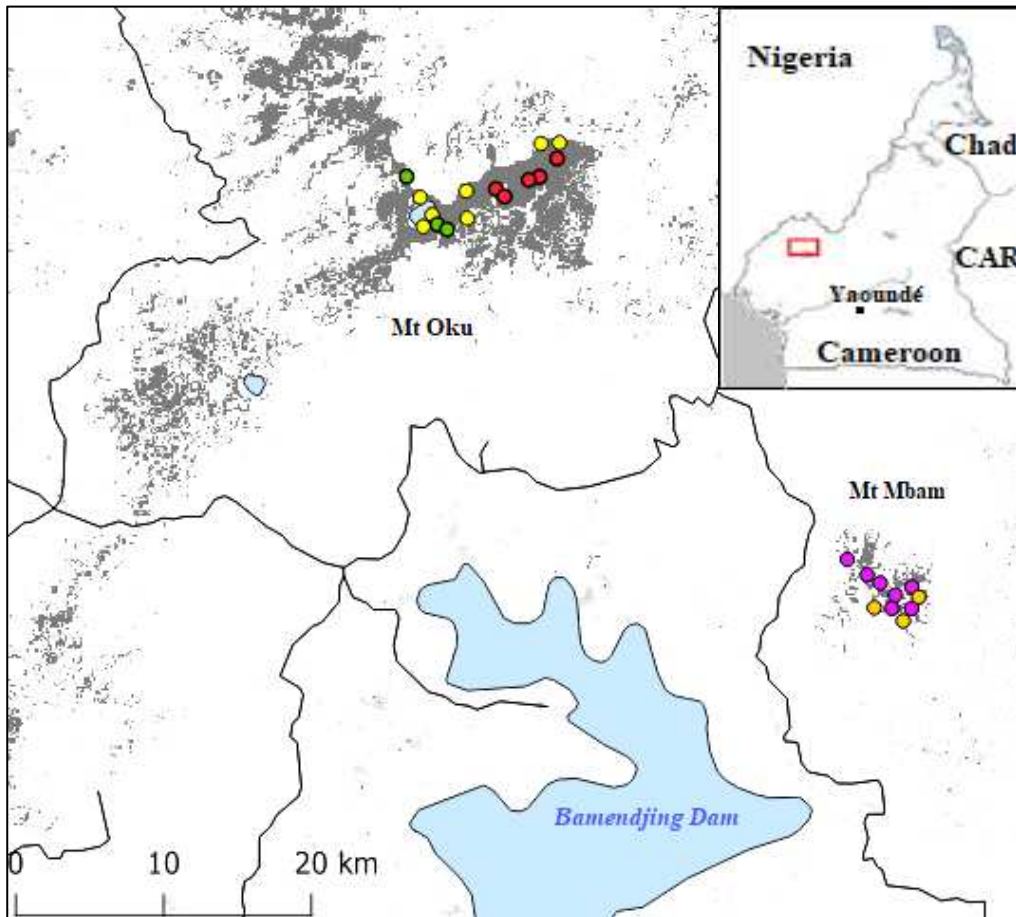


Fig. 1. Location of the montane forests studied in western Cameroon and the plots sampled in Mt. Oku and Mt. Mbam (see Fig. A1 in Appendix, for close-in views). Black lines refer to major roads, grey shading represents areas with >75% tree cover (Hansen et al., 2013). CAR refers to Central Africa Republic. Points colours: yellow = *Carapa* forests, green = *Gnidia* secondary forests, red = *Nuxia* forests, purple = ridge forests and orange = riverine forests

Fig. 2. Cluster dendrogram of similarity in tree species composition between the plots of the different forests types studied with regard to the Bray-Curtis index of dissimilarity (x-axis). Car: *Carapa* forests, Gni: *Gnidia* secondary forests, Nux: *Nuxia* forests, R: ridge forests and Riv: riverine forests. Car, Nux and Gni are found in Mt. Oku and R and Riv in Mt. Mbam.

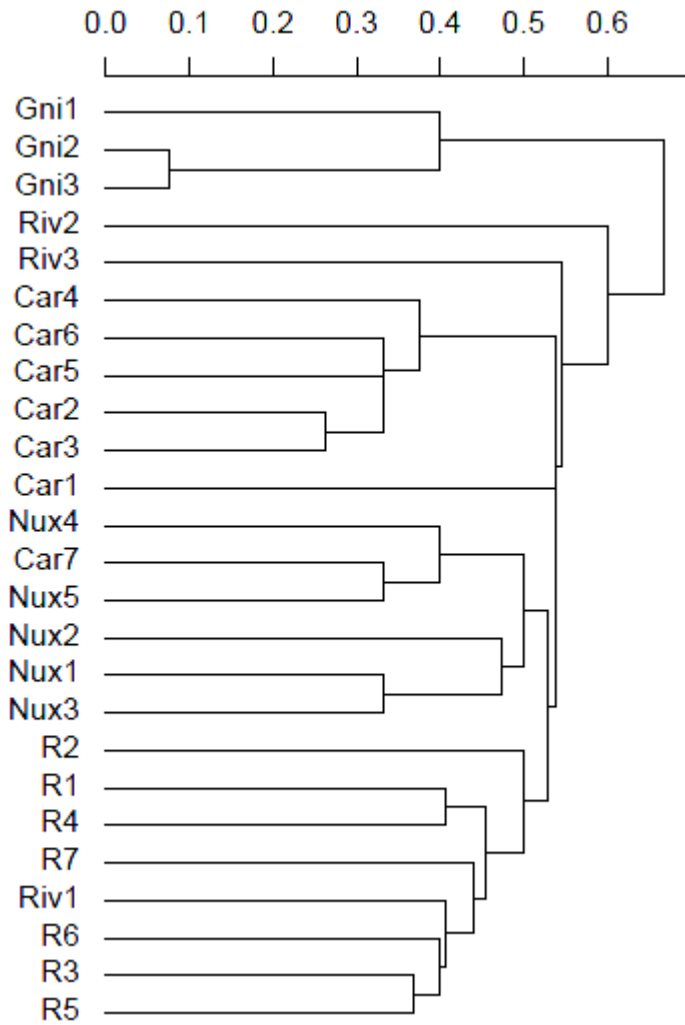
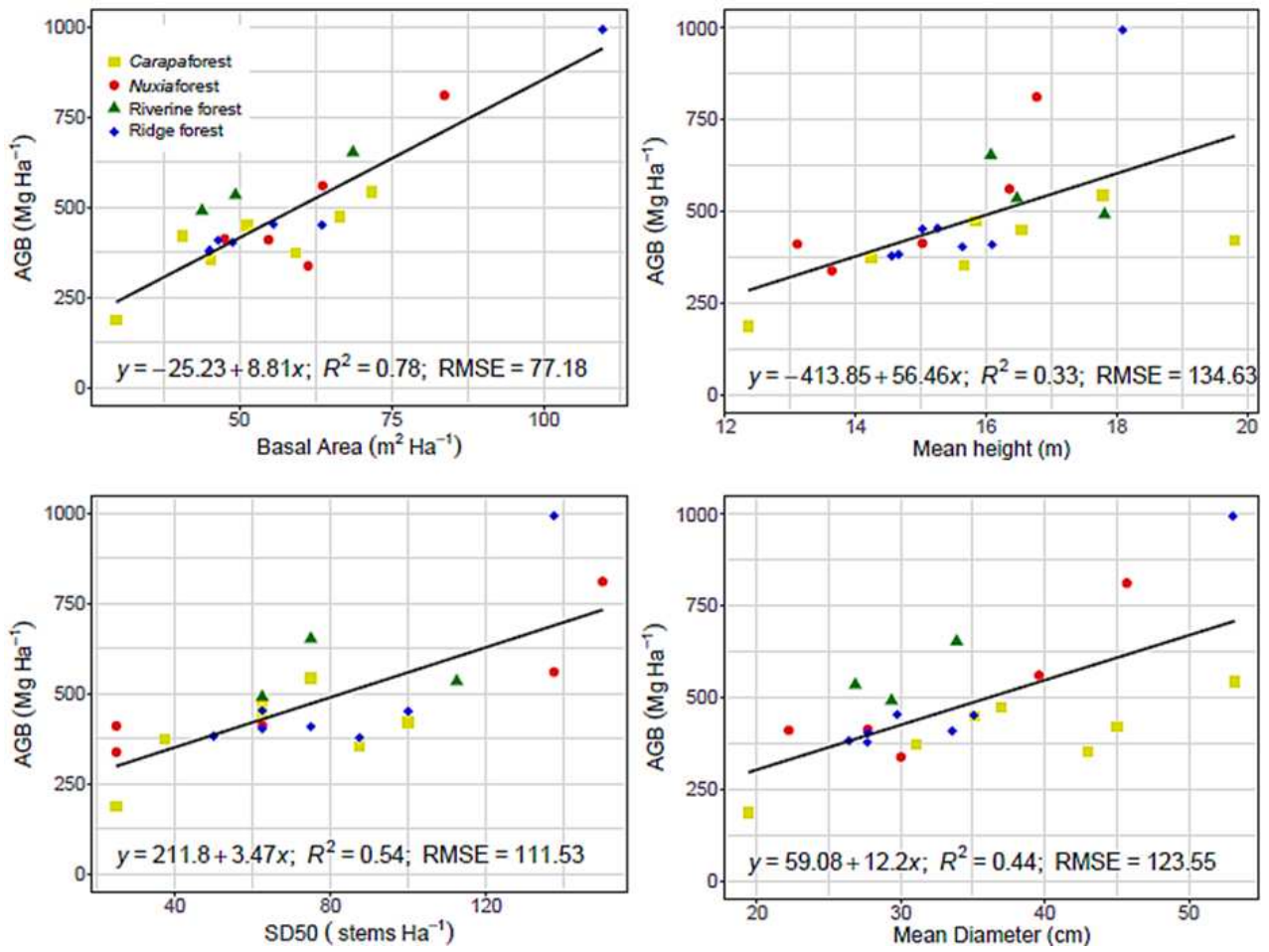


Fig. 3. Correlation between above ground biomass (AGB), and other forest attributes including: basal area, mean height, stem density of large trees (> 50 cm, SD₅₀) and mean diameter. Other forest attributes were not significantly correlated with AGB. Analysis is limited to old-growth forests.



Tables

Table 1. Mean diameter (mean diameter of all trees in the plot, D_{mean}), mean height (mean height of all trees in the plot, H_{mean}), basal area (BA), stem density (SD), stem density of large trees (with diameter $>50\text{cm}$, SD_{50}), Above ground biomass (AGB), wood mass density weighted by BA (WMD_{BA}), species richness, the rarefied species richness per 15 individuals (named Rsp), Shannon index (H') and the Pielou's evenness index (J') per forest type per mountain. Different letters within columns mark significant differences at $p < 0.05$. Values refer to mean \pm standard deviation. Note that the mean AGB of all old-growth forests is $476.3 \pm 168.7 \text{ Mg ha}^{-1}$.

Forest types	Mt. Oku			Mt. Mbam	
	Carapa forest	Nuxia forest	Gnidia forest	Riverine forest	Ridge forest
Altitude (m)	2100-2400	2500-2750	variable	1700-1900	1900-2300
Number of plots	7	5	3	3	7
D_{mean} (cm)	37.7 ± 10.8^a	33.1 ± 9.5^a	14.2 ± 0.3^b	30.1 ± 3.6^a	33.3 ± 9.3^a
H_{mean} (m)	16.0 ± 2.3^a	14.9 ± 1.6^a	11.0 ± 0.1^b	16.8 ± 0.9^a	15.6 ± 1.2^a
BA ($\text{m}^2 \text{ ha}^{-1}$)	52.1 ± 14.8^a	62.2 ± 13.5^a	15.4 ± 0.8^a	53.9 ± 13.1^a	59.2 ± 23.2^a
SD (stems ha^{-1})	380.4 ± 199.9^a	632.5 ± 322.9^{ab}	918.5 ± 6.3^b	529.2 ± 94.6^a	473.2 ± 131.4^a
SD_{50} (stems ha^{-1})	64.3 ± 26.5^a	80.1 ± 60.3^a	na	83.3 ± 26.0^a	82.1 ± 26.0^a
AGB (Mg ha^{-1})	399.9 ± 113.6^a	506.3 ± 188.7^a	49.4 ± 2.5^b	559.2 ± 83.9^a	495.7 ± 221.8^a
WMD_{BA}	0.580 ± 0.058^a	0.645 ± 0.075^a	0.519 ± 0.001^a	0.651 ± 0.043^a	0.608 ± 0.050^a
Number of species	8.7 ± 2.7^{ab}	6.8 ± 3.0^a	4.0 ± 1.7^a	13.3 ± 3.6^b	11.9 ± 2.2^b
Rsp	6.4 ± 0.9^a	4.8 ± 1.3^a	2.6 ± 0.6^b	6.6 ± 1.2^a	6.4 ± 2.6^a
H'	1.7 ± 0.3^a	1.4 ± 0.5^a	0.5 ± 0.3^b	2.1 ± 0.2^a	2.1 ± 0.3^a
J'	0.8 ± 0.1^a	0.7 ± 0.1^a	0.3 ± 0.2^b	0.8 ± 0.0^a	0.8 ± 0.1^a

Table 2. Above ground biomass (AGB in Mg ha^{-1}) as estimated using: a) field measurements of tree height and Chave et al. (2014) AGB equation (called AGB), b) Feldspauch Central Africa height-diameter allometric model and Chave et al. (2014) AGB equation (called AGB_Feld) and c) Fayolle et al. (2018) AGB equation which excludes tree height (called AGB_Fay), and the relative change in AGB (in %) between the different methods used. Values refer to mean \pm standard deviation.

	Forest types	AGB	AGB_Feld	AGB_Fay	% change method a - b	% change method a - c
Mt. Oku	Carapa forest	399.9 ± 113.6	706.8 ± 214.7	683.4 ± 212.5	76.4 ± 15.1	70 ± 14.4
	Nuxia forest	506.3 ± 188.7	905.8 ± 354.6	888.8 ± 382.3	78.5 ± 10.1	73.2 ± 10.2
Mt. Mbam	Riverine forest	559.2 ± 83.9	786.5 ± 188.8	768.4 ± 188.4	39.5 ± 12.2	36.3 ± 12.6
	Ridge forest	495.7 ± 221.8	838.9 ± 385.3	817.5 ± 389.1	68.7 ± 6.9	63.7 ± 7.1
Significance paired t-test	p value				<0.001	<0.001

