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Contribution of Tree Size and Species on Aboveground Biomass across Land Cover Types in the Taita Hills, Southern Kenya

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Abstract: Tropical landscapes comprise a variety of land cover (LC) types with characteristic canopy structure and tree species. Depending on the LC type, large-diameter trees and certain tree species can contribute disproportionately to aboveground biomass (AGB), and these patterns are not described at landscape-level in LC type specific studies. Therefore, we investigated the impact of large trees and tree species on AGB across a range of LC types in Taita Hills, Kenya. Data included 239 field plots from seven LC types: Montane forest, Plantation forest, Mixed forest, Riverine forest, Bushland, Grassland, and Cropland and homestead. Our results show that the contribution of large trees (DBH > 60 cm) on AGB was greatest in Riverine forest, Montane forest and Mixed forest (34–87%). Large trees were also common in Plantation forests and Cropland and homestead. Small trees (DBH < 20 cm) covered less than 10% of the total AGB in all forest types. In Grassland, and Cropland and homestead, smaller DBH classes made a greater contribution. Bushland differed from other classes as large trees were rare. Furthermore, the results show that each LC type had characteristic species with high AGB. In the Montane and Mixed forest, *Albizia gummifera* contributed 21.1% and 18.3% to AGB, respectively. *Eucalyptus* spp., exotic species planted in the area, were important in Mixed and Plantation forests. *Newtonia hildebrandtii* was the most important species in Riverine forests. In Bushland, *Acacia mearnsii*, species with invasive character, was abundant among trees with DBH < 30 cm. *Vachellia tortillis*, a common species in savannahs of East Africa, made the largest contribution in Grassland. Finally, in Cropland and homestead, *Grevillea robusta* was the most important species (>25% of AGB). Our results highlight the importance of conserving large trees and certain species to retain AGB stocks in the landscape. Furthermore, the results demonstrate that exotic tree species, even though invasive, can have large contribution to AGB.

Keywords: landscape; aboveground biomass; tree species; land cover; important value index

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1. Introduction

Aboveground biomass (AGB) is a crucial component of the global carbon cycle and an essential ecological variable. It has been recognized as a Global Climate Observing System (GCOS) Essential Climate Variable (ECV) and plays a critical role in the REDD+ framework (reducing emissions from deforestation and forest degradation and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries) [1]. AGB is also an important input to Earth system modeling and central to provision of food and fiber worldwide, as well as to soil, fire, and water management [2]. However, changes in land use, particularly tropical deforestation and forest degradation have led to global reduction of AGB [3]. In Africa, a considerable fraction of AGB is found outside tropical forests, for example, in savannah woodland, bushland, and agricultural landscapes [4]. This highlights the need for further research on AGB patterns across different LC types in the mosaic landscapes that consist of multiple LC types [5].

Stem diameter distribution and its links to AGB in different LC types are important for understanding carbon stocks and their dynamics [6]. Stem diameter distribution relates to a wide variety of ecosystem processes and services. In particular, large-sized trees are vital to forest structure, function, diversity [7], and regulation of ecosystem services [8,9]. Large trees make a disproportionately large contribution to the AGB of tropical forests [10–15] and their biomass production [16].

In Africa, large trees are widely distributed also outside tropical forests, for example, in woodlands, bushlands, and agroforestry systems [13,17]. Many studies have reported the important contribution of large trees to AGB in Africa [13,14,18–20], but some have revealed the important role played by the small-diameter trees in the region [21,22]. However, anthropogenic, environmental and climatic dynamics have contributed to the substantial decline of large-sized trees in Africa [23,24]. For example, illegal logging, agricultural intensification, insect and disease attacks, overgrazing, browsing, droughts and repeated wildfires can significantly reduce the number of large trees [25]. This affects the tree size distribution and hence, AGB [26]. Moreover, relatively little is known about the distribution and abundance of large trees in African savannah. This information is critical, as large trees can act as focal points for vegetation restoration in degraded agricultural landscapes and support climate change mitigation efforts through conservation [27].

Biomass allocation patterns are also influenced by tree species [13,19,28]. Only certain tree species are capable of reaching large sizes and hence, a few dominant tree species can contribute disproportionately to the AGB of a given LC type [14]. This may be due to the functional dominance of large trees [28]. Disturbance regimes that allow for the development of large-diameter trees promote the presence of these trees in an ecosystem [29]. High species richness and the presence of large tree species help to maintain vegetation structure, ecological function, and response to forest disturbance [30,31]. Landscapes with a diverse array of large tree species are better able to respond to disturbances and maintain their structure and ecological function [30]. In African savannahs, tree species are seriously impacted by megafauna, wildfires and agriculture [25], resulting in a decline in the AGB of large trees [26].

Large trees play a significant role in supporting ecosystem services and biodiversity. While all trees are valuable components of ecosystems, large old trees are typically keystone structures in forests, woodlands, savannas, agricultural landscapes, and urban areas, playing unique ecological roles not provided by younger, smaller trees [7]. The large-sized trees influence the rates and patterns of regeneration and succession [32], reduce moisture and light availability to younger trees [33], and influence the mortality of small trees [34]. They shape the structure of forests [35], occur at low stem densities, but influence spatial patterns over long inter-tree distances [36,37]. Large trees act as habitat for over 30% of vertebrate species in some ecosystems and create microenvironments with high levels of soil nutrients and plant species richness. Species dominance in landscape and LC types is important for ecosystem function and can be measured, for example, by the species important value index (IVI) [38,39]. Accurate assessments of the contribution of dominant tree species to AGB in different LC types are necessary for developing effective strategies to mitigate global climate change, but also for understanding their ecological benefits.

In this study, we examined the presence and effect of large trees and tree species on AGB in a mosaic landscape comprising of several LC types in the Taita Hills, Kenya. More specifically, we (1) studied how different sizes of trees contribute to AGB in different LC types; (2) examined which species contribute most to the large trees and AGB in different LC types; and (3) assessed ecological significance of tree species in the different LC types. We hypothesized that only a small number of the largest trees are responsible for the preponderance of AGB although there might be considerable differences between the LC types. As only certain species can develop into large individuals, we expected that total AGB is also affected by tree-species composition of the LC type.

2. Materials and Methods

2.1. Study Area

The Taita Hills are located in southeastern Kenya (Figure 1) and belong to the Eastern Arc Mountains, which are highly valuable for conservation [40]. The field plots were combined from several previous studies (see Section 2.2 below for details) and entailed variation in topography and LC types (Table 1). The area is topographically variable, and elevation ranges from approximately 600 m a.s.l. to the highest peak of the Taita Hills, Vuria (2208 m a.s.l.). The rainfall varies according to the topography between 500 mm and 1200 mm per year from plains to the hills. The soils are mostly cambisols that originate from weathered gneiss and are often gravelly to sandy-loamy and shallow [41]. Because these soils are well drained, they are less fertile. The steep slopes and transition zones are dominated by regosols, which are shallow, highly permeable, and have low water holding capacity [41]. However, due to favorable climate and edaphic conditions in the Taita Hills, as well as economic growth due to location on a transport node and tourist attractions [42], the human population in the area is growing and new agricultural land is cleared.

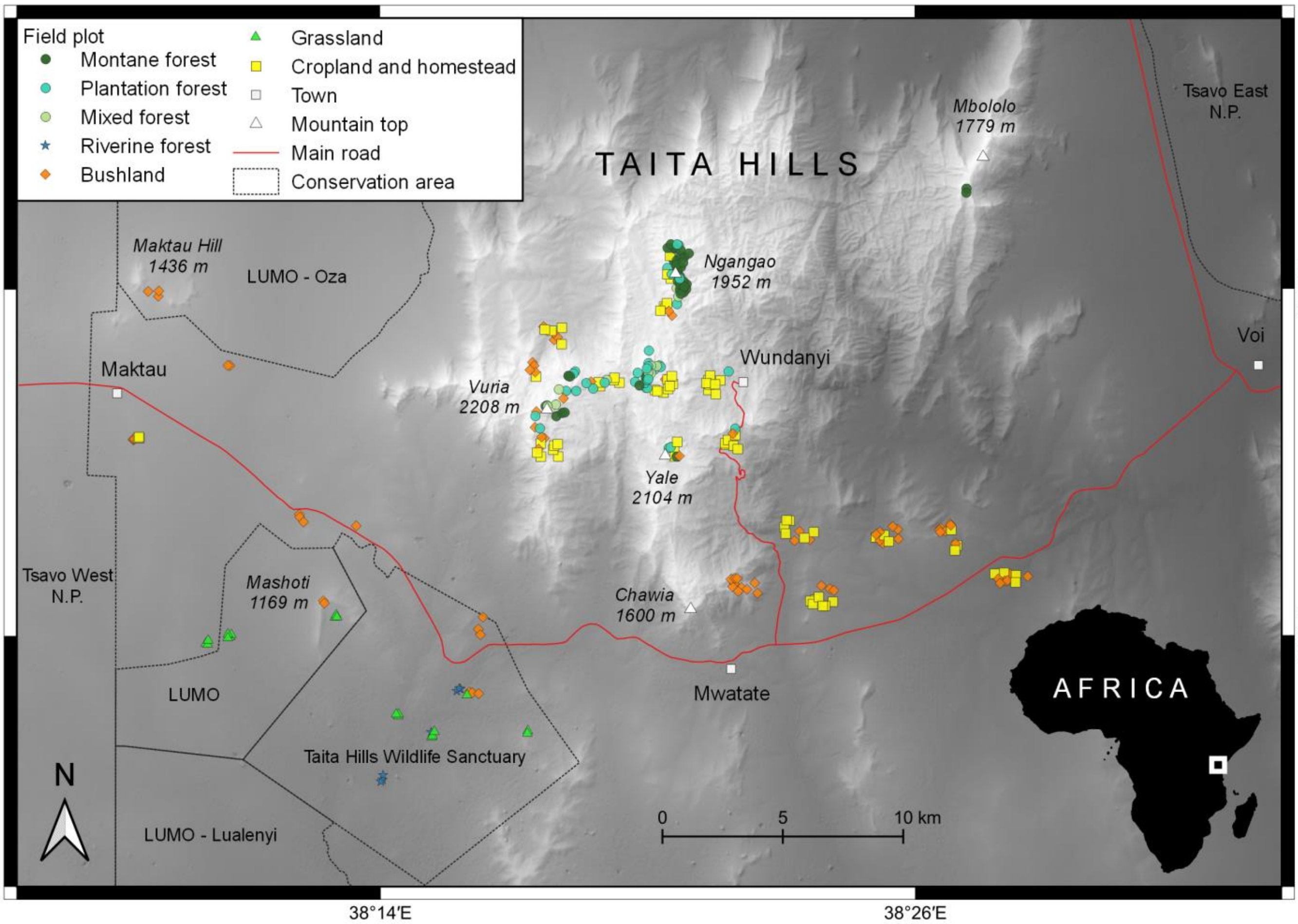

Figure 1. Location of the study area and field plots with different land cover types.

Table 1. Land cover (LC) types, number of 0.1 ha field plots in each type and elevation range.

LC Type	Description	n	Number of Tree Species	Elevation (m)
Montane forest	Montane forest of native tree species.	39	74	1506–2147
Plantation forest	Plantation forest of exotic tree species (*Eucalyptus* spp., *Cupressus lusitanica*, *Pinus* spp.)	39	30	1407–2133
Mixed forest	Montane or plantation forest with mixed species composition (<80% of the species are either native or exotic).	11	38	1641–2136
Riverine forest	Forest and woodland along the river.	7	4	859–887
Bushland	*Acacia-Commiphora* bushland and thicket in the plains and lower height *Acacia mearnsii* plantations in hills.	70	70	675–1987
Grassland	Open savanna grassland with scattered trees.	9	8	880–1049
Cropland and homestead	Open crop fields, agroforestry systems, and homestead with woody vegetation.	64	62	669–1765

African tropical montane forests have high AGB that vanishes rapidly, which along with rich biodiversity emphasize the importance of their conservation [43]. The Taita Hills are densely populated and have undergone large-scale deforestation, and as a result, the remaining forest patches are very fragmented and located near the mountaintops [44]. Some of the most common native species include *Tabernaemontana stapfiana*, *Macaranga capensis*, *Oxyanthus speciosus* and *Phoenix reclinata*, and *Celtis africana*. Plantations of exotic trees (e.g., *Eucalyptus* spp., *Pinus patula*, *Cupressus lusitanica*, and *Acacia mearnsii*) are present adjacent to the montane forests, and mixed species stands (native–exotic) are also common. Otherwise, the landscape in the hills consists of smallholder agriculture (mainly maize fields with intercropping of beans), homesteads and settlements. Agroforestry and trees outside forests (e.g., *Grevillea robusta*) are usual in the hills.

The lower elevation plains of the Taita Hills belong to the Tsavo ecosystem, which include Tsavo East and West National Parks along with several other protected areas. Livestock and wildlife populations are large in the plains. Cattle, elephants, and buffaloes constitute the most important herbivores. Some of the field plots were located within two protected areas, Taita Hills Wildlife Sanctuary (THWS) and LUMO Community Wildlife Sanctuary, where herbivores maintain open Grassland. THWS also has protected Riverine forest. The rest of the plots were located in areas outside the conservation areas, which consist of dryland agriculture and *Acacia-Commiphora* bushland and thickets. Common crops in the plains include cassava, maize, and legumes. Some typical woody species are *Vachellia tortillis*, *Commiphora baluensis*, *Vachellia xanthophloea*, *Albizia antihelmintica*, and *Commiphora schimperi*.

2.2. Field Inventory Data and Biomass Calculations

We compiled data from several field campaigns conducted between 2013 and 2018 in the study area [4,45,46]. The resulting sampling design does not follow any particular sampling scheme, as each campaign focused on different sub-areas. However, the aim of each campaign was to cover the complete variation in woody AGB in the sub-area, which should ensure that the compiled data effectively covers the variation in AGB in the study area. Furthermore, the field plots were surveyed using the same protocol in each campaign, allowing us to combine data from different campaigns. Part of the plots were randomly selected from the respective study areas, while another part of the plots was selected purposefully from areas with different assumed AGB levels and species composition (e.g., know locations of montane and plantation forests).

In all the plots, the living trees with the diameter at breast height (DBH) $\geq$ 10 cm in a circular 0.1 ha plots (17.84 m radius) were measured for diameter and identified for species [47]. The DBH measurement was made using a diameter measurement tape. In addition, tree height (H) was measured for at least three sample trees (minimum, maximum and median DBH) using either a laser range finder (Laser Technology TruPulse 360) or hypsometer (Suunto). In the plots outside forest, most trees were measured for H as there were typically very few. Furthermore, for palms, H was always measured as DBH is not good predictor of AGB. Ten forest plots surveyed in 2013 lacked H measurements and maximum H was estimated from the canopy height model (CHM) based on airborne laser scanning (ALS) data [48]. Tree species were identified by local para-taxonomists or a ranger who knows the majority of the species. The fraction of species that remained unidentified corresponds to 2% of the measured stems.

For trees with only DBH measurement, height was predicted using a two-parameter Curtis height function [49]. Furthermore, non-linear mixed effect modeling and the plot as random effects (e.g., [50]) were used to calibrate the H-DBH model for each sample plot. This was completed using the 'nlme' package [51] in the R environment [52]. The root mean square error (RMSE) of the model was 4.0 m (29.4%).

The pan-tropical allometric equation from Chave et al. [53] was used to estimate AGB (kg) for most of the trees based on wood-specific density (WD, g cm^{-3}), DBH (cm), and H (m): AGB = $0.0673 \times (WD \times DBH^2 \times H)^{0.976}$. This model is based on a destructive dataset of trees at 58 sites across a wide range of environmental and vegetation types in Africa, South America, South Asia and Australia [53]. In addition, genus-specific models were used for *Acacia* spp. (AGB = $\exp(-1.59 + 2.19 \times \log(DBH)) \times 1.05$) and *Eucalyptus* spp. (AGB = $\exp(-1.71 + 2.21 \times \log(DBH)) \times 1.29$) [54]. AGB of *Pinus* spp. were estimated using stem volume (V, m^{-2}) equation (V = $8.42 \times 10^{-4} \times DBH - 7.354 \times 10^{-3} \times DBH + 2.506 \times 10^{-2}$) [55] and biomass expansion factor for tropical pines [56]. Values of WD were obtained from the 'biomass' package [57] in R. If species-specific WD could not be obtained, we used genus-specific WD estimates, and if that was not available, we used the mean of all species present in the data (i.e., study area specific mean value).

Land cover (LC) describes the observed biophysical surface of the earth (e.g., forest, bare soil, grassland, bushland and cropland). On the other hand, land use refers to the human arrangement and activities on the earth's surface (e.g., agroforestry, pasture, and conservation). However, land use and land cover are often linked (e.g., croplands are cultivated and managed) and a classification system for a particular task can include elements of both. In our data, LC was recorded in the field but not using a consistent classification system. In addition, several people were involved in field campaigns, which can cause variation to classification. Therefore, we harmonized the LC classification and checked every plot using field-based information (e.g., if plot was cultivated or not), tree species composition (fractions of native and exotic species) and ALS data corresponding to field campaigns (canopy cover and height). The final LC classes with the number of plots in each class are shown in Table 1 and photographic examples are shown in Figure 2. If we could not classify a plot to one of these LC types (e.g., located on the border of two classes because of random sampling), we excluded the plot from this study. As a result, we used a total of 239 plots in this study.

Descriptive statistics for the plots are provided in Table 2. Mean stem density and basal area were relatively large in Montane forest, Mixed forest, and Plantation forest, and relatively small in Grassland, Cropland and homestead, Riverine forest, and Bushland. The tallest mean height was found in the Plantation forest and was relatively high in all forest types. In comparison to other types, Riverine forest had a very large mean DBH. As a result of wide variation in stand variables, mean AGB ranged from 11.6 Mg ha^{-1} in Grassland to 323.6 Mg ha^{-1} in Montane forest with the largest AGB values observed in Montane (643.2 Mg ha^{-1}) and Plantation forest (671.1 Mg ha^{-1}).

Figure 2. (**A**) Riverine forest dominated by *Vachellia xanthophloea* by Bura river, 2018. (**B**) Mixed forest dominated by *Eucalyptus* spp. with *Phoenix reclinata* in Wesu, 2021. (**C**) Agroforestry with *Mangifera indica* trees in Mwatate, 2021. (**D**) Cypress (*Cupressus lusitanica*) in the northern part of Ngangao forest, 2017. (**E**) Native montane forest, Ngangao, 2018. (**F**) *Acacia-commiphora* bushland in the lowlands in Mwatate, 2019. (**G**) Open grassland with single trees in Taita Hills Wildlife Sanctuary, 2018. (**H**) Landscape mosaic with croplands, native and plantation forests in the middle of the Taita Hills, 2018. Photos by P. Pellikka, except (**A**) by Janne Heiskanen.

Table 2. Descriptive statistics for the field plots.

LC Type	Variable	Mean	SD	Range
Montane forest (n = 39)	Density (trees ha^{-1})	664.0	220.2	150.0–1214.0
	Basal area (m^2 ha^{-1})	44.9	14.9	16.9–85.6
	Mean height (m)	13.8	2.2	8.2–18.2
	Mean DBH (cm)	24.7	15.8	10.0–123.5
	AGB (Mg ha^{-1})	323.6	134.2	117.3–643.2
Plantation forest (n = 39)	Density (trees ha^{-1})	505.0	236.6	120.0–1192.8
	Basal area (m^2 ha^{-1})	36.6	19.8	5.1–94.3
	Mean height (m)	16.4	4.4	10.1–29.7
	Mean DBH (cm)	26.8	14.7	10.0–118.5
	AGB (Mg ha^{-1})	211.4	131.7	21.5–671.1
Mixed forest (n = 11)	Density (trees ha^{-1})	646.0	200.9	411.3–1060.0
	Basal area (m^2 ha^{-1})	40.1	13.3	16.6–555.5
	Mean height (m)	11.9	2.8	7.7–16.6
	Mean DBH (cm)	23.7	14.9	10.0–110.1
	AGB (Mg ha^{-1})	223.3	95.5	85.4–388.4
Riverine forest (n = 7)	Density (trees ha^{-1})	69.0	58.1	10.0–190.7
	Basal area (m^2 ha^{-1})	21.7	12.6	61.0–42.7
	Mean height (m)	16.2	5.0	9.6–24.1
	Mean DBH (cm)	53.7	34.0	10.6–170.0
	AGB (Mg ha^{-1})	155.7	121.2	25.9–379.1
Bushland (n = 70)	Density (trees ha^{-1})	123.0	145.0	10.0–960.0
	Basal area (m^2 ha^{-1})	4.2	4.8	0.1–23.6
	Mean height (m)	7.4	2.3	3.0–13.5
	Mean DBH (cm)	18.6	9.1	10.0–109.0
	AGB (Mg ha^{-1})	15.9	23.7	0.1–127.1
Grassland (n = 9)	Density (trees ha^{-1})	59.0	53.0	20.3–171.3
	Basal area (m^2 ha^{-1})	2.4	2.1	0.4–7.3
	Mean height (m)	8.4	1.3	6.8–11.2
	Mean DBH (cm)	19.4	12.2	10.1–63.5
	AGB (Mg ha^{-1})	11.6	12.5	1.9–42.3
Cropland and homestead (n = 64)	Density (trees ha^{-1})	64.0	72.0	10.0–240
	Basal area (m^2 ha^{-1})	2.4	2.1	0.4–7.3
	Mean height (m)	8.4	1.3	3.0–20.3
	Mean DBH (cm)	21.5	11.8	10.0–100.7
	AGB (Mg ha^{-1})	15.0	21.8	0.2–108.9

2.3. Data Analysis

First, we studied how AGB is distributed in DBH classes in the LC types. All trees of each type were analyzed together and the mean AGB calculated for DBH classes from 10 cm up to >70 cm range in 10 cm intervals. The results were visualized as a bar plot. We also computed the fraction (%) that each DBH class contributed to the total AGB of each LC type. Furthermore, the contribution of different DBH classes, particularly for large trees, can vary between plots within each LC type. Therefore, we also computed the fraction of AGB covered by large trees for each plot and compared different LC types.

Next, we studied what tree species contributed most to the AGB in different LC types and DBH classes. For each type, we identified the species that made the largest contribution to total AGB, and analyzed whether, and how much, these species contributed to each DBH class. Furthermore, we studied which species were most common in different DBH classes.

Finally, we examined ecological importance of the tree species in the LC types in the landscape. The density (stems/ha), frequency (probability of occurrence by LC types), and dominance (degree to which one or several species have a major influence controlling the other species in their ecological community) of species in each plot were calculated using Equations (1)–(3). Tree density, frequency and dominance were then converted into relative density (RDE), frequency (RF) and dominance (RDO) (Equations (4)–(6)). Relative values provide more meaningful information than absolute measurement in comparing similar forest stands [58]. The relative density, frequency, and dominance were then summed to calculate the important value index (IVI) (Equation (7)) for each species in the LC types [59]. The IVI has been commonly used to assess the importance of tree species [59–61], and for understanding the share of individual tree species in the LC types [62]. It also maximizes the differences among stands with similar species composition that may not be demonstrated with just a single measure. It further represents the relative importance or dominance of a tree species in an LC type and ranged from 0 to 300. A zero value resulted when a species did not occur in an area, while a value of three hundred indicates sole dominance.

$$\text{Density} = \frac{\text{Total number of a species}}{\text{Total area sampled}} \tag{1}$$

$$\text{Frequency} = \frac{\text{Area of plots in which a species occurs}}{\text{Total area sampled}} \tag{2}$$

$$\text{Dominance} = \frac{\text{Total basal area of a species}}{\text{Total area sampled}} \tag{3}$$

$$\text{Relative density (RDE)} = \frac{\text{Number of individuals of a species}}{\text{Number of individuals of all species}} \times 100 \tag{4}$$

$$\text{Relative frequency (RF)} = \frac{\text{Frequency of a species}}{\text{Sum frequency of all species}} \times 100 \tag{5}$$

$$\text{Relative dominance (RDO)} = \frac{\text{Total basal area of the species}}{\text{Total basal area of all species}} \times 100 \tag{6}$$

$$\text{Important value index (IVI)} = \text{RF} + \text{RDE} + \text{RDO} \tag{7}$$

3. Results

3.1. Contribution of Diameter Classes to Aboveground Biomass

A high mean AGB was observed in the largest DBH classes for all LC types (Figure 3A). In all the LC types except Riverine forest, stem count decreased towards the larger DBH classes (Figure 3B). The stem count of the smaller DBH trees was the highest in Montane and Plantation forests. In Riverine forest, stem count varied the least between the DBH classes.

Percentage AGB and stem count of DBH classes varied considerably between the LC types (Figure 4). A majority of total AGB (80%) was in DBH $\geq$ 70 cm trees in Riverine forest (Figure 4A). In Montane forest, Mixed forest and Grassland, trees with DBH $\geq$ 60 cm accounted for approximately a third of the total AGB although they covered only a small proportion of the stem count (Figure 4B). Furthermore, in Plantation forest and Cropland and homestead types, large trees (DBH $\geq$ 60 cm) were common but accounted for less of the total AGB (24% and 19%, respectively). Bushland differed from the other LC types because it had a majority (56%) of the total AGB stored in the smallest DBH classes (<30 cm) (Figure 4A) and the largest proportion of the smaller DBH trees (Figure 4B). Grassland also had a high fraction of AGB in the two lowest DBH classes, and Cropland and homestead in DBH classes 20–29.9 cm and 30–39.9 cm. In the Riverine forest, the smallest DBH classes had a very small fraction of AGB.

Supplementary Figure S1 shows the contribution (%) of different DBH classes to AGB at each field plot. The plot-level analysis confirms that the patterns observed in the LC-type analysis (Figure 4) are also present in the plots, although plot-level variation is large. The median AGB contribution was always the greatest in the largest DBH class ($\geq$70 cm) in the forests. Contribution was greater than 80% in the Riverine forest plots, while it was only greater than 25% in other types. Contribution of DBH classes reduces systematically in the Montane forest towards smaller DBH classes. In the Bushland and Grassland, the smallest

DBH class (10.0–19.9 cm) had a large variation and contribution range roughly from zero to 100%. In the Cropland and homestead, the variation between the plots is the greatest. However, the greatest median contribution (approximately 75%) is observed in the largest DBH class (DBH $\geq$ 70 cm).

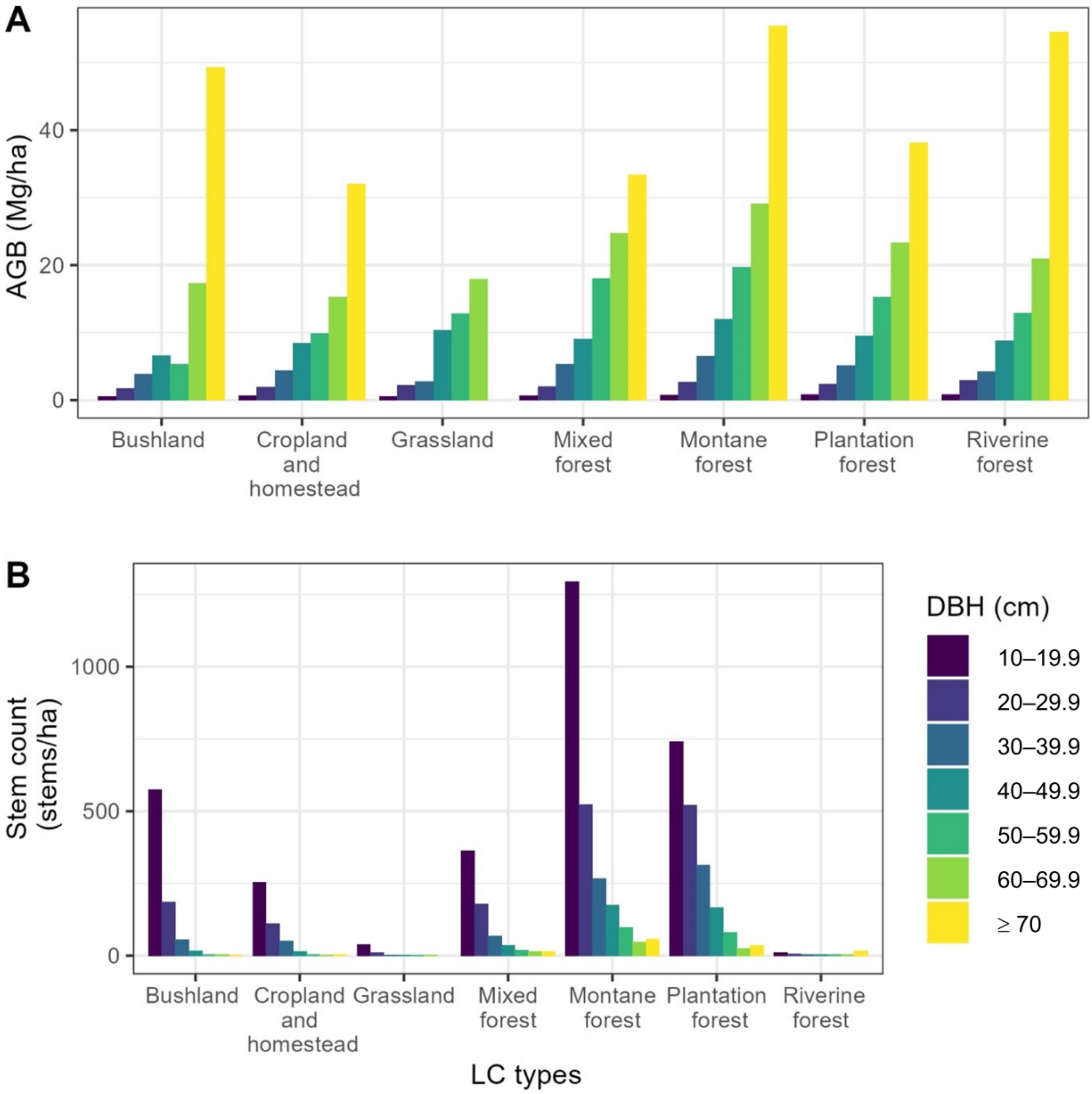

Figure 3. Mean (**A**) aboveground biomass (AGB) and (**B**) stem count in different diameter at breast height (DBH) classes and land cover (LC) types.

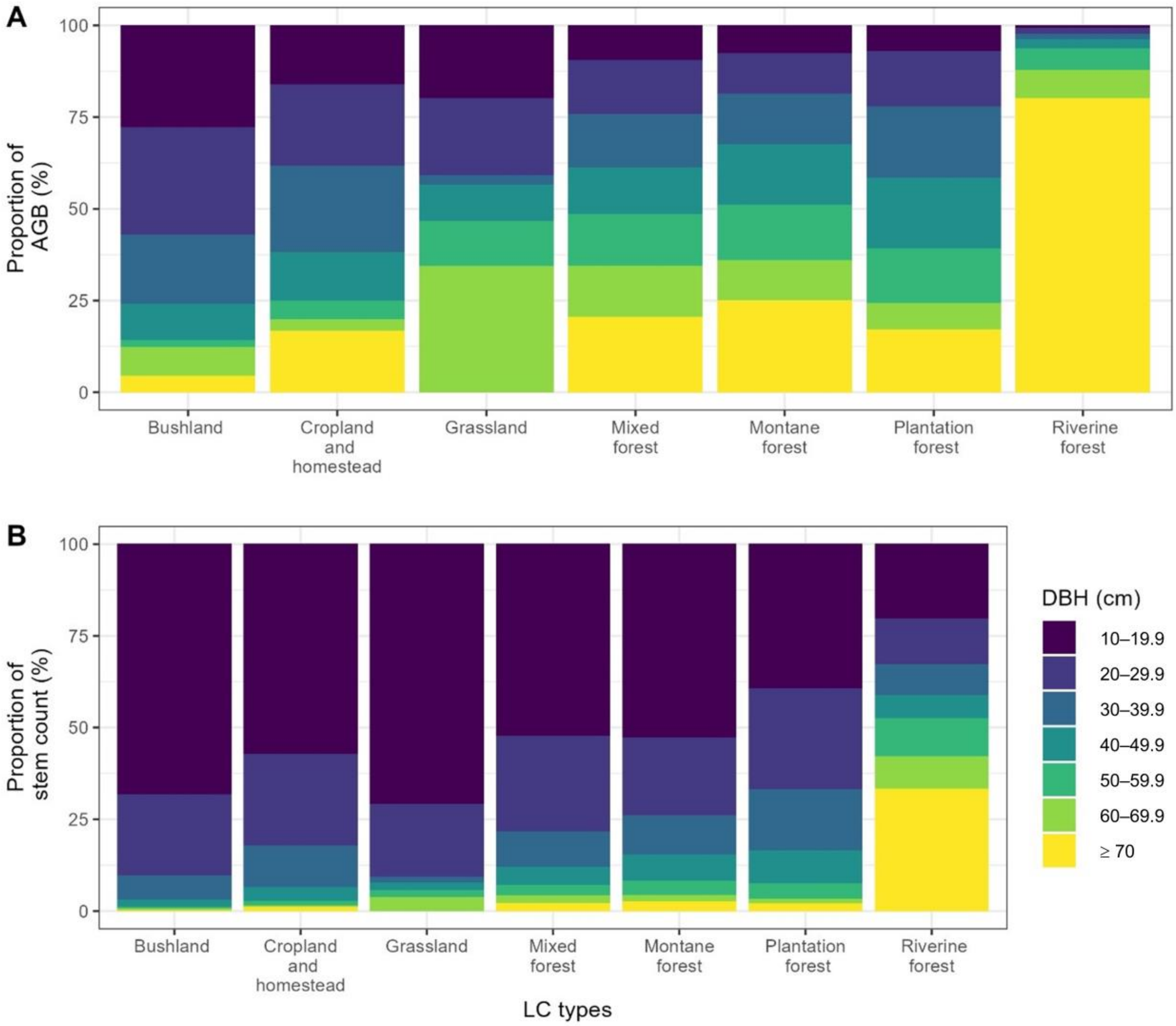

Figure 4. Proportion of (**A**) aboveground biomass (AGB) and (**B**) stems in different DBH classes and land cover (LC) types.

3.2. Contribution of Tree Species on Aboveground Biomass

Table 3 shows the tree species that contribute the most to AGB in each LC type, as well as their contribution to AGB by DBH class. *Albizia gummifera* made the largest contribution to AGB in both Montane forest and Mixed forest (21.1% and 18.3%, respectively). It had a particularly large contribution in larger DBH classes (DBH $\geq$ 40 cm). *Tabernaemontana stapfiana* also had a contribution greater than 10% to AGB in Montane forest, but it was not as common among the largest trees as *A. gummifera*. Other important Montane forest species in terms of AGB were *Macaranga capensis*, *Millettia oblata*, and *Syzygium guineense*. In the Mixed forest and Plantation forest, *Eucalyptus* spp. were the exotic species with the greatest contribution to AGB. Although present in all the DBH classes, its contribution was particularly large in the larger DBH classes. Other important species in the Plantation forest included *Cupressus lusitanica* and *Pinus* spp. The Riverine forest plots only had four tree species with DBH 10 cm or larger. *Newtonia hildebrandtii* contributed by far the greatest proportion to AGB (67.2%) with only trees larger than 30 cm in DBH.

Table 3. Contribution of the most important tree species to aboveground biomass (AGB) as a fraction of total AGB (%) in land cover (LC) type and diameter at breast height (DBH) classes.

LC Type	Species	Contribution to AGB (%)	Contribution to AGB (%) of DBH Class (cm)						
			10–19.9	20–29.9	30–39.9	40–49.9	50–59.9	60–69.9	≥70
Bushland	*Acacia mearnsii*	22.3	32.7	28.8	8.9	12.9		22.4	
	Albizia amara	17.6	2.5	12.1	30.1	40.2	37.4	41.0	
	Newtonia hildebrandtii	4.6							100.0
	Commiphora africana	4.6	3.3	5.9	5.5		46.1		
	Agauria salicifolia	4.3		2.8	9.9			22.1	
Cropland and homestead	*Grevillea robusta*	25.2	8.6	21.4	39.2	57.6	47		
	Eucalyptus sp.	12.1	6.1	4.9	16.8	16.8	29.2	76.7	
	Mangifera indica	11.6	5.7	3.4	3.6	5.3			49.4
	Ficus thonningii	4.5					13.1	23.3	18.4
	Persea americana	4.4	4.3	7.1	6.9		10.7		
Grassland	*Vachellia tortillis*	63.9	38.1	75.6		100.0	100.0	53.1	
	Acacia reficiens	16.1						46.9	
	Portulacaria afra	8.1	35.6	5.0					
	Albizia anthelmintica	7.6	4.4	19.4	100.0				
	Acacia senegal	1.8	9.3						
Mixed forest	*Albizia gummifera*	18.3	5.5	5.5	14	16.3	23.2	29.4	27.2
	Eucalyptus sp.	11.5	7.9	5.6	5.8	8.6	9.3	14.5	22.8
	Cupressus lusitanica	9.7	4.4	8.0	6.6	28.1	9.8	9.4	4.5
	Xymalos monospora	6.8	5.7	8.0	5.8	4.1		4.9	14.6
	Nuxia floribunda	6.6	1.4	4.7	8.4		18.6	5.6	6.1
Montane forest	*Albizia gummifera*	21.1	2.6	3.8	10.0	7.5	13.9	20.1	54.3
	Tabernaemontana stapfiana	12.9	12.3	20.3	19.7	17.4	17.1	9.0	2.2
	Macaranga capensis	9.3	5.0	6.7	7.0	10.5	15.1	16.8	5.3
	Millettia oblata	6.7	6.2	7.1	11.6	13.4	4.7		3.8
	Syzygium guineense	5.9	1.4	3.4	2.2	6.8	9.0	11.7	5.4
Plantation forest	*Eucalyptus sp.*	57.2	43.6	45.9	41.0	47.3	55.3	79.1	93.9
	Cupressus lusitanica	17.5	14.2	22.8	24.0	27.7	16.9	8.0	
	Pinus sp.	16.7	5.0	16.9	27.1	20.3	17.8	12.9	6.1
	Acacia mearnsii	2.5	14.6	6.1	2.0		1.0		
	Grevillea robusta	1.0	0.1	0.6	2.8	2.1			
Riverine forest	*Newtonia hildebrandtii*	67.2			72.2	39.6	15.2	77.6	72.7
	Vachellia xanthophloea	31.7	100.0	75.5	27.8	29.4	84.8	22.4	27.3
	Cordia goetzei	0.8				31.1			
	Trichilia lepidota	0.4		24.5					

Outside forests, *Acacia mearnsii* and *Albizia amara* made the largest contribution in Bushland. *A. mearnsii* is an exotic species and was very common in the smaller DBH classes (DBH < 30 cm), while *A. amara* was more common in the larger DBH classes (DBH ≥ 30 cm). In the Grassland plots, *Vachellia tortillis* made a particularly large contribution to AGB (63.9%). Finally, in the Cropland and homestead, *Grevillea robusta* made a very large share to AGB (>25%). *Eucalyptus* spp. and *M. indica* also made contributions larger than 10%, including large tree individuals. In addition, some montane forest species, such as *Ficus thonningii*, remained in the farms and contributed importantly to AGB.

In addition, we checked each DBH class for the species contributions (Supplementary Table S1). Some new species were revealed that were important in particular DBH classes, such as *A. mearnsii* in the smaller DBH classes of Cropland and homestead, and *Chrysophyllum gorungosanum* and *Pouteria adolfi-friedericii* among the largest trees in the montane forests.

3.3. Relationship between AGB and IVI of the Dominant Tree Species

The dominant tree species among all the LC types were identified based on the IVI and AGB of those species (Figure 5A). *Eucalyptus* spp. had the highest IVI and AGB. On the other hand, *C. lusitanica* had the second largest IVI but a lower AGB compared to *A. gummifera*, a native tree species with the 4th highest IVI. *T. stapfiana* and *Pinus* spp. were among the first five important species in the landscape. In general, tree species showed a strong positive correlation (R = 0.95, $p < 0.001$) between the AGB and IVI at the landscape-level (Figure 5B) and in the different LC types (Supplementary Figure S2).

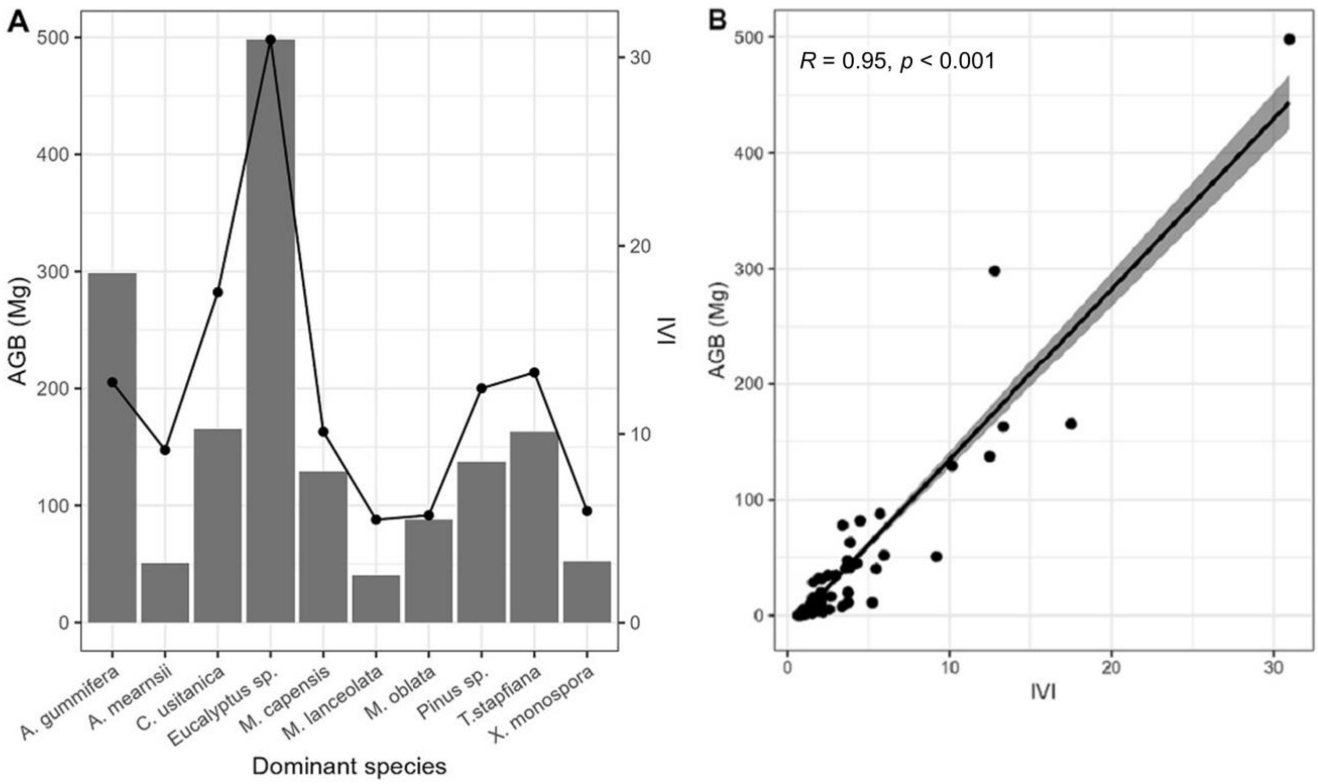

Figure 5. (**A**) Total aboveground biomass (AGB) and importance value index (IVI) of the hyperdominant tree species and (**B**) relationship between total AGB and IVI of all tree species in the landscape (i.e., across all land cover types). Linear model (AGB = 14.3 × IVI – 3.33) with 95% confidence interval is shown to demonstrate the strength of the relationship.

The IVI values showed considerable variation between the LC types (Table 4). The highest IVI values were observed for *N. hildebrandtii* (149.1) in Riverine forest, *V. tortilis* (129.5) in Grassland, *Eucalyptus* spp. (107.0) in Plantation forest, *G. robusta* (44.9) in Cropland and homestead, *A. mearnsii* (43.3) in Bushland, *T. stapfiana* (34.7) in Montane forest, and *A. gummifera* (31.9) in Mixed forest. In addition, *A. gummifera*, *A. mearnsii*, and *Eucalyptus* spp. were species with high IVI in Mixed/Montane forest, Bushland/Plantation forest, and Mixed/Plantation forest, respectively.

The three components of IVI mainly followed the same pattern as IVI, i.e., the highest values of RF, RDE, and RDO corresponded to the same species (Table 4). However, there were some notable exceptions. *Commiphora africana* had the highest RF (relative frequency) in Bushland and *Albizia anthelmintica* in Grassland. The highest values were observed for *N. hildebrandtii* (occurred in 50% of the Riverine forest plots), *V. tortilis*, and *A. anthelmintica* in Grassland (occurred in 35.7% and 21.4% of the plots, respectively). Relatively high RDE (relative density) was observed for *Maesa lanceolata* in Mixed forest and *V. xanthophloea* in Riverine forest. In terms of RDO (relative dominance), *A. amara* had a relatively high value although the highest value was achieved by *A. mearnsii*. Furthermore, *A. reficiens* in Grassland, *Eucalyptus* spp. in mixed forest, and *A. gummifera* in montane forest had high AGB in tree species with lower IVI.

Table 4. Tree species importance value (IVI) and AGB for common species in different LC types.

LC Type	Species	RF	RDE	RDO	IVI	% IVI	% AGB
Bushland	*Acacia mearnsii*	4.7	21.1	17.6	43.3	14.4	22.7
	Commiphora africana	6.1	9.0	10.2	25.3	8.4	4.5
	Commiphora schimperi	4.7	9.3	4.9	18.9	6.3	2.9
	Albizia amara	3.3	5.0	10.4	18.7	6.3	1.8
Cropland and homestead	*Grevillea robusta*	10.4	13.9	20.6	44.9	15.0	26
	Mangifera indica	4.6	9.7	10.8	25.1	8.4	11
	Persea americana	8.7	5.9	6.4	21.0	7.0	1.5
	Eucalyptus spp.	2.9	5.0	8.8	16.6	5.5	13
Grassland	*Acacia tortilis*	35.7	37.7	56.0	129.5	43.0	64
	Portulacaria afra	7.1	30.2	12.9	50.3	16.8	8.1
	Albizia anthelmintica	21.4	13.2	12.4	47.1	15.7	7.6
	Acacia reficiens	7.1	1.9	13.0	22.1	7.4	16
Mixed forest	*Albizia gummifera*	5.8	9.0	17.2	31.9	10.4	18.5
	Cupressus lusitanica	6.7	9.3	13.0	28.9	9.6	10
	Maesa lanceolata	9.6	10.6	4.8	25.0	8.3	4.5
	Eucalyptus spp.	4.8	5.7	9.1	19.6	9.9	11.2
Montane forest	*Tabernaemontana stapfiana*	5.8	14.6	14.4	34.7	11.7	13
	Albizia gummifera	5.2	5.6	16.7	27.6	9.2	21
	Macaranga capensis	4.9	8.1	10.9	23.9	8.0	9
	Milletia oblata	3.9	5.6	5.7	15.3	5.1	7
Plantation forest	*Eucalyptus* spp.	18.3	38.8	49.9	107.0	35.7	58
	Cupressus lusitanica	11.1	23.2	21.6	55.9	18.6	18
	Pinus spp.	8.7	15.9	20.6	45.2	15.4	17
	Acacia mearnsii	12.7	7.9	3.1	23.7	7.9	3.0
Riverine forest	*Newtonia hildebrandtii*	50.0	37.5	61.6	149.1	49.7	67
	Vachellia xanthophloea	30.0	58.3	37.0	125.3	41.8	32
	Cordia goetzei	10.0	2.1	1.0	13.1	4.4	0.7
	Trichilia lepidota	10.0	2.1	0.4	12.5	4.1	0.3

RF = Relative frequency; RDO = Relative dominance; RDE = Relative density; IVI = Importance value index, %IVI = percent IVI, %AGB = percentage fraction of AGB per hectare.

4. Discussion

4.1. Importance of Large Trees on Aboveground Biomass

The results revealed that large trees account for a disproportionate fraction of AGB in some of the sampled LC types in a mosaic landscape with strong human impact on current tree cover. The impact of large trees on AGB is large in forests in the hills, but large trees are scarcer in the lowlands (Bushland, Grassland). The variation in contribution is the greatest in the Cropland and homestead type, where large trees in agroforestry systems can account for substantial AGB. These results support our hypothesis that few large DBH trees contribute disproportionately to AGB in the studied landscape. The contribution of the large sized trees to the AGB is similar to that in African tropical montane forests [63], other reports from African Savannahs [31,64,65] and other areas [6,14,29,66].

Some LC types are more prone to disturbance by humans, wildlife and cattle, which contributes to the observed differences in large trees. Anthropogenic disturbance may affect the abundance and persistence of large trees. Regular disturbances such as the removal of large trees for timber, fuelwood and land clearing for agriculture by communities contribute to a lower proportion of large trees and a gradual increase in smaller-sized trees [67,68]. Moreover, exotic plantations of cypress, pine, and eucalyptus in the logged forest gaps and around forest-remnant boundaries as well as trees in Cropland and homestead type, result from active tree planting and management and therefore exhibit antropogenic patterns [68,69].

Montane, Mixed, Plantation and Riverine forest were dominated by *A. gummifera*, *Eucalyptus* spp. and *N. hildebrandtii* that are known to mature into large trees. The presence of large exotic trees mainly in Plantation and Mixed forest could be driven by fertile soil, high precipitation and elevation [70]. While slope valley bottoms with alluvial soils, and drained watershed-scale forest explains the increased tree diameter in the Riverine forest [71]. Furthermore, the desire of plantation farmers for a certain size allows trees to reach a specific size before harvest as their biomass accumulates rapidly with stand age [72]. Similar to this result are studies in semi-deciduous forest in West Africa [73,74] and for closed canopy and Riverine forest in Togo [18].

Small-size diameter trees were common in Grassland in the lowlands with shallow soils and Bushland. Considering that some of the plots were located in wildlife conservation and grazing areas, destruction of trees via movement and browsing of elephants also contribute to low AGB in the Bushland and Grassland [4,75]. Although the livelihood of communities in the Taita Hills is largely dependent on farming [44], large diameter trees still occur in the fields as an agroforestry system that is capable of connecting remaining tree stands [76]. Homesteads have trees that surround individual dwellings that are not interconnected but occur as small stands separated by agricultural fields. *M. indica*, *G. robusta*, common fruit trees and other valuable trees for human use and other ecological value (e.g., *Prunus africana*), normally grow into large sizes. Furthermore, agroforestry tree species benefit from protection by farmers, as well as an ability to grow fast, in order to fulfill their desired socioeconomic and environmental goals [77].

4.2. Most Important Tree Species Contributing to Aboveground Biomass

Although the tree species in Taita Hills are diverse, only a few species produce a disproportionately large amount of the AGB that is restricted to specific LC types and diameter sizes. This can be seen also by their high IVI. Our results show that *A. gummifera* contributed the most to the AGB of large diameter trees in Mixed and Montane forest. There is less demand for this tree as timber and fuelwood by forest dwellers, and it contributes to an increased number of large DBH sizes and the disproportionate AGB fraction. Selective harvesting of tree species of desirable traits for timber and fuelwood purpose (e.g., *P. adolfi-friedericii*), leave the non-preferred species and pioneer/transition species to contribute more to AGB. In addition, the high contribution of *A. gummifera* to the AGB of large diameter trees is in line with [5,78–80] for East Africa (Ethiopia, Kenya and Mount Kilimanjaro) and that of [81] for *S. guineense* in a woodland of Central Africa. *A. gummifera* is native to Kenya and grows at altitudes (600–2300 m) that fall within forest patches in the Taita Hills. However, their removal will threaten their role in providing ecosystem services (e.g., carbon sequestration, nitrogen-fixing, erosion control, shade or shelter) [82].

The exotic tree species play a significant role in supporting local livelihoods. *Eucalyptus* spp. in Plantation forest and Mixed forest contributed considerably to AGB in all the DBH sizes in the Taita Hills. Since they thrive well in marginal lands and grow fast, they make high AGB contribution in large DBH sizes [83]. Furthermore, despite their long-term environmental consequences [84], eucalyptus remains popular among rural farmers in Kenya [85] for providing an alternative source of income, and its ability to grow in steep rocky areas utilizing places where most crops would not do well (931–2188m) [85]. Originally, the ability of the plant to provide fast-growing wood source motivated its introduction to support railway expansion in East Africa [86–88].

Pellikka et al. [44] revealed a significant decrease in native montane forest areas in Taita Hills from 1955 to 2004 because of agricultural expansion. This transformation contributes to fewer trees with large tree sizes in Bushland. *A. mearnsii* and *A. amara* were common in all DBH classes in Bushland probably because of the invasive nature and ability for the seeds to sprout after wildfire, which is common in the Bushland and savanna grassland [82]. These tree species could be hyperdominant in Bushland. *N. hildebrandtii* was the only species in the largest DBH class (DBH $\geq$ 70 cm) in Riverine forest, but it made the greatest contribution to biomass and large diameter trees although samples included only a few Riverine forest plots. *N. hildebrandtii* is a common species in Riverine forests in the region. This may be due to certain aspects (strength of wood, rot resistance, ease of sorting and carrying) that it does not have according to local people [89] and the ability of the plant to survive in high moisture soil close to riverbanks.

Ecological and economic importance (e.g., food, fodder, fiber, timber, carbon sequestration, and soil improvement) keeps large trees on Cropland and homestead [90–93]. Our results showed few trees with a large diameter of $\geq$70 cm in Cropland and homestead. Therefore, removal of fuelwood or clearing of agricultural land could explain the scarcity of large trees in the crop fields [94]. However, certain species contributed disproportionately to AGB at different DBH classes. *G. robusta* contributed the highest fraction of AGB in most DBH classes. The maize—*G. robusta* agroforestry system in Kenya [95]—explains the popularity of *G. robusta* in Cropland and homestead type. *G. robusta* is a multipurpose tree that grows well in low fertility soil, is less competitive to food crops, and tolerates pollarding, which motivates its inclusion in agroforestry systems. Furthermore, *M. indica* (mango) made a large contribution to the AGB and the largest diameter class. This aligns with other studies in Miombo woodlands in Malawi [92] and Mozambique [90]. However, in [5], croplands and agroforestry on the inhabited slopes on Mount Kilimanjaro had more AGC than in Taita Hills, and *G. robusta* showed high AGC in Taita Hills while *A. gummifera* had the highest AGC on the side of Tanzania. Because *M. indica* is a fruit tree species, they are deliberately spared for income and food source. Therefore, they are allowed to increase (in size and number) on crop fields and homesteads.

Although Grassland inhibits the growth of tree species [96] via persistence wildfire, *V. tortillis* contributed to the highest fraction of AGB for diameters 10–69.9 cm. For trees with a diameter 10–19.9cm, 63.9% were *V. tortillis*, while in the 60–69.9 cm class, contribution was 53.1%, respectively. This shows how *V. tortillis* contributed to a significant proportion of AGB for the few large diameter trees. This result is similar to studies in Kibwezi forest in Tsavo ecosystem in Makueni County, Kenya [97], and the experimental center of Arid Forest Research Institute in India [98]. Similarly, *A. reficiens* contributed a substantial amount (46.9%) of AGB to large-sized (60–69.9 cm) trees in Grassland. The exotic tree species also contributed largely to AGB in the different DBH sizes in Plantation forest (*A. mearnsii*), Bushland (*A. mearnsii*, *A. amara*) and Riverine forest (*V. xanthophloea*). This result is similar to previous studies in the Pearl River Delta, South China [72]. Although *Acacia* spp. are important AGB pool, they create negative environmental consequences as invasive plant species that threaten the existence of native plant species [84].

4.3. Ecological Significance of the Dominant Tree Species

The results point out that the studied landscape is characterized by both exotic (*Eucalyptus* spp. and *C. lusitanica*) and native (*A. gummifera*) tree species. Rural farmers widely cultivate Eucalyptus trees due to their suitability for smallholder growers with limited resources and higher profitability compared to other tree crops [99]. Despite their invasive behavior in the region [84], most exotic tree species survive even in marginal soil and are planted on a large scale because of their economic, domestic, and ecological benefits. On the other hand, *A. gummifera*, a native tree species to Kenya account for very large AGB, as they are mainly retained as shade trees in agroforestry, and also support tree growth [100,101]. The ecological significance of these tree species supports biodiversity and biomass production, and their dominance and abundance [62]. Therefore, species with high IVI values require continuous monitoring, while species with low IVI but high ecological value require protection and conservation to aid their natural regeneration [102,103].

The results show that *A. mearnsii*, *C. africana*, *C. schimperi* and *A. amara* are dominant, and responsible for a disproportional contribution of AGB in Bushland. Similarly, the high IVI value of *A. mearnsii* supports its ecological significance as an invasive species in Bushland that replace many native tree species [84]. *G. robusta*, a common agroforestry species [104,105] in Kenya, predominates in Cropland and homestead. Furthermore, *M. indica* and *P. americana* are retained in agroforestry and homestead for their fruit, while *Eucalyptus* spp. are kept for fuel wood. These attributes (high IVI) are associated with biomass accumulation and carbon sequestration [106]. *V. tortilis* was shown to have the highest IVI in Grassland with 43%. *Portulacaria afra*, *A. anthelmintica*, and *A. reficiens* were also important tree species. *V. tortilis* also contributed the highest fraction of AGB in large trees in earlier studies [96,98,107]. One benefit of identifying the most important tree species in the landscape is that the analysis helps define target species for future remote sensing analyses in the area (e.g., [84]).

5. Conclusions

Our results show how tree size and tree species composition contribute to AGB in different LC types in the mosaic landscape with strong human influence in the Taita Hills, Kenya. Disproportionate portions of the AGB are stored in a few large standing trees that are relatively small in number. Their amount varies by LC type and those are normally protected trees in forests, agroforestry systems and homesteads near dwellings, or trees without sufficient economic value. Exotic tree species were widespread across LC types, but especially in Plantation forest, Mixed forest, and agroforestry systems in Cropland and homestead where they perform several other ecosystem services (e.g., shading, nitrogen fixation and soil conservation). Furthermore, conserved fragmented forests and large trees conserved in Cropland and homestead hold large size trees that support other ecological functions and store large fractions of AGB. Keeping large trees in the abovementioned LC types support the global climate change mitigation needs. Future research should be conducted to study how the presence of large trees and AGB relate to tree species diversity across LC types to optimize landscape-scale co-benefits of climate change mitigation and biodiversity conservation.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f14030642/s1: Figure S1: Contribution (%) of diameter at breast height (DBH) classes to plot-level aboveground biomass (AGB) in different land cover (LC) types; Figure S2: Relationship between importance value index and aboveground biomass in the different LC types: (A) Bushland; (B) Cropland and homestead; (C) Grassland; (D) Mixed forest; (E) Montane forest; (F) Plantation forest; (G) Riverine forest; Table S1. Most common tree species in different land cover (LC) types and DBH classes.

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