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Aboveground Biomass Models in the *Combretum-Terminalia* Woodlands of Ethiopia: Testing Species and Site Variation Effects

Amsalu Abich ^{1,2,*}, Mesele Negash ¹, Asmamaw Alemu ²  and Temesgen Gashaw ³

¹ Wondo Genet College of Forestry and Natural Resources, Hawassa University, Shashemene P.O. Box 128, Ethiopia; mesele@hu.edu.et

² College of Agriculture and Environmental Sciences, University of Gondar, Gondar P.O. Box 196, Ethiopia; asmamaw.alemu@uog.edu.et

³ College of Agriculture and Environmental Sciences, Bahir Dar University, Bahir Dar P.O. Box 1289, Ethiopia; temesgen.gashaw@aau.edu.et

* Correspondence: amsalu.abich@uog.edu.et; Tel.: +251-9-1881-3275

Abstract: The *Combretum-Terminalia* woodlands and wooded grasslands (CTW) are widely distributed in East Africa. While these landscapes may have the potential to act as key global carbon sinks, relatively little is known about their carbon storage capacity. Here we developed a set of novel aboveground biomass (AGB) models and tested for species and site variation effects to quantify the potential for CTW to store carbon. In total, 321 trees were sampled from 13 dominant tree species, across three sites in the Northwest lowlands of Ethiopia. Overall, fitted species-specific models performed the best, with diameter at breast height explaining 94–99% of the AGB variations. Interspecific tree allometry differences among species were more substantial than intraspecific tree allometry among sites. Incorporating wood density and height in the mixed-species models significantly improved the model performance relative mean absolute error (MAPE) of 2.4–8.0%, while site variation did not affect the model accuracy substantially. Large errors (MAPE%) were observed when using existing pantropical models, indicating that model selection remains an important source of uncertainty. Although the estimates of selected site-specific models were accurate for local sites, mixed-species and species-specific models performed better when validation data collated from different sites were incorporated together. We concluded that including site- and species-level data improved model estimates of AGB for the CTW of Ethiopia.

Keywords: aboveground biomass; tree allometry; validation; *Combretum-Terminalia* woodland; Ethiopia



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1. Introduction

Forest trees capture important amounts of atmospheric carbon dioxide through photosynthesis [1,2]. Plants in terrestrial ecosystems reportedly sequestered 3.61 Pg carbon annually between 2007 and 2016 [3]. Tropical forests, in particular, store more than half of the carbon present in the terrestrial ecosystems [4,5]. With their high species diversity, tropical forest ecosystems have been shown to have a great carbon sink capacity [3,5]. They constitute an important mitigation option for regulating climate change [3,6] as well as providing other critical ecosystem services [7]. Quantifying these multifunctional benefits is therefore critical for understanding the full potential of these ecosystems and developing effective environmental policies.

Quantification of biomass is essential to monitor the growth condition, productivity, and nutrient cycle, including carbon fluxes [8,9] and carbon storage, as outlined in the Kyoto Protocol [10,11]. Forest biomass estimations are commonly obtained via integrating remote-sensed and field inventory data with an allometric relationship [11,12]. Methods that rely on biomass allometric relationships are usually based on easily measurable tree variables, such as diameter and height. However, these approaches while widely used have been shown to have some key limitations [13]. It is therefore important that additional

information, such as tree-specific wood density and tree height [14,15], be included to improve biomass model assessments [15,16].

Numerous allometric models have been developed at the individual and multispecies levels, and some of them are compiled regionally [17–19]. The species-specific models have been proved to provide accurate estimation for the tree species of interest [20–24], but the models are less reliable when applied to other tree species or sites [23]. Differences in tree architectures and wood density within and among tree species [25] and sites [17] therefore limit the reliability of these biomass models. While developing models for each species and site will improve biomass assessment, this will require significantly more resources [26]. As such, several species-specific models are fitted with relatively small sample sizes, often as few as ≤ 13 individual trees [20,27], which can be a considerable source of model uncertainty [13,16]. This uncertainty in the aboveground biomass (AGB) estimates associated with tree species and site variations is prevalent in many regions of the world, particularly Africa.

Although several local mixed-species models have been developed to obtain better biomass estimates [26,28,29], they can generate substantial uncertainty when they are applied to other sites [23]. This is because the models are usually fitted based on a sample that is specific to a region [30]. On the other hand, a generic mixed-species or pantropical model developed based on a large dataset of many species covering a wide range of ecoregions may only be a sufficient tool for AGB estimations at larger scale because they lack specificity [22,31,32]. As such, uncertainty remains in estimates based on generic models applied to a particular site. Further, it has been argued that the choice of models can have significant uncertainty in the biomass estimate [26,33]. With the exception of a few studies such as van Breugel [26], these sources of uncertainty have been rarely addressed in the tropical ecosystems of Africa [34].

The *Combretum-Terminalia* woodlands and wooded grasslands (CTW) are a widely distributed ecosystem in East Africa including Ethiopia [35]. The CTW of Ethiopia comprise 199 woody species of which nearly 41% are endemic [36], thus having a high potential for local biodiversity conservation. In addition, it is one of the four major biomes sequestering carbon in the dryland ecosystems [37–39]. However, estimated carbon reportedly varied among studies, partly attributable to differences in wood density values used for biomass estimation. Because there are no generic mixed-species models, information on the wood density of tree species of CTW is incomplete in the country [40]. Recently, a few local mixed-species models have been developed for dry Afromontane forests in Ethiopia [30,41,42] but none for the CTW, except the recently published site-specific model of Abich [43]. Hence, development and validation of allometric models based on a dataset of many species collected from several sites are necessary to accurately estimate AGB in the CTW from plot inventories.

Therefore, in this study, we developed new aboveground biomass species-specific and site-specific (multispecies) models in Ethiopian CTW, with emphasis on the effects of tree species, model types, and site variations on the accuracy of the allometric models. The specific objectives were to: develop single-species and mixed-species allometric models of AGB using the datasets of three sites; validate the performance of the allometric models developed here with independent data collected from a different site with similar conditions; and assess the bias introduced when combining species in a single mixed-species model and using a distant model developed outside Ethiopia by plot inventory data.

2. Materials and Methods

2.1. Description of the Study Sites

The study was carried out in Metema and Quara districts located in the Amhara National Regional State and in the Homosha district located in the Benishangul Gumuz National Regional State (BNRS), Northwest lowlands of Ethiopia. These districts were selected because they reflect the high dominance of the *Combretum-Terminalia* woodland and wooded grasslands (Figure 1), which occur in the northwestern, western, and southwestern

parts of the country. The altitude ranges from 500 to 1900 m.a.s.l [35,36]. The total area cover of the CTW is estimated to be 24.5 million hectares. In addition, the vegetation is a home to diverse plant species, which are characterized by small-to-moderate-sized trees with fairly large deciduous leaves [36]. The climate is of dry tropical type, characterized by an average temperature of over 18 °C and a prolonged dry season [44].

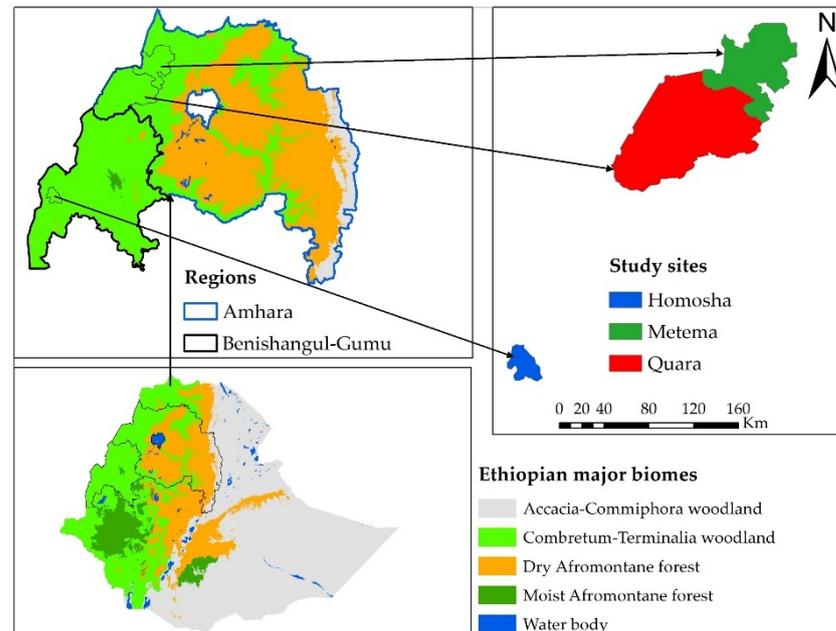


Figure 1. Map of the study sites and *Combretum-Terminalia* woodland and wooded grassland.

2.2. Topography, Climate, and Soils of the Study Sites

Metema is located between 12°30'0"–12°48'0" N latitude and 36°17'0"–36°55'0" E longitude. It is characterized by undulating land configuration with an altitudinal range of 550 to 1608 m.a.s.l. The annual rainfall ranges from 514 to 1128 mm with a mean annual rainfall of 924 mm, whereas the mean monthly minimum and maximum temperatures of the district are 19.3 °C and 35.7 °C, respectively [45]. The major soil types in Metema are vertisols and luvisols [46].

The second study site (Quara; Altash National Park, ANP) is situated between 11°47'5"–12°31'4" N latitude and 35°15'48" to 35°48'51" E longitude. Altitudinal range in the ANP is from 500 in the northern flat plain to 900 m.a.s.l in the south. The mean annual rainfall is 800 mm, with a minimum of 600 and a maximum of 1200 mm, whereas the mean monthly minimum and maximum temperatures are 25 °C and 35 °C, respectively [47]. The dominant soil types include vertisols, fluvisols, and alluvial deposits dominated by sands along with river courses (field observation).

The third study site (Homosha) is situated between 10°8'28"–10°29'0" N latitude and 34°23'44"–34°44'5" E longitude. According to the report of the BNRS Meteorological Agency (2018), the district receives a mean annual rainfall of 1200 mm, while the mean monthly minimum and maximum temperatures are 11.7 °C and 28.7 °C, respectively. This site is characterized by an altitudinal range of 1544–1634 m.a.s.l.

2.3. Field Data Collection

The development of models considered the distribution of tree species, and their size, which were collected from the three aforementioned sites. Initially, we carried out forest inventory for appropriate selection of sample trees, a total of 100 sample plots, each plot measuring 20 m × 30 m (i.e., 40 plots for Homosha in the protected area of 21,681 hectares and 60 plots for Quara in the ANP), were surveyed using systematic sampling approach. In each plot, all trees with a diameter at breast height (DBH) ≥ 5 cm and total height (H in

meter, m) were recorded and measured. The local and scientific names of the species were identified with the assistance of a local person (botanist) and the identification key [48]. Tree basal areas were estimated to determine the most dominant tree species. Accordingly, ten most dominant tree species were selected, occupying more than 80% of the total basal area of the surveyed CTW (Table A1 in Appendix A) for harvesting.

2.4. Selection of Sample Trees for Harvesting

For this study, thirteen species were considered in the development of the allometric models. The inventoried tree individuals were categorized into seven diameter classes in order to harvest representative trees covering a wide diameter and height spectrum (Table A1 in Appendix A). Accordingly, a total of 321 individual trees, comprising 102 for Quara, 118 for Homosha, and 101 for Metema, were harvested. Please note that data from Metema were obtained from a previous study [43] and used in the validation process of established models.

2.5. Biomass Measurement

Prior to felling, the DBH and diameter at stump height of a sampled tree were measured with a caliper. The AGB included all parts of the tree above the ground, excluding flower and seed parts (since it was not the onset season for flowering). The sampled tree was cut at stump height (30 cm above the ground). Then, the total height of the felled tree including its stump was measured using meter tape. Felled tree was partitioned into stump, stem, branches, and leaves. Fresh weights were measured immediately on the site using a hanging 100 kg bipod spring balance. The stump diameter and its length were also measured for the volume calculations, then converted to biomass with the wood density [49]. From each biomass component, subsamples were taken, labeled, and measured for dry-to-fresh weight ratio determination. The discs with different diameter sizes (with a width of ≥ 5 cm) were taken from the stem and branches and dried under shade for six months, whereas the leaf and twigs subsamples were oven-dried immediately. The stem and branch subsamples were oven-dried at 105 °C for 48 h, whereas the leaf and twigs were oven-dried at 70 °C for 48 h until constant weight. The fresh-to-dry weight ratios were used, afterward, to compute the total dry weight of each biomass component. Finally, the AGB of each tree felled in the field was calculated by summing all biomass components for that tree.

For basic wood density over bark determination, discs having a different thickness were taken at the bottom (at 30 cm height above the ground), DBH, mid-point between DBH and stem toward top stem, and top stem height with a width of 5 cm. The green weight for all disc samples was measured. In addition, for branches, disc samples were also taken from diameter classes of 5–10, 11–15, and >16 cm. Although the green volume of the disc can be estimated through water displacement, it was difficult for trees with a large diameter size. It was thus measured following a method described in a previous study [43].

2.6. Data Analysis

The AGB measurement dataset of Metema constituting nine species was used as independent data for validating species-specific and mixed-species models developed for Quara and Homosha. The datasets of all sites were combined for developing a general model. This is to validate the general models over species and sites.

2.6.1. Fitting and Evaluating the Allometric Models

The allometric scaling relationship (M1) was linearized using the natural logarithm, for compliance with the normality and the equal variances assumptions for the residual errors [50]. The use of the linearized form of the power-law function yielded more accurate biomass models than the nonlinear function [51,52]. Log-linear regression was thus applied to the entire datasets to fit the models. The parameters of the models were estimated using the ordinary least squares method. The data were organized as AGB datasets of (i) a given

species (species-specific, AGBss), (ii) mixed-species of a given site (site-specific, AGBsm), and (iii) a combined dataset of all species and sites referred to as the general model. All analyses were carried out using the R version 4.1.2 software [53].

$$AGB = \beta_0 DBH^{\beta_1} + \varepsilon \quad M1$$

$$\ln(AGB) = \ln(\beta_0) + \beta_1 \ln(DBH) + \varepsilon \quad M2$$

where ε and M refer to the random error and model, respectively. The bias correction factor (CF) developed by Baskerville [54] was applied to back-transformed natural logarithmic function [22]. It is computed from the residual standard error (RSE) of the fitted model as $CF = \exp(RSE^2/2)$.

A visual inspection was also used to confirm the absence of heteroscedasticity on the plot of standardized residual errors against log-transformed predicted AGB. The performance of the models was assessed on the basis of the percent relative standard error (PRSE = $(SE/|\beta|) \times 100$, where SE and $|\beta|$ refer to standard error and the absolute value of the parameter, respectively), the adjusted coefficient of determination (R^2), the proportion of variance explained by predictor variables, the relative mean error (RME%), the relative mean absolute percentage error (MAPE%), and root mean square error (RMSE, kg) [13,51]. In addition, Akaike's information criterion (AIC) was used for comparison among alternative equations with differing numbers of predictor variables [55].

Uncertainty in biomass estimate occurs when the numbers of predictor variables increase in the model due to the effect of collinearity between predictors [13]. Additional model forms (M3, M4, M5, and M6), which are described below, were tested, and their performances were assessed based on the comparison of their fit statistics with those of M2 and variance inflation factor of the models. Whereas M2, M3, M4, M5, and M6 were tested for site/multispecies models, only M2, M3, and M6 were tested for the species-specific model because wood density was incorporated in the models to account for inter-species variation.

$$\ln(AGB) = \ln(\beta_0) + \beta_1 \ln(DBH) + \beta_2 \ln(H) + \varepsilon \quad M3$$

$$\ln(AGB) = \ln(\beta_0) + \beta_1 \ln(DBH) + \beta_3 \ln(\rho) + \varepsilon \quad M4$$

$$\ln(AGB) = \ln(\beta_0) + \beta_1 \ln(DBH) + \beta_2 \ln(H) + \beta_3 \ln(\rho) + \varepsilon \quad M5$$

$$\ln(AGB) = \ln(\beta_0) + \beta_1 \ln(DBH^2 H) + \varepsilon \quad M6$$

In addition, the applicability of the following models developed for miombo woodlands [28] and pantropical forests [31,32] was evaluated.

$$AGB = 0.0763 \times (DBH^{2.2046} \times H^{0.4918}) \quad MM$$

$$AGB = 0.673 \times (DBH^2 H \rho)^{0.976} \quad Ch14$$

$$AGB = 0.112 \times (DBH^2 H \rho)^{0.916} \quad Ch5$$

where MM, Ch5, and Ch14 refer to Mugasha's [28] and Chave's [31,32] models, respectively. The Greek letter rho (ρ) denotes wood density.

2.6.2. Validation of Species-Specific and Mixed-Species Models

When a model is formulated and fitted, the assessment of its validity is critical to check if it provides acceptable performance. The assessment can be performed using various validation methods [56] and statistical inference. There are high chances of having unbiased models when they are validated using independent data (testing data) [57]. Thus, the species and mixed-species models fitted for a given site were validated using datasets of the same species and mixed-species from other sites as testing data, respectively. The mean percentage error (MPE%, Equation (1)), overall accuracy (relative error, RE% (Equation (2))),

and model efficiency (EF%) were used to evaluate the model performances [58]. To refine this validation, seven categories were formulated. The first group was formed based on species (i), where each species was considered as a factor. The other groups were formed using the site factor because species and site-specific models have less reliability outside the sites for which the data are obtained. The groups are collated trees of *Anogeissus leiocarpa* (ii), *Combretum harotomannianum* (iii), *Combretum molle* (iv), *Pterocarpus lucens* (v), *Terminalia laxiflora* (vi) and mixed-species (vii) from the sites. Then, the analysis of covariance or general linear model (GLM) was applied to assess the effects of species and site variations on the relationship between DBH and AGB. Levene's test was used to confirm homogeneity of residual variances across categories.

$$\text{MPE}\% = \frac{100}{n} \sum_{n=1}^n \frac{\text{AGB}_{\text{obs},i} - \text{AGB}_{\text{pred},i}}{\frac{1}{n} \sum \text{AGB}_{\text{obs}}} \quad (1)$$

$$\text{RE}\% = \frac{\sqrt{\text{RMSE}}}{\frac{1}{n} \sum \text{AGB}_{\text{obs}}} * 100 \quad (2)$$

$$\text{EF}\% = 1 - \sum \frac{(\text{AGB}_{\text{obs},i} - \text{AGB}_{\text{pred},i})^2}{(\text{AGB}_{\text{obs},i} - \frac{1}{n} \sum \text{AGB}_{\text{obs}})^2} * 100 \quad (3)$$

2.6.3. The Uncertainty in AGB Estimate Associated with Combining Species in a Single Mixed-Species Model

A cause of uncertainty in the AGB estimate, including the model choice, was examined based on site-based inventory. The approach of van Breugel [26] was adopted for estimating the possible bias when different tree species were combined into a single mixed-species model. This was done by comparing the plot AGB estimate obtained with the mixed-species models with that obtained with the species-specific models. For this analysis, mixed-species models including a generic model developed elsewhere outside Ethiopia [28,31,32] were applied to landscape AGB estimation. Trees not belonging to the studied species in the model development were removed from the plots. We only used tree species in the plots with 80% of the original basal area. This assisted us with directly comparing plot-level AGB estimates of the mixed-species models with estimates generated by the models of a specific tree species. Finally, the bias and accuracy of the models for each plot (plot i), plot-level, and across-plot average AGB estimates were estimated as follows.

The relative error (RE) of plot_i AGB estimates:

$$\text{RE}\% = 100 \sum \frac{\text{AGB}_{\text{ss},i} - \text{AGB}_{\text{ms},i}}{\text{AGB}_{\text{ss},i}} \quad (4)$$

The relative mean absolute error (MAPE) of plot-level AGB estimates, where N refers to the number of plots:

$$\text{MAPE}\% = \frac{100}{N} \sum_{N=1}^{100} \frac{|\text{AGB}_{\text{ss},i} - \text{AGB}_{\text{ms},i}|}{\text{AGB}_{\text{ss},i}} \quad (5)$$

The mean percentage absolute error (MPE_A) of across-plot average AGB estimates:

$$\text{MPE}_A\% = \frac{\left| \left(\frac{1}{N} \sum_{N=1}^{100} \text{AGB}_{\text{ss},i} \right) - \left(\frac{1}{N} \sum_{N=1}^{100} \text{AGB}_{\text{ms},i} \right) \right|}{\frac{1}{N} \sum_{N=1}^{100} \text{AGB}_{\text{ss},i}} \quad (6)$$

Confidence intervals (CIs) of plot-level AGB estimates by the species-specific models were estimated based on the information of the species-specific model from van

Breugel [26]. First, the relative standard error of each species model (RSE_i) was estimated using Equation (7) as:

$$RSE_i = \sqrt{\exp\left(\frac{MSE}{n-p}\right) - 1} \quad (7)$$

where MSE refers to the mean square error of the model from the regression, whereas n and p are the number of sample trees and the number of parameters in the model, respectively.

Second, the standard error for the AGB estimate for a specific species (SE_i) was estimated with Equation (8) as:

$$SE_i = RSE_i * AGB \quad (8)$$

The standard error of the plot (SE_{plot}) was estimated with Equation (9) for combinations of uncorrelated variables with different variances as:

$$SE_{plot} = \sqrt{\sum SE_1^2 + SE_2^2 + \dots + SE_{100}^2} \quad (9)$$

Lastly, the 95% CI for the AGB estimate by species-specific models was estimated as the estimated plot AGB \pm 1.96*SE_{plot}. The AGB estimates of the mixed-species models did show a significant difference when the estimates fell outside the 95% CI. Later, uncertainty in the AGB estimate due to model selection was assessed to generalize the reliability of the fitted and generic models for landscape estimation using all species datasets of the 100 plots.

3. Results

3.1. Allometric Models

Parameters of the species-specific models with their standard errors and variance inflation factors (VIFs) for each tree species are presented in Table 1 and detailed in Table A2 in Appendix B. The models with DBH alone (M2) explained 93.2–99.3% of the variation in AGB. For most tree species, however, higher VIFs and PRSEs were observed when H was included in the model. Combining the same species in a single species-specific model improved the precision (PRSE) of a parameter of the model by 0.3–37.2%. The parameters of M2 were highly significant ($p < 0.0001$) with a PRSE of $\leq 15\%$ for all species. The addition of height in M2 slightly improved the model performance of some species, and the MAPE of M3 decreased by 0.6–2.6%. Moreover, the allometric scaling of the DBH and AGB relationship differed among species, and the slopes ranged from 2.187 to 2.638 (Table 1). Using a general linear model, the difference was significant when the species were included as a factor. There was thus a significant slope and intercept difference between species.

Table 1. The best species-specific models with their parameters, a bias correction factor (CF), and fit statistics. Where MSE, R², VIF, and n refer to, respectively, the mean squared error, adjusted coefficient of determination, variance inflation factor, and the number of sample trees.

Species Name	Model Forms	n	Parameters			Fit Statistics				
			β_0	β_1	β_2	R ²	MSE	CF	VIF	MAPE
<i>A. malacophylla</i>	M3	51	−3.436	2.276	0.631	0.983	0.015	1.008	2.23	9.7
<i>A. leiocarpa</i>	M2	19	−1.462	2.299	-	0.989	0.021	1.010	-	11.4
<i>C. collinum</i>	M2	21	−2.143	2.478	-	0.982	0.040	1.020	-	16.2
<i>C. harotomannianum</i>	M3	36	−2.395	2.140	0.498	0.972	0.039	1.019	4.61	15.4
<i>C. molle</i>	M2	36	−1.535	2.187	-	0.981	0.029	1.015	-	13.8
<i>L. fruticosa</i>	M2	33	−2.089	2.348	-	0.943	0.079	1.040	-	23.6
<i>P. lucens</i>	M2	32	−2.685	2.638	-	0.977	0.043	1.022	-	15.9
<i>T. laxiflora</i>	M3	42	−2.773	2.273	0.522	0.977	0.047	1.024	4.73	17.4

The parameters (and standard errors) and the fit statistics of mixed-species models are presented in Table 2. For site-specific models, with the exception of the models (M3 and M5)

of the Quara site, the values of VIF ranged from 3.09 to 4.33. The model that combined DBH and wood density (M4) provided a more accurate estimate with an RMSE of 83.6–76.2 kg than M3, which included DBH and H with an RMSE of 93.2–104.0 kg. Adding H and wood density as a compound predictor variable in M2 substantially improved the performance of M5, with the changes in MAPE and AIC of 2.4–6.7% and 20.9–134.9, respectively (Table A3 in Appendix C). Although the estimated parameters of wood density were significantly different from zero, the precision of the parameters of M4 and M5 inflated with a PRSE of 37.5% and 47.5%, respectively, for the model of the Quara site. We observed very little or no improvement in the fit statistics of M6 that included DBH and H as a single entry (volume index), and thus the model was not further evaluated.

Table 2. The parameters, correction factors, and validation indicators of mixed-species models for CTW. The values in the parentheses refer to the standard errors of model parameters.

Model Forms	Parameters				Validation Indicators					
	β_0	β_1	β_2	β_3	R ²	CF	MRE	MAPE	RMSE	AIC
I. The allometric models of Quara site (n = 102)										
M2	−1.972 (0.115) ***	2.394 (0.039) ***	-	-	0.974	1.028	−5.7	19.4	97.9	939.2
M3	−2.447 (0.143) ***	2.022 (0.085) ***	0.688 (0.142) ***	-	0.979	1.023	−4.7	17.4	93.2	931.1
M4	−1.704 (0.150) ***	2.393 (0.038) ***	-	0.528 (0.198) **	0.975	1.026	−5.3	18.4	83.6	909.0
M5	−2.215 (0.178) ***	2.049 (0.084) ***	0.636 (0.142) ***	0.387 (0.184) *	0.979	1.022	−4.3	17.0	86.7	918.3
M6	−2.604 (0.114) ***	0.940 (0.014) ***	-	-	0.978	1.023	−4.7	17.7	96.3	935.9
II. The allometric models of Homosha site (n = 118)										
M2	−2.374 (0.145) ***	2.450 (0.048) ***	-	-	0.957	1.027	−5.2	19.0	124.3	1146.1
M3	−3.007 (0.168) ***	2.094 (0.074) ***	0.731 (0.125) ***	-	0.967	1.021	−4.1	16.6	104	1104.2
M4	−1.514 (0.133) ***	2.451 (0.035) ***	-	1.169 (0.113) ***	0.978	1.014	−2.9	13.5	76.2	1030.6
M5	−2.004 (0.168) ***	2.238 (0.059) ***	0.436 (0.101) ***	1.017 (0.111) ***	0.981	1.012	−2.3	12.3	70.2	1011.2
M6	−3.188 (0.144) ***	0.980 (0.017) ***	-	-	0.966	1.021	−3.9	17.0	101.3	1093.8
III. The general models of the combined dataset of Quara, Homosha, and Metema (n = 321)										
M2	−2.064 (0.088) ***	2.381 (0.030) ***	-	-	0.953	1.042	−8.6	24.9	149.3	3218.0
M3	−2.491 (0.106) ***	2.063 (0.056) ***	0.605 (0.093) ***	-	0.959	1.037	−7.5	23.3	127.6	3118.9
M4	−1.462 (0.078) ***	2.394 (0.023) ***	-	0.982 (0.064) ***	0.973	1.024	−4.8	17.5	96.1	2936.9
M5	−1.758 (0.098) ***	2.205 (0.045) ***	0.358 (0.075) ***	0.911 (0.064) ***	0.975	1.023	−4.6	17.0	92.7	2915.5
M6	−2.691 (0.098) ***	0.938 (0.011) ***	-	-	0.957	1.039	−7.9	23.7	120.2	3078.8

Where ***, **, and * refer to significance level at $p < 0.0001$, 0.01, and 0.04, respectively.

When combining the datasets of the three sites in a single general model, the inflated standard error of the parameters estimated from the models of specific sites decreased by a PRSE of 0.3–40.5% (Table A4 in Appendix D). Despite this, general M2 and M3 fitted poorly and yielded a relatively large MAPE, ranging from 23.3% to 24.9%. The MAPE values of models were positively correlated with AGB, with the Pearson correlation coefficient of 12.6% ($p = 0.024$) for M2 (Figure 2, blue color dots) and 3.9% ($p = 0.481$) for M3 (Figure 2, red color dots). This was improved when wood density was included in the M2 and resulted in an increased fitness with a substantial change in the MAPE and AIC values of $\leq 7.4\%$ and 281.1, respectively. H and/or wood density combined with DBH improved the model performances by an MAPE of 7.9% and AIC of 302.5 (Figure 2, black and green color dotes) compared with M2.

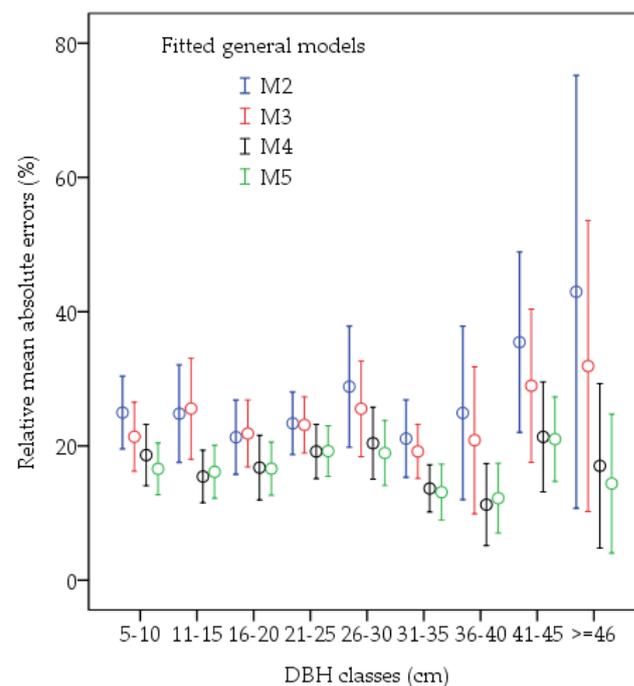


Figure 2. The relationship between relative errors and the classes of diameter at breast height (DBH) indicates the fitness of the general models. The error bar indicates the 95% confidence intervals of the mean.

3.2. The Impact of Site Variation on the Accuracy of Allometric Models

Five species with 129 trees collected from a different site were used to validate the stability of the best-performing model (M2). Variation in the intraspecific models of the species was thus observed among the sites. The validation succeeded for the *Anogeissus leiocarpa*, *Combretum molle*, and *Terminalia laxiflora*, with an EF of $\geq 90.1\%$, and the MPE ranged from -11.73% to 9.28% . However, validation failed when we applied the M2 of *Pterocarpus lucens* developed from Quara and Homosha to the testing data of the species collected from Metema, and vice versa, with MPE ranging from -25.14% to 15.17% . A similar result was attained for *Combretum harotomannianum* (Table A5 in Appendix E), explained by a significant variation among sites ($p < 0.0001$). Combining species collected from several sites into a single species-specific model, however, improved the performance of the model by up to the RE of 22.6% , resulting in unbiased models. With the exception of tree *Combretum harotomannianum*, the addition of the site factor alone or interaction with DBH in the GLM did not show a significant ($p > 0.05$) difference in both the slopes and intercepts among sites.

Furthermore, the mixed-species model that excluded wood density of Quara and Homosha poorly performed with an EF of $< 90\%$, resulting in a large bias in the AGB estimate of testing data. The MPE and RE of the models ranged from -23.50% to 19.67% and from 41.3% to 74.4% , respectively, indicating that model choice can be a source of uncertainty in AGB. This was significantly explained by variation in the sites. The model that included wood density, however, could attain a positive validation with a stable variance of residual errors (Figure 3), resulting in a substantial decrease in the MPE and RE values (Table 3), and confirmed the effect of wood density on the accuracy of AGB estimation. These validations were tested with the GLM; there were significant differences in the parameter estimates of the models among the sites but with multiple comparisons (Bonferroni method) showing that the main difference was only significant between sites when the model was based on DBH alone and/or H.

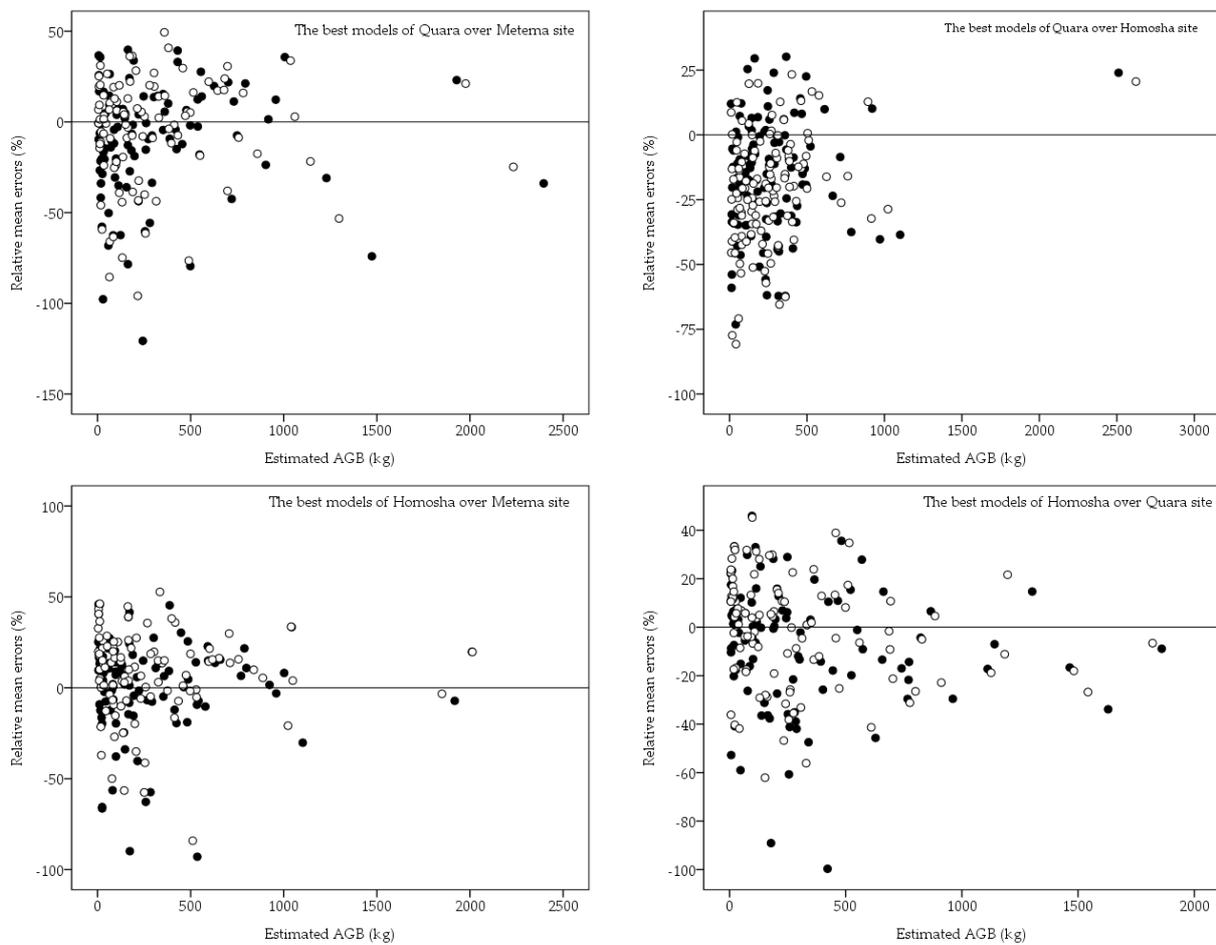


Figure 3. Validation results: the relative errors against the best models of estimated aboveground biomass (AGB in kg) when the models of a given site were applied for other sites. The symbols of white and black dots refer to the validated models 4 and 5, respectively.

Table 3. The performance of mixed-species models and their validation indicators over the testing dataset. The bolded model forms indicate the best-performing models over the testing dataset.

Model Validated	Testing Dataset	Model Forms	Validation Indicators		
			EF%	MPE%	RE%
Models of Quara	Metema	M2	66.5	−13.48	74.4
		M3	81.0	−4.26	56.1
		M4	87.3	−0.11	45.8
		M5	89.4	4.21	41.7
Models of Homosha	Homosha	M2	86.6	−23.50	51.1
		M3	90.9	−20.10	42.1
		M4	91.4	−7.80	40.8
		M5	93.4	−10.10	35.8
Models of Homosha	Metema	M2	75.0	7.60	64.3
		M3	81.6	14.78	55.1
		M4	93.2	6.58	33.4
		M5	92.6	11.22	35.0
Models of Homosha	Quara	M2	85.7	19.67	44.1
		M3	87.5	19.05	41.3
		M4	93.0	−6.52	30.8
		M5	93.4	−2.97	30.1

3.3. The Uncertainty in the AGB Estimate Associated with the Mixed-Species Model

The mixed-species M4 was better than M2 for the plot AGB estimate with a MAPE of 16.3–20.5%, and nearly 90% of plots fell within the CIs of corresponding estimations based on the species-specific models. A more accurate AGB estimate was obtained when using the models that included H with DBH and combined DBH, H, and wood density (Figure 4a, green color dots). Apart from the Homosha site, the M3 model provided similar accurate results to the across-plot AGB estimate with the MPE_A ranging from 13.6% to 14.8% (Figure 4b, red color dots). Moreover, M5 gained additional accuracy in the plot-level (MAPE ranged from 11.2 to 16.9%) and the across-plot AGB estimates with an MPE_A of 10.5–15.1% and RE of 16.6–22.5%. Similar results were attained when comparing the AGB estimates using the site-specific and general models.

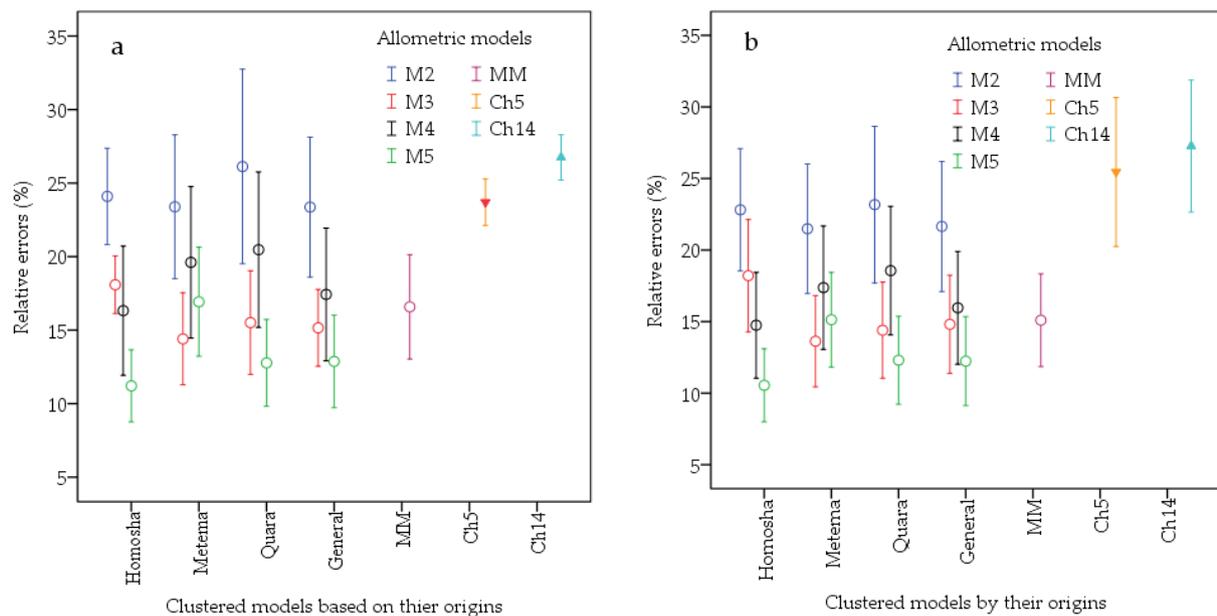


Figure 4. The relative errors in plot (a) and across-plot (b) AGB estimates result from combining the species in mixed-species models and using the distant models. The symbols of MM, Ch5, and Ch14 refer to the models of Mugasha and Chave, respectively, as defined in Section 2.6.1. The error bar indicates the 95% CIs of the mean.

The best selected model (M4) that included wood density and DBH using fit statistics and testing data at tree level was not performing well when applying the plot and across-plot AGB estimates, except for the model of Homosha (Table 4). The model produced a large bias estimate for the study sites. Similarly, for the study site, a generic model produced a large bias, resulting in a higher variation in the MAPE (23.7–26.8%) of AGB among plots (Figure 4a, orange and light blue color triangles). Likewise, an unreliable across-plot estimate was attained using the generic models with an MPE_A of 25.4–27.2% (Figure 4b) and RE of 22.2–36.4%. It was more noticeable for Chave et al.'s [31,32] models, making the selection of the model and predictor variable an important source of uncertainty.

Finally, a mean estimate of the landscape AGB ranged from 40.2 (± 2.21) to 66.1 (± 3.42) $Mg\ ha^{-1}$. This variation in AGB stocks was reflected in the variability of mixed-species models used for estimation. With the Tukey post hoc test, the differences were significant between estimates using the generic models of pantropical forests and models developed in this study ($p < 0.05$). However, the estimates were comparable and accurate when using the M3 and M5 of each site, combined dataset, and Mugasha's [28] model, with the mean AGB ranging from 55.0 (± 2.80) to 63.3 (± 3.24) $Mg\ ha^{-1}$. Moreover, the general model based on both DBH and H slightly improved the precision of landscape AGB estimate by 0.2% of the coefficient of variation when compared with the model that included DBH, H, and wood density.

Table 4. Performance of mixed-species models resulted in bias in the plot and across-plot AGB estimates.

Origins of the Models	Model Forms	Validation Indicators				
		MAPE% Std. dev.	MPEA% Std. Error	RE%		
Homosha	M2	24.1	16.52	22.8	2.15	31.3
	M3	18.1	9.85	18.2	1.98	26.8
	M4	16.3	22.16	14.7	1.86	23.7
	M5	11.2	12.35	10.5	1.29	16.6
Metema	M2	23.4	24.65	21.5	2.28	31.2
	M3	14.4	15.76	13.6	1.61	21.0
	M4	19.6	25.97	17.4	2.17	27.7
	M5	16.9	18.68	15.1	1.67	22.4
Quara	M2	26.1	33.37	23.2	2.76	35.9
	M3	15.5	17.77	14.4	1.69	22.1
	M4	20.5	26.641	18.6	2.26	29.2
	M5	12.8	14.87	12.3	1.55	19.7
Combined dataset	M2	23.4	23.96	21.6	2.29	31.4
	M3	15.2	13.20	14.8	1.73	22.7
	M4	17.4	22.74	16.0	1.99	25.4
	M5	12.9	15.87	12.2	1.57	19.8
Miombo woodlands	MM	16.6	17.88	15.1	1.63	22.2
Pantropical forests	Ch5	23.7	7.96	25.5	2.62	36.4
	Ch14	26.8	7.80	27.3	2.32	35.7

4. Discussion

The uncertainty in the AGB estimation can be generated from various sources. The first source occurs in the model, and it is called model prediction uncertainty [57]. The model building process involves three steps including formulating, fitting, and validating the model. In each step, model uncertainty can occur due to (a) inadequate predictor variables used to avoid problems of multicollinearity and lack of wood density data and (b) validating the fitted model based on the same data. The second source of uncertainty is also the application of the model developed for a given site to other site-based estimations, which has been assessed in very few studies (e.g., Paul [23]). In most previous studies, the model diagnosis and selection process has often involved the same data [28,30]. However, the uncertainty due to combining tree species into a single mixed-species model and the choice of the model using independent data, including field inventory, has been rarely assessed. Such issues were addressed in this study, using AGB measurements of 321 trees comprising 13 species collected from three sites in the CTW of Ethiopia. Moreover, the reliability of the fitted and the generic models to landscape AGB estimation was validated with the field survey of 100 plots.

4.1. Developed Allometric Models

The DBH of the sample trees in this study ranged from 5 to 65 cm, resulting in a large variation in branch architectures and stem forms and a difference in AGB among trees. Such tree growth phenomena including the structure and functional variables are expressed by the scaling relationship between DBH and AGB, called the allometric model [59]. The allometric model thus provided a reliable AGB estimate for all studied species. The variability of tree size (DBH) reflected in ontogeny impacted the model accuracy as evident in the review of Enquist [60]. For *Albizia malacophylla* species, for instance, young trees (the DBH of 5–20 cm) had the predicted universal scaling exponent and deviated to 2.062 as trees began to senesce (or reached the DBH of 31–44 cm). Therefore, the selection of sample trees used to build the model should consider all growth stages (DBH size classes) to match the target population. Then, trees can be proportionally selected in each class, as done here and also as suggested by Roxburgh [16].

Regardless of the site, three species attained the predicted universal scaling relationship between DBH and AGB, whereas most of the remaining species deviated below the theoretical scaling exponent. Similar to the present finding, a lower empirical scaling exponent from the predicted universal value was also attained elsewhere [61]. This variability in the scaling exponents may be attributed to constraints in ecological conditions [60],

resulting in structural differences across forest types, and influencing the applicability of a distant model outside its range.

Despite the non-significant variability of the scaling exponent [60,62], the predicted scaling exponents differed among species in this study. Such difference may be associated with the variation in growth conditions, resulting in marked variability of branch architectures and stem forms as detected in the studied species. Consequently, a significant wood density difference was observed among species (data not shown in this manuscript) and resulted in a difference in their allometry of AGB. Similarly, a difference in interspecific models among species was reported [26,43] that was explained by the variability in wood densities [22,26] and may be associated with a difference in the structures of tree DBH or H among species. Our result suggests that the presented species-specific models can be applied to obtain an improved estimate of tree AGB in the CTW.

A mixed-species model was developed with a different form. The results indicate that the fitted models were highly significant, providing reliable parameter estimates. The AGB of Quara was accurately determined by M3 with DBH and H together, which is consistent with comparable studies conducted in Tanzania [28] and Ethiopia [42]. In contrast, adding more predictors to the model can generate uncertainty that is associated with collinearity problems among predictors [13,28,63] and availability of wood density [64]. The issue of collinearity between DBH and H is recognized, but it has no significant impact on the overall model and associated fit statistics [51]. It has thus been argued that the models with DBH and wood density [26,32,43] and combined DBH, H, and wood density improve the accuracy of the AGB estimate [31,32,43]. The result obtained here supports this conclusion; adding wood density in M2 provided more evidence for the accuracy of AGB than adding H for all mixed-species datasets, explained by variation in wood densities among species. In addition, the performance of M2 was significantly improved when H and wood density were included as compound predictor variables, maintaining the relationship between residual errors and DBH, and gaining an advantage of decreasing uncertainty in the model.

4.2. The Impact of Site Variations on the Accuracy of Allometric Model

Here, an intraspecific allometry variation was found, resulting from the variability in geometries and wood densities among trees despite the pattern being inconsistent across species. This was explained by a difference in wood densities among trees, resulting from site variations. Similarly, a significant variation in wood densities within species was reported for tropical forests [25]. In this study, variation in sites did not adversely impact the mixed-species model accuracy and attained an unbiased AGB estimate with acceptable uncertainty, which has been previously assigned [58]. This was achieved when using the model that included wood density, maintaining a linked factor such as species and sites. It was consistent with the results showing that wood density accounted for a large proportion of the variation in AGB and improved the performance of mixed-species models [31,41,43]. The best models of a specific site thus provided an accurate AGB estimation for other sites, which is partly conditioned by similarity in species composition and climatic conditions over the sites found in the CTW biome.

Moreover, the reliability of the generic models of pantropical forest [31] has often been tested based on empirical data. The result indicates the absence of consistency in the validation results among studies: success for miombo woodland [28] and dry Afromontane forests [30,41] but failure in other studies [43,65]. In this study, the generic models produced a large error, resulting in a biased estimate, and confirmed that the use of a distant model is an important source of uncertainty. In contrast, the model developed for miombo woodland [28] provided reasonable accuracy of AGB estimation for CTW.

4.3. The Uncertainty Associated with the Selections of Mixed-Species Models

The biomass of a forest community may not vary significantly with species composition, diversity, and altitude and can be represented by a single allometric model [60,66]. This has been assumed to hold a universal scaling exponent that is predicted from individ-

ual trees [62], simplifying the issues of species-specific information. Using such theory, we quantified the uncertainty in the plot and across-plot AGB estimates associated with the use of mixed-species models based on field inventory data.

The variability of MAPE in the AGB of plots and across-plot estimates may be attributed to a variation in the tree structures and densities among plots reflected when trees that did not belong to the studied species were removed. The best mixed-species models, M5 followed by M3, of specific sites provided accurate plot and across-plot AGB estimates to the focal site. It agreed with the previous reports showing local multispecies model results in a reliable estimation for the focal site [26]. For AGB estimation with the allometric model, precision is particularly important [23] for policy involved in climate change mitigation including the REDD+ initiative [64]. In addition, the mixed-species models with an MAPE of 18–20% did not require additional validation [67]. These arguments support the results of this study, which obtained a precise across-plot AGB estimate using the M3 and M5 of Metema. When compared to the site-specific models, the general models attained a similar accuracy of the plot and across-plot AGB estimates and were slightly better than the site-specific models of the Metema site.

In contrast to the finding of van Breugel [26], the inclusion of wood density with DBH inflated the bias of plot and across-plot AGB estimates in this study. A large part of the variation in the AGB estimates was explained by M3 but performed poorly in the model building and validating process. This indicates that a model formulation and selection process based on only statistical inference, especially when the model diagnosis is performed on the same data, may reject a useful variable, which was supported by Chatfield [57]. Wood density, however, was a key predictor of AGB when it was combined with DBH and H in the model and contributed to the improvement in the accuracy of AGB estimates. It was consistent with results indicating that incorporating wood density with DBH and H in the model can reduce the effect of environmental factors on the AGB estimates of tropical forests. Moreover, assigning the threshold of PRSE alone may not be a useful indicator for evaluating model performance as found here and verified in a previous study [51]. Our result suggests that the model diagnosis should be supported by existing theory with the knowledge of experts in addition to statistical inference.

In this study, a mixed-species model based on DBH alone consistently provided an unreliable estimate of landscape AGB. For a given model form, although the evidence was not significant, the model that included H with DBH achieved slight improvement in the accuracy of the landscape AGB estimate. It was consistent with the previous result showing that a model that included wood density and DBH is unreliable to estimate landscape AGB [26]. This may be partly explained by assigning the averaged wood density of the community to the trees not belonging to the studied species. When compared to site-specific models, the selected general models did show very slight improvement in the accuracy of the landscape AGB estimate with the relative standard error of 5.1%, illustrating a negligible effect of site variations, and confirmed the advantage of combining species into a single allometric model. The general model based on both DBH and H contributed to obtaining precision in the landscape AGB estimate for CTW. This is particularly important to reduce the availability and cost of the collection of wood density data. Direct measurement of tree height is also relatively practical since the density of trees of CTW is lower than other natural forests, making an advantage of reducing error in height measurements.

Furthermore, the best mixed-species models of CTW were more accurate than the generic models of pantropical forests. The generic models significantly influenced all levels of estimations and underestimated the landscape AGB by more than 20%. This may be associated with a difference in ecological features especially structural diversity resulting from the variation in succession stages between forests. For instance, the generic models constitute a large size of trees collated from matured tropical forests growing in optimum conditions [44]. In contrast, dry woodland including CTW is characterized by a prolonged dry season and frequent fires, which affect plant growth. This variation in environmental conditions may contribute to the variability in plant growth over sites and then result in unique

phylogenetic allometry. The model that included DBH with H of miombo woodlands [28], however, provided reasonable precision of the AGB estimate for CTW, indicating the similarity in vegetation between sites. The results of this study suggest that developing a guideline for the selection of models can reduce uncertainty in AGB estimation, especially in developing countries including Ethiopia where allometric models are scarce.

5. Conclusions

The tree allometry of the DBH and AGB relationship was influenced by species and site, which indicates that applying the distant models is a potential for uncertainty in the AGB estimate. For a given species, ontogeny allometry comprising all sizes matching the target population provides an accurate AGB estimate. Tree allometry differences among species reflect the variation in the growth features of plants such as stem form, branch architecture, and then wood density among species. Although the impact of site factors was significant, the best site-specific models are sufficient tools for the estimation of other sites found in the CTW. The general models based on a dataset of several species collated from multisite could reduce the uncertainty of the AGB estimate associated with the effects of species, site variations, and model selection. Our results highlight that tree height with DBH contributed consistently to the accurate estimate from plot to landscape AGB and was comparable with the estimate using a model that combined DBH, height, and wood density. In contrast, the influence of wood density with DBH was restricted to model calibration, showing the importance of species-specific information. This suggested the need for collecting community-wide wood density data, especially for model fitting used for the estimation of landscape-scale AGB. Our best species-specific and mixed-species models can provide sufficiently reliable AGB and carbon stock estimations, providing a base for forest carbon accounting and quantifying ecosystem services of the *Combretum-Terminalia* woodlands, which is essential to support implementation of payment for environmental services.

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Appendix A

Table A1. The statistical summary of biometric variables such as diameter at breast height (D) and height (H) of the harvested tree species.

Scientific Name	Homosha			Quara			Metema		
	n	DBH (cm)	H (m)	n	DBH (cm)	H (m)	n	DBH (cm)	H (m)
		Mean (min–max)	Mean (min–max)		Mean (min–max)	Mean (min–max)		Mean (min–max)	Mean (min–max)
<i>Albizia malacophylla</i>	51	24.6 (6.8–44.3)	11.5 (4.7–15.0)	-	-	-	-	-	-
<i>Anogeissus leiocarpa</i>	-	-	-	9	29.3 (14.5–44.5)	14.6 (10.4–17.4)	10	21.4 (5.0–40.0)	10.7 (6.0–17.0)
<i>Boswellia papyrifera</i>	-	-	-	-	-	-	10	32.1 (9.0–40.0)	10.3 (6.0–14.0)
<i>Combretum collinum</i>	-	-	-	21	20.3 (5.0–46.0)	10.7 (3.5–17.5)	-	-	-
<i>Combretum harotomannianum</i>	11	10.7 (6–16.5)	6.8 (5.3–9.5)	12	15.1 (5.0–27.0)	8.7 (4.9–12.8)	13	16.9 (5–30)	8.5 (4.0–13.0)
<i>Combretum molle</i>	-	-	-	23	15.6 (5.0–31.0)	8.5 (4.5–13.4)	13	17.5 (6.0–30.0)	8.2 (4.0–12.0)
<i>Entada africana</i>	12	19.8 (7.8–32.0)	9.6 (6.0–12.2)	-	-	-	-	-	-
<i>Lannea fruticosa</i>	12	22.0 (10.2–31.5)	9.2 (6.6–11.4)	9	27.2 (14.5–43.5)	9.9 (7.3–13.3)	12	18.3 (6.0–34.0)	7.3 (4.0–10.0)
<i>Lonchocarpus laxiflorus</i>	-	-	-	-	-	-	12	18.5 (5.0–32.0)	7.9 (4.0–12.0)
<i>Pterocarpus lucens</i>	12	23 (7.5–60)	12.6 (7.0–19.5)	9	28.8 (8.5–48.6)	12.5 (6.5–17.7)	11	25.2 (8.0–41.0)	10.6 (5.0–16.0)
<i>Sterculia setigera</i>	-	-	-	-	-	-	8	39.5 (15.0–65.0)	11.3 (8–15)
<i>Syzygium guineense</i>	9	21.3 (12.5–31.0)	10.1 (7.0–14.0)	-	-	-	-	-	-
<i>Terminalia laxiflora</i>	11	21.0 (7.0–33.5)	10.9 (5.2–14.0)	19	18.8 (5.0–41.3)	8.4 (3.7–13.7)	12	25.1 (7.0–54.0)	9.8 (6.0–17.8)

Appendix B

Table A2. Species-specific models with their parameters (and standard errors) and fit statistics of the species in the *Combretum-Terminalia* woodlands (CTW). The abbreviations in the table are defined in Section 2.6.

Species Name	Model Forms	n	Parameters					Fit Statistics					
			β_0	β_1	β_2	VIF	R ²	MSE	CF	PRSE%			MAPE%
										β_0	β_1	β_2	
Species-specific equations for dataset of Quara district													
<i>A. leiocarpa</i>	M2	9	-1.285 (0.633) ***	2.244 (0.189) ***	-	-	0.946	0.030	1.015	49.3	8.4	-	13.5
	M3		-1.924 (0.874)ns	2.087 (0.240) ***	0.433 (0.411)ns	1.63	0.947	0.030	1.015	45.4	11.5	97.9	12.9
	M6		-2.514 (0.759) *	0.931 (0.081) ***	-	-	0.943	0.032	1.016	30.2	8.7	-	14.4
<i>C. collinum</i>	M2	21	-2.143 (0.217) ***	2.478 (0.075) ***	-	-	0.982	0.040	1.020	10.1	3.0	-	16.2
	M3		-2.199 (0.308) ***	2.416 (0.247) ***	0.101 (0.383)ns	10.39	0.981	0.042	1.021	14.0	10.2	379.2	16.1
	M6		-2.632 (0.262) ***	0.944 (0.032) ***	-	-	0.977	0.051	1.026	10.0	3.4	-	18.3
<i>C. harotomannianum</i>	M2	12	-1.863 (0.312) ***	2.392 (0.118) ***	-	-	0.972	0.047	1.024	16.7	4.9	-	17.6
	M3		-3.459 (0.724) **	1.412 (0.427) **	1.945 (0.825) *	19.00	0.982	0.032	1.016	20.9	30.2	42.4	12.7
	M6		-2.663 (0.296) ***	0.958 (0.040) ***	-	-	0.981	0.034	1.017	11.1	4.2	-	14.9

Table A2. Cont.

Species Name	Model Forms	n	Parameters					Fit Statistics						
			β_0	β_1	β_2	VIF	R ²	MSE	CF	PRSE%			MAPE%	
										β_0	β_1	β_2		
<i>C. molle</i>	M2	23	−1.465 (0.113) ***	2.170 (0.042) ***	-	-	0.992	0.014	1.007	7.7	1.9	-	11.6	
	M3		−1.791 (0.227) ***	2.124 (0.128) ***	0.201 (0.213)ns	4.40	0.984	0.028	1.014	12.7	6.0	106	11.9	
	M6		−2.232 (0.215) ***	0.873 (0.029) ***	-	-	0.977	0.039	1.020	9.6	3.3	-	14.0	
<i>Lankea fruticosa</i>	M2	9	−1.917 (0.711) *	2.299 (0.218) ***	-	-	0.932	0.049	1.025	37.1	9.5	-	16.4	
	M3		−1.293 (0.958)ns	2.535 (0.326) ***	−0.611 (0.625)ns	2.20	0.932	0.049	1.025	74.1	12.9	102.3	13.4	
	M6		−2.611 (1.054) *	0.930 (0.120) ***	-	-	0.881	0.085	1.044	40.4	12.9	-	23.9	
<i>P. lucens</i>	M2	9	−2.735 (0.254) ***	2.622 (0.078) ***	-	-	0.993	0.016	1.008	9.3	3.0	-	9.9	
	M3		−3.119 (0.354) ***	2.307 (0.228) ***	0.566 (0.388)ns	10.00	0.994	0.013	1.010	11.3	9.9	68.6	7.8	
	M6		−3.409 (0.261) ***	1.023 (0.029) ***	-	-	0.994	0.014	1.010	7.7	2.8	-	8.6	
<i>T. laxiflora</i>	M2	19	−2.086 (0.312) ***	2.439 (0.110) ***	-	-	0.965	0.076	1.039	15.0	4.5	-	20.8	
	M3		−2.767 (0.386) ***	1.978 (0.209) ***	0.945 (0.379) *	4.72	0.973	0.058	1.029	14.0	10.6	40.1	18.6	
	M6		−2.789 (0.290) ***	0.980 (0.037) ***	-	-	0.975	0.055	1.028	10.4	3.8	-	18.6	
Species-specific equations that were developed based on datasets of the three study sites														
<i>A. malacophylla</i>	M2	51	−2.641 (0.176) ***	2.511 (0.055) ***	-	-	0.976	0.021	1.011	6.7	2.2	-	12.3	
	M3		−3.436 (0.231) ***	2.276 (0.07) ***	0.631 (0.140) ***	2.23	0.983	0.015	1.008	6.7	3.1	22.2	9.7	
	M6		−3.901 (0.186) ***	1.051 (0.021) ***	-	-	0.980	0.017	1.009	4.8	2.0	-	11.1	
<i>A. leiocarpa</i>	M2	19	−1.462 (0.177) ***	2.299 (0.056) ***	-	-	0.989	0.021	1.010	12.1	2.4	-	11.4	
	M3		−1.705 (0.304) ***	2.162 (0.150) ***	0.268 (0.272)ns	7.11	0.989	0.021	1.010	17.8	6.9	101.5	11.1	
	M6		−2.254 (0.221) ***	0.911 (0.025) ***	-	-	0.986	0.026	1.013	9.8	2.7	-	13.4	
<i>C. collinum</i>	M2	21	−2.143 (0.217) ***	2.478 (0.075) ***	-	-	0.982	0.040	1.020	10.1	3.0	-	16.2	
	M3		−2.199 (0.308) ***	2.416 (0.247) ***	0.101 (0.383)ns	10.39	0.981	0.042	1.021	14.0	10.2	379.2	16.1	
	M6		−2.632 (0.262) ***	0.944 (0.032) ***	-	-	0.977	0.051	1.026	10.0	3.4	-	18.3	
<i>C. harotomannianum</i>	M2	36	−2.120 (0.190) ***	2.428 (0.073) ***	-	-	0.969	0.043	1.022	9.0	3.0	-	16	
	M3		−2.395 (0.219) ***	2.140 (0.148) ***	0.498 (0.227) *	4.61	0.972	0.039	1.019	9.1	6.9	45.6	15.4	
	M6		−2.596 (0.201) ***	0.935 (0.028) ***	-	-	0.970	0.042	1.021	7.7	3.0	-	16.3	
<i>Combretum molle</i>	M2	36	−1.535 (0.139) ***	2.187 (0.051) ***	-	-	0.981	0.029	1.015	9.1	2.3	-	13.8	
	M3		−2.057 (0.182) ***	1.843 (0.101) ***	0.689 (0.183) **	5.42	0.986	0.021	1.011	8.8	5.5	26.6	11.3	
	M6		−2.185 (0.130) ***	0.873 (0.017) ***	-	-	0.986	0.021	1.011	5.9	1.9	-	11.3	
<i>L. fruticosa</i>	M2	33	−2.089 (0.308) ***	2.348 (0.101) ***	-	-	0.943	0.079	1.040	14.7	4.3	-	23.6	
	M3		−1.923 (0.402) ***	2.442 (0.176) ***	−0.209 (0.320)ns	2.96	0.942	0.080	1.041	20.9	7.2	153.1	23.6	
	M6		−2.694 (0.402) ***	0.938 (0.049) ***	-	-	0.920	0.110	1.057	14.9	5.2	-	28	
<i>P. lucens</i>	M2	32	−2.685 (0.229) ***	2.638 (0.072) ***	-	-	0.977	0.043	1.022	8.5	2.7	-	15.9	
	M3		−2.998 (0.306) ***	2.451 (0.143) ***	0.368 (0.244)ns	4.06	0.978	0.041	1.021	10.2	5.8	66.3	15.1	
	M6		−3.503 (0.272) ***	1.042 (0.031) ***	-	-	0.973	0.051	1.026	7.8	3.0	-	17.5	
<i>T. laxiflora</i>	M2	42	−2.439 (0.192) ***	2.551 (0.065) ***	-	-	0.974	0.053	1.027	7.9	2.5	-	18.5	
	M3		−2.773 (0.231) ***	2.273 (0.133) ***	0.522 (0.222) *	4.73	0.977	0.047	1.024	8.3	5.9	42.5	17.4	
	M6		−3.039 (0.205) ***	1.002 (0.025) ***	-	-	0.975	0.052	1.026	6.7	2.5	-	18.9	

Where ***, **, *, and ns refer to significance level at $p < 0.0001, 0.01, 0.04,$ and non-significant, respectively.

Appendix C

Table A3. Difference in fit statistics when models based on D alone were compared with models that used compound predictor variables (combination of predictor variables) for the mixed-species data. A negative change in R^2 (ΔR^2) indicates that the second model exhibits greater R^2 value so that the second model performed better than the first model. A positive change in the relative mean absolute error ($\Delta \text{MAPE}\%$), root mean square error (ΔRMSE in kg), and Akaike's information criterion (ΔAIC) with increasing values indicates that the second model is better than the first model.

Modes	Comparison of Models Involved	Fit Statistics			
		ΔR^2	$\Delta \text{MAPE}\%$	ΔRMSE (kg)	ΔAIC
Quara	M2 using D alone–M3 using D and H	−0.004	2.0	4.7	8.1
	M2–M4 using D and ρ	−0.001	1.0	14.3	30.2
	M2–M5 using D, H, and ρ	−0.005	2.4	11.2	20.9
Homosha	M2–M3	−0.010	2.4	20.3	41.9
	M2–M4	−0.021	5.5	48.1	115.5
	M2–M5	−0.024	6.7	54.1	134.9
Combined data	M2–M3	−0.006	1.6	21.7	99.1
	M2–M4	−0.020	7.4	53.2	281.1
	M2–M5	−0.022	7.9	56.6	302.2

Appendix D

Table A4. The parameters of mixed-species models (and the standard errors) with their PRSE% of the sites and CTW.

Model	Parameters				R ²	PRSE%				VIF
	β_0	β_1	β_2	β_3		β_0	β_1	β_2	β_3	
I. Allometric models of Quara site (n = 102)										
M2	−1.972 (0.115)	2.394 (0.039)	-	-	0.974	5.8	1.6	-	-	-
M3	−2.447 (0.143)	2.022 (0.085)	0.688 (0.142)	-	0.979	5.8	4.2	20.6	-	5.73
M4	−1.704 (0.150)	2.393 (0.038)	-	0.528 (0.198)	0.975	8.8	1.6	-	37.7	-
M5	−2.215 (0.178)	2.049 (0.084)	0.636 (0.142)	0.387 (0.184)	0.979	8.0	4.1	22.3	47.5	5.90
M6	−2.604 (0.114)	0.940 (0.014)	-	-	0.978	4.4	1.5	-	-	-
II. Allometric models of Homosha site (n = 118)										
M2	−2.374 (0.145)	2.450 (0.048)	-	-	0.957	6.1	2.0	-	-	-
M3	−3.007 (0.168)	2.094 (0.074)	0.731 (0.125)	-	0.967	5.6	3.5	17.1	-	3.09
M4	−1.514 (0.133)	2.451 (0.035)	-	1.169 (0.113)	0.978	8.8	1.4	-	-	-
M5	−2.004 (0.168)	2.238 (0.059)	0.436 (0.101)	1.017 (0.111)	0.981	8.4	2.6	23.2	-	3.44
M6	3.188 (0.144)	0.980 (0.017)	-	-	0.966	4.5	1.7	-	-	-
III. Allometric models for combined dataset of Quara, Homosha, and Metema (n = 321)										
M2	−2.064 (0.088)	2.381 (0.030)	-	-	0.953	4.3	1.3	-	-	-
M3	−2.491 (0.106)	2.063 (0.056)	0.605 (0.093)	-	0.959	4.3	2.7	15.4	-	4.10
M4	−1.462 (0.078)	2.394 (0.023)	-	0.982 (0.064)	0.973	5.3	1.0	-	6.5	-
M5	−1.758 (0.098)	2.205 (0.045)	0.358 (0.075)	0.911 (0.064)	0.975	5.6	2.0	20.9	7.0	4.33
M6	−2.691 (0.092)	0.938 (0.011)	-	-	0.957	3.4	1.2	-	-	-

Appendix E

Table A5. Validation of species-specific models and fit statistics that show the effect of site variation on the accuracy of aboveground biomass.

	Best Model of Quara (QM), Homosha (HM), and Mixed Trees (MMt) over Metema Data			Best Model of Metema (MM), HM, and MMt over Quara Data				Best Model of MM, QM, and MMt over Homosha Data			
	EF%	MPE%	RE%		EF%	MPE%	RE%		EF%	MPE%	RE%
<i>Pterocarpus lucens</i>											
QM	86.4	15.17	36.3	MM	87.9	−20.89	30.3	MM	98.7	−5.31	19.8
HM	91.9	−3.07	28.3	HM	82.3	−25.14	36.7	QM	98.7	11.56	20.3
MMt	91.3	4.41	29.5	MMt	93.2	−14.87	22.8	MMt	99.7	−0.02	10.2
<i>Terminalia laxiflora</i>											
QM	97.5	6.29	20.7	MM	91.4	9.28	40.5	MM	95.0	4.24	17.7
HM	99.6	−3.47	8.2	HM	92.1	4.83	38.7	QM	95.6	0.49	16.5
MMt	99.3	2.52	10.7	MMt	90.1	6.98	43.5	MMt	95.6	0.47	16.5
<i>Combretum harotomannianum</i>											
QM	87.7	−22.73	63.2	MM	90.7	16.04	25.8	MM	90.1	−5.94	18.8
HM	82.2	19.43	25.5	HM	73.9	31.29	43.2	QM	32.8	−37.13	49.1
MMt	95.3	−5.82	39.4	MMt	93.0	10.96	22.3	MMt	80.4	−15.82	26.5
<i>Combretum molle</i>			<i>Combretum molle</i>								
QM	90.1	−11.73	25.9	MM	98.4	3.25	11.6				
MMt	90.4	−10.70	25.4	MMt	98.4	2.05	11.5				
<i>Anogeissus leiocarpa</i>											
QM	97.1	2.84	24.2	MM	91.1	−4.47	16.3				
MMt	97.3	2.25	25.4	MMt	92.3	−3.02	15.2				

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