Tree height uncertainty biases aboveground biomass estimation more than wood density in miombo woodlands

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ABSTRACT

Accurate and unbiased estimation of tree aboveground biomass (*AGB*) is essential for large-scale monitoring of forest carbon stocks. But estimating *AGB* typically requires several data imputation steps that can introduce substantial errors that are hard to quantify and correct for. Two sources of uncertainty that are thought to be particularly important but remain ~~poorly understood~~understudied are tree height – which is generally estimated using allometric models – and wood density – which is most commonly assigned from databases based on taxonomic matching. Here we used data from ~~154~~155 destructively harvested trees in Zambia's miombo woodlands that span a large range of sizes to ~~develop a framework to partition~~quantify errors in *AGB* arising from uncertainty in tree height and wood density. We found that when locally-calibrated height-diameter allometries are used to estimate missing tree height information and when wood density is imputed from species-specific values derived from public databases, *AGB* can be estimated with high precision and little or no bias. However, when tree height and wood density are imputed more coarsely using ~~generic information~~data that are not biome specific, errors in *AGB* can be substantial. ~~In particular~~Specifically, estimating tree height using a regional allometric model developed for tropical dry forests led to ~~35% underestimation of~~ underestimating *AGB*~~.~~ by 35%. Our study ~~provides an intuitive approach~~underscores the importance of accurately accounting for ~~quantifying and partitioning errors in *AGB* arising from uncertainty in~~ tree height and wood density~~,~~ to estimate *AGB*, thereby paving the way for more robust ~~mapping~~estimation of forest carbon stocks and ~~fluxes~~their uncertainties across a range of ecosystem types.

Key words: ~~Aboveground biomass, allometry, bias, error propagation,~~ forest carbon~~ stocks, forest structure, tree height, wood density~~; destructive sampling; allometry; power law scaling; Bayesian regression

1. INTRODUCTION

Forests and savannas play a crucial role in regulating the terrestrial carbon cycle by sequestering large amounts of carbon dioxide (CO_2) from the atmosphere and storing it as woody biomass ~~(Chave et al., 2014; Rathgeber et al., 2016; Mitchard, 2018; Martin et al., 2018).~~(Rathgeber et al., 2016). This potential of forests to act as long-term carbon sinks, that slow the pace of climate change by partially offsetting anthropogenic CO_2 emissions, has gained widespread attention in recent decades ~~(Hansen et al., 2013; Ipcc, 2013; Potapov et al., 2017; Grantham et al., 2020; Ellis et al., 2021; Arias et al., 2021).~~(Grantham et al., 2020; Ellis et al., 2021; Arias et al., 2021). This has led to growing interest in restoration programs centered around forest creation and expansion ~~(Lewis et al., 2019; Hua et al., 2024; Cheng et al., 2024), as well as burgeoning international forest carbon markets underpinned by programs such as REDD+ (Kalaba et al., 2013; Bomfim et al., 2022).~~(Lewis et al., 2019; Hua et al., 2024), as well as burgeoning international forest carbon markets underpinned by programs such as REDD+ (Bomfim et al., 2022) and dedicated satellite missions to map global forest carbon stocks (Quegan et al., 2019; Dubayah et al., 2020). However, a fundamental assumption of these efforts is that forest carbon stocks can be estimated accurately and without bias. In practice, this is rarely the case even at the most basic level of the individual tree ~~(Demol et al., 2024; Fareed and Numata, 2024; Terryn et al., 2024),~~(Demol et al., 2024; Fareed and Numata, 2024; Terryn et al., 2024), as there are multiple sources of uncertainty that affect tree biomass estimation and we lack a clear understanding of their relative importance and magnitude.

A fundamental unit of forest carbon stock estimation is a tree's aboveground woody biomass (*AGB*). Direct measurements of *AGB* ~~involve~~involves destructive sampling to weigh the trunk and branches, which in addition to killing the tree is laborious and costly ~~(Clark and Kellner, 2012; Colgan et al., 2013).~~(Clark and Kellner, 2012; Colgan et al., 2013). In practice, *AGB* is therefore almost always estimated using allometric equations that have been calibrated

using data from relatively small numbers of trees whose mass has been destructively measured ~~(Mugasha et al., 2013; Ngomanda et al., 2014; Kapinga et al., 2018; Handavu et al., 2021)~~(Chave et al., 2004) – although more recently terrestrial laser scanning is being increasingly used to generate accurate, non-destructive estimates of tree woody volume and *AGB* ~~(Momo Takoudjou et al., 2018; Calders et al., 2022; Demol et al., 2024).~~(Momo Takoudjou et al., 2018; Calders et al., 2022; Demol et al., 2024). These allometric biomass equations typically ~~have~~rely on some combination of stem diameter at breast height (D), tree height (H), wood density (ρ) and, in rarer cases, crown width as input variables ~~(Chave et al., 2005; Chave et al., 2014; Goodman et al., 2014; Sileshi, 2014; Ploton et al., 2016; Jucker et al., 2017).~~(Chave et al., 2014; Goodman et al., 2014; Ploton et al., 2016; Jucker et al., 2017). A myriad of such equations exist~~,~~ (Henry et al., 2013; Chojnacky et al., 2014; Zianis et al., 2005), but among the most widely used for tropical trees ~~are~~is the ~~models~~pantropical model developed by ~~(Chave et al., 2005; Chave et al., 2014),~~Chave et al. (2014), which express *AGB* as a power-law function of $D^2 \times H \times \rho$ – a compound variable that approximates a tree's trunk volume ($D^2 \times H$) and multiplies this by the density of its wood to estimate *AGB*.

~~These pantropical *AGB* equations generally perform very well when compared to data from destructive harvests. But when measured inputs are replaced with estimates derived from forest inventories, several important sources of bias and uncertainty can be introduced.~~However, the estimation of *AGB* using such models can be greatly impacted by the quality of measurements or imputation of the input variables. In particular, while D is generally recorded accurately and precisely in forest inventories, the same is not true for H and ρ. Common approaches to measuring H in the field using clinometers and laser range finders are both difficult to do accurately and time consuming. When H is measured directly in the field, estimates are therefore often uncertain and in some cases systematically biased ~~(Larjavaara and Muller-Landau, 2013; Sullivan et al., 2018; Terryn et al., 2024).~~(Larjavaara and Muller-

Landau, 2013; Sullivan et al., 2018; Terryn et al., 2024), with the height of tall trees often underestimated. More commonly, *H* is not measured at all, but is instead itself estimated from *D* using allometric equations ~~(Fayolle et al., 2016; Sullivan et al., 2018; Kafuti et al., 2022).~~(Fayolle et al., 2016; Sullivan et al., 2018). These *H*–*D* allometries not only propagate any underlying biases in the *H* ~~values~~measurements used to ~~derive~~parameterize them, but can also introduce additional sources of uncertainty that are hard to quantify once scaled to *AGB*. This includes errors arising from the choice of functional form used to model *H*–*D* allometries ~~(Fayolle et al., 2016; Ledo et al., 2016; Cano et al., 2019; Terryn et al., 2024)~~(Fayolle et al., 2016; Ledo et al., 2016; Cano et al., 2019; Terryn et al., 2024) and the fact that *H*–*D* scaling relationships can vary considerably among tree species and forest types ~~(Feldpausch et al., 2011; Banin et al., 2012; Jucker et al., 2022; Jucker et al., 2025) – something that most *H*–*D* models completely overlook.~~ (Feldpausch et al., 2011; Banin et al., 2012; Jucker et al., 2022; Jucker et al., 2025).

Similarly, ρ is very rarely measured as part of field inventories and is instead almost always assigned from global databases based on taxonomic or geographic matching ~~(Chave et al., 2009; Réjou-Méchain et al., 2017).~~(Chave et al., 2009; Réjou-Méchain et al., 2017; Fischer et al., 2026). While these databases are invaluable, they still only cover <15% of known tree species, meaning that in many cases ρ ~~values are~~is imputed using either taxonomic (e.g., genus or family-level means) or geographic proxies (e.g., plot or regional-level means). Depending on a region's taxonomic coverage in the database and the choice of imputation method, uncertainty in ρ can therefore substantially bias *AGB* estimates ~~(Flores and Coomes, 2011; Mitchard et al., 2014; Phillips et al., 2019).~~(Flores and Coomes, 2011; Mitchard et al., 2014; Phillips et al., 2019).

Here we provide a rigorous quantitative assessment of how uncertainty in both *H* and ρ propagates to tree-level *AGB* estimates, focusing specifically on southern Africa's miombo

woodlands. Like other tropical dry forests, miombo woodlands remain underrepresented in the research and conservation agenda despite ~~covering an area approximately ten times~~being among the ~~size of the UK~~most extensive tropical dry forests in Africa and globally (around 2 million km^2; (Ribeiro et al., 2020)) and storing substantial amounts of carbon in their vegetation ~~(Pennington et al., 2018; Mcnicol et al., 2018; Moonlight et al., 2021; Demol et al., 2024).~~(around 20–30 Mg C ha^{-1}; (Mcnicol et al., 2018)). To address this knowledge gap, we compiled data for ~~154~~155 trees whose *AGB* was measured via destructive ~~harvesting~~sampling in the miombo woodlands of Zambia. These trees cover a wide spectrum of sizes (D = 5.0–~~52~~68.2 cm; H = ~~3.0~~2.9–25.0 m) and represent 37 uniquely identified species that vary considerably in their wood density (ρ = 0.34–0.86 g cm^{-3}). Using these data, we set out to address ~~two key research objectives. First, we compared *AGB* estimates obtained using new biomass allometric models fit to the data with those of existing local and pantropical biomass models. Second, we systematically assessed how different approaches to imputing *H* and ρ affect tree-level *AGB* estimates.~~

three research objectives:

(1) Compare the predictive performance of existing local and pantropical biomass models that differ in their functional form;

(2) Reparametrize existing biomass models with new data to assess how this improves their fit;

(3) Determine how different approaches to imputing H and ρ affect tree-level AGB estimates.

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2. MATERIALS AND METHODS

2.1 Study system

The study was conducted using ~~multiple~~ datasets acquired in ~~Zambia's~~ miombo woodlands~~.~~ ~~These tropical dry forests~~ from three sites in the Copperbelt Province of Zambia – Mwekera, Miengwe and Katanino (Fig. 1). Miombo woodlands are characterized by the dominance of trees in the genus *Brachystegia* that form open-canopy habitats where trees and grasses co-exist. Regionally, they cover around 2 million km^2 of land, forming a belt that stretches from Angola's Atlantic coast to the Indian Ocean in Mozambique and Tanzania ~~(Ribeiro et al., 2015; Ryan et al., 2016; Dziba et al., 2020). Miombo woodlands are shaped by long dry seasons followed by months of intense rainfall, with fire playing a key role in keeping the balance between trees and grasses. Trees in this region have adapted to take advantage of short growing seasons and are able to recover remarkably quickly from wildfires and other forms of disturbance, allowing these woodlands to store surprisingly large amounts of carbon in their vegetation given the seasonally dry climate (Menicol et al., 2018; Pelletier et al., 2018; Demol et al., 2024).~~(Dziba et al., 2020). Miombo woodlands are shaped by long dry seasons (5–8 months), followed by months of intense rainfall which usually falls between November and April. Annual rainfall varies considerably across the region, from around 1600 mm in norther Zambia and southern DRC to as little as 600 mm in Angola and southern Zambia (Ribeiro et al., 2020). Accordingly, the woodlands can be dividend into wet (>1000 mm) and dry miombo (<1000 mm), which differ in their structure and species composition (White, 1983). These woodlands are further shaped by human disturbances comprising mainly of fires, wood harvesting and land clearing for agriculture (Chidumayo, 2013a). Trees have evolved and adapted to these disturbances and recover remarkably quickly (Chidumayo, 2004; Syampungani et al., 2017), with aboveground carbon stocks returning to pre-disturbance levels in around 25–40 years (Williams et al., 2008; Mcnicol et al., 2015). However, regional aboveground carbon density estimates vary significantly among studies

(15–72 Mg C ha^{-1} for mature woodlands; (Ribeiro et al., 2020)). While some of this variation reflects differences in climate, species composition and disturbance regimes (Handavu et al., 2021), it also arises from differences in the way *AGB* is estimated (Demol et al., 2024). This underscores the importance of resolving these sources of uncertainty to improve regional carbon stock estimates.

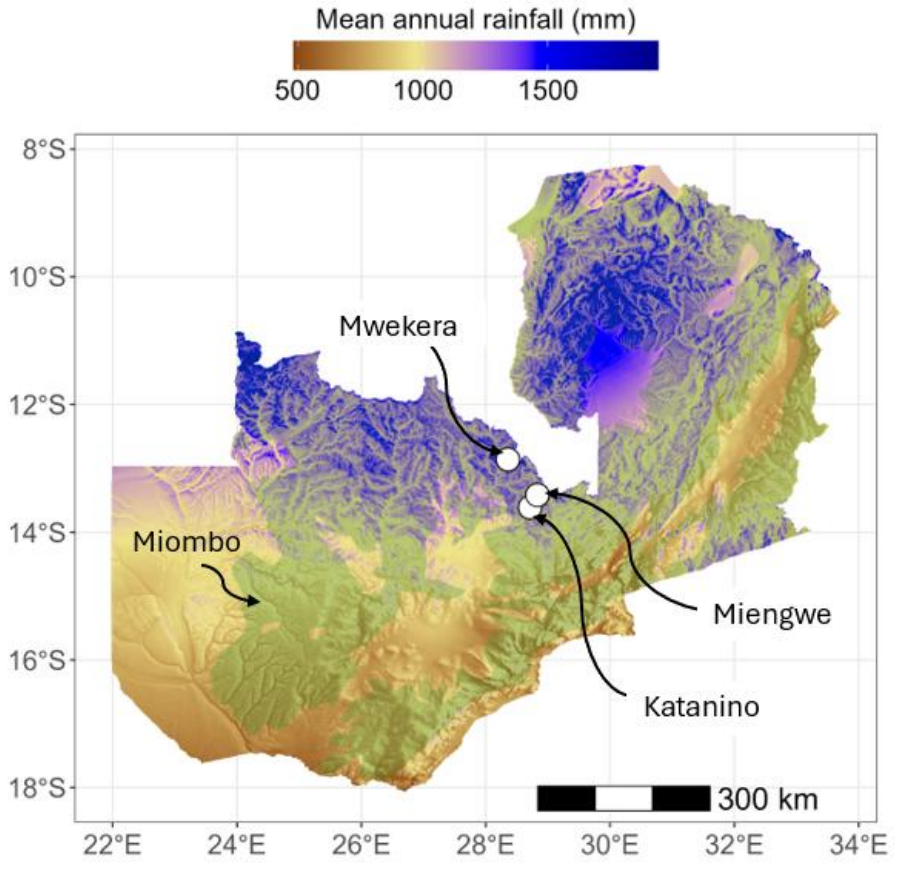


Figure 1. A map of Zambia showing the extent of the miombo woodlands (green shading) and the location of the three sites (white filled circles) from where the data used in the study were collected. The distribution of mean annual precipitation across the country shows the

approximate locations of wet miombo (northern part) and dry miombo (southern part) within Zambia. Precipitation data was extracted from the CHELSA-BIOCLIM+ database at a spatial resolution of 30 arc-seconds (approximately 1 km) (Brun et al., 2022). The shapefile for miombo woodlands extent was obtained from Poppenwimer (2022) based on the description of ecoregions by Olson et al. (2001).

2.2 Tree harvest data

~~We compiled three separate datasets where individual trees were destructively harvested to measure their aboveground biomass (*AGB*, in kg) (Kapinga et al., 2018; Handavu et al., 2021). This involved felling the trees at ground level and then cutting their stems, branches and twigs into sections so that these could be weighed to estimate the total aboveground woody mass of each tree. In addition to *AGB*, the stem diameter at breast height (*D*, in cm), tree height (*H*, in m), and wood density (ρ, in g cm^{-3}) of each tree was also measured. A total of 37 uniquely identified tree species spanning a broad range of wood densities (0.34–0.86 g cm^{-3}; median = 0.61 g cm^{-3}) were measured (Table 1). Together, the harvested trees covered a large spectrum of sizes (*D* = 5.0–52.2 cm; *H* = 3.0–25.0 m), with *AGB* ranging between 5.7–2374.4 kg (Table 1). *AGB* values were visually assessed for potential data entry errors and four trees were flagged as outliers and excluded (Fig. S1a). This left us with a total of 154 trees for fitting *AGB* models.~~

We compiled three separate datasets for which a combined total of 158 individual trees belonging to 37 tree species were destructively harvested to measure *AGB*. Prior to conducting destructive sampling, vegetation surveys were conducted to assign trees to different *D* classes (minimum *D* = 5 cm) from which a random subset was selected for harvesting. In all the three sites, *D* was measured to the nearest 0.1 cm using diameter tapes while *H* was measured using either a Suunto hypsometer (before trees were felled, at the Mwekera) or a 50 m measuring tape (after felling trees at the other two sites). Selected trees were felled at ground level (<15 cm from the ground) and then cut into manageable segments of between 1–3 m using chain

saws. The cut segments were then weighed for fresh mass in the field using the END-T3 weighing indicator with a capacity of 600 kg and a precision of 0.01 kg. Furthermore, all small branches, twigs and leaves were cut from each trunk and measured for mass (Kapinga et al., 2018; Handavu et al., 2021).

In addition to *AGB*, *D*, and *H*, the wood density (ρ, in g cm^{-3}) for each tree was also measured. Specifically, ρ was determined using sample discs cut from all wood components (trunk base, trunk segments, large and small branches) to account for variation in ρ within a tree. The cut discs were taken to the laboratory where they were oven dried at 105°C for 48 hours and then mass was determined using a scale with precision of 0.001 g. The oven dried discs were then submerged in water for 48 hours to reach saturation before determining the volume of green (fresh) wood. The volume for each disc was determined using the water displacement method using graduated cylinders. ρ was then calculated as the oven dry mass per unit volume of green wood (Kapinga et al., 2018; Handavu et al., 2021).

To rule out potential measurement errors that could unduly influence the calibration of *AGB* models, we used Cook's distance and studentized residuals to check for outliers in the bivariate relationship between *AGB* and *D* (on a log-log scale). Based on this, we identified three data points that were flagged as outliers and excluded from further analysis (Fig. S1a). This left us with 155 trees for comparing and reparametrizing *AGB* models. This dataset covered a large spectrum of sizes (*D* = 5.0–68.2 cm; *H* = 4.2–25.0 m), with *AGB* ranging between 5.7–3209.9 kg and wood density ranging between 0.34–0.86 g cm^{-3} (Table 1 and see Fig. 2 for a summary of the tree harvest data and the relationship between *AGB* and its predictors).

Table 1. Breakdown of the tree harvest dataset for the three sites in miombo woodlands, including number of trees harvested and species, as well as the median and range (in square

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brackets) of stem diameter at breast height, total tree height, wood density, aboveground biomass, elevation, mean total annual precipitation and mean annual temperature.

	Katanino forest	**Miengwe forest**	**Mwekera forest**	**Combined dataset**
Number of trees harvested	12	94	~~48~~49	~~154~~155
Number of species	9	33	5	37
Stem diameter (*D*; cm)	22.6	21.3	22.0	21.4
	[12.2 – 46.0]	[5.0 – 52.2]	[5.5 – ~~48.0~~68.2]	[5.0 – ~~52~~68.2]
Tree height (*H*; m)	13.5	12.9	~~16.5~~17.0	13.8
	[5.7 – 22.8]	[4.2 – 20.7]	[5.0 – 25.0]	[4.2 – 25.0]
Wood density (ρ; g cm^{-3})	0.64	0.60	0.64	0.61
	[0.49 – 0.86]	[0.42 – 0.82]	[0.34 – 0.85]	[0.34 – 0.86]
Aboveground biomass (*AGB*; kg)	301.0	217.7	~~225~~230.6	~~218.9~~
	[27.2 - 2149.3]	[7.8 - 2374.4]	[5.7 –	219.2
			~~1545.2~~3209.9]	[5.7 –
				~~2374.4~~3209.9]
Mean elevation (m a.s.l.)	1323	1324	1228	[1228 – 1324]
Mean annual precipitation (mm yr^{-1})	1325	1250	1198	[1198 – 1325]
Mean annual temperature (°C)	20.1	20.2	20.9	[20.1 – 20.9]

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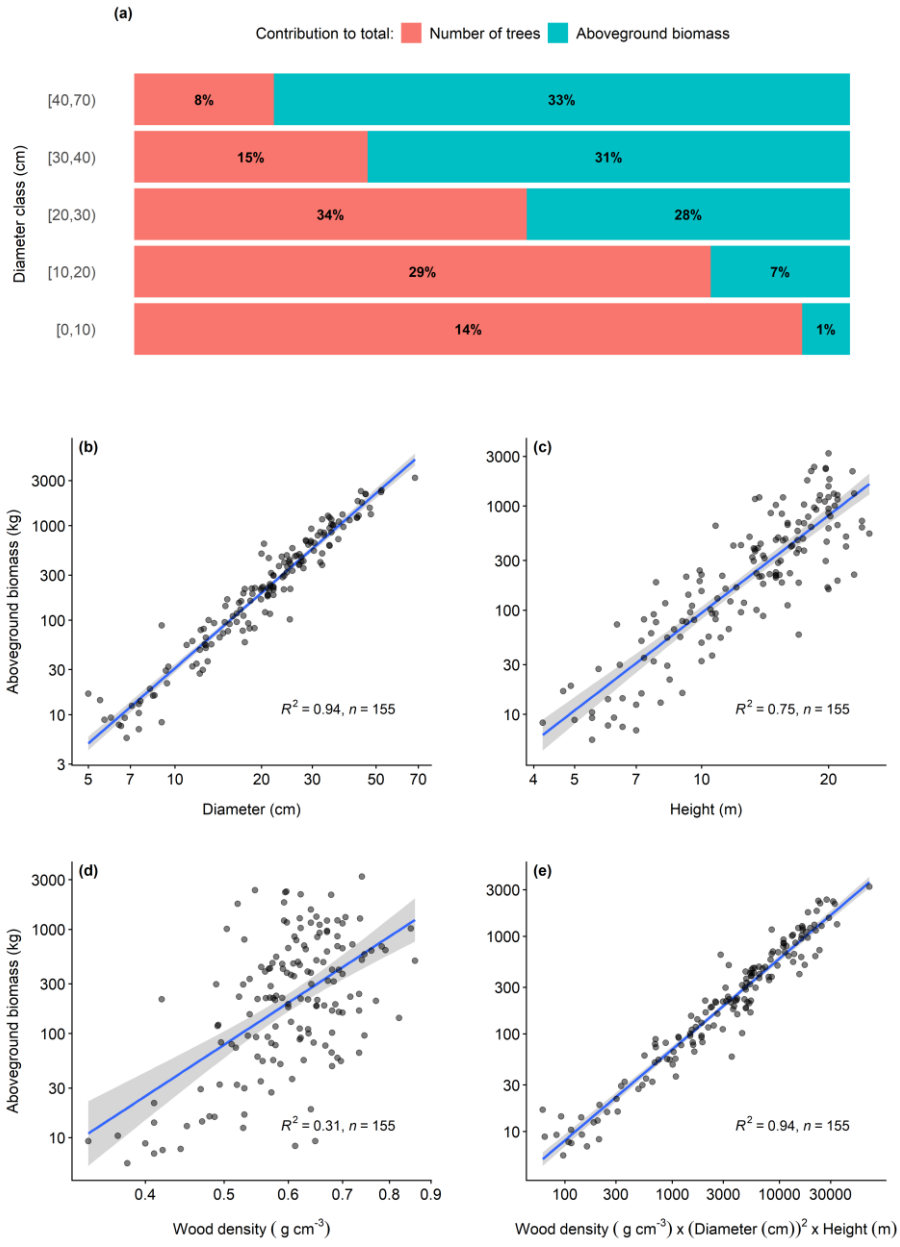


Figure 2. Overview of the tree harvest dataset. The bar plot **(a)** shows the distribution of samples across the five tree diameter classes in terms of both number of trees and their

contribution to above ground biomass (*AGB*), both expressed as percentages of the total – Note that the bars in **(a)** are not plotted to scale but merely show the percentage contribution of each *D* class to total number of trees and total *AGB*. Scatterplots show the relationship between *AGB* and the predictors used to model it, including **(b)** stem diameter (*D*), **(c)** total tree height (*H*), **(d)** wood density (ρ) and **(e)** the compound variable of *D*, *H* and ρ. The coefficient of determination (R^2) between *AGB* and each of the predictor variables is shown along with the line of best fit (blue colour) and its 95% confidence bound (grey colour). The dark grey filled circles represent the *AGB* values of each of the 155 destructively harvested trees, plotted on a log-log scale.

Apart from the tree harvest datasets used here, there are a number of other studies where destructive sampling for *AGB* has been conducted across miombo woodlands, including those in Mozambique (Ryan et al., 2011; Guedes et al., 2018), Malawi (Kachamba et al., 2016; Kuyah et al., 2016), Tanzania (Chamshama et al., 2004; Mugasha et al., 2013) and Zambia (Chidumayo, 2013b). However, all these datasets lack wood density measurements at the individual tree level and were therefore not suitable to address the core questions of our research.

2.3 Height–diameter modelling data

To determine how different approaches to ~~impute~~imputing missing tree height values impact *AGB* estimates, we compiled an additional dataset of trees from miombo woodlands in Zambia for which both *H* and *D* were measured in the field. This included forest inventory data from the three ~~sites~~study sites (Mwekera, Miengwe and Katanino) where trees were also destructively harvested to measure *AGB* ~~(Kapinga et al., 2018; Handavu et al., 2021).~~(Kapinga et al., 2018; Handavu et al., 2021). In Mwekera, 16 square plots (25×25 m) were laid out and all trees with $D \geq 5$ cm in each quadrat were identified to species level. For each tree, *D* was measured to the nearest 0.1 cm using a diameter tape while *H* was measured to the nearest 0.1

m using a Suunto hypsometer (Kapinga et al., 2018). The same forest inventory approach was used in Miengwe and Katanino forests, although in these two sites circular plots with a 20 m radius were used instead (Handavu et al., 2021). Collectively, ~~these~~ *H* and *D* were measured for a total of 4410 trees – excluding the 155 trees which were harvested for *AGB*.

We assessed the data for potential outliers by fitting a log-log linear model relating *H* and *D*. Based on the Cook's distance, a total of 223 trees were flagged as likely measurement errors and were thus excluded from further analysis (Fig. S1b). ~~represent~~This left us with 4187 trees for *H*-*D* model fitting, belonging to 79 ~~uniquely identified~~ tree species and ~~span~~spanning a similar range of tree sizes to those sampled for *AGB* (*D* = 5.0–70 cm; *H* = 2.~~0~~9–33.0 m) (~~see~~ Table ~~S3 for details). *H*–*D* relationships were visually assessed for potential~~ 2).

Table 2: Breakdown of the height-diameter modelling dataset for the three sites in wet miombo woodlands, including number of plots, trees measured, species as well as the median and range of stem diameter at breast height, total tree height, basal area, tree density, elevation, mean total annual precipitation and mean annual temperature. Climate data ~~entry errors and a small number of trees (~ 2%) were flagged as outliers and excluded (Fig.~~ were extracted from the CHELSA-BIOCLIM+ database (Brun et al., 2022) at a spatial resolution of 30 arc-seconds (approximately 1 km).~~S1b).~~ ~~This left us with a total of 4321 trees for model fitting.~~

Variable	Katanino forest	Miengwe forest	Mwekera forest	Combined dataset
Number of plots	7	55	16	-
Number of trees measured	208	3630	349	4187
Number of species	40	74	33	79
Stem diameter (*D*; cm)	16.0 [5.5 – 51.0]	13.4 [5.0 – 70.0]	20.5 [5.0 – 62.3]	14.0 [5.0 – 70.0]
Tree height (*H*; m)	10.0 [3.3 – 22.0]	9.8 [2.9 – 33.0]	12.5 [3.0 – 25.0]	10.0 [2.9 – 33.0]
Basal area (*BA*; m^2 ha^{-1})	12.0 [4.9 – 14.8]	15.5 [9.4 – 31.1]	18.1 [10.7 – 29.1]	15.5 [4.9 – 31.1]
Tree density (stems ha^{-1})	342 [104 – 414]	580 [287 – 1329]	416 [224 – 512]	565 [104 – 1329]
Elevation (m a.s.l)	1323 [1255 – 1327]	1324 [1286 – 1340]	1228	1323 [1228 – 1340]
Mean annual precipitation (mm yr^{-1})	1325 [1186 – 1353]	1250 [1130 – 1348]	1198	1249 [1130 – 1353]
Mean annual temperature (°C)	20.1 [20.1 – 20.4]	20.2 [20.1 – 20.5]	20.9	20.2 [20.1 – 20.9]

2.4 Data harmonization and analysis

All data processing and statistical analyses were conducted in R (version 4.3.1; ~~(R Core Team, 2023)) using the brms, GGally~~(R Core Team, 2023)) using the brms, GGally, geodata, terra, tidyverse, data.table, ggpmisc, cowplot, multcompView, BIOMASS, rWCVP and U.Taxonstand packages ~~(Bürkner, 2017; Réjou-Méchain et al., 2017; Wickham et al., 2019; Wilke, 2020; Schloerke et al., 2021; Hijmans, 2023; Dowle and Srinivasan, 2023; Brown et al., 2023; Zhang and Qian, 2023; Aphalo, 2024).~~(Bürkner, 2017; Réjou-Méchain et al., 2017; Wickham et al., 2019; Wilke, 2020; Schloerke et al., 2021; Hijmans, 2023; Dowle and Srinivasan, 2023; Brown et al., 2023; Zhang and Qian, 2023; Aphalo, 2024). Prior to conducting statistical analyses, we used the rWCVP and U.Taxonstand packages to harmonize tree species names ~~were harmonized~~ across all datasets using the World Checklist of Vascular Plants ~~(Govaerts et al., 2021; Brown et al., 2023).~~(Govaerts et al., 2021; Brown et al., 2023). For this step, we also cross-referenced and matched species names against the Global Wood Density Database (GWDD) which we used in subsequent analyses to assign ρ values to species ~~(Chave et al., 2009; Réjou-Méchain et al., 2017).~~using the BIOMASS package (Chave et al., 2009; Réjou-Méchain et al., 2017).

2.5 Objective 1 – Comparing ~~alternative~~ the performance of existing *AGB* models

To determine how much tree-level *AGB* estimates are influenced by the choice of biomass ~~allometry~~equation, we calculated and compared *AGB* estimates obtained using two existing ~~and two newly developed~~ biomass models. The first *AGB* ~~allometry~~equation we tested is ~~the widely~~one of most commonly used pantropical ~~model~~models developed by ~~(Chave et al., 2014),~~(Chave et al., 2014), which expresses *AGB* as the following function of *D*, *H* and ρ:

$$AGB = 0.067 \times (\rho D^2 H)^{0.976} \times \exp\left[\frac{0.357^2}{2}\right]. \quad (1)$$

~~The second is a local *AGB* model developed as part of Zambia's second integrated land-use assessment (ILUA2) which estimates *AGB* from *D* alone (Ilua, 2016; Forestry Department, 2016):~~

where $\exp\left[\frac{0.357^2}{2}\right]$ is the Baskerville correction factor defined as $\frac{\hat{\sigma}^2}{2}$, with $\hat{\sigma}$ corresponding to the estimated residual standard error of the model. The correction factor is used to account for the systematic bias introduced when back-transforming from a log-log linear model to a power law function (Baskerville, 1972). This model was developed using a large collection of tree harvest data (4004 trees) from across the tropics, including the miombo. It has been used to estimate *AGB* in tropical forests, including the miombo woodlands of Zambia (Pelletier et al., 2018; Kanja et al., 2025).

The second literature model we considered is a local *AGB* model developed as part of Zambia's second integrated land-use assessment (ILUA2) which estimates *AGB* from *D* alone (ILUA, 2016; Forestry Department, 2016):

$$AGB = 0.128 \times D^{2.342} \quad (2)$$

~~To complement these two existing *AGB* models, we used the tree harvest data described above to reparametrize a miombo-specific version of both equations. Specifically, we used the brms package to fit log-log regression models in a Bayesian framework were *AGB* was expressed as a function of either $\rho D^2 H$ or *D* alone (see S1 for details on model fitting~~As mentioned previously, there are other *AGB* models developed from destructive samples across miombo woodlands, but for the purpose of this study, we chose eq. 2 for two reasons. First, the model was developed using one of the largest collated tree harvest datasets in the region: 1319 harvested trees in Botswana, Tanzania and Zambia. The trees were harvested in *Acacia*, mopane and miombo vegetation types but with the majority of trees (~85%) coming from dry and wet miombo (Forestry Department, 2016). To our knowledge, all the other existing models

developed from destructive samples in the miombo are based on much smaller sample sizes (20–170 harvested trees). Second, this model has been adopted for use at national level in Zambia to estimate *AGB* for all vegetation types (ILUA, 2016), including to generate Zambia's forest reference emission level (FREL) submission to the United Nations Convention for Climate Change (UNFCC) (GRZ, 2016, 2021).

We used eqs. (1) and (2) to estimate the *AGB* for each of the 155 trees using measurements of *D*, *H* and ρ as inputs. ~~). The resulting fitted models were as follows:~~

~~$AGB = 0.118 \times (\rho D^2 H)^{0.924} \times \exp\left[\frac{0.373^2}{2}\right]$, and~~ ~~(3)~~

~~$AGB = 0.081 \times D^{2.600} \times \exp\left[\frac{0.385^2}{2}\right]$.~~ ~~(4)~~

We then compared the predictive ability of these ~~four~~two models on the basis of ~~two widely-used metrics that capture both the precision and bias of model predictions relative to observed *AGB* values (Huang et al., 2003; Chave et al., 2014; Sileshi, 2014):~~the root mean square error (RMSE, in kg) as a measure of precision, and percentage error (PE, in ~~%):~~%) as a measure of bias:

~~Root mean square error (RMSE) = $\sqrt{\left[\frac{1}{n}\sum_{i=1}^{n}\left(AGB_i - \widehat{AGB_i}\right)^2\right]}$, and~~ ~~(5)~~

~~Percentage error (PE) = $\left(\left(\frac{1}{n}\sum_{i=1}^{n}\left(\widehat{AGB_i} - AGB_i\right)\right) / \frac{1}{n}\sum_{i=1}^{n}\left(AGB_i\right)\right) \times 100$,~~ ~~(6)~~

RMSE = $\sqrt{\left[\frac{1}{n}\sum_{i=1}^{n}\left(AGB_i - \widehat{AGB_i}\right)^2\right]}$ (3)

PE = $\left(\left(\frac{1}{n}\sum_{i=1}^{n}\left(\widehat{AGB_i} - AGB_i\right)\right) / \frac{1}{n}\sum_{i=1}^{n}\left(AGB_i\right)\right) \times 100$ (4)

where AGB_i is the measured AGB for tree i and $\widehat{AGB_i}$ is the predicted AGB for tree i.

We used PE ~~in order~~ to ~~get~~estimate the magnitude of the mean error relative to the mean observed *AGB*. We chose PE among other metrics of model performance because it gives ~~much~~

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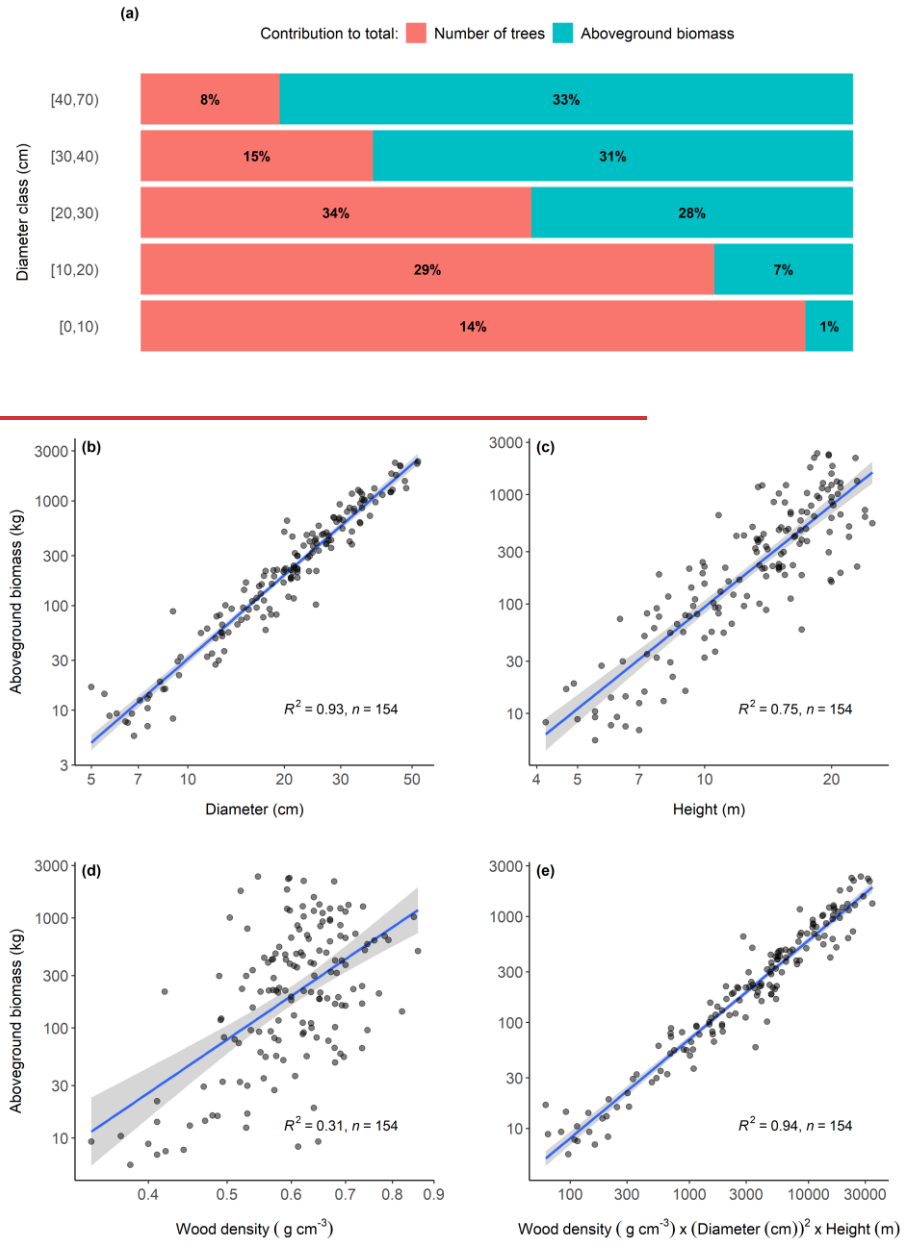
more weight to ~~the~~ large trees ~~since these have the largest errors in absolute terms. Large errors~~, which are ~~undesirable for large trees because these~~the biggest source of uncertainty in *AGB* estimation and contribute ~~the most to~~disproportionately towards total ~~*AGB*~~ forest carbon stocks (Fig. 1a; Lutz et al., 2018; Calders et al., 2022).

Finally, we also assessed the performance of the models by fitting a linear regression between observed and predicted *AGB* values and extracting the intercept and slope parameters with their associated 95% confidence intervals. If the model is unbiased, we would expect the intercept to have a value close to 0 and the slope to be approximately 1 ~~(Sileshi, 2014).~~(Sileshi, 2014).

2.6 Objective 2 – Reparametrizing *AGB* models to compare their performance to published equations

To complement the two existing *AGB* models, we used the tree harvest dataset described above to reparametrize a miombo-specific version of eqs. 1 and 2. Specifically, we fit linear regressions to log-log transformed data to model the power law relationship between *AGB* and either $\rho D^2 H$ or D alone. Models were fit in a Bayesian framework using the brms package. We used weak priors for the normalization constant (intercept) and scaling exponent (slope), which we assumed to be normally distributed. Parameter estimates were based on 6000 posterior samples drawn from 4 parallel chains after discarding 1000 burn-in draws per chain. Models were assessed based on the Gelman-Rubin statistic (Rhat = 1.00), the Bulk_ESS and Tail_ESS statistics (both >1000), and posterior predictive checks (Fig. S2), all of which confirmed that the models adequately converged and fitted the observed data well (see Appendix S1 for additional details on model fitting and validation). The resulting fitted models were as follows:

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(a)
Contribution to total:
Number of trees
Aboveground biomass
Diameter class (cm)
[40,70)
[30,40)
[20,30)
[10,20)
[0,10)
8%
33%
15%
31%
34%
28%
29%
7%
14%
1%
(b)
Aboveground biomass (kg)
Diameter (cm)
R^2 = 0.93, n = 154
(c)
Height (m)
R^2 = 0.75, n = 154
(d)
Wood density (g cm^{-3})
R^2 = 0.31, n = 154
(e)
Wood density (g cm^{-3}) x (Diameter (cm))^2 x Height (m)
R^2 = 0.94, n = 154

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$$AGB = 0.119 \times (\rho D^2 H)^{0.923} \times \exp\left[\frac{0.373^2}{2}\right] \quad (5)$$

$$AGB = 0.083 \times D^{2.590} \times \exp\left[\frac{0.384^2}{2}\right] \quad (6)$$

Having reparametrized the two literature *AGB* models (eqs 1 and 2), we then compared the performance of the four equations (1–2 and 5–6) based on RMSE and PE. This allowed us to determine which of the two functional forms is most suitable for predicting *AGB* estimation in miombo woodlands.

2.7 Objective 3 – ~~**Figure 1.** Overview of the tree harvest dataset. The bar plot **(a)** shows the distribution of samples across the five tree diameter classes in terms of both number of trees and their contribution to above ground biomass (*AGB*), both expressed as percentages of the total. Scatterplots show the relationship between *AGB* and the predictors used to model it, including **(b)** stem diameter (*D*), **(c)** total tree height (*H*), **(d)** wood density (ρ) and **(e)** the compound variable of *D*, *H* and ρ. The coefficient of determination (R^2) between *AGB* and each of the predictor variables is shown along with a line of best fit (blue colour) and its 95% confidence bound (grey colour). The dark grey filled circles represent the *AGB* values of each of the 154 destructively harvested trees, plotted on a log-log scale.~~

~~2.6~~ Influence of height and wood density uncertainty on *AGB* estimates

To better understand how different approaches to imputing H and ρ impact tree-level *AGB* estimates, we devised a series of scenarios in which we imputed values of H and ρ following commonly used practices for dealing with missing data and quantified their relative contribution to *AGB* errors. For the purposes of this analysis, we used the pantropical model of ~~(Chave et al., 2014) to predict *AGB* (Eq. (1)), as it has been widely used in the tropics, including in miombo woodlands (Pelletier et al., 2018; Grz, 2021; Kanja et al., 2025), and performed well on our dataset (see Results for details).~~(Chave et al., 2014) to predict *AGB* (eq. 1) since it performed well on our dataset (see Results for details) and is widely used by the research community. As above, model performance was assessed by comparing predicted and observed *AGB* values on the basis of RMSE and PE for the entire dataset, as well as PE when grouping trees into different D size classes (<10 cm, 10–20 cm, 20–30 cm, 30–40 cm, >40 cm).

As a starting point, we began by using ~~Eq. (~~eq. 1~~)~~ to predict the *AGB* of all ~~154~~the 155 harvested trees when using field-measured values of both H and ρ as inputs. This served as our best case scenario, in which all ~~input~~inputs data have been directly measured in the field. Next, we repeated this same process but replaced field-measured H values with estimates derived

from two alternative *H*–*D* allometries: (1) a locally-calibrated, species-specific allometry and (2) a regional, biome-specific allometry. The local allometry was derived using *H* and *D* values from the ~~4321~~4187 trees described above. The relationship was modelled as a power-law function fit to log–log transformed data~~.~~ ($H = \alpha_j \times D^{\beta_j}$), where both the scaling coefficient (α, intercept) and scaling exponent (β, slope) were allowed to vary across species (j~~) in a hierarchical Bayesian framework (see S2 for details):~~, 79 species + 1 group for 21 trees with no species identification) in a hierarchical Bayesian framework. Model fitting and assessment followed the same procedures described above for the reparametrized *AGB* models. Estimated species-level parameters are reported in Table S4, while the population-level fit (or fixed effects) was:

$$H = 1.846 \times D^{0.613} \times \exp\left[\frac{0.240^2}{2}\right] \quad (7)$$

~~$H = \alpha_j \times D^{\beta_j}$.~~

For the regional *H*–*D* allometry, we ~~instead~~ used an existing model for tropical dry forest trees developed using the Tallo database ~~(Jucker et al., 2022):~~(Jucker et al., 2022):

$$H = 2.355 \times D^{0.477} \quad (8)$$

~~.~~

Finally, we used a similar approach to vary the wood density inputs in the *AGB* equation. Specifically, we replaced field-measured ρ values with either (1) species-specific mean values (or closest taxonomic unit) obtained from the GWDD ~~or (2) with a regional mean value for African tropical forests (ρ = 0.598 g cm^{-3}; (Chave et al., 2009).~~using the BIOMASS package (Réjou-Méchain et al., 2017) or (2) with a regional mean value for African tropical forests (ρ = 0.598 g cm^{-3}; (Chave et al., 2009). When matching to the GWDD, 55% of trees were assigned species-level values, 43% genus-level means and the remaining 2% a mean of the ~~population~~dataset (0.682 g cm^{-3}).

In total, this gave us nine scenarios to compare: three possible *H* inputs into the *AGB* equation (field-measured, species-specific or biome-specific), three possible wood density

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inputs (field-measured, species-specific or biome-specific), and their respective combinations (Table 3).

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Table 3: Summary of the nine scenarios used to determine the impact of different height and wood density inputs when estimating AGB. Uncertainty, in AGB estimates, increasing from left to right for height inputs and from top to bottom for wood density.

Scenario 1	**Scenario 2**	**Scenario 3**
Height: measured	Height: species-specific *H-D*	Height: regional *H-D*
Wood density: measured	Wood density: measured	Wood density: measured
Uncertainty: low	Uncertainty: medium	Uncertainty: medium-high

Scenario 4 Height: measured Wood density: species-specific from GWDD Uncertainty: medium	**Scenario 5** Height: species-specific *H-D* Wood density: species-specific from GWDD Uncertainty: medium-high	**Scenario 6** Height: regional *H-D* Wood density: species-specific from GWDD Uncertainty: high
Scenario 7 Height: measured Wood density: regional mean Uncertainty: medium-high	**Scenario 8** Height: species-specific *H-D* Wood density: regional mean Uncertainty: high	**Scenario 9** Height: regional *H-D* Wood density: regional mean Uncertainty: very high

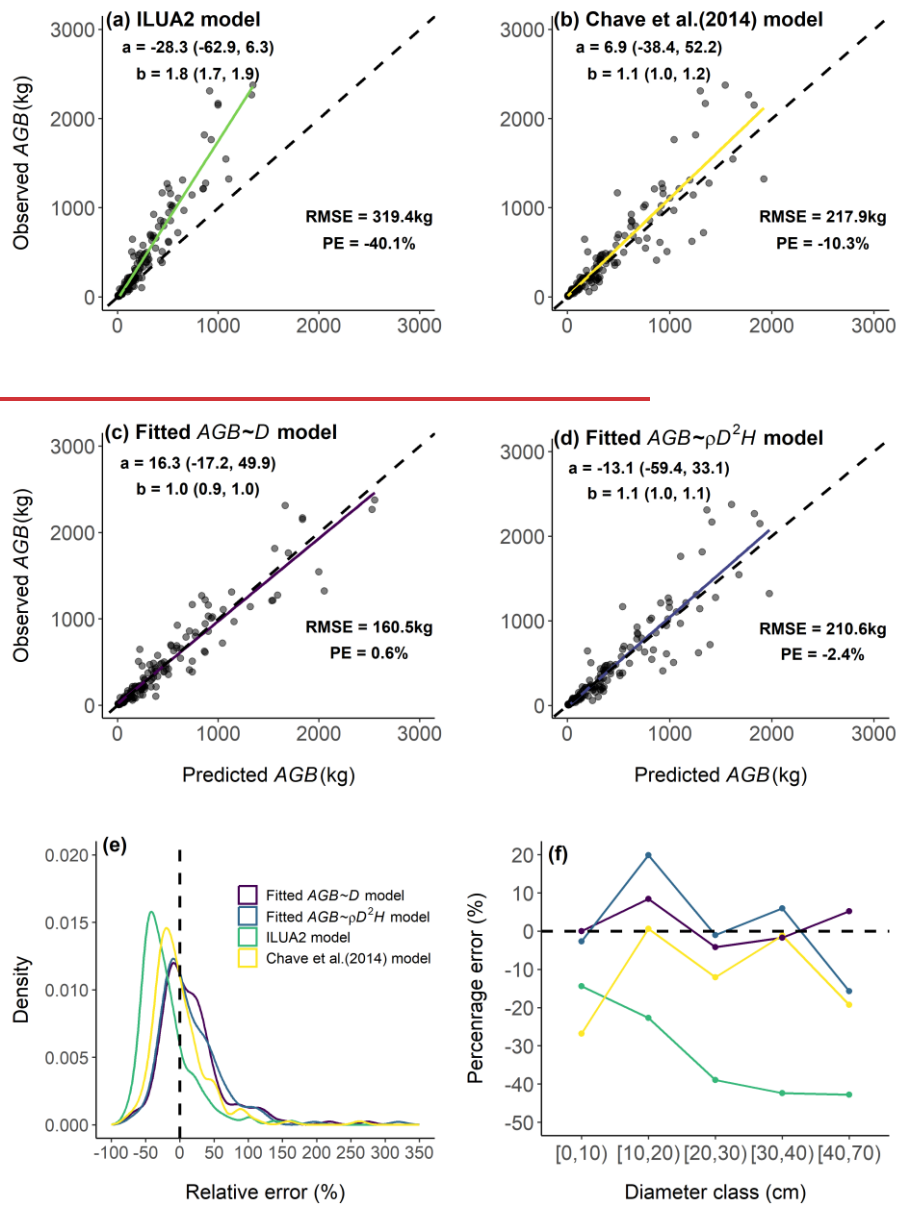
3. RESULTS

3.1 Objectives 1 and 2 – Uncertainty in *AGB* estimation due to choice of *AGB* model

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Of the four *AGB* models we compared, three performed similarly well and produced unbiased estimates of *AGB* across the range of tree sizes (Fig. 23 and Fig. S4): the two models calibrated using the tree harvest data presented in this paper (Eq. (3)eqs. 5 and Eq. (4))6) and the existing pantropical model developed by Chave et al. (2014) (Eq. (eq. 1)). Regressions). In particular, regressions between predicted and observed *AGB* values for all threeboth models that used ρD^2H as predictors (eqs. 1 and 5) had intercepts with 95% confidence intervals that overlapped with 0 (range of mean intercept values = -13.1 – 16.3) and slopes that were very closeequal to 1. Of thesethe three *AGB* models, the *D* only that performed similarly well, the reparametrized model (Fig. 2c) with ρD^2H as a predictor of *AGB* model had the lowest RMSE (160.5 kg vs 210.6 and 217.9214.2 kg) and PE (0(-1.6% vs -2.4 and -10.3%), confirming that *D* is the single strongest predictor of *AGB* (%; Fig. 1b3c). By contrast, the ILUA2 model (Eq. (eq. 2))) developed as part of Zambia's forest inventory program substantially underestimated *AGB* (Fig. 2aand had the worst performance metrics (RMSE = 323.2kg and PE = -39.2%) (Fig. 3b), especially for large trees (greenblue line in Fig. 2f).3f; see also Fig. S4). On average, predicted

values of *AGB* obtained using the ILUA2 model were around ~~40~~35% lower than those measured in the field (slope coefficient = 1.~~8~~6; Fig. 3b) and trees in the largest size class had a PE of -40% (Fig. ~~2f~~3f).


(a) ILUA2 model
a = -28.3 (-62.9, 6.3)
b = 1.8 (1.7, 1.9)
RMSE = 319.4kg
PE = -40.1%
(b) Chave et al.(2014) model
a = 6.9 (-38.4, 52.2)
b = 1.1 (1.0, 1.2)
RMSE = 217.9kg
PE = -10.3%
(c) Fitted AGB~D model
a = 16.3 (-17.2, 49.9)
b = 1.0 (0.9, 1.0)
RMSE = 160.5kg
PE = 0.6%
(d) Fitted AGB~ρD²H model
a = -13.1 (-59.4, 33.1)
b = 1.1 (1.0, 1.1)
RMSE = 210.6kg
PE = -2.4%
Observed AGB (kg)
Predicted AGB (kg)
(e)
Fitted AGB~D model
Fitted AGB~ρD²H model
ILUA2 model
Chave et al.(2014) model
Density
Relative error (%)
(f)
Percenrage error (%)
[0,10)
[10,20)
[20,30)
[30,40)
[40,70)
Diameter class (cm)

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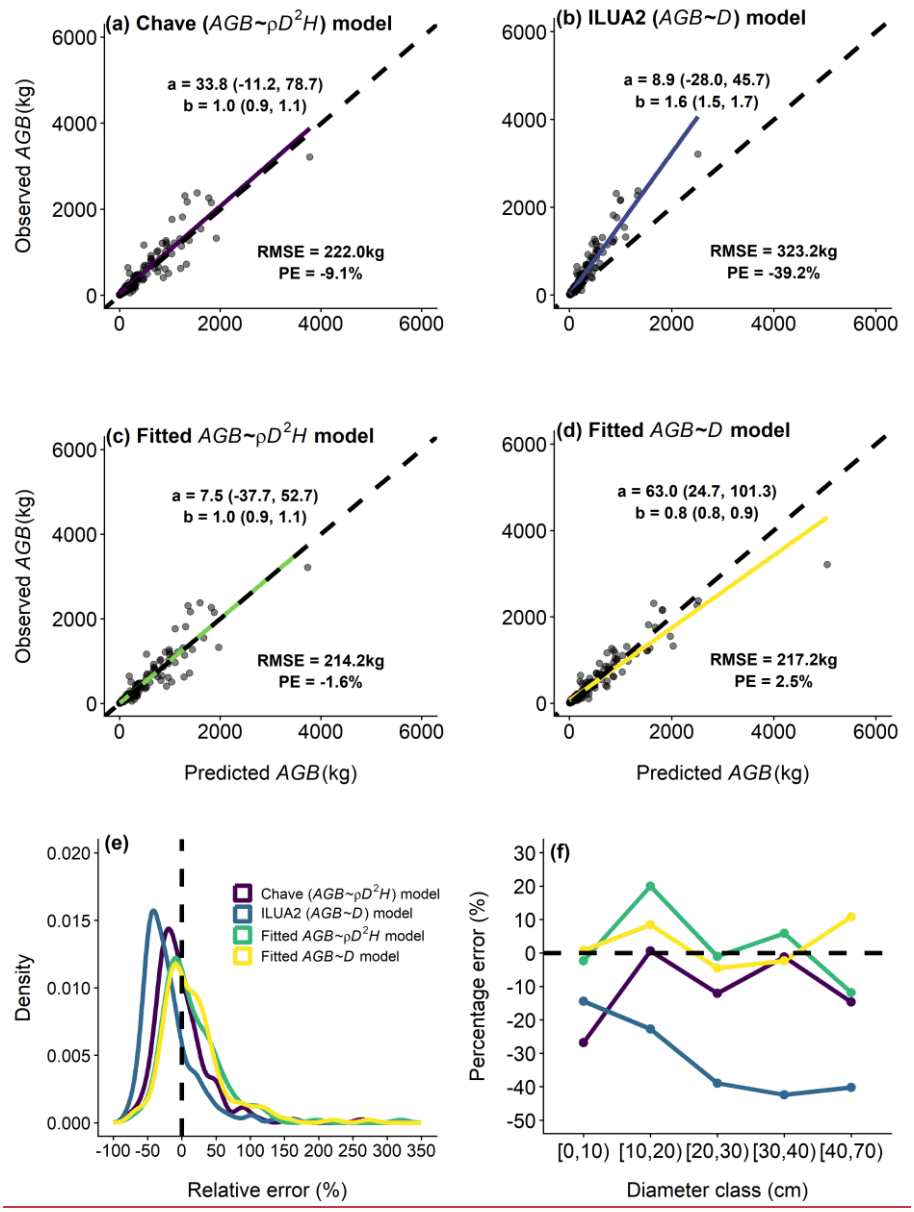


Figure ~~23~~. Predictive accuracy of the four alternative aboveground biomass (*AGB*) models. Scatterplots **(a–d)** show the relationship between observed and predicted *AGB* values across

the ~~154~~155 trees included in the dataset. Coloured lines correspond to the fit of a linear model between observed and predicted AGB values, while dashed lines illustrate a 1:1 relationship. Fit statistics for each model are reported in the panels, including the intercept ~~(~~, **a**~~),~~ and slope ~~(~~, **b**~~),~~ of the regression line with 95% confidence intervals in brackets. Model errors are visualised in the bottom two panels, including **(e)** the distribution of relative errors, as a percentage, (calculated as: ~~($\widehat{AGB_i} - AGB_i)/AGB_i) *$~~ $(\widehat{AGB_i} - AGB_i)/AGB_i) \times 100$; where AGB_i is the measured AGB for tree i; and $\widehat{AGB_i}$ is the estimated AGB for tree i) for each of the four models and (**f**) the percentage error (PE, in %) of trees grouped into ~~the~~ five stem diameter classes.

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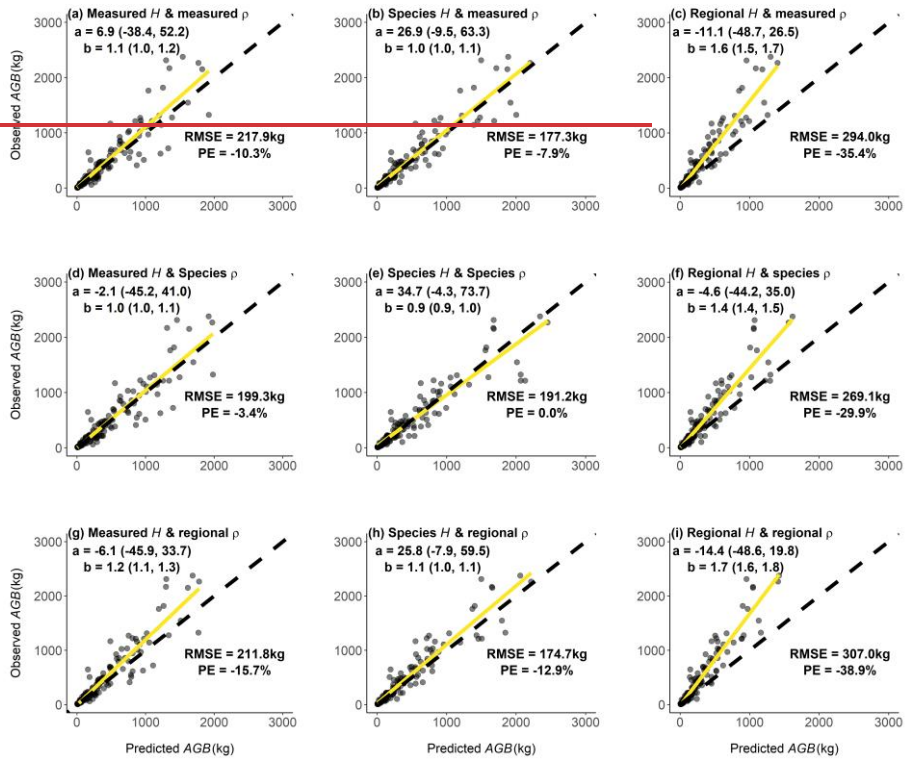
3.2 Objective 3 – Error in *AGB* estimation due to uncertainty in height and wood density

Across the nine scenarios in which we modified height (*H*) and wood density (ρ) inputs in the pantropical *AGB* model, we found that replacing field-measured values of *H* and ρ with species-specific estimates did not substantially worsen *AGB* estimates (Figs 3–4–5). In particular, height estimates obtained using the locally-calibrated, species-specific *H*–*D* allometry (Eq. (eq. 7)) were statistically indistinguishable (Fig. S5a) from those measured in the field (Fig. S5a) and consequently had little impact on predicted *AGB* values (PE = -2.6% and RMSE = 261.8 kg; Fig. 3b). Wood4b). Similarly, while species-specific wood density values obtained from the GWDD were correlated (Pearson's correlation coefficient = 0.41; Fig. S7a) but generallysignificantly higher (Fig. S5b) than those measured inon the field (Figs. S5b), and consequentlydestructively harvested trees, their use in the *AGB* model did lead to a modest reduction in underestimation of had almost no impact on *AGB* estimation (PE increase from -10.= -3% to -3.4%; Fig. 3a.0% and Fig. 3d). However, even in this case, the RMSE = 199.5 kg, with a slope coefficient between observed and of 1.0 when comparing predicted *AGB*and observed values was almost exactly 1 and the intercept very close to 0 (Fig. 3dof *AGB*; Fig. 4d).

By contrast, when *H* and ρ values were replaced with coarser regional-level estimates, errors in *AGB* increased substantially. This was most pronounced for scenarios that involved using height estimates derived from the genericregional *H*–*D* allometry for tropical dry forests (Eq. (eq. 8); right column of; Fig. 34c,f,i). Because this allometry severely underestimated tree heights by several meters (Fig. 5Figs. 6 and Fig. S6 and Table S6), by itself), its use led to a nearly 35% underestimation of *AGB* (slope coefficient between observed and predicted values = 1.63; Fig. 3c4c). A similar, albeit much weaker trend was also observed for wood density.

The regional mean ρ value for African tropical forests was only slightly lower than the mean ρ value of species sampled in our study (0.598 vs 0.607 g cm^{-3}). Therefore, replacing field-measured ρ values with a regional mean resulted in a slight increase in underestimation of *AGB* ~~from -10.3% to~~(PE = -15.~~7% (Fig. 3g;~~1% and slope coefficient = 1.2; Fig. 4g). When these two sources of errors were combined, they compounded each other and led to an underestimation of *AGB* that was comparable in magnitude to that of using the ILUA2 model to estimate *AGB* instead of the pantropical equation of Chave et al. (2014) (~~Fig. 3i;~~PE = -37.8%, RMSE = 308.6 kg and slope coefficient = 1.~~7~~5; Fig. 4i).

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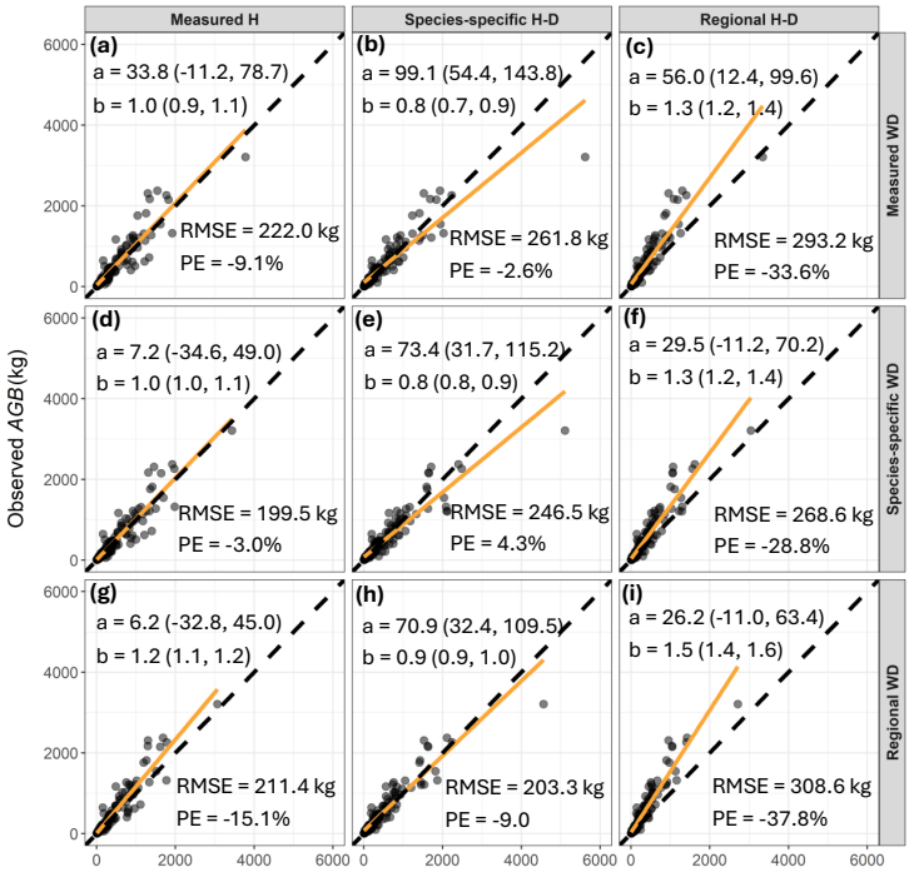


Figure ~~3~~4. Errors in aboveground biomass (*AGB*) estimation arising from uncertainty in tree height (*H*) and wood density (ρ). Each panel corresponds to one of the nine scenarios described in ~~the main text~~Table 3 in which we altered inputs of *H* and ρ in the *AGB* model developed by Chave et al. ~~(2014) (Eq. (1)). Panel (a) shows the predicted values of *AGB* when using field-measured values of both~~(2014). *H* ~~and ρ (equivalent to Fig. 2b). From~~ inputs vary in uncertainty from left to right, ~~*H* values are replaced first with~~from field measured, to those estimated using a species-specific ~~estimates derived from the locally fit *H*–*D* allometry (middle column) shown in Fig.5 and then with the~~ model (eq. 7), and finally those derived from a regional *H*–-

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D ~~allometry for tropical dry forests derived from the literature (right column) shown~~model (eq. 8). ρ inputs vary in ~~Fig. 5. From~~ uncertainty from top to bottom, from field measured ρ values ~~are replaced first with~~, to species-specific (or closest taxonomic unit) mean values derived from the Global Wood Density Database ~~(middle row),~~ and ~~then with~~finally those based on a single regional mean value for African tropical forests derived from the literature ~~(bottom row). Coloured~~. The orange coloured solid lines correspond to the fit of a linear model between observed and predicted *AGB* values, while dashed lines illustrate a 1:1 relationship. Fit statistics for each model are reported in the panels, including the intercept (a) and slope (b) of the regression line (with 95% confidence intervals in brackets ~~-~~), as well as the RMSE and PE. Refer to Fig. S8 for a similar plot but excluding the largest/observed *AGB* value which , by visual inspection, appears like an outlier when compared to other data values.

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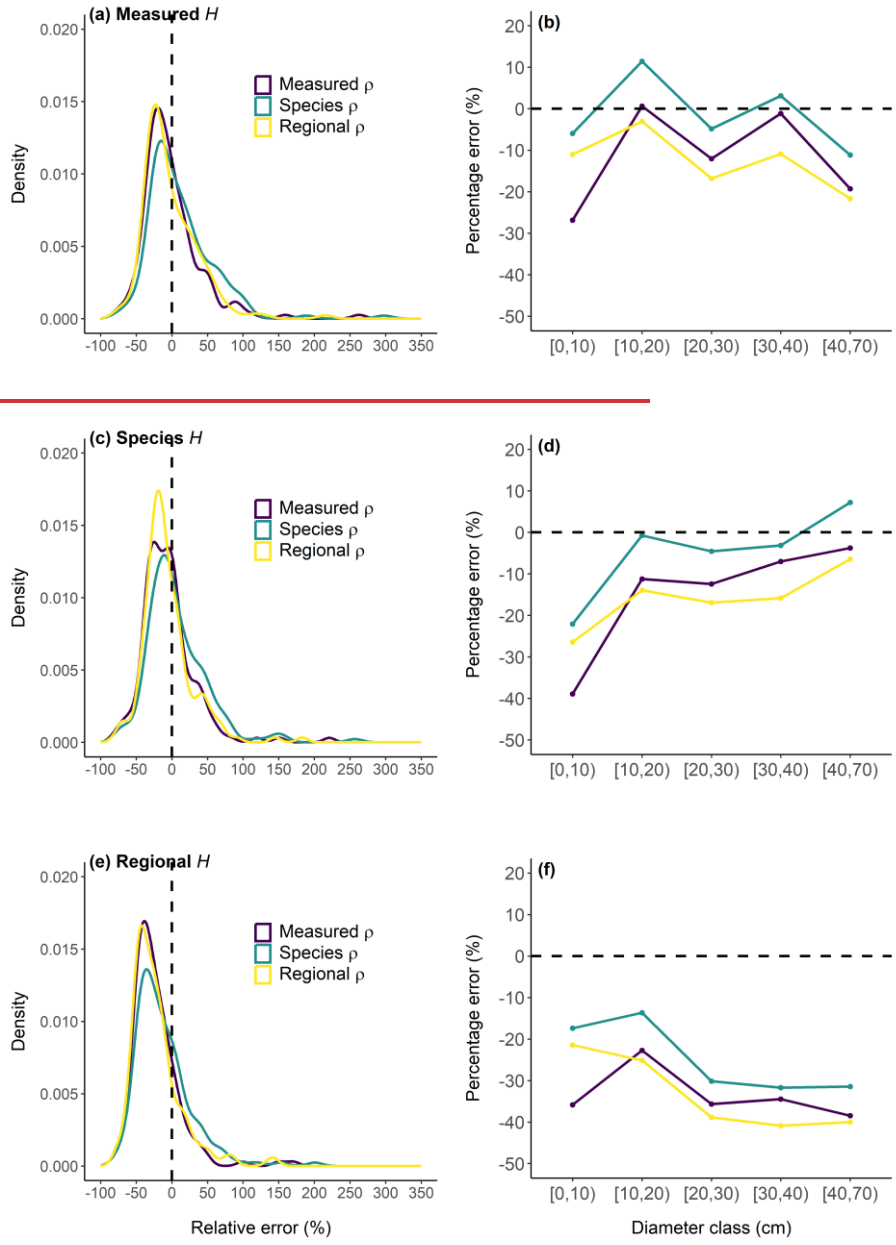
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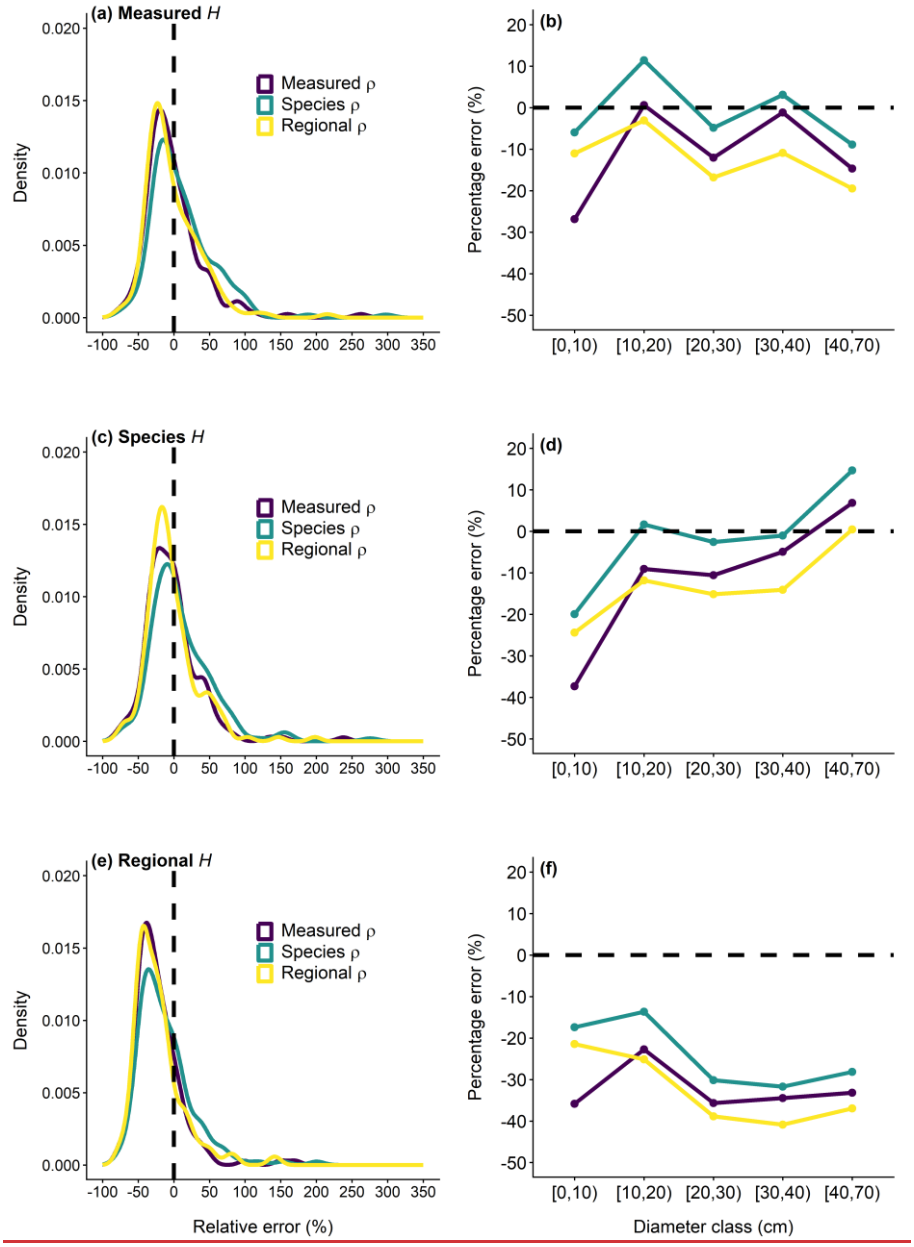
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(a) Measured H
(b)
(c) Species H
(d)
(e) Regional H
(f)
Measured ρ
Species ρ
Regional ρ
Density
Percentage error (%)
Relative error (%)
Diameter class (cm)
[0,10)
[10,20)
[20,30)
[30,40)
[40,70)

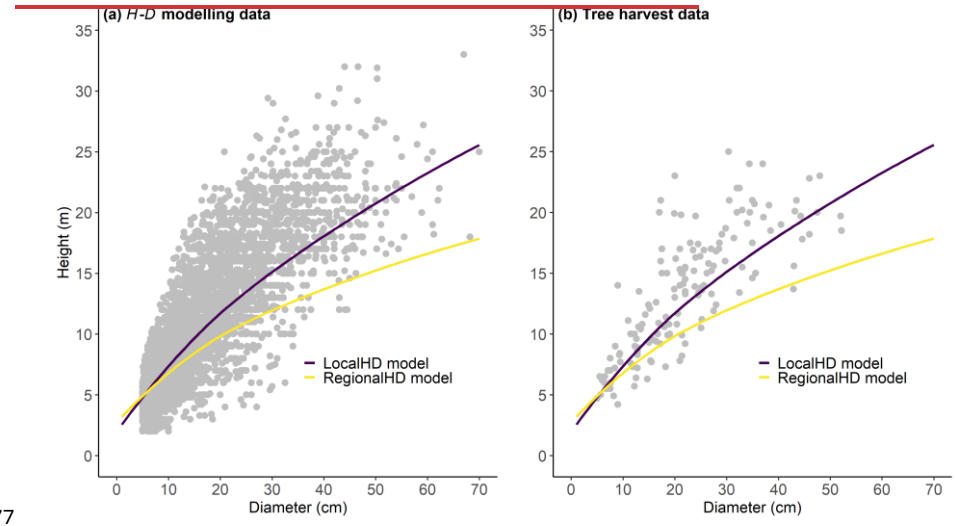
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(a) Measured H
(b)
(c) Species H
(d)
(e) Regional H
(f)
Measured ρ
Species ρ
Regional ρ
Density
Percentage error (%)
Relative error (%)
Diameter class (cm)
[0,10)
[10,20)
[20,30)
[30,40)
[40,70)

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Figure 45. Errors in aboveground biomass (AGB) estimation due to uncertainty in tree height (H) and wood density (ρ) across the nine scenarios depicted in ~~Fig.~~Table 3. Panels on the left show the distribution of relative errors, as a percentage, (calculated as: ~~$(\widehat{AGB_i} - AGB_i)/AGB_i) *$~~ $(\widehat{AGB_i} - AGB_i)/AGB_i) \times 100$; where AGB_i is the measured ~~AGB~~AGB for tree i; and $\widehat{AGB_i}$ is the estimated AGB for tree i) in AGB across the nine scenarios, while those on the right show the percentage error (PE, in %) for trees grouped into the five stem diameter classes across scenarios. In all cases, AGB was estimated using the pan-tropical model developed by Chave et al. (2014~~) (Eq. (1)).~~). Species H (Fig. 5c) refers to using eq. 7 to estimate tree H while regional H (Fig. 5e) corresponds to using eq. 8 to estimate tree H.



~~**Figure 5.** Relationship between tree height (H) and stem diameter (D) for **(a)** the 4321 trees used to develop the species-specific, local H–D allometry and **(b)** the 154 trees in the tree harvest dataset used for AGB modelling. The line of best fit of the local power-law model fit to these data (Eq. (7)) is shown in purple, while the yellow curve shows the fit of the regional H–D allometry for tropical dry forests derived from the literature (Eq. (8)). To visualise the~~

~~models, we generated a predicted *H* for *D* values in the range 1-70 cm (with 1cm interval) and converted point predictions into lines via a locally estimated scatterplot smoothing (LOESS).~~

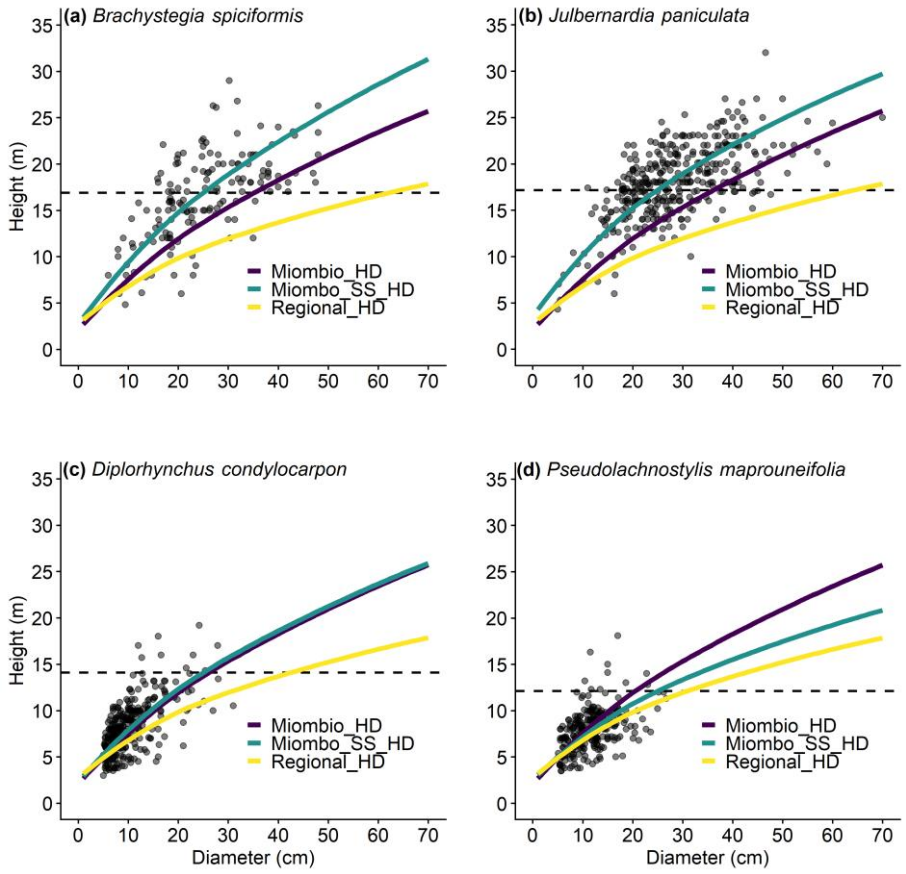


Figure 6. Variability in height-diameter (*H-D*) relationships among common miombo tree species with differing adult statures. Fitted lines correspond to the population-level fit of eq. 7(purple), the species-level deviations from the population-level fit (green; see Table S4 for species-level parameter values), and the fit of the regional *H-D* allometry derived from the Tallo database (yellow; eq. 8). The horizontal dashed black lines show the height prediction for a tree with diameter of 25 cm using the species-specific *H-D* model.

4. DISCUSSION

4.1 Strength in numbers: pantropical model provides robust estimates of *AGB*

Our study shows that when accurate measurements or estimates of tree height and wood density are available, the pantropical model developed by Chave et al. (2014) can generate unbiased estimates of *AGB*. In fact in our case, this pantropical model performed similarly well to *AGB* ~~allometries~~equations calibrated against ~~the~~new data (Fig. ~~2~~3 and Fig. S4). A key feature of this pantropical model is that compared to other regional or species-specific models that exist in the literature, it was developed using a large number of harvested trees (>4000) that span a broad range of environments and sizes. This is clearly a major strength when it comes to making predictions against new data. A priority for future research in this field should therefore be to further consolidate and expand data on harvested trees into a common database so that robust and widely applicable *AGB* models can be built.

By contrast, we found that the regional ILUA2 model developed to predict *AGB* for Zambia's forests as part of the national forest inventory severely underestimated *AGB*~~.~~, particularly that of large trees. There are two plausible reasons for this underestimation. ~~Firstly~~First, although the ILUA2 model was developed using 1319 harvested trees, these comprised mostly small to medium size trees ($D \leq$ 30cm) ~~(Forestry Department, 2016).~~(Forestry Department, 2016). Small sample sizes and/or large sample sizes with mostly smaller trees to ~~parameterise~~parameterize *AGB* models have been identified as major sources of *AGB* errors and uncertainty ~~(Chave et al., 2004). Secondly~~(Chave et al., 2004). Second, the ILUA2 model uses *D* as the sole predictor of *AGB*. While *D* is clearly the single strongest correlate of *AGB* (Fig. ~~1~~1b), in doing so~~,~~ the model does not account for differences in *H-D* scaling among species (Fig. ~~S6~~6) and forest types ~~(Timberlake et al., 2010; Munalula et al., 2020; Yambayamba et al., 2024),~~(Timberlake et al., 2010; Munalula et al., 2020; Yambayamba et al., 2025), nor does it incorporate variability in wood density which can substantially affect

AGB estimates ~~(Mitchard et al., 2014; Jucker et al., 2018; Phillips et al., 2019).~~(Mitchard et al., 2014; Jucker et al., 2018; Phillips et al., 2019). Our findings align with a recent study in the same region suggesting that commonly applied allometric models underestimate *AGB* of miombo woodlands ~~(Demol et al., 2024).~~(Demol et al., 2024). This has important practical implications, including reporting and verification of forest carbon stocks and dynamics under REDD+ ~~(Köhl et al., 2020; Grz, 2021; Melo et al., 2023) as well as~~ and emerging carbon trading initiatives~~.~~ (Köhl et al., 2020; GRZ, 2021; Melo et al., 2023), as well as the calibration and validation of satellite-derived estimates of forest carbon stocks. For instance, Zambia has previously used the ILUA2 model to estimate ~~forest reference emissions level~~FREL submissions to the ~~United Nations Framework Convention on Climate Change (~~UNFCCC~~)~~ ~~(Grz, 2016)~~ (GRZ, 2016) but most recently identified the pantropical model for consideration ~~(Grz, 2021).~~(GRZ, 2021). In this respect, our study highlights the challenges associated with accurate estimation of *AGB* stocks and therefore underscores the need for rigorous methods ~~of~~for quantifying *AGB* stocks and dynamics in miombo woodlands and beyond.

4.2 Tree height uncertainty can severely bias *AGB* estimates

Our study reiterates the recommendation of previous works to account for tree height when estimating *AGB* ~~(Feldpausch et al., 2012; Chave et al., 2014; Djomo et al., 2016; Handavu et al., 2021).~~(Feldpausch et al., 2012; Chave et al., 2014; Djomo et al., 2016; Handavu et al., 2021). However, our results also underscore how the inclusion of *H* in *AGB* models is not without its challenges ~~(Chave et al., 2014; Kapinga et al., 2018). Firstly~~(Chave et al., 2014; Kapinga et al., 2018). First, conventional field measurements of *H* are not only time consuming to take but also prone to errors, especially for large trees and in closed canopies ~~(Larjavaara and Muller-Landau, 2013; Wang et al., 2019). Secondly~~(Larjavaara and Muller-Landau, 2013; Wang et al., 2019). Second, the common practice of using *H-D* models to estimate tree height when this is not measured is equally subject to errors, especially where locally fitted *H-D*

models are unavailable ~~(Fayolle et al., 2016; Sullivan et al., 2018).~~(Fayolle et al., 2016; Sullivan et al., 2018). In line with previous studies, our results demonstrate the peril of applying generic and regional *H-D* models to specific locations that are environmentally or taxonomically distinct ~~(Feldpausch et al., 2012; Kearsley et al., 2013; Molto et al., 2014; Ledo et al., 2016; Fayolle et al., 2016).~~(Feldpausch et al., 2012; Kearsley et al., 2013; Molto et al., 2014; Ledo et al., 2016; Fayolle et al., 2016). Using a regional *H-D* model developed for tropical dry forests led to a severe underestimation of *AGB*. Worse still, this underestimation increased with *D* (Fig. ~~4f), which is particularly undesirable since larger trees contribute disproportionately to total *AGB* (Fig. 1;(Lutz et al., 2018)).~~5f), which is particularly undesirable since larger trees contribute disproportionately to total forest carbon stocks (Fig. 1a; (Lutz et al., 2018)). Our approach of fitting a locally-calibrated and species-specific *H-D* model substantially improved the accuracy of *AGB* estimates~~, but~~. However, access to high-quality local datasets to ~~parameterise~~parameterize such allometries is often limited ~~(Jucker et al., 2022).~~(Jucker et al., 2022).

The importance of tree height in *AGB* estimation has also been demonstrated in studies using remote sensing methods to map forest structure. For example, detailed reconstructions of tree architecture made possible by terrestrial laser scanning have shown that traditional allometric models can underestimate tree height and therefore *AGB* ~~(Calders et al., 2022; Terryn et al., 2024).~~(Calders et al., 2022; Terryn et al., 2024). Given the obvious challenges associated with accurate measurement of *H* using conventional field methods, we argue that improvement in *AGB* estimation in miombo woodlands requires leveraging increasingly available and affordable remote sensing technologies such as LiDAR ~~(Momo Takoudjou et al., 2018; Calders et al., 2022; Demol et al., 2022; Demol et al., 2024).~~(Momo Takoudjou et al., 2018; Calders et al., 2022; Demol et al., 2022; Demol et al., 2024). These data provide a robust way to characterise the 3D architecture of trees that can be used to describe forest structure,

functioning and dynamics with greater accuracy and across larger scales than traditional field methods ~~(Jucker et al., 2023; Battison et al., 2024).~~(Jucker et al., 2023; Battison et al., 2024).

4.3 The importance of accounting for wood density when estimating *AGB*

Wood density can vary considerably among tree species, with values ranging almost three fold from as low as 0.34 g cm^{-3} to 0.86 g cm^{-3} across those sampled in our study. As previous work in Amazonia has shown, failure to properly account for this variability in wood density among species and forest types can severely bias large-scale estimates of forest carbon stocks inferred via remote sensing ~~(Mitchard et al., 2014; Phillips et al., 2019).~~(Mitchard et al., 2014; Phillips et al., 2019). In the case of the miombo woodlands studied here, uncertainty in wood density was of secondary importance to that in tree height in driving errors in *AGB* estimation. But this is likely to differ among forest types and will depend on both the accuracy of available *H–D* allometries and the coverage of wood density databases like the GWDD.

When field-measured values of wood density were replaced with ones obtained from the GWDD, we found that overall wood density was overestimated across the population. This led to only a modest reduction in underestimation of *AGB*, as wood density values from the GWDD were generally ~~moderately~~ correlated to those measured in the field (Fig. S7). This confirms previous work showing that while wood density can vary somewhat within species, it is generally quite a conserved trait ~~(Chave et al., 2009).~~(Chave et al., 2009; Fischer et al., 2026). Therefore, provided trees have been identified to species level and that these species have matching observations in the GWDD, our results suggest that *AGB* can be estimated with limited bias. This provides a strong incentive to continue to curate and expand field reference collections of wood density to support large-scale mapping of forest carbon stocks ~~(Mo et al., 2024).~~(Fischer et al., 2026). In the context of Zambia's miombo woodlands ~~in Zambia~~, only 31 tree species (out of approximately 238 ~~uniquely~~species identified ~~species~~ in the most recent ~~extensive~~ national forest inventory ~~(Pelletier et al., 2018; Yambayamba et al., 2024))~~(Pelletier

et al., 2018; Yambayamba et al., 2025)) have wood density records ~~(Forestry Department, 2016),~~(Forestry Department, 2016), making it imperative that taxonomic coverage is increased in the future.

Uncertainty in wood density can compound the errors in *AGB* associated with the use of a generic *H*–*D* allometry, but it is easy to imagine a situation in which these errors could instead cancel each other out, making them even ~~hard~~harder to detect and quantify. In this regard, our framework provides a simple and robust way to decompose errors in *AGB* arising from uncertainty in both height and wood density. Replicating this analysis on a larger dataset, such as the pantropical *AGB* database developed by Chave et al. (2014), would provide valuable insights into the main sources of error in *AGB* estimation and how these vary across forest types and biogeographic regions.

5. CONCLUSION

Our study aimed at comparing the predictive performance of existing and reparametrized *AGB* models in miombo woodlands and quantifying the errors associated with using different approaches to imputing of height and wood density. We have shown that using *AGB* models that incorporate *H* and ρ, in addition to *D*, provide better and more transferable estimates than those that rely exclusively on *D*. The reparametrized model of Chavel et al. (2014) we develop here thus provides a good starting point for improving *AGB* estimates in miombo woodlands. However, looking ahead, we encourage the research community to continue to move towards larger, integrated databases of tree *AGB* in order to develop generalised models that can underpin accurate accounting of forest carbon stocks under REDD+ and carbon trading initiatives.

Our study further revealed that uncertainty in *H* (more than in ρ in the miombo) can lead to substantial errors in *AGB* estimates. Since *H* is typically only measured for a small sub-

sample of trees and mostly estimated using *H-D* models in conventional forest inventories, we therefore reiterate that great care is needed when selecting the approach to estimate *H* (particularly if locally available *H* data are not available to assess model performance). Collating and curating accurately measured *H-D* data and developing local species-specific *H-D* allometries remain a priority for the miombo and many other regions (particularly those in the tropics). The species-specific *H-D* models we develop here thus serve as a baseline for improving *AGB* estimation in miombo woodlands, although future work should also consider comparing different functional forms for modelling *H-D* relationships (Cano et al., 2019).

The *AGB* and *H-D* allometries developed in this study will hopefully serve as a blueprint for improving the characterization and modelling of tree allometry, ecosystem function and biomass estimation in miombo woodlands. In particular, emerging remote sensing technologies such as terrestrial and airborne LiDAR are increasingly being used to characterize tree structure and map landscape-scale carbon stocks, but require field based approaches for validation and calibration (Jucker et al., 2017; Chave et al., 2019). Similarly, improved allometries are crucial to accurate simulation of vegetation response to environmental change in dynamic global vegetation models (Fischer et al., 2019).

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AUTHOR CONTRIBUTIONS

AMY and TJ ~~conceived the idea~~ designed the study. Kondwani Kapinga (KK) did the vegetation assessment, forest inventory, destructive sampling and laboratory analysis for the ~~study.~~Mwekera forest dataset. Ferdinand Handavu (FH) did the vegetation assessment, forest inventory, destructive sampling and laboratory analysis, with assistance from KK, for the Katanino and Miengwe forests datasets. AMY did the data collating and led the analysis with assistance from TJ. ~~All~~AMY wrote the first draft of the manuscript with all the authors ~~contributed~~contributing substantially to revisions.

CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AND CODE AVAILABILITY STATEMENT

Data and R code to replicate the results of this study will be publicly archived on Zenodo following the review of this paper.

SUPPLEMENTARY MATERIAL

Additional supporting information may be found online in the Supporting Information section.

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