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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 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 destructively harvested trees in Zambia's miombo woodlands that span a large range of sizes to develop a framework to partition errors in *AGB* arising from uncertainty in tree height and wood density. We found that when locally-calibrated 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, errors in *AGB* can be substantial. In particular, estimating tree height using a regional allometric model developed for tropical dry forests led to 35% underestimation of *AGB*. Our study provides an intuitive approach for quantifying and partitioning errors in *AGB* arising from uncertainty in tree height and wood density, paving the way for more robust mapping of forest carbon stocks and fluxes.

Key words: Aboveground biomass, allometry, bias, error propagation, forest carbon stocks, forest structure, tree height, wood density

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). 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). 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). 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), 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 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). 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) – 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). These allometric biomass equations typically have 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). A myriad of such equations exist, but the most widely used for tropical trees are the models developed by (Chave et al., 2005; 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. 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). 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). These *H–D* allometries not only propagate any underlying biases in the *H* values used to derive 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) 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.

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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). While these databases are invaluable, they still only cover <15% of known tree species, meaning that in many cases ρ values are 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).

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 the size of the UK 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). To address this knowledge gap, we compiled data for 154 trees whose AGB was measured via destructive harvesting in miombo woodlands of Zambia. These trees cover a wide spectrum of sizes (D = 5.0–52.2 cm; H = 3.0–25.0 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.

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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 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 (Mcnicol et al., 2018; Pelletier et al., 2018; Demol et al., 2024).

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.

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 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	154
Number of species	9	33	5	37
Stem diameter (*D*; cm)	22.6 [12.2 – 46.0]	21.3 [5.0 – 52.2]	22.0 [5.5 – 48.0]	21.4 [5.0 – 52.2]
Tree height (*H*; m)	13.5 [5.7 – 22.8]	12.9 [4.2 – 20.7]	16.5 [5.0 – 25.0]	13.8 [4.2 – 25.0]
Wood density (ρ; g cm^{-3})	0.64 [0.49 – 0.86]	0.60 [0.42 – 0.82]	0.64 [0.34 – 0.85]	0.61 [0.34 – 0.86]
Aboveground biomass (*AGB*; kg)	301.0 [27.2 - 2149.3]	217.7 [7.8 - 2374.4]	225 [5.7 – 1545.2]	218.9 [5.7 – 2374.4]
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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2.3 Height–diameter modelling data

To determine how different approaches to impute 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 where trees were also destructively harvested to measure *AGB* (Kapinga et al., 2018; Handavu et al., 2021). Collectively, these data represent 79 uniquely identified tree species and span a similar range of tree sizes to those sampled for *AGB* (*D* = 5.0–70 cm; *H* = 2.0–33.0 m) (see Table S3 for details). *H–D* relationships were visually assessed for potential data entry errors and a small number of trees (~2%) were flagged as outliers and excluded (Fig. S1b). This left us with a total of 4321 trees for model fitting.

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, 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). Prior to conducting statistical analyses, tree species names were harmonized across all datasets using the World Checklist of Vascular Plants (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).

2.5 Comparing alternative *AGB* models

To determine how much *AGB* estimates are influenced by the choice of biomass allometry, we compared *AGB* estimates obtained using two existing and two newly-developed biomass models. The first *AGB* allometry we tested is the widely used pantropical model developed by (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):

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

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). The resulting fitted models were as follows:

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

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

We then compared the predictive ability of these four 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): root mean square error (RMSE, in kg) and percentage error (PE, in %):

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

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

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

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We used PE in order to get the magnitude of the mean error relative to the mean observed *AGB*. We chose PE among other metrics because it gives much more weight to the large trees since these have the largest errors in absolute terms. Large errors are undesirable for large trees because these contribute the most to total *AGB* (Fig. 1a).

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).

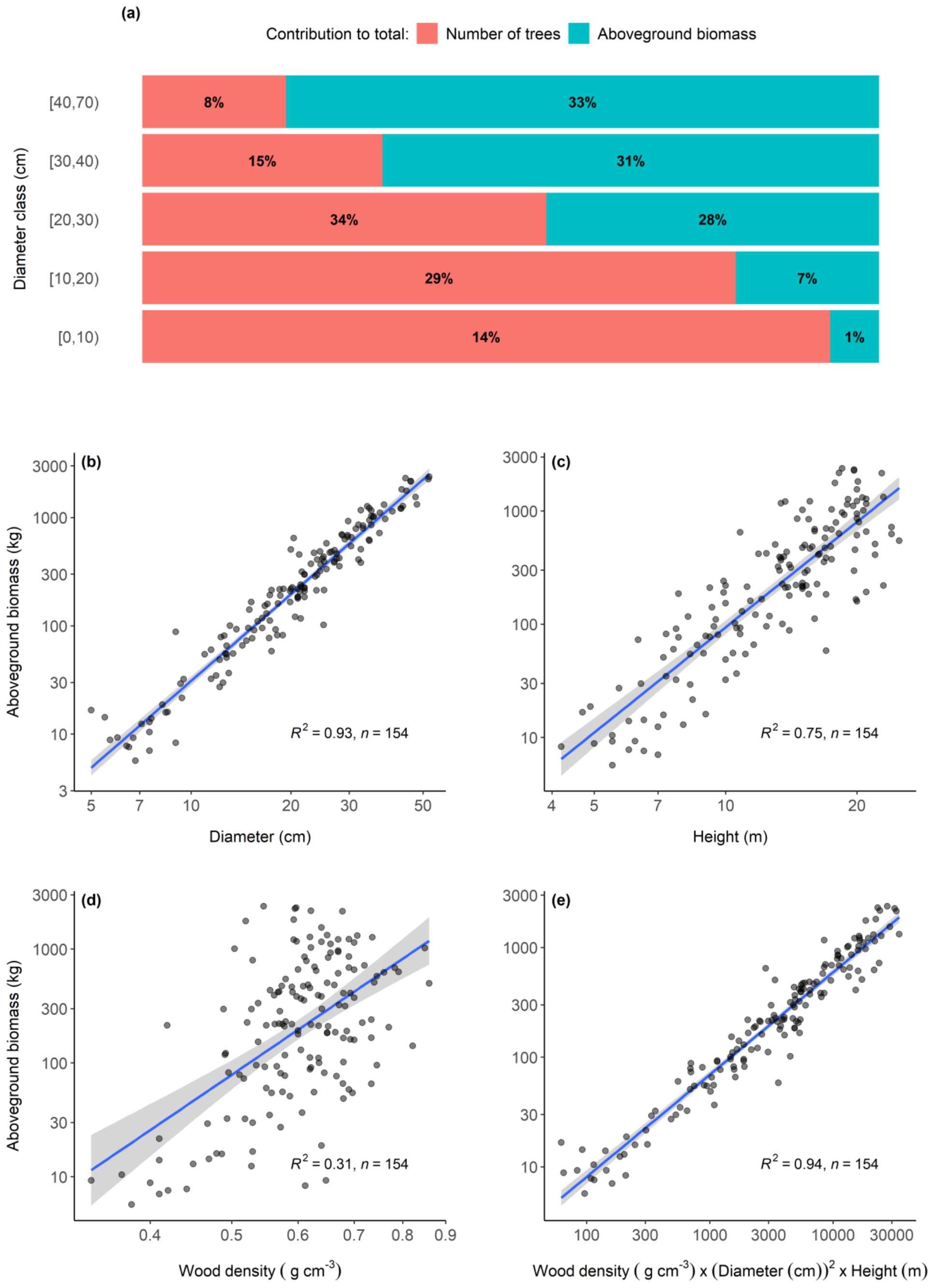

Figure 1. Overview of the tree harvest dataset. The bar plot **(a)** shows the distribution of samples across the five tree diameter classes in terms of both number of trees and their

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.

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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). 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. (1) to predict the *AGB* of all 154 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 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 trees described above. The relationship was modelled as a power-law function fit to log–log transformed data, 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):

$$H = \alpha_j \times D^{\beta_j}. \tag{7}$$

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):

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

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 ($\rho = 0.598$ 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 (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 inputs (field-measured, species-specific or biome-specific), and their respective combinations.

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3. RESULTS

3.1 Uncertainty in *AGB* estimation due to choice of *AGB* model

Of the four *AGB* models we compared, three performed similarly well and produced unbiased estimates of *AGB* across the range of tree sizes (Fig. 2): the two models calibrated using the tree harvest data presented in this paper (Eq. (3) and Eq. (4)) and the existing pantropical model developed by Chave et al. (2014) (Eq. (1)). Regressions between predicted and observed *AGB* values for all three models had intercepts with 95% confidence intervals that overlapped with 0 (range of mean intercept values = -13.1 – 16.3) and slopes that were very close to 1. Of these three *AGB* models, the *D*-only model (Fig. 2c) had the lowest RMSE (160.5 kg vs 210.6 and 217.9 kg) and PE (0.6% vs -2.4 and -10.3%), confirming that *D* is the single strongest predictor of *AGB* (Fig. 1b). By contrast, the ILUA2 model (Eq. (2)) developed as part of Zambia's forest inventory program substantially underestimated *AGB* (Fig. 2a), especially for large trees (green line in Fig. 2f). On average, predicted values of *AGB* obtained using the ILUA2 model were around 40% lower than those measured in the field (slope coefficient = 1.8) and trees in the largest size class had a PE of -40% (Fig. 2f).

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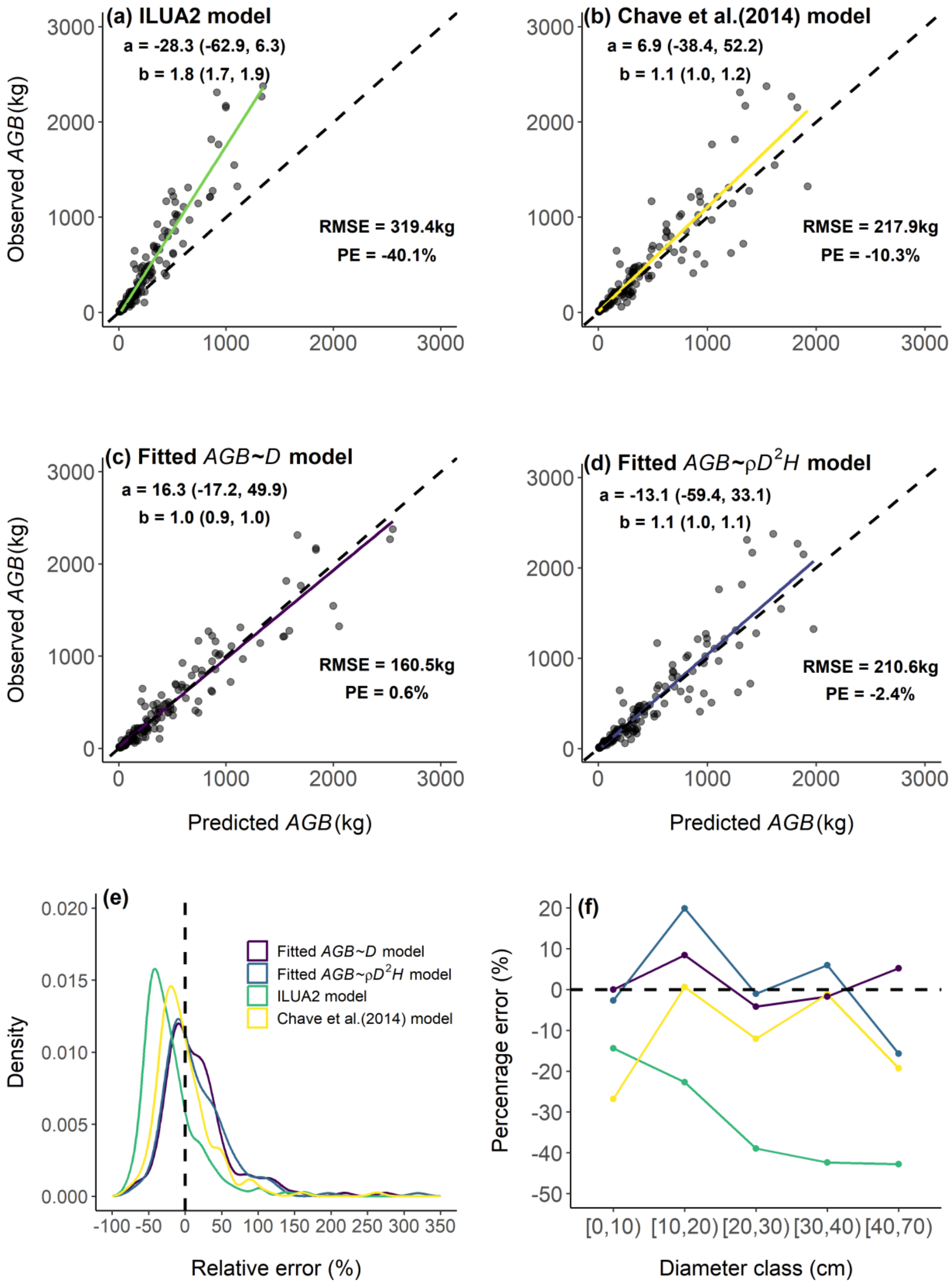

Figure 2. Predictive accuracy of the four alternative aboveground biomass (*AGB*) models. Scatterplots **(a–d)** show the relationship between observed and predicted *AGB* values across

the 154 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: $((\widehat{AGB_i} - AGB_i)/AGB_i) * 100$; 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.

3.2 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). In particular, height estimates obtained using the locally-calibrated, species-specific *H–D* allometry (Eq. (7)) were statistically indistinguishable from those measured in the field (Fig. S5a) and consequently had little impact on predicted *AGB* values (Fig. 3b). Wood density values obtained from the GWDD were correlated (Pearson's correlation coefficient = 0.41; Fig. S7a) but generally higher than those measured in the field (Figs. S5b), and consequently, their use in the *AGB* model did lead to a modest reduction in underestimation of *AGB* (PE increase from -10.3% to -3.4%; Fig. 3a and Fig. 3d). However, even in this case, the slope coefficient between observed and predicted *AGB* values was almost exactly 1 and the intercept very close to 0 (Fig. 3d).

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 generic *H–D* allometry for tropical dry forests (Eq. (8); right column of Fig. 3). Because this allometry severely underestimated tree heights by several meters (Fig. 5 and Fig. S6 and Table S6), by itself its use led to a 35% underestimation of *AGB* (slope coefficient between observed and predicted values = 1.6; Fig. 3c). 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 -15.7% (Fig. 3g; slope coefficient = 1.2). 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; slope coefficient = 1.7).

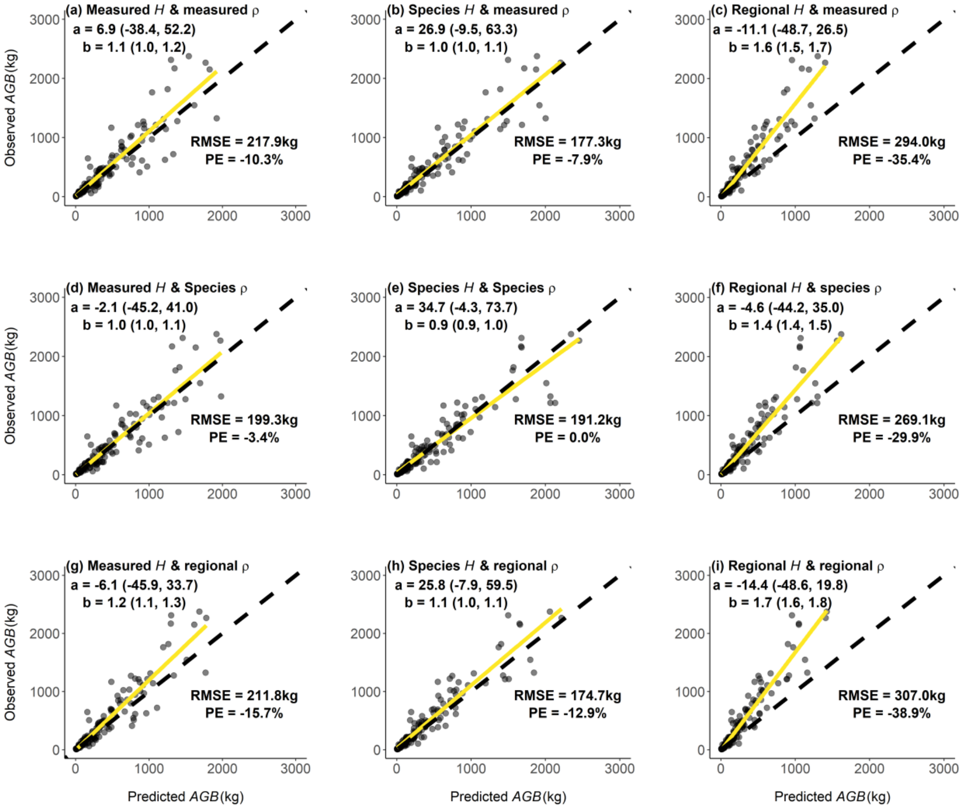

Figure 3. Errors in aboveground biomass (*AGB*) estimation arising from uncertainty in tree height (*H*) and wood density (*ρ*). Each panel corresponds to one of the nine scenarios described in the main text in which we altered inputs of *H* and *ρ* in the *AGB* model developed by Chave et al. (2014)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

with species-specific mean values derived from the Global Wood Density Database (middle row) and then with a single regional mean value for African tropical forests derived from the literature (bottom row). 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.

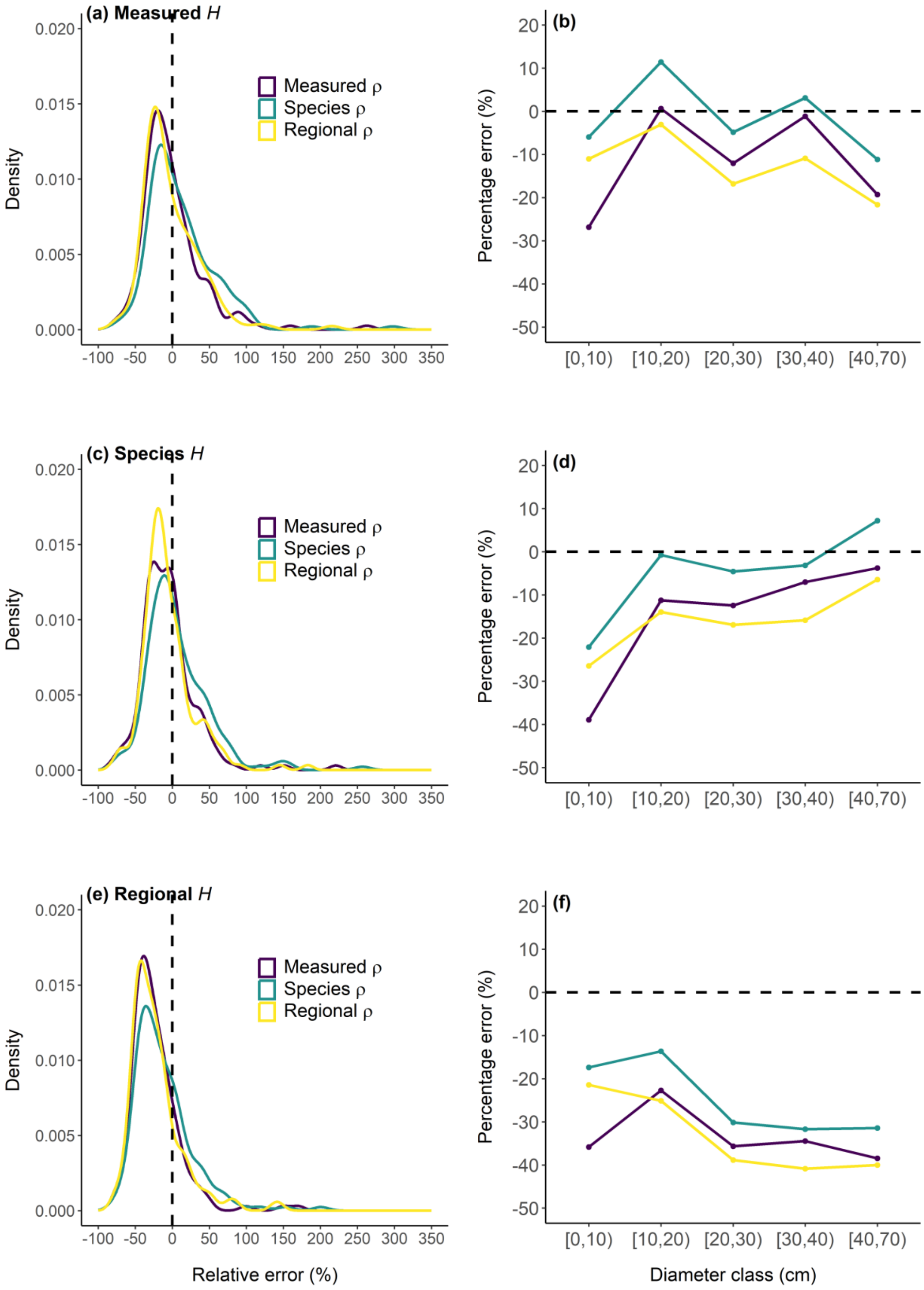
(a) Measured *H*
(b)
(c) Species *H*
(d)
(e) Regional *H*
(f)
Measured ρ
Species ρ
Regional ρ
Density
0.000
0.005
0.010
0.015
0.020
-100
-50
0
50
100
150
200
250
300
350
Relative error (%)
Percentage error (%)
20
10
0
-10
-20
-30
-40
-50
[0,10)
[10,20)
[20,30)
[30,40)
[40,70)
Diameter class (cm)

Figure 4. Errors in aboveground biomass (*AGB*) estimation due to uncertainty in tree height (*H*) and wood density (ρ) across the nine scenarios depicted in Fig. 3. Panels on the left show the distribution of relative errors, as a percentage, (calculated as: $((\widehat{AGB_i} - AGB_i)/AGB_i) * 100$; where AGB_i is the measured *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)).

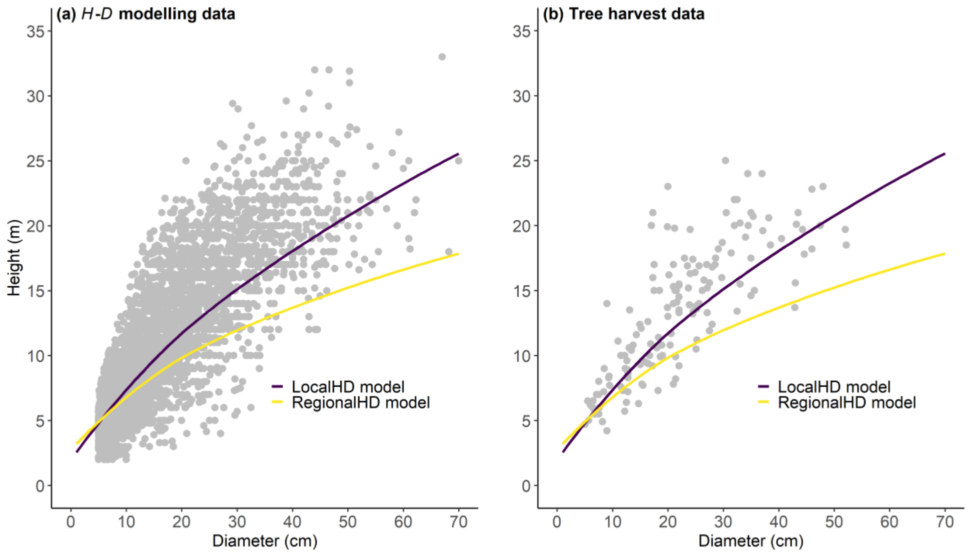

Figure 5. Relationship between tree height (*H*) and stem diameter (*D*) for **(a)** the 4321 trees used to develop the species-specific, local *H–D* allometry and **(b)** the 154 trees in the tree harvest dataset used for *AGB* modelling. The line of best-fit of the local power-law model fit to these 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).

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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 calibrated against the data (Fig. 2). 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*. There are two plausible reasons for this underestimation. Firstly, although the ILUA2 model was developed using 1319 harvested trees, these comprised mostly small to medium size trees ($D \leq$ 30cm) (Forestry Department, 2016). Small sample sizes and/or large sample sizes with mostly smaller trees to parameterise *AGB* models have been identified as major sources of *AGB* errors and uncertainty (Chave et al., 2004). Secondly, the ILUA2 model uses *D* as the sole predictor of *AGB*. While *D* is clearly the single strongest correlate of *AGB* (Fig. 1), in doing so, the model does not account for differences in *H-D* scaling among species (Fig. S6) and forest types (Timberlake et al., 2010; Munalula et al., 2020; Yambayamba et al., 2024), 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). 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). 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 emerging carbon trading initiatives. For instance, Zambia has previously used the ILUA2 model to estimate forest reference emissions level submissions to the United Nations Framework Convention on Climate Change (UNFCCC) (Grz, 2016) but most recently identified the pantropical model for consideration (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 quantifying *AGB* stocks and dynamics in miombo woodlands.

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). However, our results also underscore how the inclusion of *H* in *AGB* models is not without challenges (Chave et al., 2014; Kapinga et al., 2018). Firstly, conventional field measurements of *H* are not only time consuming but also prone to errors, especially for large trees and in closed canopies (Larjavaara and Muller-Landau, 2013; Wang et al., 2019). Secondly, 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). 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). 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)). Our approach of fitting

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a locally-calibrated and species-specific *H-D* model substantially improved the accuracy of *AGB* estimates, but access to high-quality local datasets to parameterise such allometries is often limited (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). 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). 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).

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). 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.

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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 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). 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). In the context of miombo woodlands in Zambia, only 31 tree species (out of approximately 238 uniquely identified species in the most recent extensive national forest inventory (Pelletier et al., 2018; Yambayamba et al., 2024)) have wood density records (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 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.

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AUTHOR CONTRIBUTIONS

AMY and TJ conceived the idea for the study. AMY did the data collating and led the analysis with assistance from TJ. All authors contributed 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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