Biomass estimation in mangrove forests: a comparison of allometric models incorporating species and structural information

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Abstract

Improved estimates of aboveground biomass (AGB) are required to improve our understanding of the productivity of mangrove forests to support the long-term conservation of these fragile ecosystems which are under threat from many natural and anthropogenic pressures. To understand how individual species affects biomass estimates in mangrove forests, five species-specific and four genus-specific allometric models were developed. Independent tree inventory data were collected from 140 sample plots to compare the AGB among the species-specific models and seven frequently used pan-tropical and Sundarbans-specific generic models. The effect of individual tree species was also evaluated using model parameters for wood densities (from individual trees to the whole Sundarbans) and tree heights (individual, plot average and plot top height). All nine developed models explained a high percentage of the variance in tree AGB ($R^2 = 0.97–0.99$) with the diameter at breast height and total height (H). At the individual tree level, the generic allometric models overestimated AGB from 22% to 167% compared to the species-specific models. At the plot level, mean AGB varied from 111.36 Mg ha$^{-1}$ to 299.48 Mg ha$^{-1}$, where AGB significantly differed in all generic models compared to the species-specific models ($p < 0.05$). Using measured species wood density (WD) in the allometric model showed 4.5%–9.7% less biomass than WD from published databases and other sources. When using plot top height and plot average height rather than measured individual tree height, the AGB was overestimated by 19.5% and underestimated by 8.3% ($p < 0.05$). The study demonstrates that species-specific allometric models and individual tree measurements benefit biomass estimation in mangrove forests. Tree level measurement from the inventory plots, if available, should be included in allometric models to improve the accuracy of forest biomass estimates, particularly when upscaling individual trees up to the ecosystem level.

1. Introduction

There has been a global effort to develop accurate and efficient methods to quantify aboveground carbon (measured as biomass) in mangrove forests (Hutchison et al. 2014, Ni-Meister 2015, Baccini et al. 2017, Lagomasino et al. 2019). A range of remote sensing (RS) technologies can indirectly infer forest biomass but field data are needed to calibrate and validate products (Gibbs et al. 2007, Chave et al. 2019, Réjou-Méchain et al. 2019). Destructive harvesting of trees provides the most precise estimates of aboveground biomass (AGB), yet is impractical, laborious, costly and often illegal (Komiyama et al. 2008, Edwards et al. 2019) and so mathematical models have been developed to estimate tree biomass from easily measured biophysical parameters (tree diameter at breast height (DBH), height (H), or wood density (WD)) (Brown 1997, Komiyama et al. 2005, Picard et al. 2012, Chave et al. 2014). These models are known...
as allometric models. However, this method of estimation can yield a large degree of uncertainty scaling up from individual tree biomass to plot and forest-level as uncertainties associated with individual trees are propagated (van Breugel et al. 2011, Petrokofsky et al. 2012, Réjou-Méchain et al. 2019). The choice of appropriate allometric model is therefore critical to reduce uncertainties in the estimation of forest biomass.

All allometric models have limitations since they are based on a limited number of destructively sampled trees and often the sample locations are unrepresentative of forest heterogeneity (Weiskittel et al. 2013, Hickey et al. 2018). These models also introduce an uncertainty when applied to species without the destructive sample (Mitchard et al. 2013, Ngomanda et al. 2014, Mahmood et al. 2019). For example, de Souza Pereira et al. (2018) found AGB estimation errors between minus 18% and plus 14% when using biome-specific allometries rather than species-specific ones in Brazilian mangrove forests. On the other hand, a few studies have shown that generic models can outcompete locally developed ones (Rutishauser et al. 2013, Stas et al. 2017). Uncertainties also arise from inappropriate use of regression models without considering collinearity of parameters, uncritical use of model dredging and inappropriate criteria for model selection (Sileshi 2014, Vorster et al. 2020). Recently published global and continental AGB estimates contain errors due to an under representative sample size and the exclusion of the climatic regime, geophysical and geomorphological variables, which are key to understanding the spatial distribution of biomass (Rovai et al. 2016). Inclusion of biophysical parameters such as WD and tree height can help to capture geographical heterogeneity and also act as a suitable proxy of environmental drivers such as variation in salinity which affects the growth rate, WD, species composition and tree height (Mahmood et al. 2019, Rahman et al. 2020, 2021, Virgulino-Júnior et al. 2020).

Although WD is an important variable for assessing carbon content, it is rarely measured during field inventories. Most studies identify species and then use published WD values from a database of generic values (Njana et al. 2016, Réjou-Méchain et al. 2019). Using the same, or grouped, WD in the allometric model tends to smooth species-level variations in AGB (Mitchard et al. 2013, Ni-Meister 2015). The inclusion of tree height has a large effect on individual tree and forest AGB (Feldpausch et al. 2012). Any errors introduced during individual tree height measurements can originate from the choice of methods and/or instruments and can be propagated as estimates are scaled up (Larjavaara and Muller-Landau 2013). For example, the use of height–diameter (H–D) models, developed from the height and stem diameter of individual trees, often exhibit uncertainty due to wider height-variation at different spatial scales (Feldpausch et al. 2011, Vieilledent et al. 2012). Space-borne and air-borne LiDAR and RADAR technologies can improve the accuracy of the height measurement and have been used to develop canopy height models (Fatoyinbo et al. 2021).

The Sundarbans mangrove forest is one of the largest and most bio-diverse mangroves in the world, located between Bangladesh and India. It contains the highest carbon densities (345 Mg ha$^{-1}$) in both above- and below-ground among all forests in Bangladesh (GOB 2019, Henry et al. 2021). The Bangladesh Forest Department estimated carbon stocks in the Sundarbans in 2009 and 2015 using pan-tropical allometric models and Sundarbans-specific generic models (BFD 2010, Rahman et al. 2015, Mahmood et al. 2019, Henry et al. 2021). Other studies such as Kamruzzaman et al. (2017) and Azad et al. (2020) used pan-tropical generic models to estimate AGB in selected areas. However, species-specific allometric models are not yet available to estimate AGB in the Sundarbans. Therefore, it is timely to examine whether species-specific allometric models using measured wood densities and tree heights can yield more accurate estimates of AGB in the Sundarbans and in mangrove forests more generally. The aim of this paper is to report research that compares a range of sources of uncertainty in allometric models, WD, and height measurement for AGB in the Sundarbans mangrove forest, Bangladesh. First, the study compares site- and species-specific AGB between the Sundarbans and pan-tropical generic allometric models for variability of aboveground tree biomass. Secondly, the study determines variability of AGB in the Sundarbans by comparing measured and published WD values at multiple spatial scales. Thirdly, the study quantifies the impact of different methods of tree height determination on estimates of AGB in mangrove forests.

2. Material and methods

2.1. Study area

The Bangladesh Sundarbans is situated between 21°30’ N and 22°30’ N and 89°00’ E and 89°55’ E in the lower delta plain of the Ganges–Brahmaputra–Meghna delta covering an area of 6017 km$^2$ (figure 1) (Giri et al. 2011, Aziz and Paul 2015, Sarker et al. 2016). The forest is of international significance as a Ramsar and UNESCO World Heritage site. It provides a number of valuable ecosystem services such as protecting inland areas from storms and tidal surges (Barua et al. 2020) The near-constant mean annual minimum and maximum temperature (29 °C–31 °C) and high annual rainfall (1474–2265 mm) made the climate of the Sundarbans warm and humid between 1948 and 2011 (Chowdhury et al. 2016, Sarker et al. 2016). The soil is fine-gained silt and clay and slightly calcareous (Siddiqi 2001). The Sundarbans has a distinct salinity zonation with the high salinity zone in the
west (polyhaline) to low salinity zone (oligohaline) in the east along with medium salinity zone (mesohaline) between (Siddiqi 2001, Chanda et al 2016). Salinity regulates the geomorphology and hydrological characteristics and also the morphology, growth and distribution of plant species (Sarker et al 2016, 2019a, Rahman et al 2020, 2021).

2.2. Allometric models in the Sundarbans
Species-specific allometric models are not available for all species in the Sundarbans as destructive sampling was not permitted due to an imposed felling moratorium of all species since 1989 (Mahmood et al 2019). However, four species-specific models were developed through destructive sampling in the Bangladesh Sundarbans (table 1). Three generic allometric models were recently developed for 14 species by using semi-destructive sampling methods where biomass of stems and larger branches were measured through volume and WD, and small branches and foliage through weighing after pruning (Mahmood et al 2019). Published pan-tropical models have also been used to estimate biomass in the Sundarbans (Rahman et al 2015, Kamruzzaman et al 2017, 2018).

2.3. Development of species-specific allometric model
A conceptual diagram of the research methodology is presented in the figure 2. The species-specific allometric models were developed from the semi-destructive sampling data (324 individuals, 13 species, except Sonneratia caseolaris) from Mahmood et al (2019), where AGB (kg/tree) was presented along with DBH and total height (H) (figure 1). Species-specific models for S. caseolaris were not developed as the independent tree inventory data did not have any individuals of this species. Out of 13 species, eight species (Avicennia officinalis, Avicennia marina, Bruguiera gymnorrhiza, Bruguiera sexangula, Rhizophora apiculata, Rhizophora mucronata, Xylocarpus granatum and Xylocarpus moluccensis) were merged into genus level to yield sufficient data for model fitting. Therefore, nine allometric models were developed for Aglaia cucullata, Avicennia sp., Bruguiera sp., Excoecaria agallocha, Heritiera fomes, Lumnitzera racemosa, Rhizophora sp., Sonneratia apetala, and Xylocarpus sp.

Log-linear least square regression was used to fit models to predict AGB for each species. The choice of log-linear regression over nonlinear regression was done by comparing error distribution of biomass. According to Xiao et al (2011), the linear regression of log-transformed data better characterizes multiplicative, heteroscedastic and lognormal error, whereas the nonlinear regression performs additive, homoscedastic, normal error. The goodness of fit of two models were compared and the lower value of Akaike's information criterion (AIC)
Table 1. Allometric models used for measuring aboveground biomass in the Sundarbans.

| Model no. | Site, species | Allometric model | N   | Identity in this paper and source |
|-----------|--------------|-----------------|-----|----------------------------------|
| **Bangladesh Sundarbans and species-specific** | | | | |
| 1 | *Aegialitis rotundifolia* | $\text{AGB} = 5.49 \text{GCH}^2 - 251.36 \text{H} - 0.07 \text{HCH}$  
+ $0.75 (\text{GCH} \times \text{H} \times \text{HCH})$ | 29 | Siddique *et al* (2012) |
| 2 | *Aegiceras corniculatum* | $\sqrt{\text{AGB}} = 0.48 \text{DBH} - 0.13$ | 50 | Mahmood *et al* (2016b) |
| 3 | *Ceriops decandra* | $\text{AGB} = 4.70 \text{GCH}^{4.41}$ | 48 | Mahmood *et al* (2012) |
| 4 | *Kandelia candel* | $\text{AGB} = 0.21 \text{DBH}^2 + 0.12$ | 25 | (Mahmood *et al* 2016a) |
| **Bangladesh Sundarbans and generic model** | | | | |
| 5 | For 14 species  
*Aglaia cecullata, Avicennia officinalis, Avicennia marina,*  
*Bruguiera gymnorrhiza, Bruguiera sexangula, Excoecaria agallocha,*  
*Heritiera fomes,*  
*Lumnitzera racemosa,*  
*Rhizophora acipulata,*  
*Rhizophora mucronata,*  
*Sonneratia apetala,*  
*Sonneratia caseolaris,*  
*Xylocarpus granatum,*  
*Xylocarpus moluccensis* | $\ln(\text{AGB}) = -1.9272 + 2.3517\ln(\text{DBH})$ | 260 | Mahmood_2019_D (Mahmood *et al* 2019) |
| 6 | | $\ln(\text{AGB}) = -2.4317 + 2.1341\ln(\text{DBH}) + 0.4953\ln(\text{H})$ | 260 | Mahmood_2019_DH (Mahmood *et al* 2019) |
| 7 | | $\ln(\text{AGB}) = -6.7189 + 2.1634\ln(\text{DBH}) + 0.3752\ln(\text{H}) + 0.6895\ln(\text{WD})$ | 260 | Mahmood_2019_DHW (Mahmood *et al* 2019) |
| **World or pantropical and generic model** | | | | |
| 8 | Pan-tropical, all species | $\text{AGB} = 0.0673 \times (\text{WD} \times \text{DBH}^2 \times \text{H})^{0.976}$ | 4004 | Chave_2014_DHW (Chave *et al* 2014) |
| 9 | Pan-tropical, mangrove species | $\text{AGB} = 0.0509 \times (\text{WD} \times \text{DBH}^2 \times \text{H})$ | 84 | Chave_2005_DHW (Chave *et al* 2005) |
| 10 | Pan-tropical, mangrove species | $\text{AGB} = \text{WD} \times \exp(-1.349 + 1.980\ln(\text{DBH})) + 0.207(\ln(\text{DBH}))^2 - 0.0281(\ln(\text{DBH}))^3$ | 84 | Chave_2005_DW (Chave *et al* 2005) |
| 11 | South-east Asia, mangrove species | $\text{AGB} = 0.251 \times \text{WD} \times \text{DBH}^{2.46}$ | 104 | Komiyama_2005_DW (Komiyama *et al* 2005) |

Here $\text{AGB} =$ total above ground biomass (kg), $N =$ number of destructive/semi-destructive samples, DBH = diameter at breast height (cm), H = total height (m), WD = wood density (gm cm$^{-3}$, model-7: kg m$^{-3}$), GCH = girth at collar height (cm), HCH = height of collar girth point (m).
provides significantly better fit when the magnitude of the difference of AIC is greater than 2 (Burnham and Anderson 2002). These two models were compared for all species following Xiao et al (2011). In all cases, the log-linear regression provided significantly better fit (table A.1 available online at stacks.iop.org/ERL/16/124002/mmedia). Therefore, the following six log-linear regression models were used to fit AGB as the dependent variable, and DBH and tree height (H) as independent variables

E1: \( \ln(AGB) = \ln(a) + b \ln(DBH) \)
E2: \( \ln(AGB) = \ln(a) + b \ln(H) \)
E3: \( \ln(AGB) = \ln(a) + b \ln(DBH \times H) \)
E4: \( \ln(AGB) = \ln(a) + b \ln(DBH^2 \times H) \)
E5: \( \ln(AGB) = \ln(a) + b \ln(DBH \times H^2) \)
E6: \( \ln(AGB) = \ln(a) + b \ln(DBH) + c \ln(H) \).

The underlying assumptions for the regression analysis such as normality of residuals and heteroscedasticity were used to judge the suitability of each regression model. Percent relative standard errors (PRSEs) of each regression coefficient was measured according to Sileshi (2014), where PRSE > 25 is considered an unreliable model. The multicollinearity of each model was measured with the variance inflation factor (VIF), where VIF > 5 indicates high collinearity among independent variables. Due to high multicollinearity, complex models with more independent variables were not considered in this study. After obtaining the eligible potential models for each species, the best models were selected by the lowest second-order Akaike information criterion (AICc) and residual standard error (RSE), and the highest Akaike information criterion weight (AICw) and coefficient of determination \( (R^2) \) values (Picard et al 2012, Sileshi 2014, Mahmood et al 2019, 2020). Models with non-significant parameter of estimates were not considered regardless of meeting the criteria outlined. Since, the AICw provides the likelihood of each model to be the best, it was given highest priority compared with other parameters (Sileshi 2014). For all models, the correction factor was calculated to minimize systematic bias while converting biomass from ln scale to normal scale (Sprugel 1983). The K-fold cross-validation technique was used to validate the best model. This technique randomly divides the original dataset into K subsets (ten in this case) of equal sizes, where each subset is validated with \( K-1 \) subsets (James et al 2013). The K-fold validation technique was also run for Sundarbans-specific and pantropical generic model (Model no. 7–11 in table 1) to measure tree level variability in AGB in the Sundarbans.

2.4. Tree inventory

Aboveground tree data were collected from 140 random sample plots within the Bangladesh Sundarbans (figure 1). Out of 140 sample plots, 120 plots were randomly placed within permanent sample plot (PSP) (20 × 100 m) established by the Bangladesh Forest Department whilst the remaining 20 plots were outside of the PSP. These sample plots are distributed to all 35 compartments in the Bangladesh Sundarbans covering all three salinity zones (oligohaline, mesohaline and polyhaline) and forest types (Iftekhar and

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**Figure 2.** Conceptual diagram of the research methodology. The model numbers are labeled according to table 1. Here, DBH: diameter at breast height, H: height and WD: wood density.
Saenger 2008, Sarker et al 2019b), Each plot consists of a circular plot with the radius of 11.3 m (400 m²) for measuring bigger trees (DBH > 14.5 cm) and a smaller circular plot within this of 5 m radius (79 m²) for smaller trees (DBH > 2.5–14.5 cm) (figure A.1). After establishing the plots, all individual trees (DBH > 2.5 cm) were marked, and DBH and total height (H) measured by using a diameter tape and a Vertex III hypsometer (Haglöf, Sweden), respectively. Haglöf wood increment borer (5.15 mm diameter and 300 mm bit length) was used to collect woody specimen at DBH point to determine the WD of studied species according to Wiemann and Williamson (2013). The WD (gm cm⁻³) was then measured from the volume and dry mass of the specimen. The cylindrical volume was measured in the field from the diameter and length of the specimen and brought to the laboratory for oven-drying at 105 °C until constant weight.

2.5. Variability of AGB in the Sundarbans
The magnitude and patterns of differences in AGB at plot level in the Sundarbans were compared by using different allometric models with an independent set of collected inventory data from the Sundarbans. Plot level AGB variability was measured by actual AGB difference (Mg ha⁻¹), absolute difference (Mg ha⁻¹) and relative absolute difference (%) among different allometric models.

2.5.1. AGB variability with allometric models
Measured DBH, H and WD were used in the species-specific allometric models and other site-specific and pan-tropical generic models (Model 7–11 in table 1) to assess AGB at the individual tree level. In order to compute plot-level AGB estimation per hectare (Mg ha⁻¹), a hectare expansion factor (HEF) for each stem was used according to the size of the sample plot (i.e. HEF = 25 for bigger plots, and HEF = 126.58 for smaller sub-plot) and subsequently summed up all tree biomass in each plot to get plot biomass. To estimate biomass from the species-specific models, the developed nine species-specific models were used alongside four published species-specific models (Model 1–4 in table 1). If no species-specific allometric model was available, models for similar genus or family level were applied. Since measuring the girth at collar height (GCH) for Ceriops decandra and Aegialitis rotundifolia is laborious and time consuming, DBH was measured in the field and subsequently converted to GCH from the developed relationship between DBH and GCH of 50 individuals (figure A.2).

2.5.2. AGB variability with WD
Variation of tree AGB was compared with measured and databases-sourced WD obtained from published WD databases including the global WD database (Chave et al 2009, Zanne et al 2009), World Agroforestry’s tree functional attributes and ecological databases (ICRRAF 2016) and from Bangladesh Forest Research Institute (Sattar et al 1995). The Sundarbans-specific generic allometric model (Model 7: Mahmood_2019_DHW) was used for comparison of AGB from multiple WD sources. If there was no measured WD for any species, the WD from the same genus or family was used. Instead of applying species WD, plot-level mean WD, salinity zone WD and Sundarbans level WD were used to investigate how the spatial scale of WD variation on AGB estimates in the Sundarbans. To measure salinity zone mean WD, measured WD were averaged according to three salinity zones in the Sundarbans according to Rahman et al (2021).

2.5.3. AGB variability with tree height
To derive the variation of AGB from different height measurements, mean height and maximum height from each plot was used in Model 7 (Mahmood_2019_DHW). The Model 7 was used in this case as it is originated from the Sundarbans and it contains both H and WD parameters.

2.6. Statistical analysis
All statistical analysis and graphics used R4.0.4 for Windows in RStudio Version-1.4.1106 (R Core Team 2020). The normality of residuals, heteroscedasticity and multicollinearity of each regression model were tested with Shapiro–Wilk normality test by using ‘R stats’ base package, studentized Breusch–Pagan test by using ‘lmtest’ package and VIF test using ‘car’ package, respectively (Zeileis and Hothorn 2002, Fox and Weisberg 2019). AICc for fitted regression model was assessed by 'MuMln' package (Bartoń 2020). K-fold cross validation was run using ‘caret’ package and model accuracy was compared with mean absolute error (MAE) and root mean squared error (Kuhn 2008). Pairwise comparison of tree AGB between the species-specific and other models were tested either by paired t-test if the underlying assumptions such as normality and heteroscedasticity were met; otherwise, Wilcoxon signed-rank non-parametric test was used. The 'rstatix' package was used for Wilcoxon signed-rant test and 'R stats' base package was used for paired t-test (Kassambara 2020). The graphical output was generated using the ‘ggplot2’ ‘gggeffects’ and ‘cowplot’ package (Wickham 2016, Lüdecke 2018, Wilke et al 2019).

3. Results
3.1. Species-specific allometric model
Out of 54 log-linear regression models for nine species, 26 models passed all four criteria including normality of residuals, heteroscedasticity, PRSE and VIF (table A.2). These 26 models were then fitted species-wise to the 324 semi-destructively harvested tree dataset with DBH and H: A. cucculata (19),
Table 2. Regression results for all species-specific allometric models in the Sundarbans.

| Species                | Eq. no. | Model, ln (AGB) = | \(a^*\) | \(b\) | \(c\) | Adj. \(R^2\) | RSE  | AICc  | AICcW | CF  |
|------------------------|---------|------------------|--------|------|-----|-------------|------|-------|-------|-----|
| Aglaia cucullata       | E1      | ln\(a\) + b ln \(DH\) | -1.9066 | 2.3784 | —   | 0.9915      | 0.1047 | -26.3501 | 1.00  | 1.0055 |
|                        | E5      | ln\(a\) + b ln \(DBH \times H^2\) | 3.7114 | 1.0918 | —   | 0.9585      | 0.2316 | 3.8164  | 0.00  | 1.0980 |
|                        | E2      | ln\(a\) + b ln \(H\) | 4.5809  | 3.7098 | —   | 0.8554      | 0.4324 | 27.5502 | 0.00  | 1.0272 |
| Avicennia sp.          | E1      | ln\(a\) + b ln \(DH\) | -1.5554 | 2.2069 | —   | 0.9781      | 0.2287 | 0.0103  | 0.81  | 1.0265 |
|                        | E4      | ln\(a\) + b ln \(DBH^2 \times H\) | -2.7625 | 0.9520 | —   | 0.9765      | 0.237  | 2.8854  | 0.19  | 1.0285 |
| Bruguiera sp.         | E1      | ln\(a\) + b ln \(DH\) | -1.4473 | 2.2870 | —   | 0.9845      | 0.1926 | -9.3234 | 1.00  | 1.0187 |
|                        | E3      | ln\(a\) + b ln \(DBH \times H\) | -2.7982 | 1.5246 | —   | 0.9649      | 0.2901 | 16.0743 | 0.00  | 1.0430 |
|                        | E5      | ln\(a\) + b ln \(DBH \times H^2\) | -3.1823 | 1.1004 | —   | 0.9178      | 0.4439 | 42.4386 | 0.00  | 1.1035 |
| Excoecaria agallocha  | E4      | ln\(a\) + b ln \(DBH^2 \times H\) | -2.5721 | 0.8623 | —   | 0.9903      | 0.1539 | -26.9780 | 1.00  | 1.0119 |
|                        | E3      | ln\(a\) + b ln \(DBH \times H\) | -2.9335 | 1.4173 | —   | 0.9801      | 0.2200 | -1.9475 | 0.00  | 1.0245 |
|                        | E5      | ln\(a\) + b ln \(DBH \times H^2\) | -3.3198 | 1.0359 | —   | 0.9591      | 0.3152 | 50.1953 | 0.00  | 1.0509 |
|                        | E2      | ln\(a\) + b ln \(H\) | -4.0227 | 3.6582 | —   | 0.8558      | 0.5919 | 67.3342 | 0.00  | 1.1915 |
| Heritiera fomes       | E1      | ln\(a\) + b ln \(DH\) | -1.9944 | 2.4603 | —   | 0.9931      | 0.1434 | -97.2721 | 1.00  | 1.0103 |
| Luminitzera racemosa  | E1      | ln\(a\) + b ln \(DH\) | -2.1151 | 2.4187 | —   | 0.9858      | 0.1342 | -8.8255 | 0.94  | 1.0090 |
|                        | E4      | ln\(a\) + b ln \(DBH^2 \times H\) | -3.2562 | 1.0631 | —   | 0.9783      | 0.1663 | -3.2570 | 0.06  | 1.0139 |
|                        | E3      | ln\(a\) + b ln \(DBH \times H\) | -4.0458 | 1.8671 | —   | 0.9558      | 0.2373 | 5.9931  | 0.00  | 1.0286 |
|                        | E5      | ln\(a\) + b ln \(DBH \times H^2\) | -4.9734 | 1.4650 | —   | 0.8994      | 0.3579 | 16.6722 | 0.00  | 1.0661 |
| Rhizophora sp.        | E4      | ln\(a\) + b ln \(DBH^2 \times H\) | -2.3744 | 0.8953 | —   | 0.9467      | 0.2226 | 2.8788  | 0.82  | 1.0251 |
|                        | E3      | ln\(a\) + b ln \(DBH \times H\) | -2.8960 | 1.5009 | —   | 0.9358      | 0.2443 | 6.0407  | 0.17  | 1.0303 |
|                        | E5      | ln\(a\) + b ln \(DBH \times H^2\) | -3.4321 | 1.1161 | —   | 0.9065      | 0.2948 | 12.4334 | 0.01  | 1.0444 |
| Sonneratia apetala    | E4      | ln\(a\) + b ln \(DBH^2 \times H\) | -2.8869 | 0.9170 | —   | 0.9938      | 0.1633 | -10.3304 | 0.71  | 1.0134 |
|                        | E6      | ln\(a\) + b ln \(DBH \times H\) + c ln(H) | -2.6715 | 1.9068 | 0.7430 | 0.9939      | 0.1625 | -8.5123 | 0.29  | 1.0133 |
|                        | E3      | ln\(a\) + b ln \(DBH \times H\) | -3.6314 | 1.5533 | —   | 0.9854      | 0.2518 | 6.9904  | 0.00  | 1.0322 |
|                        | E5      | ln\(a\) + b ln \(DBH \times H^2\) | -4.4509 | 1.1706 | —   | 0.9582      | 0.4256 | 27.9819 | 0.00  | 1.0948 |
|                        | E2      | ln\(a\) + b ln \(H\) | -5.6705 | 4.2261 | —   | 0.7723      | 0.9932 | 61.8759 | 0.00  | 1.6575 |
| Xylocarpus sp.        | E1      | ln\(a\) + b ln \(DH\) | -1.9174 | 2.3100 | —   | 0.9720      | 0.1989 | -15.5125 | 1.00  | 1.0200 |

Here bold and light grey shaded models are the best model for each species, \(a^*\) stands for ln \(a\), all parameters of estimates \((a, b, c)\) are significant at \(p < 0.05\), \(R^2\): coefficient of determination, RSE: residual standard error, AICc: with small sample bias adjustment, AICcW: weighted AIC, CF = correction factor for converting log scale in to normal scale.
Avicennia sp. (41), Bruguiera sp. (31), E. agallocha (35), H. fomes (97), L. racemosa (13), Rhizophora sp. (17), S. apetala (20), and Xylocarpus sp. (51).

Out of 26 models, the best nine species-specific models are presented for each species group (table 2; figure 3). The AICw shows that the best-chosen models for A. cucullata, Bruguiera sp., E. agallocha, H. fomes, and Xylocarpus sp. have 100% chance for being the best model, while Avicennia sp., L. racemosa, Rhizophora sp. and S. apetala have respectively 81%, 94%, 82%, and 71% chance to be the best model (table 3). In the case of S. apetala, while E6 models had the highest and lowest RSE and AIC value, the E4 model was chosen based on higher AICw for its greater chance for being the best model. The adjusted coefficient of determination ($R^2$) varied from 0.77 to 0.99 for all models. All species-specific models comprised single predictor value with only DBH for six species: A. cucullata, Avicennia sp., Bruguiera sp., H. fomes, L. racemosa, and Xylocarpus sp. and with combination of DBH and H (DBH$^2 \times H$) for E. agallocha, S. apetala, and Rhizophora sp.

The ten-fold cross validation showed that the species-specific model gives the lowest average MAE of all species in comparison to three Sundarbans-specific and four pan-tropical generic allometric models (figure 4, table A.4). The lowest average MAE revealed that the species-specific models performed well to predict the AGB in the Sundarbans. AGB estimation at tree level had mean relative absolute difference in MAE between 21.85% with Mahmood_2019_DHW model to the maximum 167.43% with Komiyama_2005_DW model followed by Chave_2005_DHW and Chave_2014_DHW (table A.4). The paired $t$-test of MAE for species-specific models with generic models showed that there is no significant difference of MAE with three Sundarbans-specific models ($p > 0.05$); however, all four pan-tropical models showed significantly higher MAE than the species specific-model ($p < 0.05$). The largest error was obtained for E. agallocha with Komiyama_2005_DW.

### 3.2. Aboveground tree biomass in the Sundarbans

The tree inventory in the Bangladesh Sundarbans indicates a total of 24 tree species. The mean DBH, height, measured and database-sourced WD of all tree species are presented in the table 3. The DBH and H distribution are presented in the supplementary figures A.3 and A.4. Frequency distribution of the topmost ten species based on basal area (m$^2$ ha$^{-1}$) and tree density (trees ha$^{-1}$) showed that E. agallocha, H. fomes and C. decandra comprise 90% of the stems in the Sundarbans, although they represent 60% in
Table 3. List of tree species found in the Sundarbans with taxonomy and structural parameters.  

| Sl No. | Latin name                          | Local name       | Family            | Mean DBH (cm ± s.d.) | Mean height (m ± s.d.) | Measured mean wood density (gm cm$^{-3}$ ± s.d.) | Mean wood density from database (gm cm$^{-3}$ ± s.d.) |
|--------|-------------------------------------|------------------|-------------------|----------------------|------------------------|-------------------------------------------------|-----------------------------------------------------|
| 1.     | Aegialitis rotundifolia (Roxb.)     | Nunia            | Plumbaginaceae    | 6.86 ($\pm$ 2.85)   | 3.94 ($\pm$ 1.71)     | 0.50 ($\pm$ 0.05)                                               |                                                     |
| 2.     | Aegiceras corniculatum (L.) Blanco  | Kholshi          | Primulaceae       | 5.69 ($\pm$ 2.67)   | 5.73 ($\pm$ 2.18)     | 0.74 ($\pm$ 0.08)                                               |                                                     |
| 3.     | Aglaia cucullata (Roxb.) Pellegr.   | Kela Kela        | Meliaceae         | 3.58 ($\pm$ 1.16)   | 4.70 ($\pm$ 1.62)     | 0.59 ($\pm$ 0.09)                                               |                                                     |
| 4.     | Avicennia alba (Blume.)             | Sada Baen        | Avicenniaceae     | 14.10 ($\pm$ 0.85)  | 8.70 ($\pm$ 2.40)     | 0.65 ($\pm$ 0.07)                                               |                                                     |
| 5.     | Avicennia marina (Forssk.) Vierh.   | Moricha Baen     | Avicenniaceae     | 10.40 ($\pm$ 5.26)  | 10.87 ($\pm$ 5.77)    | 0.76 ($\pm$ 0.08)                                               |                                                     |
| 6.     | Avicennia officinalis L.             | Kala Baen        | Avicenniaceae     | 21.20 ($\pm$ 13.40) | 11.56 ($\pm$ 5.13)    | 0.83 ($\pm$ 0.08)                                               |                                                     |
| 7.     | Bruguiera gymnorrhiza (L.) Lam.     | Lal Kakra        | Rhizophoraceae    | 7.40                  | 5.80                   | 0.72 ($\pm$ 0.03)                                               |                                                     |
| 8.     | Bruguiera sexangula (Lour.) Poir.   | Holud Kakra      | Rhizophoraceae    | 15.75 ($\pm$ 3.95)  | 6.96 ($\pm$ 3.02)     | 0.84 ($\pm$ 0.10)                                               |                                                     |
| 9.     | Cerbera manghas L.                  | Dakar            | Apocynaceae       | 8.92 ($\pm$ 0.08)   | 0.72 ($\pm$ 0.08)     | 0.35 ($\pm$ 0.01)                                               |                                                     |
| 10.    | Ceriops decandra (Griff.) Ding Hou | Hahal Kogra      | Rhizophoraceae    | 3.31 ($\pm$ 0.80)   | 3.97 ($\pm$ 0.95)     | 0.66 ($\pm$ 0.07)                                               |                                                     |
| 11.    | Cynometra ramiflora L.              | Singa            | Fabaceae          | 4.25 ($\pm$ 0.15)   | 6.93 ($\pm$ 0.41)     | 0.42 ($\pm$ 0.08)                                               |                                                     |
| 12.    | Cynometra ramiflora L.              | Singa            | Fabaceae          | 6.60                  | 6.80                   | 0.41 ($\pm$ 0.07)                                               |                                                     |
| 13.    | Excoecaria agallocha L.             | Gewa             | Euphorbiaceae     | 6.93 ($\pm$ 4.04)   | 6.71 ($\pm$ 2.49)     | 0.42 ($\pm$ 0.08)                                               |                                                     |
| 14.    | Excoecaria indica (Willd.) Muell. Ar. | Batul           | Euphorbiaceae     | 6.60                  | 6.80                   | 0.41 ($\pm$ 0.07)                                               |                                                     |
| 15.    | Heritiera fomes Buch.-Ham.           | Sundri           | Malvaceae         | 8.57 ($\pm$ 6.58)   | 8.03 ($\pm$ 4.16)     | 0.57 ($\pm$ 0.81)                                               |                                                     |
| 16.    | Hibiscus rosa-sinensis L.            | Bula             | Malvaceae         | 8.57 ($\pm$ 6.58)   | 8.03 ($\pm$ 4.16)     | 0.57 ($\pm$ 0.81)                                               |                                                     |
| 17.    | Intsia bijuga (Colebr.) Kuntze      | Bhai/Bhola       | Malvaceae         | 4.39                  | 5.00                   | 0.57 ($\pm$ 0.81)                                               |                                                     |
| 18.    | Inula bracteata (L.) Prance         | Vakathi          | Palmaeae          | 4.40 ($\pm$ 0.59)   | 5.17 ($\pm$ 0.81)     | 0.58 ($\pm$ 0.05)                                               |                                                     |
| 19.    | Karaya (L.) Panigrahi               | Karya            | Fabaceae          | 5.70                  | 6.50                   | 0.55 ($\pm$ 0.13)                                               |                                                     |
| 20.    | Kandelia candel (L.) Druce          | Karanja          | Lecythidaceae     | 13.54                 | 10.28                  | 0.85 ($\pm$ 0.11)                                               |                                                     |
| 21.    | Rhizophora mucronata Lam.           | Jhana Garjan     | Rhizophoraceae    | 15.42 ($\pm$ 3.72)  | 10.38 ($\pm$ 2.65)    | 0.85 ($\pm$ 0.11)                                               |                                                     |
| 22.    | Sonneratia alba (Buch.-Ham.)        | Keora            | Lythraceae        | 29.35 ($\pm$ 12.81) | 17.97 ($\pm$ 5.30)    | 0.85 ($\pm$ 0.11)                                               |                                                     |
| 23.    | Xylocarpus granatum K.D. Koen.      | Dunda            | Meliaceae         | 18.77 ($\pm$ 12.03) | 8.08 ($\pm$ 2.66)     | 0.67 ($\pm$ 0.09)                                               |                                                     |
| 24.    | Xylocarpus moluccensis (Lam.) M. Roem | Passur          | Meliaceae         | 15.51 ($\pm$ 10.80) | 9.39 ($\pm$ 5.89)     | 0.65 ($\pm$ 0.09)                                               |                                                     |

*Indicates mangrove associates according to Tomlinson (2016). Abbreviation: DBH = diameter at breast height. Values without s.d. indicates single observation.

**Multiple wood density values from different sources.
terms of basal area (figure 5). *E. agallocha* and *H. fomes* was within the top two species in both categories; *C. decandra* was the third in terms of tree density, however, the sixth in case of basal area for its lower DBH.

The mean AGB varied from 111.36 Mg ha$^{-1}$ with the Chave_2005_DHW model to the highest 299.48 Mg ha$^{-1}$ for Chave_2005_DW model (figure 6). Except for Chave_2005_DHW and Chave_2014_DHW, all other models yielded higher AGB than the species-specific model (123 Mg ha$^{-1}$). The mean relative absolute difference in AGB ranged from 9% with Mahmood_2019_DHW to 142% with Chave_2005_DW. Pairwise comparison with the Wilcoxon signed-rank test between species-specific and other models showed that all generic models measured significantly different AGB than the species-specific model in the Sundarbans ($p < 0.05$). Both Chave_2005_DW and Komiyama_2005_DW overestimated AGB (supplementary table A.5). The absolute difference between allometric models tended to increase with DBH in all species, suggesting that larger trees are crucial for estimating AGB with a variety of available allometric model leading to a greater error and uncertainty.

AGB was significantly higher when models used published WD compared to species-specific measured WD (Wilcoxon signed-rank test, $p < 0.05$) (figure 7(A), table 4). The maximum mean relative difference biomass was for Sundarbans mean WD.
followed by salinity zone mean WD and database-derived WD. Looking at different sources of height data, using plot top height tended to overestimate AGB by 19.46%, while using average height underestimated AGB by 8.31% compared to the measurements from individual species (figure 7(B), table 4).

4. Discussion

The results show that the species-specific allometric models provide the lowest average MAE for all species in the Sundarbans (figure 4, table A.4). However, the three Sundarbans-specific generic models showed no significant difference of mean MAE at tree-level compared with the species-specific models (table A.4). At plot-level, all local and pan-tropical generic models either overestimated or underestimated AGB when compared to local species-specific models (figure 6). Several studies have concluded that site-specific AGB models estimate biomass or carbon with less error than regional or pan-tropical models; for example, Sundarbans mangrove forest (Mahmood et al. 2019), lowland Dipterocarp forest in Indonesia (Basuki et al. 2009), degraded landscape in Northern Ethiopia (Mokria et al. 2018), central African forest (Ngomanda et al. 2014) and Mexican tropical humid forests (Martínez-Sánchez et al. 2020). In contrast, only a few studies report better performance from regional or pan-tropical models and these appear result from large uncertainties in the data used to build the local model; for example, West Africa (Aabeyir et al. 2020). The accuracy of these generic models for a particular forest depends on whether these models incorporate sufficient samples from that forest. Chave et al. (2014) point out that the discrepancy between local models and their own model (Chave_2014_DHW) in wet forests (including mangroves) is largely due to failure to address the wider variation of tree form and other characteristics like

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**Figure 6.** Comparison of aboveground biomass (Mg ha\(^{-1}\)) with different allometric models. The models are arranged from the highest median AGB to the lowest. The black horizontal line of box plot for each model represents the median and the width of violin plot represents the proportion of the data located there as a measure of kernel probability density. The black dots represent the outliers, which are 1.5 times of the interquartile range above the upper quartile and below the lower quartile (McGill et al. 1978).

**Figure 7.** Comparison of aboveground biomass with (A) different wood density and (B) different height parameters. The parameters are arranged from the highest median AGB to the lowest. For details of the violin-box plot, see figure 6.
Table 4. Pairwise comparison test of plot-level AGB from species-specific and other allometric models.

| Model comparison                          | Mean difference biomass (Mg ha\(^{-1}\)) | Mean absolute difference biomass (Mg ha\(^{-1}\)) | Mean relative absolute difference (%) | Wilcoxon signed-rank test (Z), p-value |
|------------------------------------------|-----------------------------------------|-----------------------------------------------|-------------------------------------|------------------------------------------|
| **Comparison of different allometric model**                                      |                                         |                                               |                                     |                                          |
| Species-specific—Mahmood_2019_DHW         | –5.18                                   | 11.38                                         | 9.21                                | Z = –5.13, p < 0.05                        |
| Species-specific—Chave_2014_DHW           | 0.79                                    | 17.38                                         | 14.07                               | Z = –2.89, p < 0.05                        |
| Species-specific—Mahmood_2019_D           | –12.66                                  | 19.66                                         | 15.92                               | Z = –6.40, p < 0.05                        |
| Species-specific—Chave_2005_DHW            | 12.59                                   | 21.07                                         | 17.06                               | Z = –6.51, p < 0.05                        |
| Species-specific—Mahmood_2019_DH           | –21.27                                  | 23.37                                         | 18.92                               | Z = –7.95, p < 0.05                        |
| Species-specific—Komiyama_2005_DW          | –52.47                                  | 52.57                                         | 42.57                               | Z = –10.26, p < 0.05                       |
| Species-specific—Chave_2005_DW             | –175.67                                 | 175.75                                        | 142.31                              | Z = –10.26, p < 0.05                       |
| **Comparison from different wood density (WD)**                                     |                                         |                                               |                                     |                                          |
| Measured WD—plot mean WD                 | –3.16                                   | 5.83                                          | 4.53                                | Z = –5.86, p < 0.05                        |
| Measured WD—database WD                   | –4.82                                   | 9.91                                          | 7.70                                | Z = –3.83, p < 0.05                        |
| Measured WD—salinity zone mean WD          | –4.08                                   | 12.46                                         | 9.68                                | Z = –3.54, p < 0.05                        |
| Measured WD—Sundarbans mean WD            | –4.29                                   | 12.47                                         | 9.69                                | Z = –3.59, p < 0.05                        |
| **Comparison from different Tree Height (m)**                                      |                                         |                                               |                                     |                                          |
| Individual height—plot mean height        | 10.70                                   | 10.70                                         | 8.31                                | Z = –13.68, p < 0.05                       |
| Individual height—plot top height         | –25.04                                  | 25.04                                         | 19.46                               | Z = –13.68, p < 0.05                       |
butresses, which are common in the Sundarbans. Their previous model (Chave_2005_DW) overestimated AGB in the Sundarbans because of its inability to estimate biomass from larger trees (DBH > 42 cm) (Chave et al. 2005). However, surprisingly, the worldwide generic models for mangroves also overestimate AGB, possibly because of the samples drawn from the mangroves of Asia-Pacific and Australia (Komiyama et al. 2008).

The structure and morphological characteristics of all mangroves vary according to their ability to adapt to environmental conditions such as salinity, which is less pronounced in other wet and dry tropical areas (Ball and Pidsley 1995, Tomlinson 2016). Environmental drivers such as salinity and water deficit are considered the main stressors for the growth and development of mangroves, including the Sundarbans. For example, the third most abundant species in the Sundarbans, C. decandra, is a multi-stemmed bushy species, on the other hand, the top two, H. fomes and E. agallocha are tree-like structures. The pantropical models yielded a large error in the dwarf, bushy species and other true mangrove species in the Sundarbans (table A.5). Moreover, the extreme salinity has reduced the stature (Rahman et al. 2015), trunk diameter (Rahman et al. 2020) and the leaf area (Khan et al. 2020) of H. fomes and S. apetala, present in all three salinity zones in the Sundarbans. Due to these wider morphological variation, Banerjee et al. (2013) highlighted the importance of developing models based on salinity zonation.

This study demonstrates that when using measured wood densities and individual tree heights, generic equations yield accurate estimates of AGB in mangroves at the plot scale (figure 7). Most species had a higher published WD than the measured value seen in table 3 (Henry et al. 2010). The use of WD from different databases such as the Global WD database resulted in a 9% variation for species having multiple values, which could provide a significant variation in AGB if upscaled (Réjou-Méchain et al. 2019). Averaging WD at the plot scale, salinity zone scale or ecosystem scale also introduces errors. While WD is considered an important variable to capture a range of characteristics such as high density versus low density timber species, climax versus pioneer species or primary versus secondary species, the use of WD value from the secondary sources or averaging them in the higher scales might not reflect the true biomass (Slik et al. 2008, Kenzo et al. 2009). Phillips et al. (2019) noted significant AGB error in the Amazon rainforest while scaling up from the plot level to forest and amazon-wide level. Yuen et al. (2016) observed 31 Mg ha$^{-1}$ higher AGB with the difference of measured and published WD of only 0.13 gm cm$^{-3}$.

Among nine developed models, six models showed that DBH alone is a strong predictor of AGB across the Bangladesh Sundarbans. The remaining three models of E. agallocha, S. apetala, and Rhizophora sp. showed sensitivity to height. However, the inclusion of top height or average height instead of using individual tree height can increase the error at the plot level and above. Kearsley et al. (2013) observed 24% overestimation of AGB in the central Congo Basin by using a regional height–diameter relationship developed by Feldpausch et al. (2012) compared to the local relationship. On the other hand, using mean height could reduce the difficulty of taking height measurements in dense forests, yet may lead to a significant underestimation of AGB (Hunter et al. 2013). The difficulty of measuring height under a dense forest canopy allows researchers to use H-D relationship or to use bioclimatic variables in allometric models. However, these also lead to non-uniform bias in biomass estimation (Réjou-Méchain et al. 2019).

Although species-specific WD and individual height data can be used to accurately estimate AGB at the plot and ecosystem level, collecting species information is impractical in highly diverse mixed tropical forests such as in Amazonia, Southeast Asia and the Congo basin, which comprise of more than 53 000 tree species (Feldpausch et al. 2012, Slik et al. 2015). Mangroves, by comparison exhibit less diversity. Developing allometric models for dominant species could improve the biomass inventory. For example, in the Sundarbans only 28 species were recorded (24 in this survey) and just three species (E. agallocha, H. fomes and C. decandra) constitute about 90% of stand density (figure 5), which implies that developing three allometric models is enough to produce acceptable AGB estimates in the Sundarbans (GOB 2019). The model used for C. decandra was developed by destructive sampling from Hossain et al. (2012) and so this study recommends developing models with destructive samples from all salinity zones for H. fomes and E. agallocha.

The errors and uncertainties in the individual tree and plot level AGB estimates will result in large errors when scaling up to the ecosystem, region or country level by RS techniques. Réjou-Méchain et al. (2019) described the errors due to poor choice of allometric models and failure to capture variabilities of WD and H as uniform and non-uniform bias. Uniform bias systematically propagates over- or under-estimation whereas non-uniform bias is related to an inability to capture the variabilities across landscapes, for example, WD and H variation among successional stages or environmental gradients such as the salinity in the Sundarbans (Rahman et al. 2020). These two types of bias, in addition to mapping errors resulting from the use of RS, may result in serious anomalies in national and global carbon budgets and result in poor understanding of species contribution to ecosystem processes and function in mangroves.
5. Conclusion

This study developed and tested five species-specific and four genus-specific allometric models for the nine most important species in the Sundarbans. All developed models explained a high percentage of the variance in tree AGB ($R^2 = 0.97–0.99$) using measured DBH and total height (H) data. At the individual tree level, the generic allometric models overestimated AGB between 22% and 167% compared to the species-specific models and at the plot level, they showed statistically significant AGB differences compared to the species-specific models ($p < 0.05$). Measured WD showed 3%–10% less biomass than WD from databases and other sources and AGB was overestimated by up to 20% when using plot top height and underestimated by 8% using plot average height data rather than individual tree heights. The study concludes that biomass estimation in mangroves forests always benefit from species-specific models and individual tree measurements when appropriate input data are available. Tree level measurements from inventory plots play an important role for the improved estimation of forest biomass while scaling from individual trees up to the ecosystem level. Improved estimates of AGB will improve our understanding of the productivity of mangrove forests, information that is needed for the long-term conservation of these fragile ecosystems that face many natural and anthropogenic pressures.

Data availability statement

The primary inventory data from the Bangladesh Sundarbans are available in TRY database (www.try-db.org/TryWeb/Home.php). The used semi-destructive sampling data for the Sundarbans is publicly available in the supplementary files of Mahmood et al (2019). The data that support the findings of this study are openly available at the following URL/DOI: 10.5281/zenodo.5544398. Data will be available from 30 June 2022.

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Conflict of interest

The authors agreed that they have no conflict of interest.

Credit authorship contribution statement

Md Saidur Rahman: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing.

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References

Aabeeir R, Adu-Bredu S, Agyare W A and Weir M J C 2020 Allometric models for estimating aboveground biomass in the tropical woodlands of Ghana, West Africa For. Ecosyst. 7 41
Azad M S, Kamruzzaman M and Osawa A 2020 Quantification and understanding of above and belowground biomass in medium saline zone of the Sundarbans, Bangladesh: the relationships with forest attributes J. Sustain. For. 39 331–45
Aziz A and Paul A R 2015 Bangladesh Sundarbans: present status of the environment and biota Diversity 7 242–69
Baccini A, Walker W, Carvalho L, Farina M, Sulla-Menashe D and Houghton R A 2017 Tropical forests are a net carbon source based on aboveground measurements of gain and loss Science 358 230–4
Ball M C and Pidsley S M 1995 Growth responses to salinity in relation to distribution of two mangrove species, Sonneratia alba and S. lanceolata, in northern Australia Funct. Ecol. 9 77–85
Banerjee K, Sen Gupta K, Raha A and Mitra A 2013 Salinity based allometric equations for biomass estimation of Sundarban mangroves Biomass Bioenergy 56 382–91
Bartoli K 2020 MuMln: multi-model inference. R package version 1.43.17 (available at: https://CRAN.R-project.org/package=MuMln) (Accessed 01 March 2020)
Barua S K, Boscolo M and Animon J I 2020 Valuing forest-based ecosystem services in Bangladesh: implications for research and policies Ecosyst. Serv. 42 101069
Basuki T M, van Laake P E, Skidmore A K and Hussin Y A 2009 Allometric equations for estimating the above-ground biomass in tropical lowland Dipterocarp forests For. Ecol. Manage. 257 1684–94
BFD 2010 Integrated Resource Management Plans for the Sundarbans (2010–2020) (Dhaka: Nishorgo Network, Forest Department, Government of Bangladesh)
Brown S 1997 Estimating biomass and biomass change of tropical forests: a primer (Rome: FAO Forestry Paper 134)
Burnham K P and Anderson D R 2002 Information and Likelihood Theory: A Basis for Model Selection and Inference A practical information-theoretic approach. Model Selection and Multimodel Inference 2nd edn vol 2 K P Burnham and D R Anderson (Berlin: Springer) pp 49–97
Chanda A et al 2016 Blue carbon stock of the Bangladesh Sundarban mangroves: what could be the scenario after a century? Wetlands 36 1033–45
Chave J et al 2005 Tree allometry and improved estimation of carbon stocks and balance in tropical forests Oecologia 145 87–99
Chave J et al 2014 Improved allometric models to estimate the aboveground biomass of tropical trees Glob. Change Biol. 20 2177–90
Chave J et al 2019 Ground data are essential for biomass remote sensing missions Surv. Geophys. 40 863–80
Chave J, Coomes D, Jansen S, Lewis S L, Swenson N G and Zanne A E 2009 Towards a worldwide wood economics spectrum Ecol. Lett. 12 351–66
Chowdury M Q, de Riddler M and Beechman H 2016 Climatic signals in tree rings of Heritiera fomes Buch.-Ham. in the Sundarbans, Bangladesh PlaS One 13 e0149788
de Souza Pereira F R, Kampel M, Gomes Soares M L, Estrada G C D, Bentz C and Vincent G 2018 Reducing uncertainty in mapping of mangrove aboveground biomass using airborne discrete return lidar data Remote Sens. 10 637
Edwards D P, Scolar J B, Mills S C, Burivalova Z, Koh L P and Wilcove D S 2019 Conservation of tropical forests in the anthropocene Curr. Biol. 29 R1008–R20
Fatoyinbo T et al 2021 The NASA AfriSAR campaign: airborne SAR and lidar measurements of tropical forest structure and biomass in support of current and future space missions Remote Sens. Environ. 264 112533
Feldpausch T R et al 2011 Height-diameter allometry of tropical forest trees Biogeosciences 8 1081–106
Feldpausch T R et al 2012 Tree height integrated into pantropical forest biomass estimates Biogeosciences 9 4381–403
Fox J and Weisberg S 2019 An [R] Companion to Applied Regression (Thousand Oaks, CA: Sage)
Gibbs H K, Brown S, Niles J O and Foley J A 2007 Monitoring and estimating tropical forest carbon stocks: making REDD a reality Environ. Res. Lett. 2 045023
Giri C, Ochieng E, Tieszen L L, Zhu Z, Singh A, Loveland T, Maske J and Duke N 2011 Status and distribution of mangrove forests of the world using earth observation satellite data Glob. Ecol. Biogeogr. 20 154–9
GOB 2019 Tree and forest resources of Bangladesh: report on the Bangladesh forest inventory Forest Department, Ministry of Environment, Forest and Climate Change, Government of the People’s Republic of Bangladesh, Dhaka, Bangladesh.
Henry M et al 2021 A multi-purpose National Forest Inventory in Bangladesh: design, operationalisation and key results For. Ecosyst. 8 12
Henry M, Besnard A, Asante W A, Eshun J, Adu-Bredu S, Valentini R, Bernoux M and Saint-André L 2010 Wood density, phytomass variations within and among trees, and allometric equations in a tropical rainforest of Africa For. Ecol. Manage. 260 1375–88
Hickey S M, Callow N J, Phinn S, Loveock C E and Duarte C M 2018 Spatial complexities in aboveground carbon stocks of a semi-arid mangrove community: a remote sensing height-biomass-carbon approach Estuar. Coast. Shelf Sci. 200 194–201
Hossain M, Saha C, Rubaiot Abdullah S M, Saha S and Siddique M R H 2016a Allometric biomass, nutrient and carbon stock models for Kandelia candel of the Sundarbans, Bangladesh Treet 30 709–17
Hossain M, Shaikh M A A, Saha C, Abdullah S M R, Saha S and Siddique M R H 2016b Above-ground biomass, nutrients and carbon in Aegiceras corniculata of the Sundarbans Open J. For. 6 72–81
Hossain M, Siddique M R H, Bose A, Limon S H, Chowdhury M R K and Saha S 2012 Allometry, above-ground biomass and nutrient distribution in Ceriops decandra (Griffith) Ding Hou dominated forest types of the Sundarbans mangrove forest, Bangladesh Wetlands Ecol. Manage. 20 339–48
Hunter M O, Keller M, Victoria D and Morton D C 2013 Tree height and tropical forest biomass estimation Biogeosciences 10 8385–99
Hutchison J, Manica A, Swetnam R, Balmford A and Spalding M 2014 Predicting global patterns in mangrove forest biomass Conserv. Lett. 7 335–40
ICRAF 2016 Tree Functional attributes and Ecological Databases: Wood density (available at: http://db.worldagroforestry.org/) (Accessed 25 March 2020)
Iftekhar M and Saenger P 2008 Vegetation dynamics in the Bangladesh Sundarbans mangroves: a review of forest inventories Wetlands Ecol. Manage. 16 291–312
James G, Witten D, Hastie T and Tibshirani R 2013 An Introduction to Statistical Learning vol 112 (Berlin: Springer)
Kamruzzaman M, Ahmed S and Osawa A 2017 Biomass and net primary productivity of mangrove communities along the oligohaline zone of Sundarbans, Bangladesh For. Ecosyst. 4 16
Kamruzzaman M, Ahmed S, Paul S, Rahman M M and Osawa A 2018 Stand structure and carbon storage in the oligohaline zone of the Sundarbans mangrove forest, Bangladesh For. Sci. Technol. 14 23–28
Kassambara A 2020 Rstat: pipe-friendly framework for basic statistical tests (available at: https://cran.r-project.org/web/packages/rrstatix/) (Accessed 25 March 2020)
Kearsley E et al 2013 Conventional tree height–diameter relationships significantly overestimate aboveground carbon stocks in the Central Congo Basin Nat. Commun. 4 2269
Kenzo T et al 2009 Development of allometric relationships for accurate estimation of above- and below-ground biomass in tropical secondary forests in Sarawak, Malaysia J. Trop. Ecol. 25 371–80
Khan M N I, Khattam S, Azad M S and Mollick A S 2020 Leaf morphology and anatomical plasticity in Sundri (Heritiera fomes Buch.-Ham.) along different canopy light and salinity zones in the Sundarbans mangrove forest, Bangladesh Glob. Ecol. Conserv. 23 e01127
Komiyama A, Ong J E and Pougprarn S 2008 Allometry, biomass, and productivity of mangrove forests: a review Aquat. Bot. 89 169–180
Komiyama A, Pougprarn S and Kato S 2005 Common allometric equations for estimating the tree weight of mangroves J. Trop. Ecol. 21 471–7
Kuhn M 2008 Building predictive models in R using the caret package J. Stat. Softw. 28 1–26
Lagomasino D, Fatoyinbo T, Lee S, Feliciano E, Trettin C, Shapiro A and Mangora M M 2019 Measuring mangrove carbon loss and gain in deltas Environ. Res. Lett. 14 R10202
Larjavaara M and Muller-Landau H C 2013 Measuring tree height: a quantitative comparison of two common field methods in a moist tropical forest Methods Ecol. Evol. 4 793–801
Lüdecke D 2018 ggeffects: tidy data frames of marginal effects from regression models (available at: http://db.worldagroforestry.org/) (Accessed 25 March 2020)
Matieu H, Iqbal M Z and Akhter M 2020 Semi-destructive felling of the Sundarbans Mangroves: a review Estuar. Coast. Shelf Sci. 234 28–38
M Rahman et al 2018 Spatial complexities in aboveground carbon stocks of a tropical forest: implications for climate change and future carbon cycle Estuar. Coast. Shelf Sci. 201 15–24
M Rahman et al et al 2020 Leaf allometry and improved estimation of carbon stocks and balance in tropical forests Oecologia 145 87–99
McMullan R et al 2011a A multi-purpose National Forest Inventory in Bangladesh: design, operationalisation and key results For. Ecosyst. 8 12
Mehdi M, Besnard A, Asante W A, Eshun J, Adu-Bredu S, Valentini R, Bernoux M and Saint-André L 2010 Wood density, phytomass variations within and among trees, and allometric equations in a tropical rainforest of Africa For. Ecol. Manage. 260 1375–88
Mehdi M, Besnard A, Asante W A, Eshun J, Adu-Bredu S, Valentini R, Bernoux M and Saint-André L 2010 Wood density, phytomass variations within and among trees, and allometric equations in a tropical rainforest of Africa For. Ecol. Manage. 260 1375–88
M Rahman et al 2018 Spatial complexities in aboveground carbon stocks of a tropical forest: implications for climate change and future carbon cycle Estuar. Coast. Shelf Sci. 201 15–24
Mahmood H, Siddique M R H, Abdullah S M R, Islam S M Z, Matieu H, Ishqal M Z and Akhter M 2020 Semi-destructive
method to derive allometric aboveground biomass model for village forest of Bangladesh: comparison of regional and pantropical models. *J. Trop. For. Sci.* 32 246–56

Mahmood H, Siddique M R H, Rubaiota Abdullah S M, Costello L, Matieu H, Iqbal M Z and Akhter M 2019 Which option best estimates the above-ground biomass of mangroves of Bangladesh: pantropical or site- and species-specific models? *Wetlands Ecol. Manage.* 27 553–69

Martínez-Sánchez J L, Martínez-Garza C, Cámara L and Castillo O 2020 Species-specific or generic allometric equations: which option is better when estimating the biomass of Mexican tropical humid forests? *Carbon Manage.* 11 241–9

McGill R, Tukey J W and Larsen W A 1978 Variations of box plots *Am. Stat.* 32 12–16

Mitchard E T, Saatchi S, Baccini A, Asner G P, Goetz S J, McGill R, Tukey J W and Larsen W A 1978 Variations of box plots

Rahman M M, Khan M N I, Hoque A K F and Ahmed I 2015

R Core Team 2020

Picard N, Saint-André L and Henry M 2012

Njana M A, Meilby H, Eid T, Zahabu E and Malimbwi R E 2016

Mitchard E T, Saatchi S S, Baccini A, Asner G P, Goetz S J, McGill R, Tukey J W and Larsen W A 1978 Variations of box plots

Rahman M S, Sass-Klaassen U, Zuidema P A, Chowdhury M Q, Harris N J and Brown S 2013 Uncertainty in the spatial distribution of tropical forest biomass: a comparison of pantropical maps *Carbon Balance Manage.* 8 10

Mokria M, Melkuria W, Gebekirstos A, Aynekulu E, Belay B, Gashaw T and Bräuning A 2018 Mixed-species allometric equations and estimation of aboveground biomass and carbon stocks in restored degraded landscape in northern Ethiopia *Environ. Res. Lett.* 13 024022

Ngomanda A et al 2014 Site-specific versus pantropical allometric equations: which option to elaborate the biomass of a moist central African forest? *For. Ecol. Manage.* 312 1–9

Ni-Meister W 2015 Aboveground terrestrial biomass and carbon stock estimations from multisensor remote sensing *Land Resources Monitoring, Modeling, and Mapping with Remote Sensing II* ed P S Thenkabail (Boca Raton, FL: CRC Press) pp 47–67

Njana M A, Mbillhy H, Eit D, Zahabu E and Malimbwi R E 2016 Importance of tree basic density in biomass estimation and associated uncertainties: a case of three mangrove species in Tanzania *Ann. For. Sci.* 73 1073–87

Petrockofsky G, Kanamaru H, Achar D, Goetz S J, Joosten H, Holmgren P, Leptonen A, Menton M C S, Pullin A S and Wattenbach M 2012 Comparison of methods for measuring and assessing carbon stocks and carbon stock changes in terrestrial carbon pools. How do the accuracy and precision of current methods compare? A systematic review protocol *Environ. Evidence* 1 6

Phillips O L, Sullivan M J P, Baker T R, Monteagudo Mendoza A, Vargas P N and Vásquez R 2019 Species matter: wood density influences tropical forest biomass at multiple scales *Surv. Geophys.* 40 913–35

Picard N, Saint-André L and Henry M 2012 *Manual for Building Tree Volume and Biomass Allometric Equations: From Field Measurement to Prediction Food and Agricultural Organization of the United Nations, Rome, and Centre de Coopération Internationale en Recherche Agronomique pour le Développement, Montpellier*

R Core Team 2020 *R: A Language and Environment for Statistical Computing* (Vienna: R Foundation for Statistical Computing)

Rahman M M, Khan M N I, Hoque A K F and Ahmed I 2015

Carbon stock in the Sundarbans mangrove forest: spatial variations in vegetation types and salinity zones *Wetlands Ecol. Manage.* 23 269–83

Rahman M S, Donoghue D N M and Bracken L J 2021 Is soil organic carbon underestimated in the largest mangrove forest ecosystems? Evidence from the Bangladesh Sundarbans *CATENA* 200 105159

Rahman M S, Sass-Klaassen U, Zuidema P A, Chowdhury M Q and Beekman H 2020 Salinity drives growth dynamics of the mangrove tree *Sonneratia apetala* Buch.-Ham. in the Sundarbans, *Bangladesh Dendrochronology* 62 125711

Rouix-Méchain M et al 2019 Upscaling forest biomass from field to satellite measurements: sources of errors and ways to reduce them *Surv. Geophys.* 40 881–911

Rovai A et al 2016 Scaling mangrove aboveground biomass from site-level to continental-scale *Glob. Ecol. Biogeogr.* 25 286–98

Rutishauser E, Noor-an F, Laumonier Y, Halperin J, Ruftie, Herguoa-l’C K and Verchot L 2013 Generic allometric models including height best estimate forest biomass and carbon stocks in Indonesia *For. Ecol. Manage.* 307 219–25

Sarker S K, Matthiopoulos J, Mitchell S N, Ahmed Z U, Mamun M B A and Reeve R 2019a 1980s–2010s: the world’s largest mangrove ecosystem is becoming homogeneous *Biol. Conserv.* 236 79–91

Sarker S K, Reeve R, Paul N K and Matthiopoulos J 2019b Modelling spatial biodiversity in the world’s largest mangrove ecosystem—the Bangladesh Sundarbans: a baseline for conservation *Divers. Distrib.* 25 729–42

Sarker S K, Reeve R, Thompson J, Paul N K and Matthiopoulos J 2016 Are we failing to protect threatened mangroves in the Sundarbans world heritage ecosystem? *Sci. Rep.* 6 21234

Sattar M A, Bhattacharjee D K and Sarker S B 1995 Physical, mechanical and seasoning properties of 45 lesser used or unused forest timbers of Bangladesh and their uses *Bangladesh J. For.* 24 11–21

Siddiqui N A 2001 *Mangrove Forestry in Bangladesh* (Chittagong: Institute of Forestry & Environmental Sciences, University of Chittagong)

Siddique M R H, Mahmood H and Chowdhury M R K 2012 Allometric relationships for estimating above-ground biomass of *Aegialitis rotundifolia* Roxb. of Sundarbans mangrove forest, in Bangladesh *J. For. Res.* 23 23–28

Silesi G W 2014 A critical review of forest biomass estimation models, common mistakes and corrective measures *For. Ecol. Manage.* 329 237–54

Silk J W F et al 2015 An estimate of the number of tropical tree species *Proc. Natl Acad. Sci.* 112 7472–7

Silk J W F, Bernard C S, Breman F C, van Beek M, Salim A and Sheil D 2008 Wood density as a conservation tool: quantification of disturbance and identification of conservation-priority areas in tropical forests *Conserv. Biol.* 22 1299–308

Sprugel D 1983 Correcting for bias in log-transformed allometric equations *Ecology* 64 209–10

Stas M S, Rutishauser E, Chave J, Anten N P R and Laumonier Y 2017 Estimating the aboveground biomass in an old secondary forest on limestone in the Moluccas, Indonesia: comparing locally developed versus existing allometric models *For. Ecol. Manage.* 389 27–34

Tomlinson P B 2016 *The Botany of Mangroves* (Cambridge: Cambridge University Press)

van Breugel M, Ransijn J, Craven D, Bongers F and Hall J S 2011 Estimating carbon stock in secondary forests: decisions and uncertainties associated with allometric biomass models *For. Ecol. Manage.* 262 1648–57

Vieilledent G, Vaudry R, Andriamanohisoa S F D, Rakotonarivo O S, Randrianasolo H Z, Razafindrabe H N, Rakotoarivo C B, Ebeling J and Rasamoelina M 2012 Comparing locally developed versus existing allometric equations *Ecol. Appl.* 22 572–84

Virkulino-Höriger P C C, Carneiro D N, Nascimento W R Jr., Cougo M F and Fernandes M E B 2020 Biomass and carbon estimation for scrub mangrove forests and examination of their allometric associated uncertainties *PLoS One* 15 e0230008

Vorster A G, Evangelista P H, Stovall A E L and Ex S 2020 Variability and uncertainty in forest biomass estimates from the tree to landscape scale: the role of allometric equations *Carbon Balance and Management* 15 8

Weinkittel A, MacFarlane D W, Radtke P J, Affleck D L R, Temesgen H, Woodall C W, Westfall J A and Coulston J W 2015 A call to improve methods for estimating tree biomass for regional and national assessments *J. For.* 113 414–24

Wickham H 2016 *Ggplot2: Elegant Graphics for Data Analysis* (Berlin: Springer)
Wiemann M C and Williamson G B 2013 Biomass determination using wood specific gravity from increment cores General Technical Report, FPL-GTR-225 Forest Products Laboratory, USDA Forest Service vol 9 p 225
Wilke C O, Wickham H and Wilke M C O 2019 Streamlined Plot Theme and Plot Annotations for ‘ggplot2’ (available at: https://wilkelab.org/cowplot/index.html) (Accessed 01 March 2020)
Xiao X, White E P, Hooten M B and Durham S L 2011 On the use of log-transformation vs. nonlinear regression for analyzing biological power laws Ecology 92 1887–94
Yuen J Q, Fung T and Ziegler A D 2016 Review of allometric equations for major land covers in SE Asia: uncertainty and implications for above- and below-ground carbon estimates For. Ecol. Manage. 360 323–40
Zanne A E, Lopez-Gonzalez G, Coomes D A, Ilic J, Jansen S, Lewis S L, Miller R B, Swenson N G, Wiemann M C and Chave J 2009 Data from: towards a worldwide wood economics spectrum, Dryad, dataset (https://doi.org/10.5061/dryad.234)
Zeileis A and Hothorn T 2002 Diagnostic checking in regression relationships R News 2 7–10