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# Predicting biomass of hyperdiverse and structurally complex Central Amazon forests – a virtual approach using extensive field data

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Abstract

Old-growth forests are subject to substantial changes in structure and species composition due to the intensification of human activities, gradual climate change and extreme weather events. Trees store ca. 90 % of the total AGB above-ground biomass in tropical forests and AGB estimation models are crucial for forest management and conservation. In the Central Amazon, predicting AGB at large spatial-scales is a challenging task due to the heterogeneity of successional stages, high tree species diversity and inherent variations in allometry and architecture. We parameterized generic AGB estimation models applicable across species and a wide range of structural and compositional variation related to species sorting into height layers as well as frequent natural disturbances. We used 727 trees from 101 genera and at least 135 species harvested in a contiguous forest near Manaus, Brazil. Sampling from this dataset we assembled six scenarios designed to span existing gradients in floristic composition and size distribution in order to select models that best predict AGB at the landscape-level across successional gradients. We found that good individual tree model fits do not necessarily translate into good predictions of AGB at the landscape level. When predicting AGB (dry mass) over scenarios using our different models and an available pantropical model, we observed systematic biases ranging from -31 % (pantropical) to +39 %, with RMSE root-mean-square error values of up to 130 Mg ha<sup>-1</sup> (pantropical). Our first and second best models had both low mean biases (0.8 and 3.9 %, respectively) and RMSE (9.4 and 18.6 Mg ha<sup>-1</sup>) when applied over scenarios. Predicting biomass correctly at the landscape-level in complex tropical forests, especially allowing good performance at the margins of data availability for model parametrization, requires the inclusion of predictors related to species architecture. The model of interest should comprise the floristic composition and size-distribution variability of the target forest, implying that even generic global or pantropical biomass estimation models can lead to strong biases. Reliable biomass assessments for the Amazon basin still depend on the collection of destructive allometry data at the local/regional scale and forest inven-

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tories including species-specific attributes, which are often unavailable or estimated imprecisely in most regions.

## 1 Introduction

Allometries describe how relationships between different dimensions (e.g. length, surface area and weight) of organisms change non-proportionally as they grow (Huxley and Teissier, 1936). The lack of proportionality arises from the fact that organisms change their shape while they grow (i.e. the dimensions differ in their relative growth rates). As one important application, allometric relationships can be used to relate simple dimensions of trees (e.g. DBH diameter at breast height or  $H$  tree height) to dimensions more relevant for forest managers and basic ecological research, such as wood volume or whole tree biomass (Brown et al., 1989; Higuchi et al., 1998; Saldarriaga et al., 1998).

Allometric relationships and biomass estimation models can differ substantially between different tree species, especially in species-rich regions with a high variation in tree sizes and architectures such as in the tropical rainforests (Banin et al., 2012; Nelson et al., 1999; Poorter et al., 2003). This variation reflects differences in growth strategy and life history, such as tree species occupying different strata when mature (e.g. understory, canopy, or emergent species), successional niches (e.g. pioneer or light demanding species, e.g. *Cecropia* spp. and *Pourouma* spp., in contrast to late-successional or shade tolerant, e.g. *Cariniana* spp. and *Dipteryx* spp.) or environmental microsites, e.g. gap and non-gap (Clark and Clark, 1992; King, 1996; Swaine and Whitmore, 1988).

Important and highly variable architectural attributes of tropical tree species include stem shape (e.g. slender to stout form), branch form and branching intensity (e.g. plagiotropic, orthotropic and unbranched), crown contour (e.g. round, elongated and irregular), crown position (e.g. understory, canopy and emergent), maximum DBH and Height (Hallé, 1974; Hallé et al., 1978). In addition, there is large variation in growth

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rate (the speed at which a certain space is filled) (Silva et al., 2002) and consequently in wood anatomy among species. WD wood density, which is particularly important for biomass estimation, varies significantly across regions (Muller-Landau, 2004) and can differ between species by more than one order of magnitude (Chave et al., 2006). Given these sources of variation, it is not surprising that different allometries were reported when comparing species (Nelson et al., 1999), successional stages (Ribeiro et al., 2014), ontogenies (Sterck and Bongers, 1998), and regions (Lima et al., 2012). Unfortunately, transferring such species-, size-, ontogeny- and site-specific biomass estimation models to other contexts – other species, other size ranges, other life-stages, other sites or successional stages – typically leads to strongly biased predictions, especially when predictor ranges are limited or neglected (Clark and Kellner, 2012; Sileshi, 2014).

In temperate and boreal forests, the size-, ontogeny-, site-variation has been captured by the development of generic species-specific biomass estimation models (Wirth et al., 2004; Wutzler et al., 2008) based on data from hundreds of individuals from a single species. However, this approach is prohibitive in the tropics where thousands of tree species coexist (Slik et al., 2015; ter Steege et al., 2013). Instead, the challenge is to develop generic local or regional multivariate formulations that generalize also across species (Higuchi et al., 1998; Lima et al., 2012; Nelson et al., 1999; Saldarriaga et al., 1998). Ideally, they contain predictor variables that (1) jointly capture a large fraction of the variation induced by the underlying morphological and anatomical gradients and are (2) still easy enough to obtain or measure.

The development and application of such multivariate generic models valid across species, tree sizes and sites poses a number of challenges. Finding the appropriate model structure and estimating the model coefficients requires a design matrix with a large number of individual measurements containing the variable of interest (here AGB above-ground biomass) and the predictor variables (i.e. DBH,  $H$ , SG species' successional group (ranging from pioneer to late-successional species) and WD). Importantly, the design matrix should ideally cover all possible real-world combinations of predictor values in order to avoid error-prone extrapolations and biased predictions.

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adult survivors, and thereby including different successional groups (pioneers, mid- and late-successional species), tree sizes and with a broader range of architectures than old-growth forests (Chambers et al., 2009a; Marra et al., 2014). Once floristic composition changes and structural gradients increase to this extent, allometry becomes more complex and reliable landscape-level biomass estimates rely on well designed and well tested generic biomass models.

We report here a new allometric dataset of 727 trees harvested in a contiguous terra firme forest near Manaus, Brazil. This dataset includes biomass measurements from 101 genera and at least 135 tree species that vary in architecture and are from different successional groups. These trees span a wide range of DBH (from 5 to 85 cm),  $H$  (from 3.9 to 34.5 m) and WD (from 0.348 to 1.000 g cm<sup>-3</sup>). This data matrix was used to develop generic AGB estimation models for Central Amazon forests applicable across species and a wide range of structural and compositional variation, using various subsets of the available predictors; i.e. size (DBH and  $H$ ), SG and WD.

We next evaluated our models, as well as the current pantropical model from Chave et al. (2014) at the landscape-level using a virtual approach. We created scenarios of simulated 100 ha forest plots by assembling subsets of the 727 known-biomass trees in our data matrix. These scenarios were designed to span gradients in (1) floristic composition by assembling stands with specific proportions of pioneer, mid- and late-successional species, and (2) size distributions. We compared the known biomass of these forest assemblage scenarios to predictions based on the generic models, with the goal of answering the following questions: (1) Which variance modeling approach and combinations of predictors produced the best individual tree AGB estimation model? (2) Which model most reliably predicted AGB at landscape-level, i.e. across successional gradients? We expected that the best model, the one reducing both bias and error of single and landscape-level biomass prediction, would require species-specific variables as well as an additional parameter allowing the modeling of heteroscedastic variance. Our approach and the independence of our dataset allowed us to evaluate whether is still important to build local/regional models or whether avail-

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able pantropical/global models suitable for landscape biomass assessments – under the assumption that they predict biomass satisfactory over all sorts of tropical forest types and successional stages.

## 2 Material and methods

## 2.1 Study site

Our study site is located at the Estação Experimental de Silvicultura Tropical (EEST), a 21.000 ha research reserve (Fig. 1) managed by the Laboratório de Manejo Florestal (LMF) of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil (2°56' S, 60°26' W). Mean annual temperature in this region is about 26 °C and rainfall averages to 2600 mm year<sup>-1</sup> (Sombroek, 2001) with annual peaks of up to 3450 mm (Silva et al., 2002). From July to September there is a distinct dry season with usually less than 100 mm of rain per month. Topography is undulating with relative altitude between valleys and plateaus varying from 50 to 100 m (Braga, 1979). Soils on upland plateaus and the upper portions of slopes have high clay content (Oxisols), while soils on slope bottoms and valleys have high sand content (Spodosols) and are subject to seasonal flooding (Telles et al., 2003).

The EEST is mainly covered by a contiguous closed canopy old-growth terra firme forest with high tree species diversity and dense understory (Braga, 1979; Ribeiro et al., 1999). The terra firme forests are the predominant forest type in the Brazilian Amazon (Braga, 1979; Higuchi et al., 2004) and ca. 93 % of the total plant biomass is stored in trees with DBH  $\geq 5$  cm (Lima et al., 2012; Silva, 2007). The tree density (DBH  $\geq 10$  cm) in the EEST is  $593 \pm 28$  trees  $\text{ha}^{-1}$  (mean  $\pm 99$  % confidence interval) (Marra et al., 2014). Trees larger than 100 cm in DBH are rare ( $< 1$  individual  $\text{ha}^{-1}$ ) and those with DBH  $> 60$  cm accounted for only 16.7 % of the AGB (Vieira et al., 2004).

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## 2.2 Allometric data

We used data from 727 trees harvested in this region, each with measured biomass and predictor variables. This dataset comprised 101 genera and at least 135 species with DBH  $\geq 5.0$  cm (Table 1; all data are given in Table S1 in the Supplement). The trees were harvested through the plot-based harvest method in an old-growth forest and in two secondary forests (14 year-old regrowth following slash and burn and 23 year-old regrowth following a clear cut) (Fig. 1). Rather than an individual selection, our plot-based method relies on the harvesting of all trees found in selected plots. This method allows for a valid/faithful representation of the DBH-distribution of our target forests (Higuchi et al., 1998). In the old-growth forest the trees were harvested in eight plateau and three valley plots (10 m  $\times$  10 m) randomly selected within an area of 3.6 ha (Silva, 2007). In each of the secondary forests the trees were harvest in five plots (20 m  $\times$  20 m) randomly selected within a 1 ha plateau area (Santos, 1996; Silva, 2007). By including data from the two secondary forests, we were able to increase the variation in floristic composition and consequently the range of species-related variation in architecture and allometry (Tables 1 and S1).

Trees were harvested at ground level. For each tree, the DBH (cm),  $H$  (m) and fresh mass (kg) were recorded in the field by using a diameter tape, a meter tape and a mechanical metal scale (300 kg  $\times$  200 g), respectively. The DBH was measured before, while  $H$  was measured after harvesting. For trees with buttresses or irregular trunk shape, the diameter was measured above these parts. Each tree component (stem, branches and leaves) was weighted separately. For large trees, stems were cut into smaller sections. The mass of sawdust was collected and weighted together with its respective stem section. Leaves and reproductive material, when available, were collected to allow species identification accordingly to the Angiosperm Phylogeny Group (APG III) classification (Stevens, 2012). Botanical samples were incorporated in the EEST collection. The water content for each tree was determined from three discs (2–5 cm in thickness) collected from the top, middle and bottle of the bole, and samples

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(~ 2 kg) of small branches and leaves. The samples were oven-dried at 65°C to constant dry mass. The dry mass data was calculated by using the corresponding water content of each component (Lima et al., 2012; Silva, 2007). Dry mass for each tree was used for subsequent model fits and comparisons.

## 2.3 Species' architecture attributes

Each of our tree species or genera were assigned to one of three successional groups known to vary in their architecture, namely pioneer, mid- and late-successional. To make this assignment, we considered several attributes related to species' architecture (i.e. shape and life history), growth position (i.e. stratum), morphology, wood density and ecology (Tables S1 and S2). We validated this approach by checking our assignments against those of classic studies (Clark and Clark, 1992; Denslow, 1980; Saldarriaga et al., 1998; Shugart and West, 1980; Swaine and Whitmore, 1988), local/regional studies conducted in the Amazon (Amaral et al., 2009; Chambers et al., 2009a; Kammesheidt, 2000; Marra et al., 2014) and species description available in the Missouri Botanical Garden (<http://www.tropicos.org>), speciesLink (<http://www.splink.cria.org.br>) and Lista de Espécies da Flora do Brasil (<http://www.floradobrasil.jbrj.gov.br/>). More importantly, we considered empirical field observations, architectural information from our allometric dataset, and data for species presence/absence from a network of permanent plots representing a wide range of successional stages in Central Amazon. This network includes plots in old-growth (LMF unpublished data – census from 1996 to 2012; Silva et al., 2002), secondary forests (Carvalho Jr et al., 1995; Santos, 1996), small and large canopy gaps ( $\geq c. 2000 \text{ m}^2$ ) created by windthrows with 4, 7, 14, 17, 24 and 27 year-old (LMF unpublished data; Marra et al., 2014).

Since WD values vary strongly among studies (Chave et al., 2006) and sites (Muller-Landau, 2004), we compiled WD values mainly from studies carried out in the Brazilian Amazon (Chave et al., 2009; Fearnside, 1997; Laurance et al., 2006; Nogueira et al., 2005, 2007). For species where WD data were not available for the Brazilian Amazon, we considered studies from other Amazonian regions (Chave et al., 2009). For species

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where no published WD was available, or where the identification was carried out to the genus level (64 in total), we used the mean value for all species from the same genus occurring in Central Amazon. For trees identified only to the family level (7 in total), we used the mean value of genera from that family excluding those not reported in the Central Amazon (Table S1).

## 2.4 Statistical analyses

### 2.4.1 Individual tree biomass estimation model fits

The AGB estimation models we applied varied in the number and combination of our predictor variables (eight combinations/series) as well as the strategy of modeling the variance (three model types – see below), yielding a set of 24 candidate models (Table 2). We used four predictors: DBH diameter at breast height (cm), SG species' successional group (categorical predictor: 1 = pioneer, 2 = mid- and 3 = late-successional species), WD wood density ( $\text{g cm}^{-3}$ ) and  $H$  tree height. We tested variables for collinearity by calculating the VIF variance inflation factor. A conservative VIF > 2.0 indicates significant collinearity among variables (Graham, 2003; Petraitis et al., 1996). Model series 1–4 had VIF < 1.5 (Table 2), which indicated no significant collinearity among predictors. For model series 5–8, we found VIF > 2.0 for DBH and  $H$ , which indicates significant collinearity between these two variable. This pattern was previously reported for other allometric datasets from Amazon and other tropical regions (Lima et al., 2012; Ribeiro et al., 2014; Sileshi, 2014).

We fit models representing the eight different predictor combinations to our entire dataset of 727 trees using three variance modeling approaches: non-linear least square (NLS), ordinary least square with log-linear regression (OLS) and a non-linear approach in which we modeled the heteroscedastic variance of the dataset (MOV). The MOV approach models variance as a function of DBH with a normally distributed

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We fit the AGB estimation models with non-informative uniform priors using WinBUGS 1.4.1 (Lunn et al., 2000; Spiegelhalter et al., 2002). For each model, three chains were run in parallel, and convergence of the posterior distribution for each parameter was assessed by convergence to one of the ratio of pooled to mean within-chain central 80 % intervals or by the stability of both intervals (Brooks and Gelman, 1998; Brooks and Roberts, 1998).

To select the best model we calculated the DIC Deviance Information Criterion. The DIC is a generalization of *AIC* Akaike's Information Criterion and consists of a cross-validatory term that expresses both the goodness of the fit and the models' complexity. The lower the value the better the predictive ability and parsimony (Spiegelhalter et al., 2002). We also checked whether the 95 % credible intervals of the coefficient's posterior distributions excluded zero. However, we did not attempt to test the null hypothesis that a particular parameter is zero (Bolker et al., 2013; Bolker, 2008). Contrasts were evaluated by monitoring differences between parameters or predictions based on their posterior distribution. For communicating the results we consider two parameters significantly different if the 95 % credible interval of the posterior distribution of their difference does not include zero.

To support the selection of the best model, and to allow for comparisons with the available literature, we calculated the  $R^2_{\text{adj}}$  adjusted coefficient of determination and the Syx% relative standard error as a percentage. The Syx% was calculated as follows:

$$\text{Syx}\% = \left( \frac{2s}{\hat{y}\sqrt{N}} \right), \quad (3)$$

where  $s$ ,  $\hat{y}$  and  $N$  are the standard deviation of the regression, the mean of the focal independent variable and the number of observations, respectively. For the OLS approach including log-transformed variables, we calculated the Syx% using untransformed data. To correct for the bias introduced by the log-transformed data, a CF cor-



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To address variations in size-distribution, we varied the proportion of small and big trees fixing a threshold value of 21 cm, which represents the mean DBH (trees with DBH  $\geq 10$  cm) of our studied forest (Marra et al., 2014). Our size-distribution scenarios included: a small-sized stand, 90 % from small (DBH  $< 21$  cm) and 10 % from big trees (DBH  $\geq 21$  cm); a mid-sized stand with equal numbers of small and big trees; and a large-sized stand, with 10 % small and 90 % big trees (Fig. 2b and d). As for our floristic composition scenarios, in order to produce reliable size-distribution scenarios, we constrained our sampling effort to a basal area value of  $30.3 \text{ m}^2 \text{ ha}^{-1}$  also typical for our studied old growth forest (trees with DBH  $\geq 5$  cm) (Marra et al., 2014; Suwa et al., 2012). Both our floristic and size-distribution scenarios produced the J-inverse distribution pattern, typical of tropical forests (Clark and Clark, 1992; Denslow, 1980).

AGB at the landscape-level was determined by adding up the measured AGB for “sampled” trees in each scenario. To test how well our biomass estimation models predicted the AGB at the stand level, we related biases and RMSE root-mean-square error. Because data on tree height is normally unavailable or estimated imprecisely in Amazon forest inventories, we focused on models including only DBH, WD and SG as predictors. In addition to the “internal evaluation” of our models, we tested the pantropical model from Chave et al. (2014):

$$\log \text{AGB} \sim -1.803 - 0.976E + 0.976[\log \text{WD}] + 2.673[\log \text{DBH}] - 0.0299[\log \text{DBH}]^2, \quad (5)$$

which was parameterized with data from 4004 trees (DBH  $\geq 5$  cm) harvested in 53 old-growth and five secondary forests. This model has DBH,  $H$  (estimated from a DBH :  $H$  relationship), WD and a variable  $E$  (environmental stress) as predictors, and was suggested for estimating tree AGB in the absence of height measurements.

All tests were performed using the R 3.2.1 software platform (R Core Team, 2014). All codes used in this study were written by ourselves. Figures were produced using the ggplot2 package (Wickham, 2009).



3 Results

3.1 Individual tree biomass estimation model fits

The models M33 (DBH and WD as predictors) and M43 (DBH, SG and WD) were the two best fitting models across all tree individuals (high  $R^2_{adj}$  and both low Syx% and DIC values). These two models were also better in our landscape predictions (see Sect. 3.2). The statistics for the goodness of fit for the 24 models are given in Table 3. Although the NLS approach produced models with overall higher values of  $R^2_{adj}$  and lower values of Syx%, the DIC values indicated that the OLS and the MOV approaches produced the best models. For the models fit with OLS, which rely on log-transformed variables, the addition of other predictors together with DBH systematically decreased the CF values. This pattern suggests a reduction in the biases resulting from back-transformation.

As expected, the addition of other predictors to a model containing only DBH systematically increased the models' parsimony, as indicated by the lower DIC values (Table 3). The inclusion of the SG resulted in models with slightly lower  $R^2_{adj}$  and higher Syx% compared to the same model structure without SG.

We observed differences with respect to the coefficients  $b$  and  $c$  among pioneer, mid- and late-successional species in most of the models that included the SG assignment (Table S3 and Fig. S1). The late-successional species tended to have higher intercepts and steeper slopes. Pioneer and mid-successional species had lower differences in intercepts but still strong differences in the slope coefficients.

An evaluation of AGB predictions for individual trees from our two best models (as described in the Sect. 3.2), as well from the tested pantropical model (Chave et al., 2014) are presented in the Supplement of this study (Fig. S1). Our two best models had lower biases (overestimation of 0.6 and 3.5 %) than the tested pantropical model (underestimation of 30 %).

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### 3.2 Landscape-level biomass predictions across scenarios

To search for the model that best predicts AGB at the landscape-level, we tested our models (excluding those with  $H$  as a predictor, Table 2) across the 100 1 ha plots assembled for each of our six forest-scenarios (Figs. 3–5) as well as jointly for all of them (Fig. 6).

The “true” AGB (from the summed mass of trees used to assemble the forest scenarios) varied from 198.1 to 314.3 (early- to late-succession scenarios) and 101.4 to 391.8 Mg ha<sup>-1</sup> (small- to large-sized scenarios). The ability of the various biomass estimation models to predict the “true” virtual biomass values generally reflected the goodness of fit of the models for predicting individual tree data (Table 3 and Figs. 3–6). The same pattern was observed when evaluating the pantropical model from Chave et al. (2014), which underestimated both the AGB of individual trees (Fig. S1) and in all of our scenarios (Table S4 and Fig. S2).

While some models produced accurate and satisfactory predictions across all scenarios, others systematically under- or overestimated the observed AGB in our 1 ha plots (Fig. 3 and Fig. S2). The agreement between models and observations was not only influenced by the different combinations of predictors, but the different methods to model the variance. Interestingly, despite producing the best fits to the individual tree data, models fit with NLS produced the least reliable landscape-level predictions, with model M11 (only DBH as predictor) being the unique exception for the mid- and late-succession scenarios (Fig. 3).

We observed systematic biases ranging from -14% (underestimation) to 38.8% (overestimation) in estimated landscape-level AGB (Fig. 4). The models fit with NLS tended to overestimate landscape-level AGB, with biases ranging from -3.6 up to 38.8%, both extreme values from model series 1 (only DBH as predictor). Overall, the models fit with NLS tended to deal slightly better with changes in floristic composition compared to tree size-distribution. The tested pantropical model systematically

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underestimated landscape-level biomass, with a mean bias of  $-29.7\%$  (Table S4 and Fig. S2).

The models fit with the OLS and particularly with the MOV approaches were clearly better at capturing the variation in floristic composition and size-distribution of trees.

5 Consequently, these models produced the most reliable landscape-level predictions within the scenarios (Fig. 3). As also indicated by the individual tree model fits, the MOV approach produced more reliable predictions, especially with model series 2 and 4.

10 In general, the models fit with the OLS and MOV approaches did not show systematic trends in under- or overestimation. The models fit with the OLS approach had biases ranging from  $-13.8$  to  $11.1$  %, with extreme values from model series 1 and 2, respectively. The models fit with the MOV approach had biases ranging from  $-14$  to  $10.5$  %, also with extreme values from model series 1 and 2, respectively (Fig. 4).

The reported systematic biases led to strong differences between the predicted and the observed AGB (Fig. 5). The models fit with NLS resulted in RMSE values ranging from 16.8 up to 125.8 Mg ha<sup>-1</sup>. For the models fit with OLS, the RMSE values ranged from 5.1 to 57.6 Mg ha<sup>-1</sup>. The MOV models had RMSE ranging from 5.5 to 58.7 Mg ha<sup>-1</sup>. The pantropical model's predictions had a mean RMSE of 102.6 Mg ha<sup>-1</sup> (Table S4).

By combining the bias and RMSE values, we could observe the overall models' performance in predicting AGB across scenarios (Fig. 6). When challenged to predict biomass across all scenarios, the models fit with the MOV approach produced more reliable predictions (smaller range of biases and RMSE), except for model series 1 (only DBH as a predictor), for which the OLS approach performed better. Independently of applied predictors, the NLS approach had the highest mean and range of values for bias and RMSE.

As we expected, the addition of SG and WD improved the quality of the joint prediction. This was evidenced by the systematic reduction of models' bias and RMSE. Notably for the NLS approach, the inclusion of SG led to strong reduction of the bias

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and RMSE (Fig. 6). Interestingly, for this approach the addition of WD alone did not improve the estimations accuracy.

## 4 Discussion

### 4.1 Individual tree biomass estimation model fits

The best-performing allometry model structures for predicting the biomass of individual trees included species-specific predictors and either the OLS or MOV fitting approaches (Figs. 3 and 6 and Table S3). As we hypothesized, including both the SG and WD as predictors greatly increased the models' performance. When taken alone, adding either of these two predictors to the basic DBH model yielded a better model than adding  $H$  (Table S3). This pattern was true for all the three variance modeling approaches and supports that having the species' identification (i.e. further assignment into successional groups) and/or coherent wood density values, is crucial when aiming for precise tree AGB predictions. Since old-growth forests comprise a mosaic of different successional stages, with trees of various architectures and sorted into different forest layers/strata, these variables are of great importance when aiming for reliable AGB predictions at the landscape-level (see Sect. 4.2).

Although the NLS approach fits our dataset better (higher  $R^2_{adj}$  and lower  $Syx\%$ ), the assumption of a constant-variance violates the natural heteroscedasticity of allometric datasets. With the log-transformation of the OLS approach, homoscedasticity is reached but in a way that does not exactly reflect how variance actually changes. As previously reported for terra firme forests in Amazon (Chambers et al., 2001; Lima et al., 2012), models fit with the OLS approach tend to overestimate the biomass of large-sized trees.

Indeed, the best models are obtained using the OLS and MOV approaches, in which we explicitly modeled variance depending on the main predictor (DBH). This explains why the models fit with these approaches produced more reliable (i.e. least biased)

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AGB estimates as compared to those fit with the NLS approach. We included the latter approach mainly for illustration purposes. The NLS approach is still frequently found in the literature (Sileshi, 2014), despite the fact that assuming constant variance is not a good choice for allometric datasets.

Despite the highly heterogeneous nature of our dataset (Tables 1 and S1), DBH alone still captures a large fraction of the variation in AGB. This could be confirmed by lower Syx% values within model series 1 in comparison to the other model series (Table 2). This illustrates that ignoring selection criteria capturing a model's capacity to make predictions for new predictor combinations (e.g. different region or successional stage) such as the DIC or our landscape-level evaluation (see Sect. 4.2), can lead to the wrong choice. The basic models containing only DBH had a higher DIC in comparison to other model series and consequently did poorly in predicting the AGB of our different landscape scenarios (Fig. 6).

Our dataset contains a large number of species, which allowed for the maximum expression of architectural attributes. In comparison to species-specific biomass estimation models (Nelson et al., 1999) or models fit from data collected in undisturbed and homogenous forests (Higuchi et al., 1998; Lima et al., 2012), we expected the addition of predictors reflecting architectural and anatomical variation to improve model parsimony. This pattern was observed when adding SG and WD (Fig. 6 and Table S3).

The differences related to the coefficients  $b$  and  $c$  we found among our successional groups highlighted the importance of using SG as a predictor of the architectural attributes that influence allometry, especially when WD is not available (Table S3). In the models containing SG, the significant variation of the coefficients  $b$  and  $c$  between pioneers, mid- and late-successional species, highlights the importance of architectural attributes on defining allometries (Nelson et al., 1999). Often, these differences were neglected in previous studies that dealt with heterogeneous datasets and aimed at parameterizing global/pantropical models biomass estimation models.

Interestingly, when compared to our two best models, the tested Chave et al. (2014)'s pantropical model produced the largest bias (overestimation) for individual tree

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## 4.2 Landscape-level biomass predictions across scenarios

The different combinations of floristic composition and structure (i.e. tree density and basal area) used in our virtual approach reflected forest changes along succession (Chambers et al., 2009a; Marra et al., 2014; Norden et al., 2015), including realistic variations in AGB reported for Central Amazon stands differing in successional stage (from early-succession to old-growth) (Carvalho Jr et al., 1995; Higuchi et al., 2004; Lima et al., 2007). When taking into account the accuracy of landscape-level predictions across scenarios, the best models were those fit by using the MOV approach. From this approach, the models M33, M43 and M23 were the first, second and third best models, respectively (Fig. 6).

Modeling the variance properly as in the MOV approach is particularly important when both small and large trees – at the respective endpoints of the size predictors DBH and  $H$  – are to be estimated precisely. Assuming homoscedastic variance in allometric data gives a stronger weight to the information of large trees (which have large residuals) and reduces the “strength” of the small trees (with small residuals) on the estimation of the coefficients. This almost invariably leads to models that overestimate the biomass of small trees (i.e. large trees pulling the “line” upwards). This effect can be clearly seen in Fig. 4 where the NLS models dramatically overestimated the biomass particularly in the small-sized and the early successional scenario. The OLS approach tends to produce the opposite effect. The log-transformation shrinks the size of the residuals of the large-sized trees and inflates it for the small-sized trees. The influence of positive residuals or large-sized trees that often have a strong lever is reduced, and the lever of very small trees is increased. This may (although not as extremely as in the NLS case) lead to an underestimation of the biomass of big trees. A slight tendency of this effect is also visible in Fig. 4 when the OLS and MOV models are compared in the model series 2 and 3. The model evaluation with our virtual forests thus clearly illustrates that a balanced modeling of the variance, i.e. giving the small and large trees equal weight, is very important when (1) the design matrices are very heterogeneous

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or unbalanced with respect to size and when (2) predictions are to be made at landscape-level across stands that vary in the mean size/shape of trees.

Models containing only size-predictors (such as DBH) are particularly sensitive to this problem. Including SG and WD as predictors captured part of the interspecific variation in architecture and anatomy and partly alleviated the above-mentioned problems of the NLS and OLS models. Thus, although a simple allometric model (e.g.  $AGB \sim b1DBH^{b2}$ ) can accurately describe the DBH:AGB relationship at the individual-level (Tables 3 and S3), our results demonstrate that obtaining good estimates of biomass in heterogeneous landscapes (i.e. mixtures of successional stages and tree sizes) requires correct modeling of the size-related variance (Sileshi, 2014; Todeschini et al., 2004) and including suitable predictors of species-specific attributes reflecting ecological, architectural and anatomical variation.

Our model evaluation using “virtual forests” was used to test what level of model complexity and appropriateness of variance modeling is needed to avoid “distortions” and make satisfying predictions at the fringes of our predictor space. However, since we constructed the forest scenarios with trees of the design matrix, this is an “internal evaluation” and not a test of model behavior in the face of new predictor combinations. Furthermore, we used DIC as parsimony-based model selection criterion, which was designed to exactly approximate this capacity and typically yields similar results as cross-validation (Wirth et al., 2004). The DIC is therefore particularly important for judging the quality of the model, especially for application in other regions or for other species. Unlike the virtual forest approach, where the M33 (DBH and WD as predictors with modeled variance) appeared as best model (lowest bias and RMSE at the same time) (Fig. 6), the DIC invariably requires the full model complexity irrespective of whether  $H$  is considered or not (Table 3).

As reported in other studies (Alvarez et al., 2012; Lima et al., 2012; Ngomanda et al., 2014; Nogueira Junior et al., 2014), using Chave et al. (2014)’s pantropical biomass estimation model for landscape-level predictions led to strong biases in the case of our Central Amazon forest scenarios. Thus, our recommendation is not to assume that

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their model is equally applicable across all tropical forests, especially for secondary or hyperdiverse tropical forests. In this context, we alert researches and managers about the importance of applying local or regional generic models when estimating biomass, and the importance of species composition information in plot studies.

5 **4.3 Suitability of the chosen predictors for practical application**

As we have seen, predicting biomass correctly at the landscape-level and in particular improving performance at the fringes or outside the predictor space, requires the inclusion of predictors related to species architecture (DBH in combination with  $H$  [when available], WD and/or SG). Knowledge of these last two variables depends on the identification of species, further assignment into successional groups and measurement or compilation of species-specific WD values. For the purposes of our study, these variables were successfully addressed.

However, we understand that reliable biomass estimation models also require variables that can be easily and confidently acquired or measured. As we discuss below, this is not the case for  $H$ , species identification and, consequently, in many cases for WD and SG.

The tree species diversity in the Amazon is high (de Oliveira and Mori, 1999; ter Steege et al., 2013). Species identification requires extensive field work (i.e. collection of botanical samples) and joint effort of parobotanists, botanists and taxonomists. In many cases, this task might pose a major problem.

For WD, values can vary widely not only between species (Chave et al., 2006) – which we exploit in our modeling approach – but also between different sites/regions (Muller-Landau, 2004), within individuals of the same species or even in an individual tree (density varying along the tree bole) (Higuchi et al., 1998; Nogueira et al., 2005). Ideally, WD measures should be carried out in situ following a method that allows for sampling both heart- and sapwood. Still, at temperatures below 100 °C, the wood bound water content can not be removed (Williamson and Wiemann, 2010). Thus, measuring WD from non-representative samples and applying measures from

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environmental and neighbor effects (Henry and Aarssen, 1999; Sterck and Bongers, 1998). Consequently, the error of AGB estimates can increase when applying  $H$  values estimated from regional or global models (Feldpausch et al., 2011, 2012; Hunter et al., 2013; Santos Jr et al., 2006). As observed in our (Table 2) and other allometry datasets (Sileshi, 2014), the high collinearity between DBH and  $H$  can distort coefficient values, inflate standard errors and lead to biased estimates. The increased availability of new tools such as Lidar can improve the quality and resolution of  $H$  and thus biomass (Marvin et al., 2014; Sawada et al., 2015), but currently the areas where such data are available are limited.

Extra care should be taken when using biomass estimation models to assess biomass dynamics (e.g. biomass recovery after disturbances). Earlier stages of recovery can have a higher proportion of small trees from pioneers species (Norden et al., 2015), which have lower wood density (Chambers et al., 2009a; Marra et al., 2014; Saldarriaga et al., 1998) and a particular type of architecture (Hallé et al., 1978; Swaine and Whitmore, 1988). Once floristic composition changes and structural gradients increase, allometry becomes more complex and reliable landscape-level biomass estimates may require models that include predictors approximating species-specific architecture and anatomy.

Reliable biomass predictions for the entire Amazon basin are still highly dependent on the collection of plot-based allometric data and forest inventories including information on species composition, tree height and wood density, which are often unavailable or estimated imprecisely in most regions. We recommend the use of the best models fit in this study (M33 and M43) when aiming to reliable landscape biomass estimations for Central Amazon terra firme forests, especially those under complex disturbance regimes and for which specific/local models are not available. If data on species composition and wood density are available or could be accurately compiled from the literature, we encourage the use of the model M33. In case WD data is not available, or available in insufficient resolution, the model M33 could be replaced by the model M23 still with satisfactory results.

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**Table 1.** Summary of the dataset applied in this study. Trees were harvested in the Estação Experimental de Silvicultura Tropical (EEST), a contiguous terra firme forest reserve near Manaus, Central Amazon, Brazil.

Variables	Old growth forest	Secondary forest (23 year-old)	Secondary forest (14 year-old)
NT	131	346	250
SR	82	63	51
DBH	5.0–85.0	5.0–37.2	5.0–33.1
<i>H</i>	5.9–34.5	3.9–27.0	9.0–15.5
WD	0.348–0.940	0.389–1.000	0.395–1.000
AGB	8.3–7509.1	5.4–1690.2	7.5–1562.8

Variables: NT number of trees; SR species richness; DBH diameter at breast height (cm); *H* tree height (m); WD wood density ( $\text{g cm}^{-3}$ ); and AGB above-ground biomass (dry mass in kg).

**Table 2.** Tested equations for estimating AGB above-ground tree biomass in a terra firme forest near Manaus, Central Amazon, Brazil.

Series	Model	Equation	Variance modeling approach	VIF (range)
1	M11	$AGB \sim b1DBH^{b2}$	NLS	1
	M12	$\log(AGB) \sim \log(b1) + b2(\log DBH)$	OLS	1
	M13	$AGB \sim b1DBH^{b2}$	MOV	
2	M21	$AGB \sim b1[SG]DBH^{b2[SG]}$	NLS	1.001
	M22	$\log(AGB) \sim \log(b1[SG]) + b2(\log DBH[SG])$	OLS	1.005
	M23	$AGB \sim b1[SG]DBH^{b2[SG]}$	MOV	
3	M31	$AGB \sim b1DBH^{b2}WD^{b3}$	NLS	1.007
	M32	$\log(AGB) \sim \log(b1) + b2(\log DBH) + b3(\log WD)$	OLS	1.017
	M33	$AGB \sim b1DBH^{b2}WD^{b3}$	MOV	
4	M41	$AGB \sim b1[SG]DBH^{b2[SG]}WD^{b3[SG]}$	NLS	1.016–1.468
	M42	$\log(AGB) \sim \log(b1[SG]) + b2(\log DBH[SG]) + b3(\log WD[SG])$	OLS	1.017–1.395
	M43	$AGB \sim b1[SG]DBH^{b2[SG]}WD^{b3[SG]}$	MOV	
5	M51	$AGB \sim b1DBH^{b2}H^{b3}$	NLS	3.382
	M52	$\log(AGB) \sim \log(b1) + b2(\log DBH) + b3(\log H)$	OLS	3.342
	M53	$AGB \sim b1DBH^{b2}H^{b3}$	MOV	
6	M61	$AGB \sim b1[SG]DBH^{b2[SG]}H^{b3[SG]}$	NLS	1.019–3.439
	M62	$\log(AGB) \sim \log(b1[SG]) + b2(\log DBH[SG]) + b3(\log H[SG])$	OLS	1.010–3.360
	M63	$AGB \sim b1[SG]DBH^{b2[SG]}H^{b3[SG]}$	MOV	
7	M71	$AGB \sim b1DBH^{b2}H^{b3}WD^{b4}$	NLS	1.014–3.428
	M72	$\log(AGB) \sim \log(b1) + b2(\log DBH) + b3(\log H) + b4(\log WD)$	OLS	1.038–3.469
	M73	$AGB \sim b1DBH^{b2}H^{b3}WD^{b4}$	MOV	
8	M81	$AGB \sim b1[SG]DBH^{b2[SG]}H^{b3[SG]}WD^{b4[SG]}$	NLS	1.523–3.624
	M82	$\log(AGB) \sim \log(b1[SG]) + b2(\log DBH[SG]) + b3(\log H[SG]) + b4(\log WD[SG])$	OLS	1.422–3.547
	M83	$AGB \sim b1[SG]DBH^{b2[SG]}H^{b3[SG]}WD^{b4[SG]}$	MOV	

Predictors: DBH diameter at breast height (cm); SG species' successional group (pioneers, mid- and late-successional);  $H$  tree height (m); and WD wood density ( $\text{g cm}^{-3}$ ). Variance modeling approach: NLS non-linear least square; OLS ordinary least square with log-linear regression; and MOV non-linear with modeled variance. Since NLS and MOV rely on the same equation, they have analogue VIF variation inflation factor values.

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**Table 3.** Statistics of AGB above-ground tree biomass estimation models parameterized from a dataset of 727 trees harvested in a terra firme forest near Manaus, Central Amazon, Brazil. See Table 2 for predictors and applied variance modeling approaches, and Table A3 for the coefficients.

Series	Model	Dev	pD	DIC	$R^2$ adj	Syx%	CF
1	M11	9694.5	2.919	9697.4	0.894	3.130	1.066
	M12	6808.0	2.990	6811.3	0.865	3.542	
	M13	6821.0	3.856	6825.2	0.864	3.544	
2	M21	9336.0	-3.608	9332.1	0.935	2.453	1.061
	M22	6751.0	6.992	6758.4	0.541	6.449	
	M23	6741.0	10.373	6751.3	0.556	6.360	
3	M31	9291.0	4.052	9294.7	0.939	2.373	1.056
	M32	6683.0	4.062	6687.0	0.884	3.280	
	M33	6698.0	4.918	6702.5	0.865	3.527	
4	M41	9144.4	1.909	9146.3	0.949	2.155	1.054
	M42	6658.0	10.037	6667.7	0.698	5.214	
	M43	6650.0	12.956	6663.3	0.703	5.192	
5	M51	9479.0	0.023	9479.3	0.921	2.702	1.055
	M52	6680.0	4.017	6684.3	0.898	3.060	
	M53	6720.0	4.674	6724.7	0.896	3.103	
6	M61	9184.0	-50.750	9131.9	0.947	2.214	1.050
	M62	6613.0	9.902	6622.4	0.754	4.713	
	M63	6631.0	11.484	6642.0	0.747	4.800	
7	M71	8998.0	0.951	8999.1	0.959	1.942	1.047
	M72	6570.0	5.023	6574.9	0.933	2.480	
	M73	6610.0	5.697	6615.4	0.920	2.707	
8	M81	8875.0	-49.607	8825.1	0.965	1.794	1.046
	M82	6547.0	13.284	6560.7	0.813	4.097	
	M83	6566.0	13.645	6580.0	0.804	4.214	

Parameters: Dev models' deviance; pD effective number of parameters; DIC deviance information criterion;  $R^2$  adj R-squared adjusted; Syx% standard deviation of the mean (%); and CF correction factor for models fit from ordinary least square with log-linear regression.

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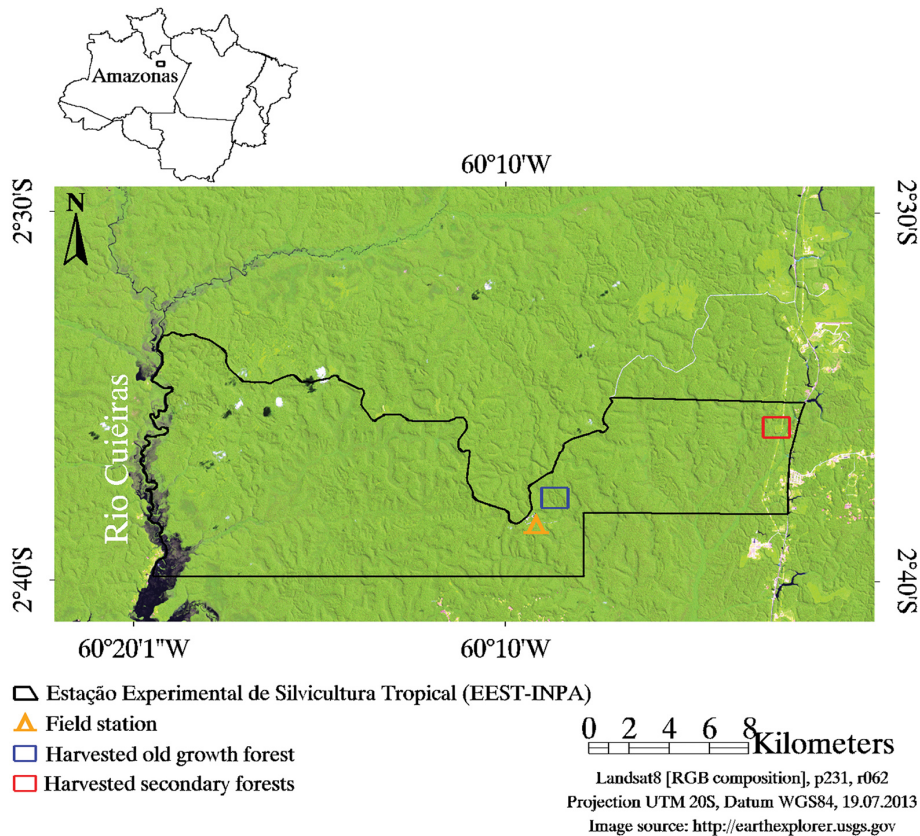
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**Figure 1.** Study site of terra firme forest near Manaus, Central Amazon, Brazil.

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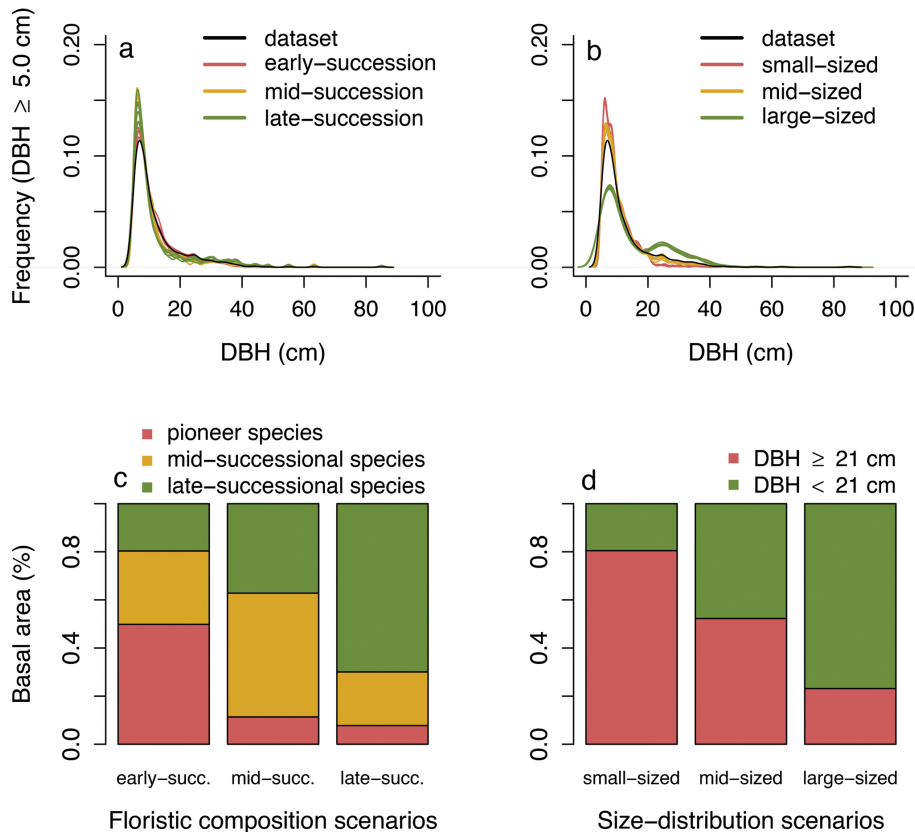
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**Figure 2.** Sampling schemes applied to assemble six forest-scenarios designed to reflect changes in floristic composition and size-distribution of trees in a terra firme forest near Manaus, Central Amazon, Brazil.

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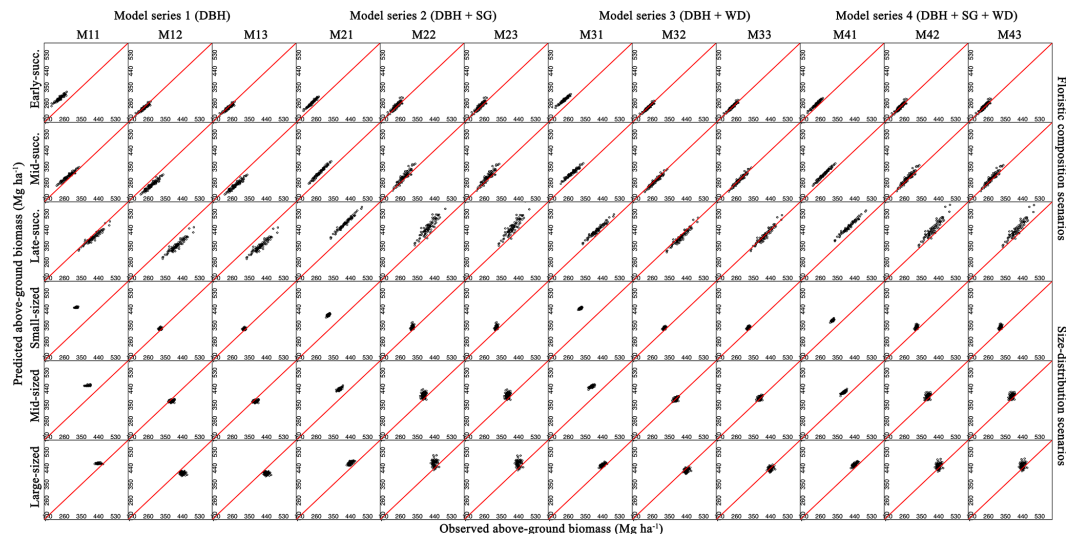
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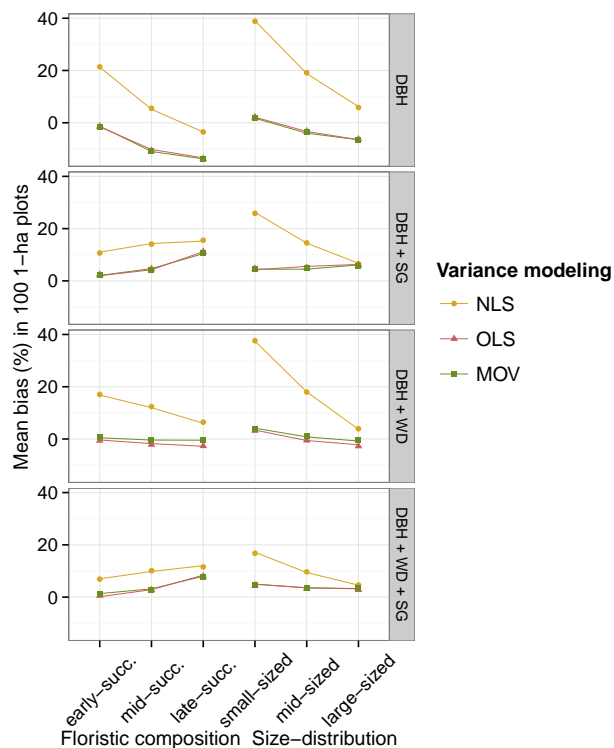
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**Figure 3.** Predicted vs. observed above-ground tree biomass (dry) of 100 randomly sampled 1 ha plots from the design matrix of 727 trees, harvested near Manaus, Central Amazon, Brazil. The line of equality (1 : 1 line) is shown as a red/straight line. Floristic composition and size-distribution scenarios followed the sampling scheme described in Fig. 2 of this study. See Table 2 for the variance modeling approach of different equations. Predictors: DBH diameter at breast height (cm); SG species' successional group (pioneers, mid- and late-successional); and WD wood density ( $\text{g cm}^{-3}$ ). Note that models containing *H* tree height as predictor were excluded here.

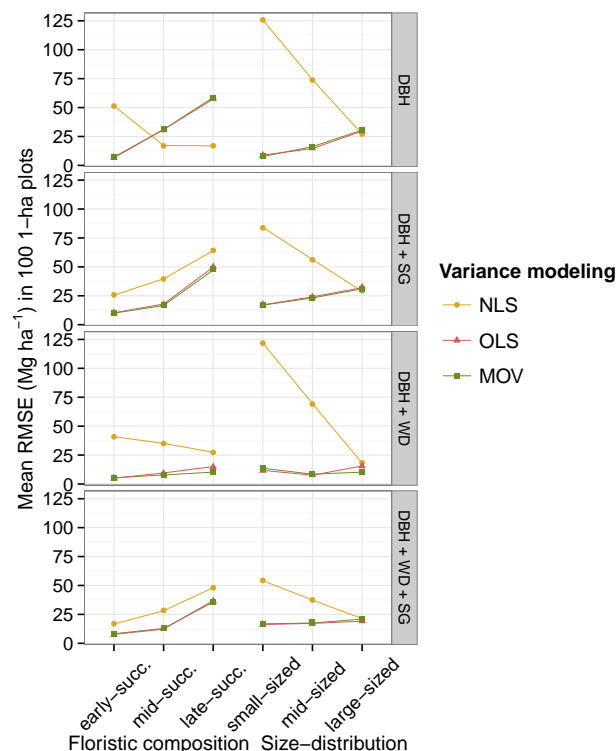
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**Figure 4.** Profiles relating the bias of 12 above-ground biomass estimation models across six 1 ha forest-scenarios designed to reflect changes in floristic composition and size-distribution in a terra firme forest near Manaus, Central Amazon, Brazil. Predictors: DBH diameter at breast height (cm); SG species' successional group (pioneers, mid- and late-successional); and WD wood density ( $\text{gcm}^3$ ). Variance modeling approaches: NLS non-linear least square; OLS ordinary least square with log-linear regression; and MOV non-linear with modeled variance. Note that models containing *H* tree height as predictor were excluded here.

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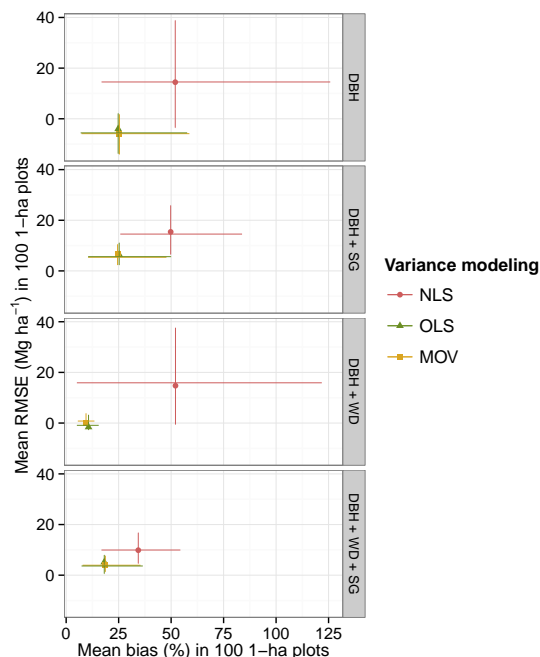


**Figure 5.** Profiles relating the RMSE root-mean-square error of 12 AGB above-ground biomass estimation models along six forest-scenarios designed to reflect changes in floristic composition and size-distribution in a terra firme forest near Manaus, Central Amazon, Brazil. Predictors: DBH diameter at breast height (cm); SG species' successional group (pioneers, mid- and late-successional); and WD wood density ( $\text{g cm}^{-3}$ ). Variance modeling approaches: NLS non-linear least square; OLS ordinary least square with log-linear regression; and MOV non-linear with modeled variance. Note that models containing  $H$  tree height as predictor were excluded here.

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**Figure 6.** Performance of 12 models for joint estimation of AGB across the six forest-scenarios included in this study. The scenarios reflect the landscape-level variation in floristic composition and size-distribution in a terra firme forest near Manaus, Central Amazon, Brazil. Models are rated by the absolute mean bias and RMSE root-mean-square error. Solid points and bars represent absolute mean and range values, respectively. Predictors: DBH diameter at breast (cm) height; SG species' successional group (pioneers, mid- and late-successional); and WD wood density ( $\text{g cm}^3$ ). Variance modeling approaches: NLS non-linear least square; OLS ordinary least square with log-linear regression; and MOV non-linear with modeled variance. Note that models containing  $H$  tree height as predictor were excluded here.

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