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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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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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However, in multivariate models with several predictors, this precondition is rarely met, not even by large design matrices. The ultimate prediction is typically at the landscape-level, which requires summing up individual predictions for several thousands of trees varying in size, architecture and species assignment. The larger the multivariate variation of predictor values within a stand, the higher is the likelihood that extrapolation errors occur. This calls for a validation at the landscape-level which, however, requires a plot-based harvest method. For obvious reasons, this has rarely been attempted (Carvalho Jr et al., 1995; Chambers et al., 2001; Higuchi et al., 1998; Lima et al., 2012).

Notable effort has already been made to parameterize global/pantropical AGB estimation models (Brown et al., 1989; Chave et al., 2005, 2014). Commonly, these models are derived using several different datasets, each of which is comprised of relatively few trees and species. Although few opportunities exist to evaluate these models at the landscape-level, they are used worldwide in different contexts, sites and across successional stages. For instance, the pantropical model from Chave et al. (2005) (DBH and WD as predictors) overestimated biomass when tested against trees in Gabon (Ngomanda et al., 2014), Peru (Goodman et al., 2014), Colombia (Alvarez et al., 2012) and Brazil (Lima et al., 2012), but also underestimated the AGB in mixed-species Atlantic Forest stands, Brazil (Nogueira Junior et al., 2014).

The availability of such generic AGB estimation models applicable to many species and contexts is particularly important for management, ecological and biogeochemical research in tropical forest landscapes that encompass a particularly wide spectrum of floristic and structural variation. For example, in the Central Amazon terra firme forests, one hectare of old-growth forest can hold more than 280 tree species (DBH ≥ 10 cm) (de Oliveira and Mori, 1999) with a wide range of architectures and anatomies (Braga, 1979; Muller-Landau, 2004; Ribeiro et al., 1999). At the landscape scale, this region encompasses a mosaic of successional stages promoted by windthrows (Asner, 2013; Chambers et al., 2009b, 2013; Negrón-Juárez et al., 2010, 2011). Disturbed areas include a diverse set of species representing the range from new regrowth to

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⁻³). 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⁻¹ (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 ≥ 5 cm (Lima et al., 2012; Silva, 2007). The tree density (DBH ≥ 10 cm) in the EEST is 593 ± 28 trees ha⁻¹ (mean ±99% confidence interval) (Marra et al., 2014). Trees larger than 100 cm in DBH are rare (< 1 individual 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 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 (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_{adj} adjusted coefficient of determination and the $Syx\%$ relative standard error as a percentage. The $Syx\%$ was calculated as follows:

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

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-

rection factor was calculated as follows:

$$CF = \exp\left(\frac{SSE^2}{2}\right), \quad (4)$$

where SSE is the standard error of the estimate (Sprugel, 1983).

2.4.2 Landscape-level biomass predictions across scenarios

5 To evaluate the models outlined in Table 2, we predicted AGB at the landscape-level for six forest-scenarios assembled by a stratified random selection of individual trees from our design matrix of 727 trees. Our scenarios were designed to span a successional gradient created by natural disturbances in which the interaction of tree mortality intensity and species vulnerability and resilience produce complex communities varying
10 in species composition and size-distribution of trees (Chambers et al., 2009a, 2013; Marra et al., 2014). We assembled three scenarios to reflect variations in floristic composition and three scenarios to reflect variations in size-distribution. Each scenario was sampled a 100 times resulting in 100 1 ha plot per scenario with different combination of trees randomly (with replacement) assembled according to the scenario-specific design principles.

To address the effect of variations in floristic composition on estimated AGB, we created scenarios where we varied the proportion of pioneer, mid- and late-successional species. The early-succession scenario comprised 50 % from trees sampled randomly from the species classified as pioneer, 40 % of mid- and 10 % of late-successional species (as survivors of disturbances). The mid-succession scenario comprised 10 % from trees sampled randomly from the species classified as pioneer, 70 % of mid- and 20 % of late-successional species. The late-succession scenario comprised 10 % from trees sampled randomly from the species classified as pioneer, 40 % of mid- and 50 % of late-successional species (Fig. 2a and c). We constrained our floristic composition scenarios to a stem density of 1255 trees ha⁻¹ (DBH ≥ 5 cm) typical for the old-growth
25 terra firme forests at the EEST (Lima et al., 2007; Marra et al., 2014; Suwa et al., 2012).

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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⁻¹ (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.

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.

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^{-1} . For the models fit with OLS, the RMSE values ranged from 5.1 to 57.6 Mg ha^{-1} . The MOV models had RMSE ranging from 5.5 to 58.7 Mg ha^{-1} . The pantropical model's predictions had a mean RMSE of 102.6 Mg ha^{-1} (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 $Sy\%$), 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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biomass prediction (Fig. S1 and Sect. 3.1). As previously mentioned, underestimation was also reported when applying the Chave et al. (2005)'s pantropical model in Atlantic Forest stands, Brazil (Nogueira Junior et al., 2014). For our study, we attribute part of this pattern to strong differences in forest structure and tree allometry/architecture between our Central Amazon dataset and that used to parameterize the pantropical model of Chave et al. (2014). Although the DBH and H range of the trees used in our study is well represented by the pantropical dataset, the two datasets vary strongly with respect to the DBH and H distribution of trees (Fig. S3). Our dataset clearly has a much higher density of small-sized and a much lower density of large-sized trees. The pantropical dataset comprises $\sim 8\%$ ($n = 329$) of trees with DBH ≥ 60 cm and mean H of 39.3 m (and even a tree with 212 cm DBH and another one with 70.7 m H). Interestingly, none of these 329 large-sized trees were found in Central Amazon. Note that the largest tree in our dataset has 85 cm DBH and 33 m H (Tables 1 and S1), and as previously reported, trees with DBH ≥ 60 cm account for less than 17% of the total AGB in Central Amazon terra firme forests (Vieira et al., 2004). Thus the structure and biomass of these Central Amazon forests is not well-predicted from the ‘‘improved’’ pantropical equation (Chave et al., 2014).

Observed differences on the relationship between predictor variables (DBH and WD) and AGB of trees from our dataset and the pantropical dataset highlight part of the variation in tree allometry and architecture that was not represented by the pantropical dataset (Fig. S4). As for the differences in forest structure, these differences in tree allometry and architecture reflect typical differences in species composition among successional stages (Clark and Clark, 1992; Denslow, 1980; Marra et al., 2014). By including our two secondary forests, we added a greater proportion of allometric variation in our models compared to the Chave et al. (2014) dataset (Fig. S5). Our results indicate that neglecting variations in tree allometry and architecture related to floristic composition can lead to strong bias when predicting individual tree AGB, especially when complex old-growth and secondary forests (Asner, 2013; Chambers et al., 2013; Norden et al., 2015) are not accounted for the model parameterization.

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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Bolker, B. M.: *Ecological Models and Data in R*, Princeton University Press, New Jersey, 2008.

Bolker, B. M., Gardner, B., Maunder, M., Berg, C. W., Brooks, M., Comita, L., Crone, E., Cubaynes, S., Davies, T., de Valpine, P., Ford, J., Gimenez, O., Kéry, M., Kim, E. J., Lennert-Cody, C., Magnusson, A., Martell, S., Nash, J., Nielsen, A., Regetz, J., Skaug, H., and Zipkin, E.: Strategies for fitting nonlinear ecological models in R, *AD Model Builder*, and *BUGS*, *Methods Ecol. Evol.*, 4, 501–512, 2013.

Braga, P. I. S.: Subdivisão fitogeográfica, tipos de vegetação, conservação e inventário florístico da floresta amazônica, *Acta Amaz.*, 9, 53–80, 1979.

Brooks, S. P. and Gelman, A.: General methods for monitoring convergence of iterative simulations, *J. Comput. Graph. Stat.*, 7, 434–455, 1998.

Brooks, S. P. and Roberts, G. O.: Convergence assessment techniques for Markov chain Monte Carlo, *Stat. Comput.*, 8, 319–335, 1998.

Brown, S., Gillespie, A. J. R., and Lugo, A. E.: Biomass estimation methods for tropical forests with applications to forest inventory data, *For. Sci.*, 35, 881–902, 1989.

Carvalho Jr, J. A., Santos, J. M., Santos, J. C., Leitão, M. M., and Higuchi, N.: A tropical rain-forest clearing experiment by biomass burning in the Manaus region, *Atmos. Environ.*, 29, 2301–2309, 1995.

Chambers, J. Q., Santos, J. dos, Ribeiro, R. J., and Higuchi, N.: Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest, *Forest Ecol. Manage.*, 152, 73–84, 2001.

Chambers, J. Q., Robertson, A. L., Carneiro, V. M. C., Lima, A. J. N., Smith, M. L., Plourde, L. C., and Higuchi, N.: Hyperspectral remote detection of niche partitioning among canopy trees driven by blowdown gap disturbances in the Central Amazon, *Oecologia*, 160, 107–117, 2009a.

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- Chambers, J. Q., Negrón-Juárez, R. I., Hurtt, G. C., Marra, D. M., and Higuchi, N.: Lack of intermediate-scale disturbance data prevents robust extrapolation of plot-level tree mortality rates for old-growth tropical forests, *Ecol. Lett.*, 12, E22–E25, 2009b.
- Chambers, J. Q., Negron-Juarez, R. I., Marra, D. M., Di Vittorio, A., Tews, J., Roberts, D., Ribeiro, G. H. P. M., Trumbore, S. E., and Higuchi, N.: The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape., *P. Natl. Acad. Sci. USA*, 110, 3949–54, 2013.
- Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J. P., Nelson, B. W., Ogawa, H., Puig, H., Riéra, B., and Yamakura, T.: Tree allometry and improved estimation of carbon stocks and balance in tropical forests, *Oecologia*, 145, 87–99, 2005.
- Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., ter Steege, H., and Webb, C. O.: Regional and phylogenetic variation of wood density across 2456 neotropical tree species, *Ecol. Appl.*, 16, 2356–2367, 2006.
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., and Zanne, A. E.: Towards a worldwide wood economics spectrum., *Ecol. Lett.*, 12, 351–66, 2009.
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrizar, A., Mugasha, W., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G., and Vieilledent, G.: Improved allometric models to estimate the aboveground biomass of tropical trees, *Glob. Change Biol.*, 3177–3190, 2014.
- Clark, D. A. and Clark, D. B.: Life history diversity of canopy and emergent trees in a neotropical rain forest, *Ecol. Monogr.*, 62, 315–344, 1992.
- Clark, D. B. and Kellner, J. R.: Tropical forest biomass estimation and the fallacy of misplaced concreteness, *J. Veg. Sci.*, 23, 1191–1196, 2012.
- da Silva, R. P.: Alometria, estoque e dinâmica da biomassa de florestas primárias e secundárias na região de Manaus (AM), Ph.D. thesis, Universidade Federal do Amazonas, Brazil, available at: http://www.inpa.gov.br/arquivos/Tese_Biomassa_Roseana_Silva.pdf (last access: 20 August 2015), 2007.
- da Silva, R. P., Santos, J. dos, Tribuzy, E. S., Chambers, J. Q., Nakamura, S., and Higuchi, N.: Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil, *Forest Ecol. Manage.*, 166, 295–301, 2002.

- Denslow, J. S.: Patterns of plant species diversity during succession under different disturbance regimes, *Oecologia*, 46, 18–21, 1980.
- dos Santos, J.: Análise de modelos de regressão para estimar a fitomassa da floresta tropical úmida de terra-firme da Amazônia Brasileira, Ph.D. thesis, Universidade Federal de Viçosa, Minas-Gerais, Brazil, 1996.
- Fearnside, P. M.: Wood density for estimating forest biomass in Brazilian Amazonia, *Forest Ecol. Manage.*, 90, 59–87, 1997.
- Feldpausch, T. R., Banin, L., Phillips, O. L., Baker, T. R., Lewis, S. L., Quesada, C. A., Affum-Baffoe, K., Arets, E. J. M. M., Berry, N. J., Bird, M., Brondizio, E. S., de Camargo, P., Chave, J., Djagbletey, G., Domingues, T. F., Drescher, M., Fearnside, P. M., França, M. B., Fyllas, N. M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M. O., Iida, Y., Salim, K. A., Kassim, A. R., Keller, M., Kemp, J., King, D. A., Lovett, J. C., Marimon, B. S., Marimon-Junior, B. H., Lenza, E., Marshall, A. R., Metcalfe, D. J., Mitchard, E. T. A., Moran, E. F., Nelson, B. W., Nilus, R., Nogueira, E. M., Palace, M., Patiño, S., Peh, K. S.-H., Raventos, M. T., Reitsma, J. M., Saiz, G., Schrodt, F., Sonké, B., Taedoumg, H. E., Tan, S., White, L., Wöll, H., and Lloyd, J.: Height-diameter allometry of tropical forest trees, *Biogeosciences*, 8, 1081–1106, doi:10.5194/bg-8-1081-2011, 2011.
- Feldpausch, T. R., Lloyd, J., Lewis, S. L., Brienen, R. J. W., Gloor, M., Monteagudo Mendoza, A., Lopez-Gonzalez, G., Banin, L., Abu Salim, K., Affum-Baffoe, K., Alexiades, M., Almeida, S., Amaral, I., Andrade, A., Aragão, L. E. O. C., Araujo Murakami, A., Arets, E. J. M. M., Arroyo, L., Aymard C., G. A., Baker, T. R., Bánki, O. S., Berry, N. J., Cardozo, N., Chave, J., Comiskey, J. A., Alvarez, E., de Oliveira, A., Di Fiore, A., Djagbletey, G., Domingues, T. F., Erwin, T. L., Fearnside, P. M., França, M. B., Freitas, M. A., Higuchi, N., E. Honorio C., Iida, Y., Jiménez, E., Kassim, A. R., Killeen, T. J., Laurance, W. F., Lovett, J. C., Malhi, Y., Marimon, B. S., Marimon-Junior, B. H., Lenza, E., Marshall, A. R., Mendoza, C., Metcalfe, D. J., Mitchard, E. T. A., Neill, D. A., Nelson, B. W., Nilus, R., Nogueira, E. M., Parada, A., Peh, K. S.-H., Pena Cruz, A., Peñuela, M. C., Pitman, N. C. A., Prieto, A., Quesada, C. A., Ramírez, F., Ramírez-Angulo, H., Reitsma, J. M., Rudas, A., Saiz, G., Salomão, R. P., Schwarz, M., Silva, N., Silva-Espejo, J. E., Silveira, M., Sonké, B., Stropp, J., Taedoumg, H. E., Tan, S., ter Steege, H., Terborgh, J., Torello-Raventos, M., van der Heijden, G. M. F., Vásquez, R., Vilanova, E., Vos, V. A., White, L., Willcock, S., Woell, H., and Phillips, O. L.: Tree height integrated into pantropical forest biomass estimates, *Biogeosciences*, 9, 3381–3403, doi:10.5194/bg-9-3381-2012, 2012.

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- Goodman, R. C., Phillips, O. L., and Baker, T. R.: The importance of crown dimensions to improve tropical tree biomass estimates, *Ecol. Appl.*, 24, 680–698, 2014.
- Graham, M. H.: Confronting multicollinearity in ecological multiple regression, *Ecology*, 84, 2809–2815, 2003.
- 5 Hallé, F.: Architecture of trees in the rain forest of Morobe District, New Guinea, *Biotropica*, 6, 43–50, 1974.
- Hallé, F., Oldeman, R. A. A., and Tomlinson, P. B.: *Tropical Trees and Forests: an Architectural Analysis*, Springer-Verlag, Berlin, German Federal Republic, 1978.
- Henry, H. A. L. and Aarssen, L. W.: The interpretation of stem diameter-height allometry in trees: Biomechanical constraints, neighbour effects, or biased regressions?, *Ecol. Lett.*, 2, 89–97, 1999.
- 10 Higuchi, N., Santos, J. dos, Ribeiro, R. J., Minette, L., and Biot, Y.: Biomassa da parte aérea da vegetação da floresta tropical úmida de terra-firme da Amazônia brasileira, *Acta Amaz.*, 28, 153–166, 1998.
- 15 Higuchi, N., Chambers, J. Q., Santos, J. dos, Ribeiro, R. J., Pinto, A. C. M., Silva, R. P. da, Rocha, R. de M., and Tribuzy, E. S.: Dinâmica e balanço do carbono da vegetação primária da Amazônia Central, *Floresta*, 34, 295–304, 2004.
- Hunter, M. O., Keller, M., Victoria, D., and Morton, D. C.: Tree height and tropical forest biomass estimation, *Biogeosciences*, 10, 8385–8399, doi:10.5194/bg-10-8385-2013, 2013.
- 20 Huxley, J. and Teissier, G.: Terminology of relative growth, *Nature*, 137, 780–781, 1936.
- Isik, F. and Li, B.: Rapid assessment of wood density of live trees using the Resistograph for selection in tree improvement programs, *Can. J. Forest Res.*, 33, 2426–2435, 2003.
- Kammesheidt, L.: Some autecological characteristics of early to late successional tree species in Venezuela, *Acta Oecol.*, 21, 37–48, 2000.
- 25 King, D. A.: Allometry and life history of tropical trees, *J. Trop. Ecol.*, 12, 25–44, 1996.
- Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Fearnside, P. M., Ribeiro, J. E. L., and Capretz, R. L.: Rain forest fragmentation and the proliferation of successional trees, *Ecology*, 87, 469–482, 2006.
- Lima, A. J. N., Teixeira, L. M., Carneiro, V. M. C., Santos, J. dos and Higuchi, N.: Análise da estrutura e do estoque de fitomassa de uma floresta secundária da região de Manaus AM, dez anos após corte raso seguido de fogo, *Acta Amaz.*, 37, 49–54, 2007.
- 30 Lima, A. J. N., Suwa, R., Ribeiro, G. H. P. M., Kajimoto, T., Santos, J. dos, Silva, R. P. da, Souza, C. A. S. de, Barros, P. C. de, Noguchi, H., Ishizuka, M., and Higuchi, N.: Allomet-

ric models for estimating above- and below-ground biomass in Amazonian forests at São Gabriel da Cachoeira in the upper Rio Negro, Brazil, *Forest Ecol. Manage.*, 277, 163–172, 2012.

Lin, C. J., Kao, Y. C., Lin, T. T., Tsai, M. J., Wang, S. Y., Lin, L. D., Wang, Y. N., and Chan, M. H.: Application of an ultrasonic tomographic technique for detecting defects in standing trees, *Int. Biodeter. Biodegr.*, 62, 434–441, 2008.

Lunn, D. J., Thomas, A., Best, N., and Spiegelhalter, D.: WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility, available at: <http://www.mrc-bsu.cam.ac.uk/software/bugs/> (last acces: 20 September 2015), 2000.

Marra, D. M., Chambers, J. Q., Higuchi, N., Trumbore, S. E., Ribeiro, G. H. P. M., Santos, J. dos, Negrón-Juárez, R., Reu, B., and Wirth, C.: Large-scale wind disturbances promote tree diversity in a central Amazon forest, *PLoS One*, 9, e103711, 1–16, 2014.

Marvin, D. C., Asner, G. P., Knapp, D. E., Anderson, C. B., Martin, R. E., Sinca, F., and Tupayachi, R.: Amazonian landscapes and the bias in field studies of forest structure and biomass, *P. Natl. Acad. Sci.*, 111, E5224–E5232, 2014.

Muller-Landau, H. C.: Interspecific and inter-site variation in wood specific gravity of tropical trees, *Biotropica*, 36, 20–32, 2004.

Negrón-Juárez, R. I., Chambers, J. Q., Guimaraes, G., Zeng, H., Raupp, C. F. M., Marra, D. M., Ribeiro, G. H. P. M., Saatchi, S. S., Nelson, B. W., and Higuchi, N.: Widespread Amazon forest tree mortality from a single cross-basin squall line event, *Geophys. Res. Lett.*, 37, 1–5, 2010.

Negrón-Juárez, R. I., Chambers, J. Q., Marra, D. M., Ribeiro, G. H. P. M., Rifai, S. W., Higuchi, N., and Roberts, D.: Detection of subpixel treefall gaps with Landsat imagery in Central Amazon forests, *Remote Sens. Environ.*, 115, 3322–3328, 2011.

Nelson, B. W., Mesquita, R. C. G., Pereira, J. L. G., de Souza, S. G. A., Batista, G. T., and Couto, L. B.: Allometric regressions for improved estimate of secondary forest biomass in the central Amazon, *Forest Ecol. Manage.*, 117, 149–167, 1999.

Ngomanda, A., Obiang, N. L. E., Lebamba, J., Mavouroulou, Q. M., Gomat, H., Mankou, G. S., Loumeto, J., Iponga, D. M., Ditsouga, F. K., Koumba, R. Z., Bobé, K. H. B., Okouyi, C. M., Nyangadouma, R., Lépengué, N., Mbatchi, B., and Picard, N.: Site-specific vs. pantropical allometric equations: which option to estimate the biomass of a moist central African forest?, *Forest Ecol. Manage.*, 312, 1–9, 2014.

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- Nogueira, E. M., Nelson, B. W., and Fearnside, P. M.: Wood density in a dense forest in central Amazonia, Brazil, *Forest Ecol. Manage.*, 208, 261–286, 2005.
- Nogueira, E. M., Fearnside, P. M., Nelson, B. W., and França, M. B.: Wood density in forests of Brazil's "arc of deforestation": implications for biomass and flux of carbon from land-use change in Amazonia, *Forest Ecol. Manage.*, 248, 119–135, 2007.
- Nogueira Junior, L. R., Engel, V. L., Parrotta, J. A., Melo, A. C. G., and Ré, D. S.: Allometric equations for estimating tree biomass in restored mixed-species Atlantic, *Biota Neotrop.*, 14, 1–9, 2014.
- Norden, N., Angarita, H. A., Bongers, F., Martiñez-Ramos, M., Granzow-de la Cerda, I., van Breugelf, M., Lebrija-Trejos, E., Meavei, J. A., Vandermeer, J., Williamson, G. B., Finegan, B., Mesquita, R., and Chazdon, R. L.: Successional dynamics in Neotropical forests are as uncertain as they are predictable, *P. Natl. Acad. Sci. USA*, 112, 8013–8018, 2015.
- De Oliveira, A. A. and Mori, S. A.: A central Amazonian terra firme forest. I. High tree species richness on poor soils, *Biodivers. Conserv.*, 8, 1219–1244, 1999.
- Petratis, P. S., Dunham, A. E., and Niewiarowski, P. H.: Inferring multiple causality: the limitations of path analysis, *Funct. Ecol.*, 10, 421–431, 1996.
- Poorter, L., Bongers, F., Sterck, F. J., and Wöll, H.: Architecture of 53 rain forest tree species differing in adult stature and shade tolerance, *Ecology*, 84, 602–608, 2003.
- R Core Team: R: a language and environment for statistical computing, Available at: <http://www.r-project.org> (last access: 1 August 2015), 2014.
- Ribeiro, G. H. P. M., Suwa, R., Marra, D. M., Kajimoto, T., Ishizuka, M., and Higuchi, N.: Allometry for juvenile trees in an Amazonian forest after wind disturbance, *JARQ*, 48, 213–219, 2014.
- Ribeiro, J. E. L. S., Hopkins, M. J. G., Vicentini, A., Sothers, C. A., Costa, M. A. da S., Brito, J. M. de, Souza, M. A. D. de, Martins, L. H. P., Lohmann, L. G., Assunção, P. A. C. L., Pereira, E. da C., Silva, C. F. da, Mesquita, M. R., and Procópio, L. C.: Flora da Reserva Ducke: Guia de Identificação das Plantas Vasculares de uma Floresta de Terra-firme na Amazônia Central, INPA, Manaus, 1999.
- Saldarriaga, J. G., West, D. C., Tharp, M. L., and Uhl, C.: Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela, *J. Ecol.*, 76, 938–958, 1998.
- dos Santos Jr, U. M., Gonçalves, J. F. de, and Feldpausch, T. R.: Growth, leaf nutrient concentration and photosynthetic nutrient use efficiency in tropical tree species planted in degraded areas in central Amazonia, *Forest Ecol. Manage.*, 226, 299–309, 2006.

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Sawada, Y., Suwa, R., Jindo, K., Endo, T., Oki, K., Sawada, H., Arai, E., Shimabukuro, Y. E., Celes, C. H. S., Campos, M. A. A., Higuchi, F. G., Lima, A. J. N., Higuchi, N., Kajimoto, T., and Ishizuka, M.: A new 500 m resolution map of canopy height for Amazon forest using spaceborne LiDAR and cloud-free MODIS imagery, *Int. J. Appl. Earth Obs.*, 43, 92–101, 2015.

Schinker, M. G., Hansen, N., and Spiecker, H.: High-frequency densitometry – a new method for the rapid evaluation of wood density variations, *IAWA J.*, 24, 231–239, 2003.

Shugart, H. H. and West, D. C.: Forest succession models, *BioScience*, 30, 308–313, 1980.

Sileshi, G. W.: A critical review of forest biomass estimation models, common mistakes and corrective measures, *Forest Ecol. Manage.*, 329, 237–254, 2014.

Slik, J. W. F., Arroyo-Rodríguez, V., Aiba, S., Alvarez-Loayza, P., Alves, L. F., Ashton, P., Balvanera, P., Bastian, M. L., Bellingham, P. J., van den Berg, E., Bernacci, L., Bispo, P. da C., Blanc, L., Böhning-Gaese, K., Boeckx, P., Bongers, F., Boyle, B., Bradford, M., Brearley, F. Q., Hockemba, M. B., Bunyavejchewin, S., Matos, D. C. L., Castillo-Santiago, M., Catharino, E. L. M., Chai, S., Chen, Y., Colwell, R. K., Chazdon, R. L., Clark, C., Clark, D. B., Clark, D. A., Culmsee, H., Damas, K., Dattaraja, H. S., Dauby, G., Davidar, P., DeWalt, S. J., Doucet, J., Duque, A., Durigan, G., Eichhorn, K. A. O., Eisenlohr, P. V., Eler, E., Ewango, C., Farwig, N., Feeley, K. J., Ferreira, L., Field, R., Oliveira Filho, A. T. de, Fletcher, C., Forshed, O., Franco, G., Fredriksson, G., Gillespie, T., Gillet, J., Amarnath, G., Griffith, D. M., Grogan, J., Gunatilleke, N., Harris, D., Harrison, R., Hector, A., Homeier, J., Imai, N., Itoh, A., Jansen, P. A., Joly, C. A., Jong, B. H. J. de, Kartawinata, K., Kearsley, E., Kelly, D. L., Kenfack, D., Kessler, M., Kitayama, K., Kooyman, R., Larney, E., Laumonier, Y., Laurance, S., Laurance, W. F., Lawes, M. J., Amaral, I. L. do, Letcher, S. G., Lindsell, J., Lu, X., Mansor, A., Marjokorpi, A., Marti, E. H., Meilby, H., Melo, F. P. L., Metcalfe, D. J., Medjibe, V. P., Metzger, J. P., Millet, J., Mohandass, D., Montero, J. C., Valeriano, M. de M., Mugerwa, B., Nagamasu, H., Nilus, R., Ochoa-Gaona, S., Onrizal, Page, N., Parolin, P., Parren, M., Parthasarathy, N., Paudel, E., Permana, A., Piedade, M. T. F., Pitman, N. C. A., Poorter, L., Poulsen, A. D., Poulsen, J., Powers, J., Prasad, R. C., Puyravaud, J., Razafimahaimodison, J., Reitsma, J., dos Santos, J. R., Spironello, W. R., Romero-Saltos, H., Rovero, F., Rozak, A. H., Ruokolainen, K., Rutishauser, E., Saiter, F., Saner, P., Santos, B. A., Santos, F., Sarker, S. K., Satdichanh, M., Schmitt, C. B., Schöngart, J., Schulze, M., Suganuma, M. S., Sheil, D., Pinheiro, E. da S., Sist, P., Stevart, T., Sukumar, R., Sun, I., Sunderand, T., Suresh, H. S., Suzuki, E., Tabarelli, M., Tang, J., Targhetta, N., Theilade, I., Thomas, D. W.,

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Sombroek, W.: Spatial and temporal patterns of amazon rainfall, *J. Hum. Environ.*, 30, 388–396, 2001.

Spiegelhalter, D. J., Best, N. G., Carlin, B. P., and van der Linde, A.: Bayesian measures of model complexity and fit, *J. Roy. Stat. Soc. B*, 64, 583–639, 2002.

Sprugel, D. G.: Correcting for bias in log-transformed allometric equations, *Ecology*, 64, 209–210, 1983.

ter Steege, H., Pitman, N. C., Sabatier, D., Baraloto, C., Salomão, R. P., Guevara, J. E., Phillips, O. L., Castilho, C. V., Magnusson, W. E., Molino, J., Monteagudo, A., Vargas, P. N., Montero, J. C., Feldpausch, T. R., Coronado, E. N. H., Killeen, T. J., Mostacedo, B., Vasquez, R., Assis, R. L., Terborgh, J., Wittmann, F., Andrade, A., Laurance, W. F., Laurance, S., Marimon, B. S., Marimon, B., Vieira, I. C. G., Amaral, I. L., Brienen, R., Castellanos, H., López, D. C., Duivenvoorden, J. F., Mogollón, H. F., Matos, F. D. de A., Dávila, N., García-Villacorta, R., Diaz, P. R. S., Costa, F., Emilio, T., Levis, C., Schiatti, J., Souza, P., Alonso, A., Dallmeier, F., Montoya, A. J. D., Fernandez Piedade, M. T., Araujo-Murakami, A., Arroyo, L., Gribel, R., Fine, P., Peres, C., Toledo, M., Aymard, C. G., Baker, T. R., Cerón, C., Engel, J., Henkel, T. W., Maas, P., Petronelli, P., Stropp, J., Zartman, C. E., Daly, D., Neill, D., Silveira, M., Paredes, M. R., Chave, J., Lima Filho, D. de A., Jørgensen, P. M., Fuentes, A., Schöngart, J., Cornejo Valverde, F., Di Fiore, A., Jimenez, E. M., Peñuela Mora, M. C., Phillips, J. F., Rivas, G., van Andel, T. R., von Hildebrand, P., Hoffman, B., Zent, E. L., Malhi, Y., Prieto, A., Rudas, A., Ruschell, A. R., Silva, N., Vos, V., Zent, S., Oliveira, A. A., Schutz, A. C., Gonzales, T., Nascimento, M. T., Ramirez-Angulo, H., Sierra, R., Tirado, M., Medina, M. N. U., van der Heijden, G., Vela, C. I., Torre, E. V., Vriesendorp, C., Wang, O., Young, K. R., Baider, C., Balslev, H., Ferreira, C., Mesones, I., Torres-Lezama, A., Giraldo, L. E. U., Zagt, R., Alexiades, M. N., Hernandez, L., Huamantupa-Chuquimaco, I., Milliken, W., Cuenca, W. P., Pauletto, D., Sandoval, E. V., Gamarra, L. V., Dexter, K. G., Feeley, K., Lopez-Gonzalez, G., and Silman, M. R.: Hyperdominance in the Amazonian tree flora, *Science*, 342, 1243092, doi:10.1126/science.1243092, 2013.

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Sterck, F. J. and Bongers, F.: Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees, *Am. J. Bot.*, 85, 266–272, 1998.

Stevens, P. F.: Angiosperm Phylogeny Website, version 12, available at: <http://www.mobot.org/MOBOT/research/APweb/> (last access: 20 August 2015), 2012.

5 Suwa, R., Kajimoto, T., Ishizuka, M., Pinto, A. C. M., Trindade, A. S., Silva, R. O., and Higuchi, N.: Comparative study of forest structure between plateau and valley bottom in a central Amazonian forest, *Kantoshinrinkenkyuu*, 63, 85–88, 2012.

Swaine, M. D. and Whitmore, T. C.: On the definition of ecological species groups in tropical rain forests, *Vegetatio*, 75, 81–86, 1988.

10 Telles, E. C., Camargo, P. B., Martinelli, L. A., Trumbore, S. E., Costa, E. S., Santos, J., Higuchi, N., and Oliveira Jr, C.: Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia, *Global Biogeochem. Cy.*, 17, 1–12, 2003.

Todeschini, R., Consonni, V., Mauri, A., and Pavan, M.: Detecting “bad” regression models: multicriteria fitness functions in regression analysis, *Anal. Chim. Acta*, 515, 199–208, 2004.

15 Vieira, S., de Camargo, P. B., Selhorst, D., da Silva, R., Hutyra, L., Chambers, J. Q., Brown, I. F., Higuchi, N., Santos, J. dos, Wofsy, S. C., Trumbore, S. E., and Martinelli, L. A.: Forest structure and carbon dynamics in Amazonian tropical rain forests, *Oecologia*, 140, 468–479, 2004.

Wickham, H.: *ggplot2: Elegant Graphics for Data Analysis*, Springer, New York, 2009.

20 Williamson, B. G. and Wiemann, M. C.: Measuring wood specific gravity correctly, *Am. J. Bot.*, 97, 519–524, 2010.

Wirth, C., Schumacher, J., and Schulze, E.: Generic biomass functions for Norway spruce in Central Europe – a meta-analysis approach toward prediction and uncertainty estimation, *Tree Physiol.*, 24, 121–139, 2004.

25 Wutzler, T., Wirth, C., and Schumacher, J.: Generic biomass functions for common beech (*Fagus sylvatica* L.) in Central Europe – predictions and components of uncertainty, *Can. J. Forest Res.*, 38, 1661–1675, 2008.

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

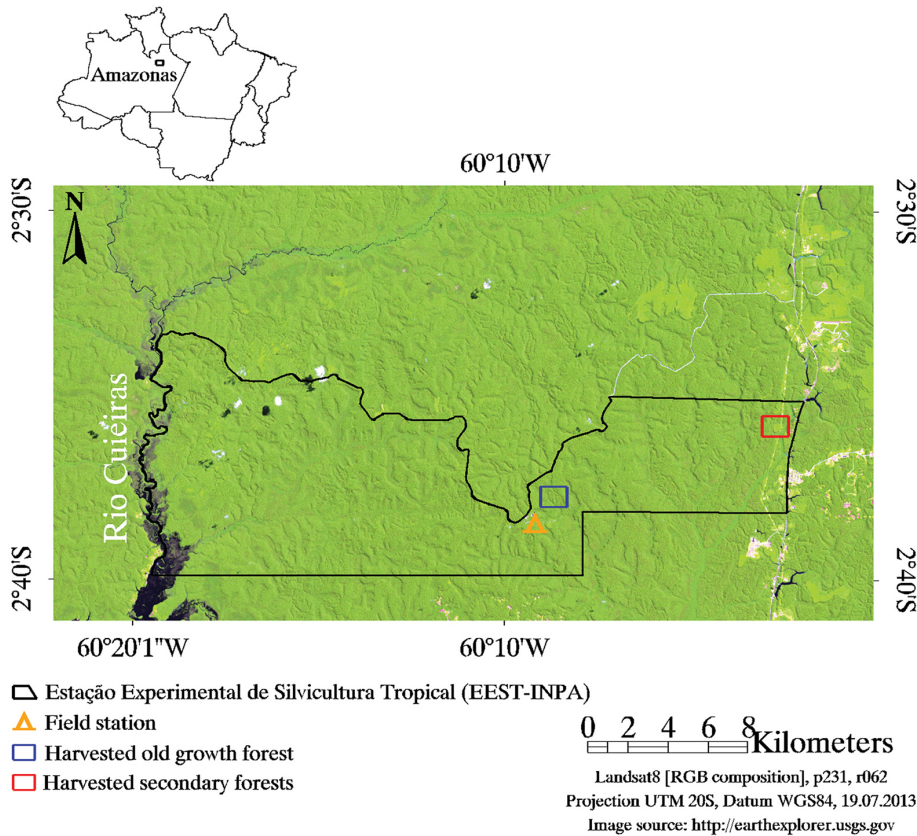


Figure 1. Study site of terra firme forest near Manaus, Central Amazon, Brazil.

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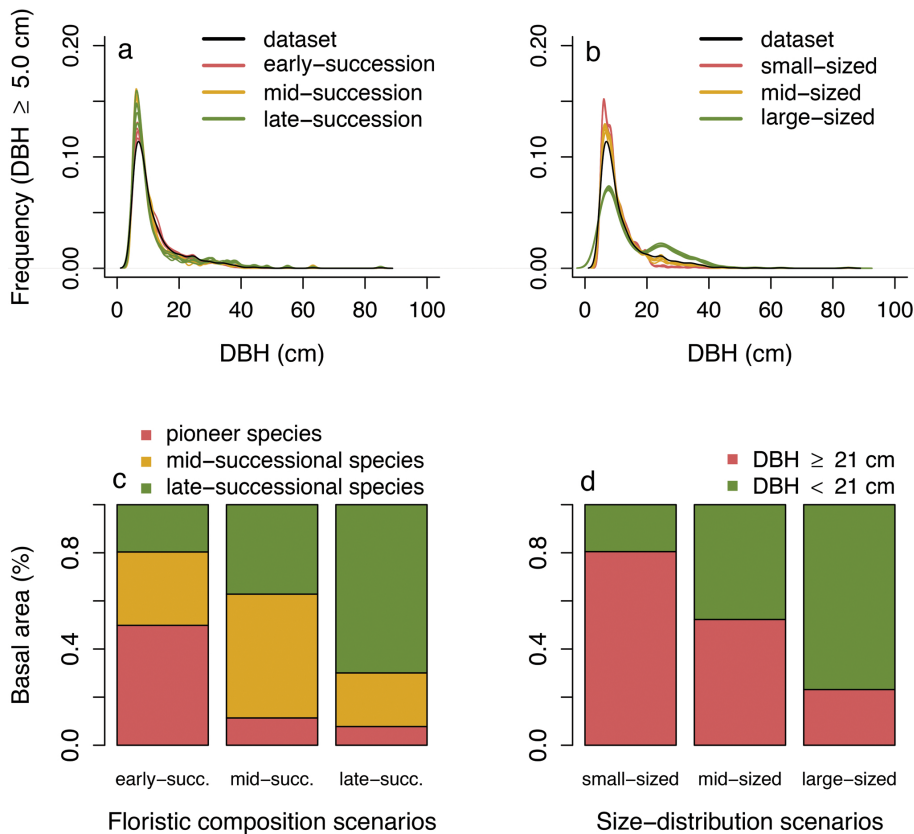


Figure 2. Sampling schemes applied to assemble six forest-scenarios designed to reflect changes in floristic composition and size-distribution of trees in a terra firme forest near Manaus, Central Amazon, Brazil.

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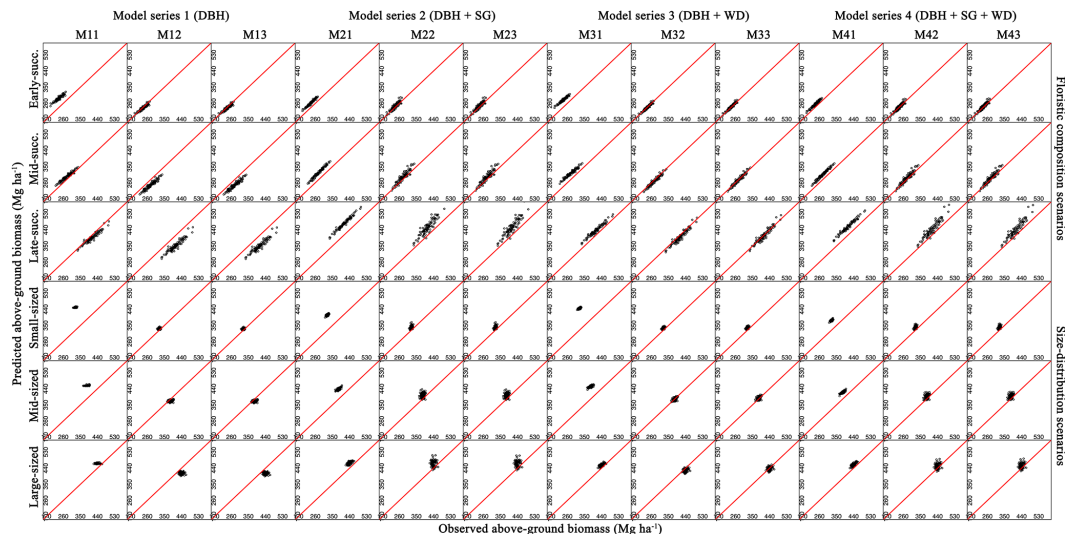


Figure 3. Predicted vs. observed above-ground tree biomass (dry) of 100 randomly sampled 1 ha plots from the design matrix of 727 trees, harvested near Manaus, Central Amazon, Brazil. The line of equality (1 : 1 line) is shown as a red/straight line. Floristic composition and size-distribution scenarios 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 (g cm^{-3}). Note that models containing *H* tree height as predictor were excluded here.

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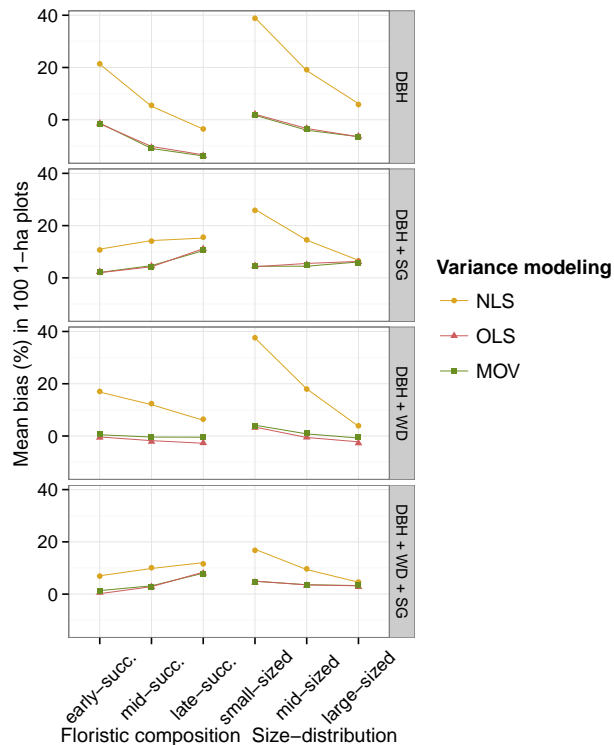


Figure 4. Profiles relating the bias of 12 above-ground biomass estimation models across six 1 ha forest-scenarios designed to reflect changes in floristic composition and size-distribution in a terra firme forest near Manaus, Central Amazon, Brazil. Predictors: DBH diameter at breast height (cm); SG species' successional group (pioneers, mid- and late-successional); and WD wood density (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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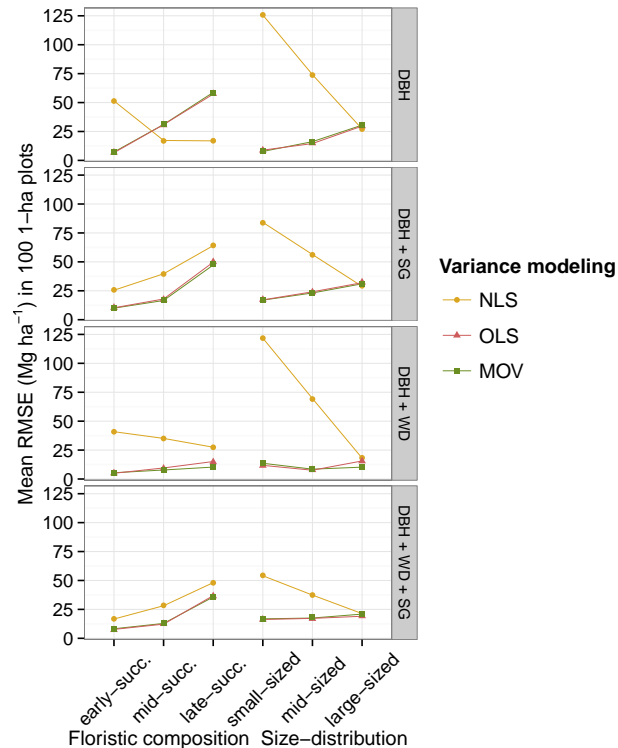
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Figure 5. Profiles relating the RMSE root-mean-square error of 12 AGB above-ground biomass estimation models along six forest-scenarios designed to reflect changes in floristic composition and size-distribution in a terra firme forest near Manaus, Central Amazon, Brazil. Predictors: DBH diameter at breast height (cm); SG species' successional group (pioneers, mid- and late-successional); and WD wood density (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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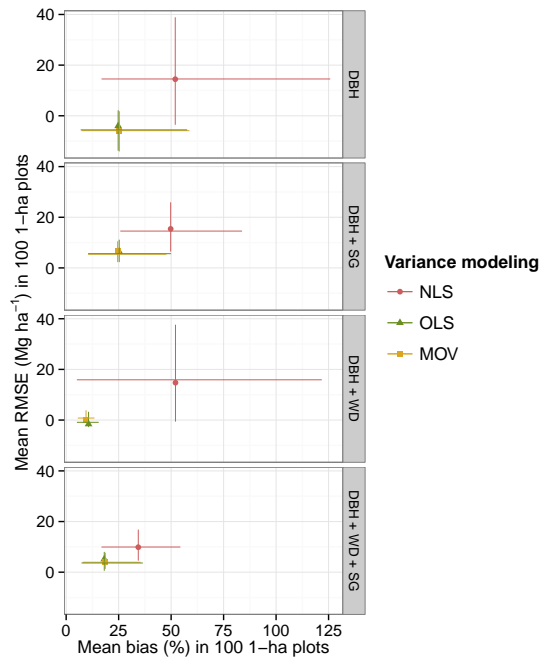


Figure 6. Performance of 12 models for joint estimation of AGB across the six forest-scenarios included in this study. The scenarios reflect the landscape-level variation in floristic composition and size-distribution in a terra firme forest near Manaus, Central Amazon, Brazil. Models are rated by the 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 (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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