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 aboveground biomass (AGB) in tropical forests and precise tree biomass estimation models are crucial for 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 tree 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 (diameter at breast height ≥ 5 cm) 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 reliable 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^{-1} (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^{-1}) when applied over scenarios. Predicting biomass correctly at the landscape-level in hyperdiverse and structurally complex tropical forests, especially allowing good performance at the margins of data availability for model construction/calibration, requires the inclusion of predictors that express inherent variations in 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 (i.e. secondary forests) still depend on the collection of allometric data at the local/regional scale and forest inventories 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. diameter at breast height [DBH] or tree total height [*H*]) 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 groups (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 (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 H (Hallé, 1974; Hallé et al., 1978). In addition, there is large variation in growth rate (the speed at which a certain space is filled) and consequently in wood anatomy among species (Bowman et al., 2013; Silva et al., 2002; Worbes et al., 2003). Wood density (WD), 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 predictions that deviate strongly from observations, especially when the sampling design does not allow the selection of relevant data for proper estimation of the parameters of interest (Gregoire et al., 2016) or 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 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 generic models valid across species, tree sizes and sites poses a number of challenges. Finding the appropriate model structure and estimating the model parameters requires a dataset with a large number of individual measurements containing the variable of interest (here AGB) and the predictor variables (i.e. DBH, *H*, species' successional group [SG] and WD). Importantly, the dataset should ideally cover all possible real-world combinations of predictor values in order to avoid error-prone extrapolations and unreliable predictions. However, in multiple regression models, 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 and species assignment. The larger the 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 theses 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 + 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., 2013; Negrón-Juárez et al., 2010; Nelson et al., 1994). 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., 2009; 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 novel 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 (pioneers, mid- and late-successional). 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}). We used this dataset to parameterize generic AGB estimation models for Central Amazon *terra firme* forests applicable across species and a wide range of structural and compositional variation (i.e. secondary forests), using various subsets of the available predictors; i.e. size (DBH and *H*), SG (ranging from pioneer to late-successional species) and WD.

We next evaluated our models, as well as the pantropical model from Chave et al. (2014) at the landscape-level using a virtual approach. We created scenarios of simulated 100 1-ha forest plots by assembling subsets of the 727 known-biomass trees in our dataset. These scenarios were designed to span gradients in (1) floristic composition by assembling stands with specific proportions of pioneer, mid- and late-succession species, and (2) size distributions of trees. 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 biomass 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 mean deviation 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 available pantropical/global models are 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 Brazilian Institute for Amazon Research (INPA), Manaus, Amazonas, Brazil (2°56'S, 60°26'W). Averaged annual temperature in Manaus was 26.7 °C for the 1910-1983 period (Chambers et al., 2004). Averaged annual precipitation ca. 50 km east of our study site was 2610 mm for the 1980-2000 period (Silva et al., 2003) 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 altitude ranging from 40–180 m a.s.l. 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). In contrast to floodplains (i.e. igapó and várzea) associated with large Amazon rivers (e.g. Rio Negro and Rio Amazonas), valleys associated with streams and low-order rivers can be affected by local rain events and thus have a polymodal and not predictable flood-pulse pattern with many short and sporadic inundations (Junk et al., 2011).

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; Marra et al., 2014). The *terra firme* forests are among the predominant forest types 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). In the study region, tree mortality rates can be influenced by variations in topography (Marra et al., 2014; Toledo et al., 2012). Floristic composition and species demography can also vary with the vertical distance from drainage (Schietti et al., 2013).

2.2 Allometric data

We used data from 727 trees harvested in this region (Santos, 1996; Silva, 2007), each with measured biomass and predictor variables. This dataset comprised 101 genera and at least 135 species with DBH ≥ 5.0 cm (Table 1; all data are given in Table S1). The trees were harvested through the plot-based harvest method in an old-growth forest and in two contiguous 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 the target forests and a landscape validation of the fitted models (Higuchi et al., 1998; Lima et al., 2012).

Before selecting plots, we surveyed both the old-growth and secondary forests to assure that no strong differences in structure and floristic composition existed; also that the selected patches were representative of our different successional stages. In the old-growth forest the trees were harvested in eight plateau and three valley plots (10 m x 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 x 20 m) randomly selected within a 1 ha plateau area, each (Santos, 1996; Silva, 2007). By including trees from secondary forests we were able to increase the variation in floristic composition and consequently the range of species-related variation in architecture and allometry (Tab. 1 and Tab. S1). Since our secondary forests were inserted in the contiguous matrix from which old-growth plots were sampled, we also controlled for the effects of important drivers of tree allometry and architecture, such as variations in environmental conditions (e.g. soil, precipitation rates and distribution), forest structure and wood density (Banin et al., 2012); the last, intrinsically related to variation ins floristic composition.

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 x 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 (i.e. stem, branches and leaves) was weighted separately. For large trees, stems were cut into smaller sections before weighing. 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 APGIII system (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 bottom of the bole, and samples (ca. 2 kg) of small branches and leaves. The samples were oven-dried at 65 ºC 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 was assigned to one of three successional groups known to vary in their architecture, namely pioneer, mid- and late-successional groups. 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 (Tab. S1 and Tab. 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., 2009; 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 dataset, and data for species presence/absence from a network of permanent plots representing a wide range of successional stages in Central Amazon (Tab. S2). 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 (≥ ca. 2000 m^2) created by windthrows with four, seven, 14, 17, 24 and 27 year-old (LMF unpublished data; Marra et al., 2014).

Since reported WD values for the same species or genera can vary strongly among different 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 where no published WD was available, or where the identification was carried out to the genus level (63 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 study region (Tab. 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 (Tab. 2). We used DBH (cm), WD (g cm^{-3}) and *H* (m) as predictors. Furthermore, we used the species' successional group (SG) assignment as a 'categorical predictor' (factor: 1 = pioneer, 2 = mid- and 3 = late-successional species), thereby representing functional diversity along a main axis of tree successional strategies, functional and architectural variation. Depending on the model-type parameters, the continuous variables were allowed to vary for capturing the successional aspects of functional diversity. We consider the SG grouping factor as integral part of the model. Fitting all SG's in one model in an Markov chain Monte Carlo (MCMC) context is different from fitting separate models because the joint model also absorbs the covariance structure of the parameters across groups, especially in models were not all parameters are allowed to vary between SGs.

We tested variables for collinearity by calculating the variance inflation factor (VIF). A conservative VIF > 2.0 indicates significant collinearity among variables (Graham, 2003; Petraitis et al., 1996). Model series 1-4 had VIF < 1.5 (Tab. 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 variables. This pattern was previously reported for other 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). In the MOV approach we modeled the variance as a function of *DBH* with a normally distributed residual error:

$\varepsilon_{i} = N(\hat{y}_{i}, \sigma_{i})$ (1),

where i is the subscript for individuals (i = 1, …, n) and σ_i is modeled with a heteroscedastic variance according to:

$\sigma_{i} = c_{i} * DBH_{i}^{c_{2}}$ (2).

Model series 1 (M11, M12 and M13) used DBH as the sole predictor (Tab 2). For model series 2 (M21, M22 and M23), we allowed the b regression parameters and c heteroscedastic variance to vary according to the SG assignment (1, 2 or 3). This approach allowed us to account for differences among the groups without splitting the dataset into three different groups. This method has increased analytical power and allowed us to assess the relationships between tree allometry and architecture.

For model series 3 (M31, M32 and M33), we ignored the SG assignment but introduced WD (which did not correlate strongly with SG). For model series 4 (M41, M42 and M43) we allowed each SG to have its own wood density effect. For model series 5 and 6, we replaced the WD by *H*. In model series 5 (M51, M52 and M53), we restricted the SG-variation of b and c, while in series 6 (M61, M62 and M63) we allowed these parameters to vary according to SG. For model series 7 (M71, M72 and M73), we combined DBH, *H* and WD but restricted the SG-variation of b and c. Finally, for model series 8 (M81, M82 and M83), we combined DBH, *H* and WD, and allowed b and c to vary with SG (Tab. 2).

In contrast to prior approaches, we did not test models based on compound (e.g. log[AGB] ~ log[b1] + b2[logDBH^{2}HWD]) or quadratic/cubic derivatives (e.g. log[AGB] ~ log[b1] + b2[logDBH] + b3[logDBH^2] + b4[logDBH^3]) (Brown et al., 1989; Chave et al., 2005, 2014; Ngomanda et al., 2014). These structures would have limited our ability to include biological variation by defining SG-specific parameters for DBH, *H* and WD, separately.

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 Deviance Information Criterion (DIC). The DIC is a generalization of Akaike's Information Criterion (AIC) and consists of a cross-validatory term that expresses both the goodness of the fit and the models' complexity. The lower the value the higher the predictive ability and parsimony (Spiegelhalter et al., 2002). We also checked whether the 95% credible intervals of the parameter'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, B, 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 allow for comparisons of different model structures and approaches with the available literature, we calculated the coefficient of determination (R^2), the adjusted coefficient of determination (R^2adj) and the relative standard error ($S_{yx\%}$). The $S_{yx\%}$ was calculated as follows:

$$S_{yx\%} = \left(\frac{2s}{\bar{y}\sqrt{N}}\right) \text{ (3),}$$

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. As in all allometric datasets relating linear to volume-proportional data, there is indeed heteroscedascity in our data, which makes the $S_{yx\%}$ an inappropriate measure for model selection.

For the OLS approach including log-transformed variables, we calculated the $S_{yx\%}$ using untransformed data. To correct for the bias introduced by the log-transformed data, a correction factor (CF) was calculated as follows:

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

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

2.4.2 Landscape-level biomass predictions across scenarios

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 dataset 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 in species composition and size-distribution of trees (Chambers et al., 2009, 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 100 times resulting in 100 1-ha plots 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 2c). We constrained our floristic composition scenarios to a stem density of 1255 trees ha^{-1} (DBH ≥ 5 cm) typical for the old-growth *terra firme* forests at the EEST (Lima et al., 2007; Marra et al., 2014; Suwa et al., 2012).

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* ≥ 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 ≥ 21 cm); a mid-sized stand with equal numbers of trees smaller and greater or equal to 21 cm in DBH; and a large-sized stand, with 10 % small and 90 % big trees (Fig. 2b and 2d). 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 m^2 ha^{-1} also typical for our studied old growth forest (trees with DBH ≥ 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 root-mean-square error (RMSE). In order to assess the accuracy of different predictions in the context of models’ uncertainty, we additionally reported the overall performance of the tested models along all forest-scenarios. When doing so, we present the bias and RMSE in the same unit (Mg), which allow for assessing the magnitudes of deviations in model predictions (Gregoire et al., 2016; McRoberts and Westfall, 2014). 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):

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

which was parameterized with data from 4004 trees (DBH ≥ 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.

We performed all analysis using the R 3.2.1 software platform (R Core Team, 2014). We use the R2WinBUGS (Sturtz et al., 2005) package for running WinBUGS from R, and the ggplot2 package (Wickham, 2009) for producing figures, with the exception of Fig. 1, which was produced in the Environment for Visualizing Images software (ENVI, ITT Industries, Inc, Boulder CO, USA). All codes used in this study were written by ourselves.

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 and R^2adj, and low $S_{yx\%}$ and DIC values compared to other models). These two models also produced more reliable landscape predictions (see section 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 and R^2adj, and lower values of $S_{yx\%}$, 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 (Tab. 3). The inclusion of the SG assignment resulted in models with slightly lower R^2adj and higher $S_{yx\%}$ compared to the same model structure without SG.

We observed differences with respect to the parameters b and c among pioneer, mid- and late-successional species in most of the models that included the SG assignment (Tab. 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 slopes.

An evaluation of AGB predictions for individual trees from our two best models (as described in the section 3.2), as well from the 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 %).

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 [Tab. 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 (Tab. 3 and Figs. 3-6). The same pattern was observed when evaluating the tested pantropical model, which underestimated both the AGB of individual trees (Fig. S1) and in all of our scenarios (Tab. S4 and Fig. S2).

While some models produced accurate and satisfactory predictions across all scenarios, others systematically under- or overestimated the observed AGB (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 capture changes in floristic composition better than in tree size-distribution. The tested pantropical model systematically underestimated landscape-level biomass, with a mean bias of -29.7% (Tab. S4 and Fig. S2).

The models fit with the OLS and particularly with the MOV approaches were clearly more efficient 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 AGB 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} (Tab. 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 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 (Fig. 3, Fig. 6 and Tab. 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 consistent model than adding *H* (Tab. 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 section 4.2).

Although the NLS approach fits our dataset better (higher R^2adj and lower $S_{yx\%}$), 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* forest 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 MOV and OLS 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. smaller differences between predictions and observations) 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 an appropriated choice for allometric datasets.

Despite the highly heterogeneous nature of our dataset (Tab. 1 and Tab. S1), DBH alone still captures a large fraction of the variation in AGB. This could be confirmed by lower $S_{yx\%}$ values within model series 1 in comparison to the other model series (Tab. 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 section 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 both SG and WD (Fig. 6 and Tab. S3).

The differences related to the parameters 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 in disturbed or secondary forests where WD is not available (Tab. S3). In the models containing SG, the significant variation of the parameters *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 biomass prediction (Fig. S1 and section 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 ca. 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* (Tab. 1 and Tab. 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 that used in the pantropical model highlight part of the variation in tree allometry and architecture that was not represented in 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., 2009; 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 parameters. 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 or unbalanced with respect to size and when (2) predictions are to 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 ~ b1DBH^{b2}) can accurately describe the DBH:AGB relationship at the individual-level (Tab. 3 and Tab. S3), our results demonstrate that reliable 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. This approach also allowed us to asses the magnitude of RMSE in model predictions in relation to the bias of these predictions. Our best performance models produced predictions with RMSE similar (i.e. M23 and M33) to the bias associated to these prediction, which indicates that model deviations can be attributed to ramdon variation and possibly be ignored (Gregoire et al., 2016; McRoberts and Westfall, 2014). However, since we constructed the forest-scenarios with trees from our dataset, 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 DBH + WD with modeled variance (M33) 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 (Tab. 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 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.

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 the species identification, *H* 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 parabotanists, 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. Measuring WD from non-representative samples and applying measures from studies in which samples were oven-dried at different temperatures can produce complication. At temperatures below 100 °C, the wood bound water content can not be removed (Williamson and Wiemann, 2010). This requires improvement of available methods and tools (e.g. resistography, X-ray, ultrasonic tomography, near-infrared-spectroscopy, acoustic/ultrasonic wave propagation and high-frequency densiometry) (Isik and Li, 2003; Lin et al., 2008; Schinker et al., 2003) that in the future may allow the measurement of WD in live trees from hyperdiverse tropical forests (thousands of species). However, the acquisition of WD data is still expensive and is not easily conducted simultaneously with forest inventories.

In the Amazon, information on WD is not available at the species-level for most regions, and the available WD data have been acquired using a wide range of methods. Thus, the compilation of WD data from different sources without filtering criteria may introduce an unpredictable source of error. As a result, researchers and managers need to establish robust criteria and test whether including WD information compiled from the available literature can really increase the quality of biomass predictions (as shown in our study). These limitations become critical when adjusting biomass estimation models both from small or even large/combined datasets collected without a plot-based harvest method that allows for a landscape-level evaluation of models derived using individual trees (Carvalho Jr et al., 1995; Higuchi et al., 1998; Lima et al., 2012; Silva, 2007). One important result of our study is that correct assignment of species into successional groups can satisfactorily replace the use of WD despite the fact WD and SG were not trivially correlated (Tab. 2).

Most of the available biomass estimation models include *H* as a predictor. Indeed, we expected the inclusion of *H* to substantially improve our individual tree fits and landscape-level predictions. Although *H* is a powerful predictor of AGB, because together with DBH it defines the slenderness of trees and also indicates the life-time light availability (suppressed trees with typically short crowns have a high *H:*DBH ratio), acquiring these data is still costly and difficult in tall and complex tropical forest canopies. As a consequence, *H* is often measured imprecisely or not at all in most existing forest inventories across the Amazon. *H* varies with plant ontogeny and can be affected by 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 (Tab. 2) and other datasets (Sileshi, 2014), the high collinearity between DBH and *H* can distort coefficient values, inflate standard errors and lead to unreliable estimates. The increased availability of new tools such as Lidar can improve the resolution of data on tree height and thus biomass (Marvin et al., 2014; Sawada et al., 2015), but currently the areas where such data are available are limited. The calibration of remote sensing based biomass models for diverse tropical forest still relies on the degree of uncertainty associated to plot-level AGB estimates (Chen et al., 2015).

Despite uncertainties associated with global estimates of carbon stocks, tropical forests storage ca. 25% of the terrestrial carbon (Bonan, 2008; Saatchi et al., 2011) and provide resources (e.g. food, fuel, timber and water) essential for humankind (Trumbore et al., 2015). Nonetheless, old-growth tropical forests are under rapidly change and degradation due to the intensification of human activities, gradual climate change and extreme weather events (FAO, 2010; IPCC, 2014). The Reducing Emissions from Deforestation and Forest Degradation (REDD+) program from the United Nations Framework Convention on Climate Change (UNFCCC) establishes rewarding for actions that mitigate carbon emission through prevention of forest loss and degradation. For countries with large forest cover (e.g. Brazil and other Amazon countries), such programs emerge as an economical alternative against historically more lucrative land uses resulting in forest degradation or suppression. However, we showed that reliable estimates of forest biomass are complex to be obtained and prone to large uncertainty. Reliable predictions of biomass/carbon stocks over large regions of structurally complex and hyperdiverse tropical forests such as the Amazon still depend 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.

Natural and anthropogenic tropical secondary forests are widely distributed and account for ca. 50% of the global forest cover (FAO, 2010). Although highly productive and resilient (Poorter et al., 2016), Neotropical forests can take unpredictable successional trajectories (Norden et al., 2015). During forest succession, 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. 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, which have lower wood density (Chambers et al., 2009; Marra et al., 2014; Saldarriaga et al., 1998) and a particular type of architecture (Hallé et al., 1978; Swaine and Whitmore, 1988).

We recommend the use of the best models fit in this study when aiming for reliable landscape AGB 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 or M23. In case these data are not available, or available in insufficient resolution, the model M13 could be applied and produce satisfactory results.

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Tables

Table 1. Summary of the dataset applied in this study. Trees were harvested in the Estação Experimental de Silvicultura Tropical, a contiguous *terra firme* forest reserve near Manaus, Amazonas, 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
H	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: number of trees (NT); species richness (SR); diameter at breast height (DBH) (cm); tree total height (H) (m); wood density (WD) (g cm^{-3}); and aboveground biomass (AGB) (dry mass in kg).

Table 2. Tested equations for estimating tree aboveground biomass (AGB) 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) ~ log(b1) + b2(logDBH)	OLS	1
	M13	$AGB \sim b1DBH^{b2}$	MOV	
2	M21	$AGB \sim b1[SG]DBH^{b2[SG]}$	NLS	1.001
	M22	log(AGB) ~ log(b1[SG]) + b2(logDBH[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) ~ log(b1) + b2(logDBH) + b3(logWD)	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) ~ log(b1[SG]) + b2(logDBH[SG]) + b3(logWD[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) ~ log(b1) + b2(logDBH) + b3(logH)	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) ~ log(b1[SG]) + b2(logDBH[SG]) + b3(logH[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) ~ log(b1) + b2(logDBH) + b3(logH) + b4(logWD)	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) ~ log(b1[SG]) + b2(logDBH[SG]) + b3(logH[SG]) + b4(logWD[SG])	OLS	1.422 - 3.547

M83	AGB ~ b1[SG]DBH$^{b2[SG]}$H$^{b3[SG]}$WD$^{b4[SG]}$	MOV

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

Table 3. Statistics of aboveground biomass (AGB) estimation models fit in a *terra firme* forest near Manaus, Central Amazon, Brazil. See Tab. 2 for predictors and applied variance modeling approaches, and Tab. A3 for the models' parameters.

Series	Model	Dev	pD	DIC	R^2	R^2adj	$S_{yx\%}$	CF
1	M11	9694.5	2.919	9697.4	0.894	0.894	3.130	
	M12	6808.0	2.990	6811.3	0.865	0.865	3.542	1.066
	M13	6821.0	3.856	6825.2	0.864	0.864	3.544	
2	M21	9216.0	3.773	9219.9	0.946	0.945	2.259	
	M22	6751.0	6.943	6758.3	0.557	0.540	6.458	1.061
	M23	6739.0	10.465	6749.5	0.558	0.554	6.381	
3	M31	9291.0	4.052	9294.7	0.949	0.939	2.373	
	M32	6683.0	4.062	6687.0	0.885	0.884	3.280	1.056
	M33	6698.0	4.918	6702.5	0.865	0.865	3.527	
4	M41	9057.0	2.303	9059.8	0.957	0.956	2.030	
	M42	6657.0	10.006	6667.5	0.701	0.699	5.215	1.054
	M43	6649.0	13.059	6661.6	0.701	0.699	5.239	
5	M51	9479.0	0.023	9479.3	0.921	0.921	2.702	
	M52	6680.0	4.017	6684.3	0.899	0.898	3.060	1.055
	M53	6720.0	4.674	6724.7	0.897	0.896	3.103	
6	M61	9183.9	-71.746	9112.2	0.948	0.947	2.214	

	M62	6614.0	10.078	6624.1	0.754	0.750	4.845	1.050
	M63	6631.0	11.754	6642.9	0.740	0.737	4.896	
7	M71	8998.0	0.951	8999.1	0.959	0.959	1.942	
	M72	6570.0	5.023	6574.9	0.934	0.933	2.480	1.047
	M73	6610.0	5.697	6615.4	0.922	0.920	2.707	
8	M81	8812.0	-42.073	8770.3	0.968	0.967	1.719	
	M82	6548.0	13.031	6561.3	0.811	0.804	4.200	1.046
	M83	6566.0	13.778	6580.0	0.801	0.800	4.262	

Parameters: models' deviance (Dev); effective number of parameters (pD); Deviance Information Criterion (DIC); coefficient of determination (R^2); adjusted coefficient of determination (R^2adj); relative standard error ($S_{yx\%}$); and correction factor (CF) for models fit from ordinary least square with log-linear regressions.

Figures

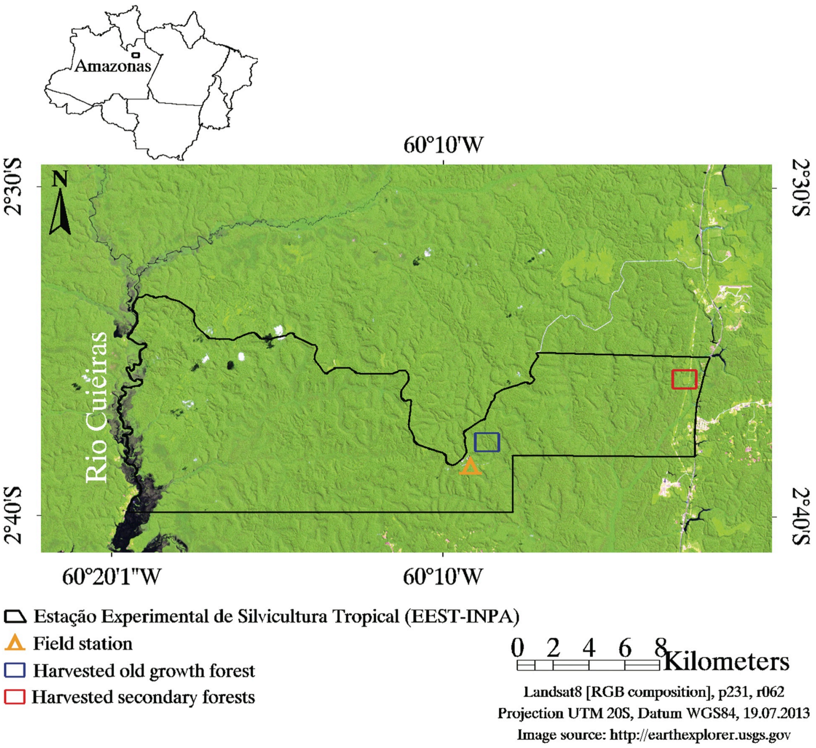

Figure 1. Study site of *terra firme* forest near Manaus, Central Amazon, Brazil.

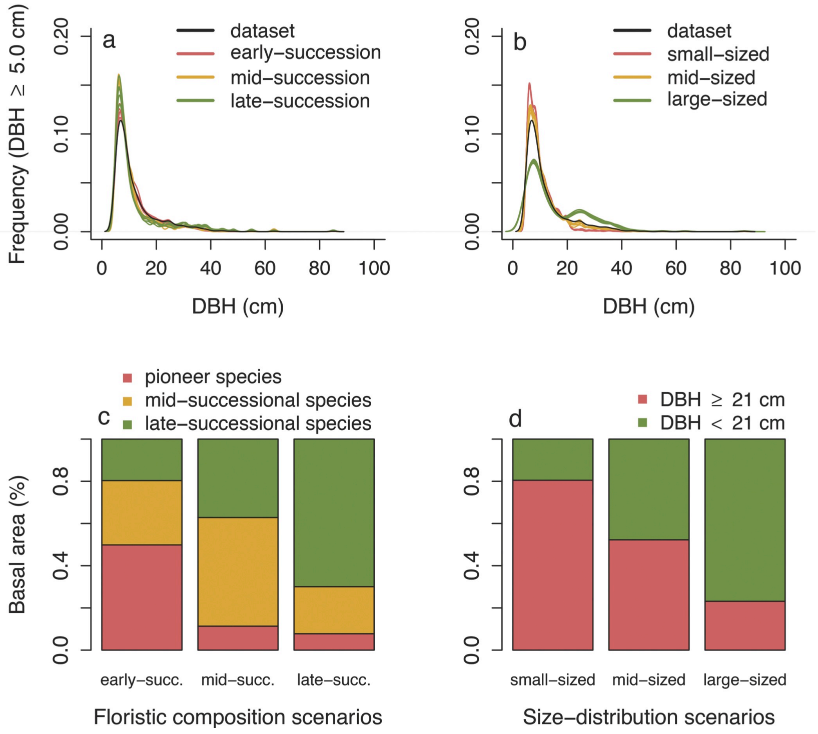

Figure 2. Sampling schemes applied to assemble the six forest-scenarios designed to reflect changes in floristic composition and size-distribution of trees, typical of Central Amazon *terra firme* forests.

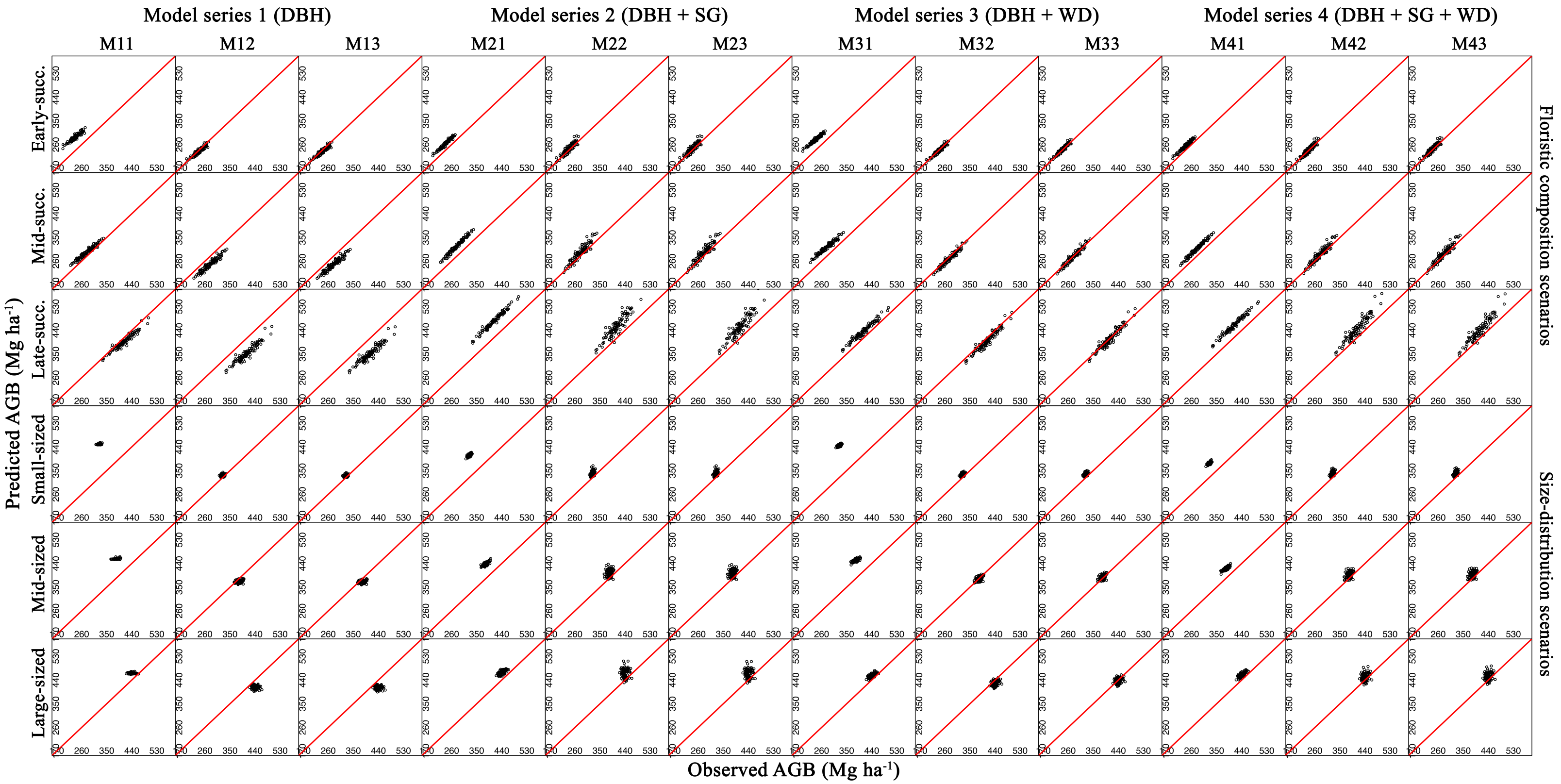

Figure 3. Predicted vs. observed aboveground biomass (AGB) along six forest-scenarios composed of 100 1-ha plots. The line of equality (1:1 line) is shown as a red/straight line. Forest scenarios were designed to reflect landscape-level variations in floristic composition and size-distribution of trees, typical of Central Amazon terra firme forests. Floristic composition and size-distribution scenarios followed the sampling scheme described in section 2.4.2 (Fig. 2) of this study. Models' predictors: diameter at breast height (DBH) (cm), species' successional group (SG) (pioneers, mid- and late-successional) and wood density (WD) (g cm^{-3}). See Tab. 2 for the variance modeling approach of different equations. Note that models containing total tree height (*H*) as predictor were excluded here.

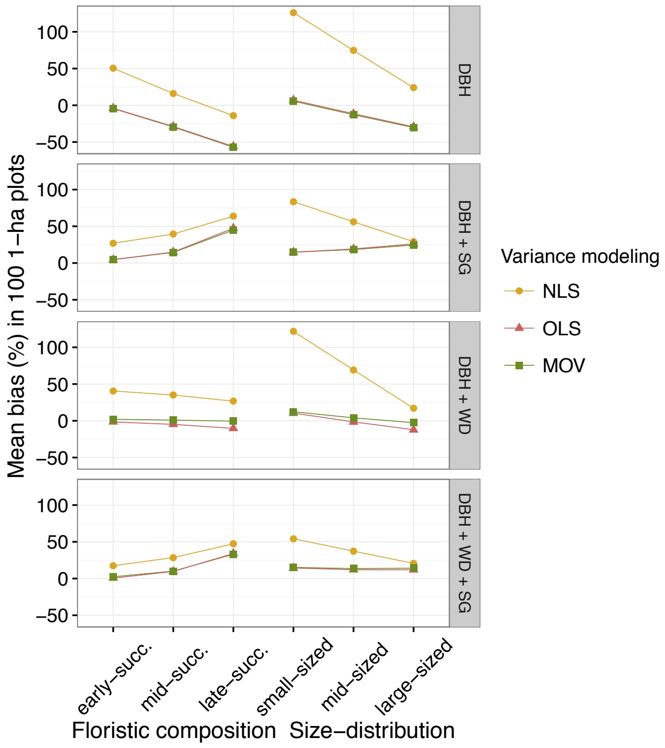

Figure 4. Profiles relating the bias of 12 tree aboveground biomass estimation models tested along six forest scenarios composed of 100 1-ha plots. Forest scenarios were designed to reflect landscape-level variations in floristic composition and size-distribution of trees, typical of Central Amazon terra firme forests. Models' predictors: diameter at breast height (DBH) (cm), species' successional group (SG) (pioneers, mid- and late-successional) and wood density (WD) (g cm^{-3}). Variance modeling approaches: non-linear least square (NLS), ordinary least square with log-linear regression (OLS) and non-linear with modeled variance (MOV). Note that models containing *H* tree height as predictor were excluded here.

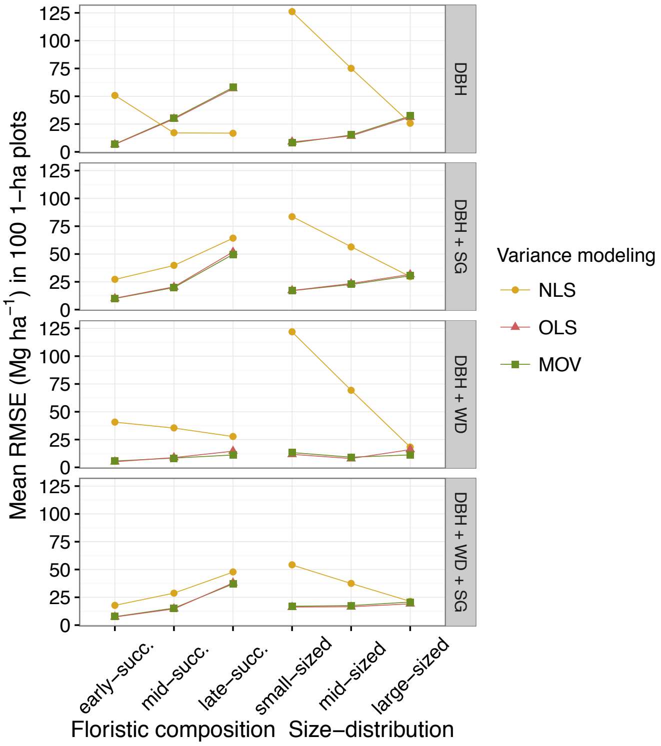

Figure 5. Profiles relating the RMSE root-mean-square error of 12 tree aboveground biomass estimation models tested along six forest scenarios composed of 100 1-ha plots. Forest scenarios were designed to reflect landscape-level variations in floristic composition and size-distribution of trees, typical of Central Amazon terra firme forests. Models' predictors: diameter at breast height (DBH) (cm), species' successional group (SG) (pioneers, mid- and late-successional) and wood density (WD) (g cm^{-3}). Variance modeling approaches: non-linear least square (NLS), ordinary least square with log-linear regression (OLS) and non-linear with modeled variance (MOV). Note that models containing *H* tree height as predictor were excluded here.

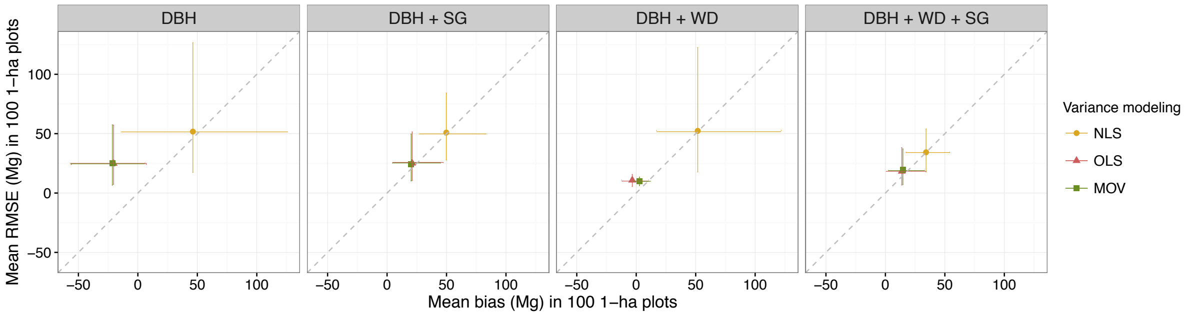

Figure 6. Overall performance of 12 tree aboveground estimation models along six forest-scenarios composed of 100 1-ha plots. Forest scenarios were designed to reflect landscape-

level variations in floristic composition and size-distribution of trees, typical of Central Amazon terra firme forests. Models are rated by the absolute mean bias and root-mean-square error (RMSE), both in Mg. Solid points and bars represent absolute mean and range values, respectively. Models' predictors: diameter at breast height (DBH) (cm), species' successional group (SG) (pioneers, mid- and late-successional) and wood density (WD) (g cm^{-3}). Variance modeling approaches: non-linear least square (NLS), ordinary least square with log-linear regression (OLS) and non-linear with modeled variance (MOV). Note that models containing *H* tree height as predictor were excluded here.