

Multilevel mixed-effect models to predict wood volume in a hyperdiverse Amazon forest

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ABSTRACT

Accurate wood volume predictions are critical in hyperdiverse forests because each species has specific size and shape traits. Although generic models at a multispecies level were widely used in Amazonian managed forests, they are subject to more significant bias due to interspecific variability. We used an extensive database of wood volume collected in managed forests to test the hypothesis that generic models violate the independence assumption due to that predictions vary with species-specific size. Our hypothesis was proved as residuals of the generic model were conditioned to species and specific size. The multilevel models were more accurate both in fitting and validation procedures, and accounted for variance derived from species and specific size, providing a more reliable prediction. However, we found that the size-specific models have a similar predictive ability to species-specific models for new predictions. This implies more practical estimates in hyperdiverse forests where fitting species-specific models can be complex. The findings are crucial for sustainable forest management as they allow for more reliable wood volume estimates, leading to less financial uncertainty and preventing damage to forest stocks through under or over-exploitation.

KEYWORDS: forest management, volume prediction, multispecies generic model, model improvement

Modelos multinível de efeito misto para prever o volume de madeira em uma floresta amazônica hiperdiversa

RESUMO

Previsões precisas do volume de madeira são críticas em florestas hiperdiversas, pois cada espécie tem características específicas de tamanho e forma. Embora modelos genéricos em nível multiespécie sejam amplamente utilizados em florestas manejadas na Amazônia, eles estão sujeitos a maiores vieses devido à variabilidade interespecífica. Usamos um extenso banco de dados de volume de madeira coletado em florestas manejadas para testar a hipótese de que modelos genéricos violam a suposição de independência, pois as previsões variam de acordo com o tamanho específico da espécie. Nossa hipótese foi comprovada pois os resíduos do modelo genérico foram condicionados à espécie e ao tamanho específico. Os modelos multiníveis foram mais precisos nos procedimentos de ajuste e de validação e contabilizaram a variância derivada de espécies e do tamanho específico, fornecendo previsões mais confiáveis. Descobrimos que os modelos específicos de tamanho têm capacidade preditiva semelhante aos específicos da espécie para novas previsões. Isto implica em estimativas mais práticas em florestas hiperdiversas, onde pode ser complexo o ajuste de modelos específicos por espécies. As conclusões são cruciais para o manejo florestal sustentável, pois permitem estimativas mais confiáveis do volume de madeira, conduzindo a menor incerteza financeira e evitando danos aos estoques florestais devido à sub ou superexploração.

PALAVRAS-CHAVE: manejo florestal, previsão de volume, modelo genérico multiespécie, melhoria do modelo

INTRODUCTION

Accurate predictions of individual tree volume are essential for forest management planning. These estimates are critical in hyperdiverse forests since each species has specific size and shape traits. Given this, local-specific volume models are required by the Brazilian forestry law (Brasil 2009) to control wood volume derived from managed forests in the Amazon (Leão et al. 2021). Allometric models in hyperdiverse forests are classified into two categories: species-specific, which often provides more accurate estimates, and generic or multispecies, which groups several species in a single equation and may lead to biased estimates due to the high interspecific allometry variability (Bojórquez et al. 2020; Magalhães et al. 2021). Some recent studies proved the greater accuracy of species-specific equations for volume predictions in Amazonian managed forests (Santos et al. 2020; Silva et al. 2022). However, it is still unclear how species may affect volume estimates, and further studies are needed to elucidate mechanisms for developing specific volume equations (Lima et al. 2020).

Another critical methodological issue is the ordinary least squares (OLS) fitting method, the primary method applied to fit allometric models (Zar 1968; Brown et al. 1989). Some error assumptions should be met by the data to fit OLS models, such as independence, normality, and homoscedasticity (Burnham and Anderson 2002; Zuur et al. 2010). These assumptions are often ignored, inducing incorrect research conclusions and biased predictions (Dutcă et al. 2018). Allometric models are not independent when data are hierarchically clustered into other variables, e.g., trees from the same species, plot/site, or age may be more similar in allometry (Kearsley et al. 2017). In these situations, models are subjected to nested sources of variability (Hall and Bailey 2001) derived from hierarchical data structure.

When OLS models violate the independence assumption in hierarchical data, another modeling approach is highly recommended (Dutcă et al. 2018). Mixed-effect models may be a suitable approach to account for the non-independence and error autocorrelation (Banin et al. 2012). This approach finds simultaneous estimators for all levels, incorporating random effects that provide hierarchical predictions (Robinson and Hamann 2011; Nascimento et al. 2020). Multilevel mixed-effects models are helpful in a wide range of forestry applications (Hall and Bailey 2001). Although significant improvements were obtained in monospecific stands, mixed models have been applied less frequently in tropical forests, where predictive gains could be high given the high species diversity and allometric variability (Colmanetti et al. 2020). Additionally, few studies used this approach for the improvement of volume estimates (Vismara et al. 2015), particularly in Amazonia.

We hypothesized that local generic models violate the independence assumption because predictions vary with species-specific size. If this hypothesis is not rejected, disregarding data hierarchical structure, two consequences are assumed for wood volume prediction in Amazonian managed forests: (1) generic models tend to underestimate the volume of large-sized species and overestimate the volume of small-sized species; and (2) this tendency can bias new predictions. In this context, this study aimed to apply multilevel mixed-effects modeling to evaluate the effects of hierarchical data on generic volume predictions, comparing the results with a generic multispecies model.

MATERIAL AND METHODS

Study area and field data

The study area is Jamari National Forest (JNF), Rondônia state, southwestern Brazilian Amazon (09°30'00"S, 63°16'64"W). The local climate is classified as Kw, with a well-defined dry period in winter according to the Köppen system, with 2,400 mm of mean annual precipitation and 25 °C of mean annual temperature (Alvares et al. 2013). The vegetation is evergreen tropical rainforest, varying between open and dense forest types (Cysneiros et al. 2017a). JNF is a protected area of sustainable use, in which a part of the landscape is destined for forest management under reduced impact logging by authorized companies (Brasil 2000). We used an extensive local database of tree volume collected between 2014 and 2015 in managed forests. Wood volume (V) from 5,010 harvested trees (diameter at breast height, DBH ≥ 50 cm) was measured by Smalian's method (Machado and Figueiredo Filho 2014). The database included 21 species, with 80% (4,008) of trees used for model fitting and 20% (1,002) for validation. Datasets were randomly selected, maintaining the sampling ratio constant (80:20) for each species (Table 1).

Species-specific size

The maximum individual diameter and volume per species were used as size descriptors for clustering species in size groups. We specified three groups *a priori* by k-means clustering ($k = 3$), using the Ward method and Euclidian distance in *factoextra* R package (Kassambara and Mundt 2020). This procedure resulted in three hierarchical size groups (small, medium, and large) (Figure 1a), with distinct allometric patterns (Figure 1b,c). Average DBH and average wood volume were of up to 76 cm and 6.4 m³, respectively, for small-sized species; up to 98 cm and 10.5 m³ for medium-sized species; and up to 120 cm and 17 m³ for large-sized species.

Generic model

Only single predictor models were used to test our hypothesis. A generic model (GM) was fitted at a multispecies level to predict wood volume (V) as a function of diameter

Table 1. Sample size (N), DBH (diameter at breast height) and volume (Vol) of timber tree species from Jamari National Forest (Rondônia, Brazil) used in this study. Values are the mean ± standard deviation for each size group (small, medium, and large trees, see Material and Methods for size definitions). Id is the identification of species name acronyms (see Table 1).

Species	Family	Id	Fitting			Validation		
			N	DBH (cm)	Vol (m ³)	N	DBH (cm)	Vol (m ³)
Small sized								
<i>Brosimum rubescens</i> Taub.	Moraceae	rub	103	75.6 ± 14.3	5.49 ± 2.3	26	76.5 ± 10.7	5.58 ± 1.8
<i>Clarisia racemosa</i> Ruiz & Pav.	Moraceae	rac	233	69.9 ± 9.9	4.29 ± 1.3	58	72.7 ± 9.2	5.03 ± 1.8
<i>Dipteryx odorata</i> (Aubl.) Willd.	Fabaceae	odo	230	75.1 ± 15.4	5.53 ± 2.7	57	73.5 ± 15.0	5.62 ± 3.2
<i>Erisma fuscum</i> Ducke	Vochysiaceae	fus	70	75.4 ± 16.3	6.03 ± 2.4	17	73.0 ± 12.7	5.22 ± 1.8
<i>Hymenaea intermedia</i> Ducke	Fabaceae	int	62	71.7 ± 13.8	6.34 ± 2.6	15	74.8 ± 15.6	6.21 ± 2.0
<i>Peltogyne paniculata</i> Benth.	Fabaceae	pan	590	67.7 ± 10.4	4.13 ± 1.4	148	69.7 ± 11.1	4.07 ± 1.5
<i>Pouteria guianensis</i> Aubl.	Sapotaceae	gui	52	64.5 ± 9.7	4.02 ± 1.2	13	65.2 ± 9.1	3.70 ± 0.8
<i>Qualea paraensis</i> Ducke	Vochysiaceae	par	195	67.7 ± 11.9	5.32 ± 2.2	49	68.7 ± 12.3	5.55 ± 2.4
Medium sized								
<i>Allantoma decandra</i> (Ducke)	Lecythidaceae	dec	56	80.8 ± 18.1	7.30 ± 3.9	14	79.2 ± 16.0	6.46 ± 3.0
<i>Apuleia leiocarpa</i> (Vogel) J.F.Macbr.	Fabaceae	lei	121	87.0 ± 19.7	8.04 ± 3.9	30	89.9 ± 19.5	10.42 ± 5.3
<i>Astronium lecointei</i> Ducke	Anacardiaceae	lec	612	75.8 ± 13.7	7.61 ± 3.2	153	74.9 ± 15.2	8.20 ± 3.8
<i>Caryocar glabrum</i> Pers.	Caryocaraceae	gla	114	79.6 ± 16.8	5.81 ± 2.8	29	81.2 ± 16.3	6.12 ± 3.3
<i>Caryocar villosum</i> (Aubl.) Pers.	Caryocaraceae	vil	55	90.1 ± 16.3	7.34 ± 3.3	14	91.4 ± 16.8	7.49 ± 3.2
<i>Cedrelinga cateniformis</i> Ducke	Fabaceae	cat	45	95.2 ± 24.0	9.47 ± 5.4	11	97.9 ± 21.7	11.35 ± 6.5
<i>Erisma bicolor</i> Ducke	Vochysiaceae	bic	82	79.8 ± 17.9	6.42 ± 3.4	21	84.2 ± 16.3	6.66 ± 3.2
<i>Goupia glabra</i> Aubl.	Goupiaceae	ggl	147	83.3 ± 17.7	5.79 ± 2.7	37	82.9 ± 15.9	6.85 ± 4.1
<i>Handroanthus incanus</i> (Gentry) Grose	Bignoniaceae	inc	50	73.1 ± 13.3	6.53 ± 3.6	12	83.8 ± 21.1	7.38 ± 4.3
Large Sized								
<i>Cariniana micrantha</i> Ducke	Lecythidaceae	mic	98	112.7 ± 30.9	16.50 ± 8.5	25	120.7 ± 31.7	16.92 ± 8.6
<i>Couratari stellata</i> A.C.Sm.	Lecythidaceae	ste	404	88.3 ± 18.4	10.81 ± 5.3	101	86.7 ± 18.0	9.97 ± 4.2
<i>Dinizia excelsa</i> Ducke	Fabaceae	exc	434	104.3 ± 25.3	13.97 ± 7.3	109	106.5 ± 26.0	14.40 ± 6.8
<i>Hymenolobium heterocarpum</i> Ducke	Fabaceae	het	254	93.3 ± 24.9	10.52 ± 6.1	64	95.7 ± 24.5	11.25 ± 6.6

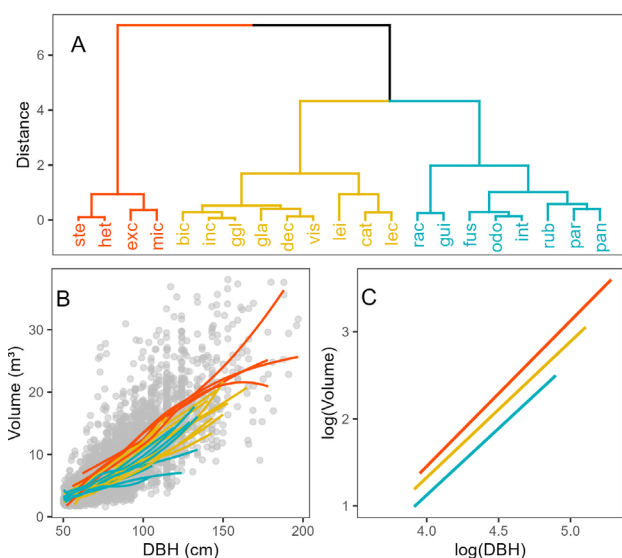


Figure 1. Grouping of 21 timber tree species from Jamari National Forest (Rondônia, Brazil) according to their specific size (maximum DBH and volume (V) in the sample). A – hierarchical clustering into three size groups: small (blue), medium (yellow), and large (red); B – V × DBH relationship by species (colors indicate the size group as in A and dots indicate the V × DBH measurements); C – size-group mean logV × logDBH relationship. See Table 1 for the correspondence of species name acronyms in (A).

at breast height (DBH). GM was fitted by the ordinary least squares (OLS) method. Log transformation was applied to obtain a linear relationship between volume and diameter (Figure 1c). This transformation is commonly used to describe tree allometric relationships with advantages for modeling performance (Brown et al. 1989), as it can produce more accurate estimations of parameters and confidence intervals (Xiao et al. 2011). Back-transformation biases were corrected by the correction factor given by the square of residual variance divided by two (Baskerville 1972). All statistics were computed using corrected predictions. Data normality was assessed with the Shapiro-Wilk test and variance homogeneity by the non-constant variance score test.

Due to non-constant residuals, an explicit model for the variance was needed (Kangas et al. 2022). The variance was modeled as the power of DBH (Robinson and Hamann 2011). This provided significantly better fitting (likelihood ratio test, $P < 0.001$) than the previous OLS model, in which error was modeled as constant variance. The form of the final generic model was expressed as in Equation 1:

$$\log(V) = \beta_0 + \beta_1 * \log(DBH_{ij}) + \epsilon_{ij} \quad (1)$$

where V is the stem volume (m^3), DBH is the stem diameter at breast height (cm), β_0 is the intercept coefficient, β_1 is the slope coefficient, and ε_{ij} is the error assumed as a power of DBH .

This model does not consider the hierarchical structure of the data (Dutcă et al. 2018), however, several sources of variation may affect it (Robinson and Hamann 2011), including the differences among species (Hulshof et al. 2015).

Multilevel mixed models

Mixed-effects modeling account for intra and interspecific variability (Magalhães et al. 2021). These models were named multilevel (Hall and Bailey 2001) to alude at the purpose of the model to estimate hierarchical predictions simultaneously for different levels. We incorporated species and species-specific size as random effects, as specific size and allometric relationships ($V \times DBH$) vary among the species (Figure 1b,c). Three hierarchical forms were compared to test the model's random structure: 1) fixed model, no random effects (Equation 1); 2) random intercept and fixed slope model (Equation 2); and 3) random intercept and slope model, both varying across levels (Equation 3).

$$\log(V) = (\beta_0 + b_{0i}) + \beta_1 * \log(DBH_{ij}) + \varepsilon_{ij} \quad (2)$$

$$\log(V) = (\beta_0 + b_{0i}) + (\beta_1 + b_{1i}) * \log(DBH_{ij}) + \varepsilon_{ij} \quad (3)$$

where β_0 and β_1 are the fixed terms, respectively the intercept and slope coefficients of the general relationship; b_{0i} and b_{1i} are the random effect terms of β_0 and β_1 , under effect of i levels, that express the intraspecific effect and size-specific effect; and ε_{ij} is the model error assumed as level-dependent.

These models were tested to accommodate species and species size, assuming specific $V \times DBH$ relationships (Nascimento et al. 2020), so that predictions are provided for each hierarchical level of the database. The random structure selection was based on Akaike's information criterion (AIC) and likelihood ratio tests (LRT). In addition, we reported the marginal R^2 , which includes the variance of fixed effects, and conditional R^2 , which includes the variance of fixed and random effects (Nakagawa and Schielzeth 2013). The mixed models were fitted using the restricted maximum likelihood method (REML) to test the significance of including the random effects (Kearsley et al. 2017).

Data analysis

To test our hypothesis, the residuals of the generic model were evaluated by species and species size. ANOVA was used to test if residuals were level-dependent. Tukey's post-hoc test was used to verify how residuals differ between species and species size. The intraclass correlation coefficient (ICC) (Equation 4) was computed to evaluate the performance of multilevel models to account for error autocorrelation. ICC shows the proportion of variance derived from the differences between levels (Dutcă et al. 2018) and varies between 0 and 1: values close to 0 indicate that most of the variance derives

from differences between trees within levels, and values close to 1 indicate a strong correlation between trees and that the variance results from differences between levels.

$$ICC = \tau^2 / (\tau^2 + \sigma^2) \quad (4)$$

where τ^2 is the random variance caused by variation between levels; and σ^2 is the residual variance caused by difference between trees within levels.

Bias (Equation 5), root mean square error (RMSE) (Equation 6), relative root mean square error (RRMSE) (Equation 7), coefficient of determination (R^2) (Equation 8), and AIC values (Equation 9) were computed to compare the goodness-of-fit of the approaches. The validation dataset was used to test the models' predictive performance, using bias, RMSE, and RRMSE. We used a Tukey's test to compare the observed and estimated volume by species size to evaluate the expectation of bias propagation to new predictions. All statistical tests were performed at a 1% significance level. The models were fitted using the *nlme* R package (Pinheiro et al. 2021). Statistical assumptions of normality and variance homogeneity were checked for all models. All statistical analyses were performed using R version 4.0.3 (R Core Team 2021).

$$Bias = (\sum(y_i - \hat{y}_i)) / n \quad (5)$$

$$RMSE (m^3) = \sqrt{((\sum(y_i - \hat{y}_i)^2) / (n-1))} \quad (6)$$

$$RRMSE (\%) = ((RMSE(m^3)) / (\sum(y_i) / n)) * 100 \quad (7)$$

$$R^2 = 1 - [(\sum(y_i - \hat{y}_i)^2) / (\sum(y_i - \bar{y})^2)] \quad (8)$$

$$AIC = -2\log L_i + 2P_i \quad (9)$$

where y_i is the observed stem volume (m^3), \hat{y}_i is the predicted stem volume, \bar{y} is the mean of observed stem volume, n is the number of observations (measured trees), L_i is model maximum likelihood, and P_i is the number of model coefficients.

RESULTS

Generic model

The hypothesis of independence violation for the generic model was accepted as residuals were dependent on species and species size (Tukey's test for species: $P < 0.01$; Tukey's test for size: $P < 0.01$; Figure 2). This means that the errors of the generic model were not random, but related to groups displaced from the overall mean (Figure 2). Although residuals for species may show distinct patterns, in general they followed the expected tendency of underestimation for large species and overestimation for small species. This tendency was more evident for species size, as expected for generic models in hyperdiverse forests. Residuals were significantly higher for large species and lower for small species (Tukey's test: $P < 0.01$), suggesting that generic models can be more accurate for medium-sized species and less accurate for smaller and larger species.

Multilevel mixed models

The mixed-effects model structure (Table 2) confirmed the occurrence of species-specific size allometry (Figure 1) as intercept and slope coefficients varied significantly with species and species size (Supplementary Material, Table S1). All coefficients of mixed models were significant ($P < 0.01$), with high variation between levels. Species- and size-specific models with random intercept and slope were obtained after the structure selection in a mixed modeling approach (Table 2). These were the most parsimonious models, significantly improving volume modeling (likelihood ratio tests: $P < 0.01$). Improvements were also obtained to account for the residual autocorrelation and deal with independence violation (low ICC), suggesting that multilevel mixed models can provide more reliable volume predictions in hyperdiverse forests.

Model comparison

The accuracy significantly differed among modeling approaches in fitting and validation procedures (Table 3). Compared to the generic model, the fit of multilevel mixed models improved the volume explanation by 8.4% (species-specific model) and 6.3% (size-specific model), while accuracy increased by 4.9% (0.38 m^3) and 3.6% (0.28 m^3), respectively. The species-specific model showed the best goodness of fit. Still, the size-specific model showed a lower residual autocorrelation (Table 2), appropriate for dealing with

hierarchical data structure. When applied to the validation dataset, multilevel mixed models increased accuracy by 4.1% (0.33 m^3) and 3.0% (0.25 m^3), respectively. The validation procedure confirmed the second expected consequence derived from our hypothesis (that tendency of the generic model is propagated to new predictions) (Figure 3). The

Table 2. Selection of mixed-effect model structure to predict wood volume as a function of DBH for a dataset of 21 timber tree species from Jamari National Forest (Rondônia, Brazil). R^2_m is the variance explained by fixed effects; all effects explain R^2_c ; AIC is the Akaike information criterion; ICC is the intraclass correlation; LRT is the likelihood ratio test; GM = generic model; MMsp = species-specific multilevel model; MMsZ = size-specific multilevel model.

Model	R^2_m	R^2_c	AIC	ICC	LRT	Structure
Do V x DBH relationships differ by species?						
GM		0.608	2916			no random effects
MMsp1	0.568	0.665	1875	0.223	**	β_0 random, β_1 fixed
MMsp2	0.564	0.674	1853	0.251	**	β_{0i} , β_1 random
Do V x DBH relationships differ by species size?						
GM		0.608	2916			no random effects
MMsz1	0.534	0.623	2351	0.191	**	β_0 random, β_1 fixed
MMsz2	0.531	0.620	2348	0.193	**	β_{0i} , β_1 random

** significant at the 0.01 level.

Table 3. Comparison of fit and validation performance among a generic model (GM), a species-specific multilevel model (MMsp), and a size-specific multilevel model (MMsz) to predict wood volume as a function of DBH for a dataset of 21 timber tree species from Jamari National Forest (Rondônia, Brazil). RMSE = root mean square error; RRMSE = relative root mean square error; R^2 = coefficient of determination; AIC = Akaike's information criterion.

Model	Fitting					Validation		
	Bias	RMSE (m^3)	RRMSE (%)	R^2	AIC	Bias	RMSE (m^3)	RRMSE (%)
GM	0.446	3.378	43.26	0.608	2916	0.533	3.267	40.31
MMsp	0.018	2.994	38.35	0.692	1853	0.146	2.937	36.24
MMsz	0.021	3.097	39.66	0.671	2348	0.134	3.021	37.28

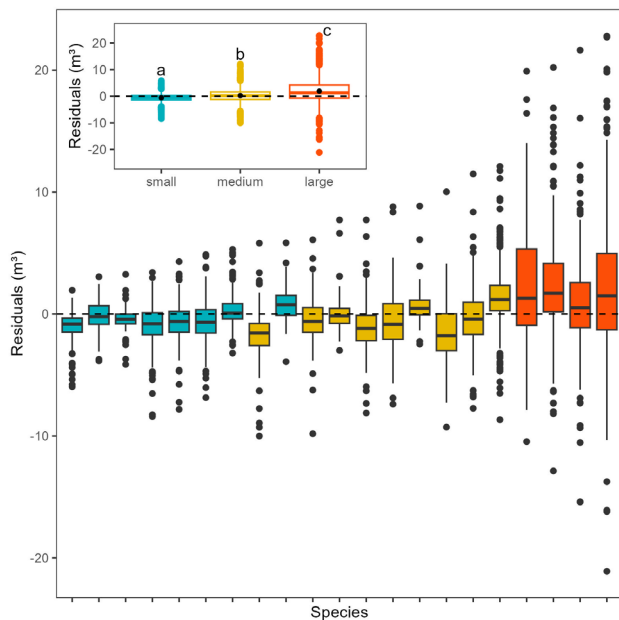


Figure 2. Residuals for species and tree size groups of the generic model fitted at multispecies level to predict wood volume as a function of DBH for a dataset of 21 timber tree species from Jamari National Forest (Rondônia, Brazil). Different letters above the averages of size group residuals indicate statistically significant differences according to Tukey's test. In the boxplots, the box represents the interquartile range (IQR) of the residuals from the first quartile (Q1) to the third quartile (Q3); the solid line is the median of the residuals; the points are outlier residuals; and the whiskers are the range of the residuals outside the IQR (minimum and maximum values, respectively).

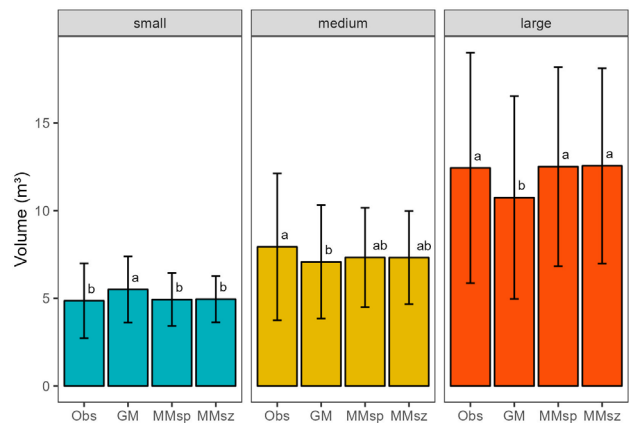


Figure 3. Comparison of measured volume (Obs) and volume predicted by the generic model (GM), species-specific multilevel model (MMsp), and size-specific multilevel model (MMsz) using the validation dataset of 21 timber tree species from Jamari National Forest (Rondônia, Brazil). Columns represent the mean and bars the standard deviation of the predicted volume. Different letters above the columns indicate statistically significant differences within size groups according to Tukey's test.

generic model significantly underestimated the volume of medium and large species and overestimated that of small species (Tukey's test: $P < 0.01$). Species- and size-specific models provided predictions significantly adherent to the observed volume ($P > 0.01$).

DISCUSSION

Most timber volume models fitted in the Brazilian Amazon are multispecies, although they do not consider the hierarchical structure of the data. This study showed that generic models are less recommendable for volume stock assessments in hyperdiverse forests because predictions depend on species-specific traits. Our results also demonstrated that multilevel mixed models improve volume predictions because they can account for the effects of species and species size. Additionally, species- and size-specific models presented a similar performance for new predictions. This carries practical applications to managing hyperdiverse forests, where occasionally it is not easy to fit species-specific models.

Non-independence of generic models

Generic multispecies models have been widely used for volume estimation in Amazonian managed forests (Tonini and Borges 2015; Gimenez *et al.* 2016; Romero *et al.* 2020) because they require only DBH measurements to be applied (Colmanetti *et al.* 2020). However, our results showed that the predictions of generic models cannot be considered independent in hyperdiverse forests because data are grouped within species. Due to the hierarchical data structure, the variance among trees is associated with intra- and interspecific variability, particularly relative to size allometry (Dutcă *et al.* 2018). Consequently, the residuals generated by the generic model were autocorrelated. As models that ignore clustered data often report biased results (Dutcă *et al.* 2018), the volume predictions varied among our size groups as expected, with underestimations in large-sized species and overestimations in small-sized species, propagating these biases to new predictions.

Improvements using multilevel mixed modeling

Including random effects improved model performance, especially in dealing with independence assumptions that compromise modeling inference (Hall and Bailey 2001). Mixed models improve volume predictions because they account for intraspecific variability, as a given DBH value can differ largely in its associated volume among levels. Therefore, our fitted mixed models accommodated the variance produced by species and species size, correcting prediction errors (Dutcă *et al.* 2018). Our results agree with previous studies that found that hierarchical models by species provide more accurate estimates than generic models (Bojórquez *et al.* 2020; Nascimento *et al.* 2020; Magalhães *et al.* 2021; Abreu *et al.* 2022). Compared to traditional

modeling, mixed-effects fitting usually requires fewer sampled trees, reducing the sampling cost (Colmanetti *et al.* 2020). In addition, this approach easily allows additional hierarchies to be incorporated into fitted models (Lam *et al.* 2017). Mixed models also exclude the need to fit an equation for each species once a single model provides hierarchical predictions at several levels (Nascimento *et al.* 2020; Abreu *et al.* 2022).

Implications for volume prediction

Similarity among models in their species- and size-specific predictive ability suggest some practical implications for volume prediction in hyperdiverse forests. First, fitting mixed models are usually restricted to the same set of species, which is challenging in hyperdiverse forests (Colmanetti *et al.* 2020). Second, rare species, which are common in the Amazon forest (Schulze *et al.* 2008) are limiting for species-specific model fitting (Cysneiros *et al.* 2017a). Grouping species by size may solve this issue, but a large sample size is required to reliably classify new species into a size group (Cysneiros *et al.* 2017b). However, mixed models are efficient only when random effects are expressive (Vismara *et al.* 2015), i.e., if a random effect is similar to the population mean no benefit will be observed in using these models, and the fixed-effects models may be more appropriate (Colmanetti *et al.* 2020). Furthermore, even using species-specific equations, parameters can vary depending on the location (Colmanetti *et al.* 2020), which must be controlled when using equations across different sites.

The validation procedure showed that mixed models were more accurate than the tested generic model. Although the prediction deviation among models was numerically small, it represents a substantial wood volume. From an overall wood volume of 8,128 m³ in the validation dataset, 535 m³ were underestimated by the generic model, against 146 m³ by the species-specific and 134 m³ by the size-specific models. Considering the average Amazon logwood price as US\$ 164 per m³ (ITTO 2023), the biased predictions of the generic model represent a financial uncertainty of approximately US\$ 87,740, which represents only 20% (the validation dataset) of all trees harvested over two years at our study site. Notably, the bias was higher for large species, which is crucial for forest planning as large timber species are spatially clustered in the study area (Péllico Netto *et al.* 2017).

Allometric predictions are frequently based on variables measured in forest inventories for wood stock assessment in large areas (McRoberts and Westfall 2016; Leão *et al.* 2021) thus biased wood volume estimates can generate significant financial uncertainty and lack of control over remaining and managed stocks (Rolim *et al.* 2006; Leão *et al.* 2021). Sustainable forest management depends on reliable estimates of wood volume at tree and stand level, especially in hyperdiverse tropical forests. Further studies are needed to quantify the consequences of biased predictions for forest management financial and tactical planning, and improve the

estimates that regulate virtual credits for wood in Amazonian forests (Andrade et al. 2023).

CONCLUSIONS

Our study showed that generic multispecies models for volume prediction violate the independence assumption in hyperdiverse forests and can fail to make new predictions based on species and species size, proving the expected consequences deriving from our hypothesis. The tendency to underestimate the volume of large-sized species and overestimate the volume of small-sized species was propagated to new predictions. Multilevel mixed models accounted for interspecific variability and reduced error autocorrelation, providing more accurate predictions of timber wood volume and reducing financial uncertainty and potential damage to forest stocks.

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REFERENCES

- Abreu, J.C.; Lima, R.B.; Rabelo, F.G.; Santos, H.K.V.; Silva, T.T.; Santos, M.M. 2022. Mixed-effect models for volumetric estimation of lumber from native Amazon species. *Floresta*, 52: 384-393.
- Alvares, C.A.; Stape, J.L.; Sentelhas, P.C.; de Moraes Gonçalves, J.L.; Sparovek, G. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, 22: 711-728.
- Andrade, K.D.C.; Santos, A.P.F.; Emmert, F.; Santos, J.; Lima, A.J.N.; Higuchi, N. 2023. Volumetric yield coefficient: the key to regulating virtual credits for Amazon wood. *Acta Amazonica*, 53: 1-8. doi.org/10.1590/1809-4392202101602
- Banin, L.; Feldpausch, T.R.; Phillips, O.L.; Baker, T.R.; Lloyd, J.; Affum-Baffoe, K.; et al. 2012. What controls tropical forest architecture? Testing environmental, structural and floristic drivers: Determinants of tropical forest architecture. *Global Ecology and Biogeography*, 21: 1179-1190.
- Baskerville, G.L. 1972. Use of logarithmic regression in the estimation of plant biomass. *Canadian Journal of Forest Research*, 2: 49-53.
- Bojórquez, A.; Martínez-Yrizar, A.; Búrquez, A.; Jaramillo, V.J.; Mora, F.; Balvanera, P.; Álvarez-Yépiz, J.C. 2020. Improving the accuracy of aboveground biomass estimations in secondary tropical dry forests. *Forest Ecology and Management*, 474: 118384.
- Brasil. 2000. Lei Federal Nº 9.985, de 18 de julho de 2000. Federal law that creates the National System of Nature Conservation Units of Brazil. (http://www.planalto.gov.br/ccivil_03/LEIS/L9985.htm). Accessed on 21 July 2022.
- Brasil. 2009. Resolução Conama nº 406, de 02 de fevereiro de 2009. Establishes technical parameters for sustainable forest management plans in Brazil. (<https://www.ibama.gov.br/component/legislacao/?view=legislacao&legislacao=114762>). Accessed on 18 Jan 2023
- Brown, S.; Gillespie, A.; Lugo, A.E. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Science*, 35: 881-902.
- Burnham, K.P.; Anderson, D.R. 2002. *Model Selection and Inference: A Practical Information-Theoretic Approach*, 2nd ed. Springer, New York, 355p.
- Colmanetti, M.A.A.; Weiskittel, A.; Scolforo, H.F.; Sotomayor, J.F.M.; Couto, H.T.Z. 2020. Calibrating individual tree biomass models for contrasting tropical species at an uneven-aged site in the native Atlantic Forest of Brazil: A direct comparison of alternative approaches, sample sizes, and sample selection methods. *Forest Ecology and Management*, 473: 118306.
- Cysneiros, V.C.; Pelissari, A.L.; Machado, S.A.; Figueiredo Filho, A.; Souza, L. 2017a. Modelos genéricos e específicos para estimativa do volume comercial em uma floresta sob concessão na Amazônia. *Scientia Forestalis*, 45: 295-304.
- Cysneiros, V.C.; Pelissari, A.L.; Machado, S.A.; Figueiredo-Filho, A.; David, H.C. 2017b. Cluster and discriminant analyses for stem volume modelling of tree species groups in an Amazon rainforest. *Journal of Tropical Forest Science*, 29: 325-333.
- Dutcă, I.; Stăncioiu, P.T.; Abrudan, I.V.; Ioras, F. 2018. Using clustered data to develop biomass allometric models: The consequences of ignoring the clustered data structure *PLoS ONE*, 13: e0200123.
- Gimenez, B.O.; Danielli, F.E.; Oliveira, C.K.A.; Santos, J.; Higuchi, N. 2015. Equações volumétricas para espécies comerciais madeireiras do sul do estado de Roraima. *Scientia Forestalis*, 43: 291-301.
- Hall, D.B.; Bailey, R.L. 2001. Modeling and prediction of forest growth variables based on multilevel nonlinear mixed models. *Forest Science*, 47: 311-321.
- Hulshof, C.M.; Swenson, N.G.; Weiser, M.D. 2015. Tree height-diameter allometry across the United States. *Ecology and Evolution*, 5: 1193-1204.
- ITTO. 2023. *ITTO Tropical Timber Market Report*. 27:16. 32p. (https://www.atibt.org/files/upload/news/ITTO/MIS_1-15_Aug2023.pdf). Accessed on 04 Sep 2023.
- Kangas, A.; Pitkänen, T.P.; Mehtätalo, L.; Heikkinen, J. 2022. Mixed linear and non-linear tree volume models with regional parameters to main tree species in Finland. *Forestry*, 96: 1-19. doi:10.1093/forestry/cpac038
- Kassambara, A.; Mundt, F. 2020. *Factoextra: Extract and Visualize the Results of Multivariate Data Analyses*. R Package Version 1.0.7. (<https://CRAN.R-project.org/package=factoextra>).
- Kearsley, E.; Moonen, P.C.; Hufkens, K.; Doetterl, S.; Lisingo, J.; Boyemba Bosela, F.; Boeckx, P.; Beeckman, H.; Verbbeeck, H. 2017. Model performance of tree height-diameter relationships in the central Congo Basin. *Annals of Forest Science*, 74: 7. doi:10.1007/s13595-016-0611-0

- Lam, T.Y.; Kershaw, J.A.; Hajar, Z.S.N.; Rahman, K.A.; Weiskittel, A.R.; Potts, M.D. 2017. Evaluating and modelling genus and species variation in height-to-diameter relationships for Tropical Hill Forests in Peninsular Malaysia. *Forestry*, 90: 268-278.
- Leão, F.M.; Nascimento, R.G.N.; Emmert, F.; Santos, G.G.A.; Caldeira, N.A.M.; Miranda, I.S. 2021. How many trees are necessary to fit an accurate volume model for the Amazon Forest? A site-dependent analysis. *Forest Ecology and Management*, 480: 118652.
- Lima, R.B.; Ferreira, R.L.C.; Silva, J.A.A.; Guedes, M.C.; Abreu, J.C.; Oliveira, C.P.; et al. 2020. Improving the forecasts of commercial timber volume in transition forest in the northern Brazilian Amazon. *Southern Forests*, 82: 148-158.
- Machado, S.M.; Figueiredo Filho, A. 2014. *Dendrometria*, 2nd ed. Editora Unicentro, Guarapuava, 316p.
- Magalhães, T.M.; Cossa, V.N.; Guedes, B.S.; Fanheiro, A.S.M. 2021. Species-specific biomass allometric models and expansion factors for indigenous and planted forests of Mozambique highlands. *Journal of Forestry Research*, 32: 1047-1065.
- McRoberts, R.E.; Westfall, J.A. 2016. Effects of uncertainty in model predictions of individual tree volume on large area volume estimates. *Forest Science*, 60: 34-42.
- Nakagawa, S.; Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4: 133-142.
- Nascimento, R.G.M.; Vanclay, J.K.; Figueiredo Filho, A.; Machado, S.A.; Ruschel, A.R.; Hiramatsu, N.A.; Freitas, L.J.M. 2020. The tree height estimated by non-power models on volumetric models provides reliable predictions of wood volume: The Amazon species height modelling issue. *Trees, Forests and People*, 2: 100028.
- Péllico Netto, S.; Pelissari, A.L.; Cysneiros, V.C.; Bonazza, M.; Sanquetta, C.R. 2017. Sampling procedures for inventory of commercial volume tree species in Amazon Forest. *Anais da Academia Brasileira de Ciências*, 89: 1829-1840.
- Pinheiro, J.; Bates, D.; DebRoy, S. 2021. *nlme: Linear and Nonlinear Mixed Effects Models*. R package version R 4.1. (<https://CRAN.R-project.org/package=nlme>).
- R Core Team. 2021. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Robinson, A.; Hamann, J.D. 2011. *Forest Analytics with R: An Introduction*. Springer, New York, 354p.
- Rolim, S.G.; Couto, H.D.; Jesus, R.D.; França, J.T. 2006. Modelos volumétricos para a Floresta Nacional do Tapirapé-Aquirí, Serra dos Carajás (PA). *Acta Amazonica*, 36: 107-114.
- Romero, F.M.B.; Jacovine, L.A.G.; Ribeiro, S.C.; Torres, C.M.M.E.; Silva, L.F.; Gaspar, R.O.; Rocha, S.J.S.S.; Staudhammer, C.L.; Fearnside, P.M. 2020. Allometric equations for volume, biomass, and carbon in commercial stems harvested in a managed forest in the southwestern Amazon: A case study. *Forests*, 11: 814. doi:10.3390/f11080874
- Santos, M.F.; Figueiredo Filho, A.; Gama, J.R.V.; Retslaff, F.A.S.; Costa, D.L. 2020. Species-specific equations: Greater precision in commercial volume estimation in managed forests in the Amazon. *Cerne*, 26: 315-330.
- Schulze, M.; Grogan, J.; Landis, R.M.; Vidal, E. 2008. How rare is too rare to harvest? Management challenges posed by timber species occurring at low densities in the Brazilian Amazon. *Forest Ecology and Management*, 256: 1443-1457.
- Silva, I.C.O.; Garlet, J.; Morais, V.A.; Araújo, E.J.G.; Silva, J.R.O.; Curto, R.D.A. 2022. Equations and Form Factor by species increase the precision and accuracy for estimating tree volume in the Amazon. *Floresta*, 52: 268-276.
- Tonini, H.; Borges, R.A. 2015. Equação de volume para espécies comerciais em Floresta Ombrófila Densa no sul de Roraima. *Pesquisa Florestal Brasileira*, 35: 111-117.
- Vismara, E.S.; Mehtälö, L.; Batista, J.L.F. 2015. Linear mixed-effects models and calibration applied to volume models in two rotations of *Eucalyptus grandis* plantations. *Canadian Journal of Forest Research*, 24: 132-141.
- Xiao, X.; White, E.P.; Hooten, M.B.; Durham, S.L. 2011. On the use of log-transformation vs. nonlinear regression for analyzing biological power laws. *Ecology*, 92: 1887-1894.
- Zar, J. H. 1968. Calculation and miscalculation of the allometric equation as a model in biological data. *Bioscience*, 18: 1118-1120.
- Zuur, A.F.; Ieno, E.N.; Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1: 3-14.

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DATA AVAILABILITY

The data that support the findings of this study are available, upon reasonable request from the corresponding author.



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SUPPLEMENTARY MATERIAL

Cysneiros *et al.* Multilevel mixed-effect models to predict wood volume in a hyperdiverse Amazon forest

Table S1. Fixed and random coefficients of the generic model (GM), species-specific multilevel model (MMsp), and size-specific multilevel model (MMsz) used to predict wood volume as a function of DBH for a dataset of 21 timber tree species from Jamari National Forest (Rondônia, Brazil). See Table 1 for the correspondence of species name acronyms used in MMsp levels with random effects.

Coefficients	GM		MMsp		MMsz			
	β_0	β_1	Level	$\beta_0 + b_{0i}$	$\beta_1 + b_{1i}$	Level	$\beta_0 + b_{0i}$	$\beta_1 + b_{1i}$
Fixed effects	-6.634	1.948	Species	-5.337	1.642	Size	-5.058	1.59
	(0.104)	(0.024)		(0.199)	(0.047)		(0.110)	(0.032)
Random effects			bic	-5.264	1.610	Small	4.898	1.544
			cat	-6.033	1.796	Medium	5.094	1.589
			dec	-6.233	1.853	Large	5.282	1.634
			exc	-4.829	1.586			
			fus	-4.998	1.564			
			ggl	-5.284	1.579			
			gla	-5.453	1.632			
			gui	-4.841	1.492			
			het	-5.997	1.818			
			in	-5.215	1.641			
			inc	-6.083	1.835			
			lec	-5.347	1.691			
			lei	-5.227	1.622			
			mic	-4.967	1.625			
			odo	-5.895	1.744			
			pan	-3.904	1.253			
			par	-5.460	1.680			
			rac	-5.069	1.530			
			rub	-5.127	1.567			
			ste	-5.372	1.712			
			vis	-5.486	1.647			