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Improved tree height estimation of secondary forests in the Brazilian Amazon

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ABSTRACT

This paper presents a novel approach for estimating the height of individual trees in secondary forests at two study sites: Manaus (central Amazon) and Santarém (eastern Amazon) in the Brazilian Amazon region. The approach consists of adjusting tree height-diameter at breast height (H:DBH) models in each study site by ecological species groups: pioneers, early secondary, and late secondary. Overall, the DBH and corresponding height (H) of 1,178 individual trees were measured during two field campaigns: August 2014 in Manaus and September 2015 in Santarém. We tested the five most commonly used log-linear and nonlinear H:DBH models, as determined by the available literature. The hyperbolic model: $H = a.DBH/(b+DBH)$ was found to present the best fit when evaluated using validation data. Significant differences in the fitted parameters were found between pioneer and secondary species from Manaus and Santarém by F-test, meaning that site-specific and also ecological-group H:DBH models should be used to more accurately predict H as a function of DBH. This novel approach provides specific equations to estimate height of secondary forest trees for particular sites and ecological species groups. The presented set of equations will allow better biomass and carbon stock estimates in secondary forests of the Brazilian Amazon.

KEYWORDS: tree height-diameter (H:DBH) model; nested model; indicative variable; height growth; ecological species groups

Estimativa melhorada de altura de árvores em florestas secundárias da Amazônia brasileira

RESUMO

Este trabalho apresenta uma nova abordagem para a estimativa de altura de árvores em florestas secundárias em duas áreas de estudo na Amazônia brasileira: Manaus (Amazônia central) e Santarém (Amazônia oriental). A abordagem consistiu em ajustar modelos hipsométricos separados por área de estudo e grupos ecológicos de espécies: pioneiras, secundárias iniciais e secundárias tardias. No total, 1178 árvores foram medidas em diâmetro e altura em duas etapas de campo: agosto de 2014 em Manaus e Setembro de 2015 em Santarém. Foram testados cinco modelos log-lineares e não lineares mais utilizados na literatura. O modelo hiperbólico: $H = a.D/(b+D)$ foi o que apresentou o melhor ajuste quando avaliado com os dados de validação. Diferenças significativas nos parâmetros de ajuste foram observadas entre as espécies pioneiras e secundárias de Manaus e Santarém pelo teste F, significando que equações específicas por grupos ecológicos e área de estudo deveriam ser utilizadas para estimar a altura (H) a partir do diâmetro (D) com maior acurácia. Esta nova abordagem fornece equações específicas para localidade e grupo ecológico, para estimar a altura das árvores em florestas secundárias. O conjunto de equações desenvolvidas permitirá melhorar as estimativas de biomassa e a quantificação dos estoques de carbono nas florestas secundárias da Amazônia brasileira.

PALAVRAS-CHAVE: modelos hipsométricos; modelos aninhados; variável indicadora; taxa de crescimento em altura; grupos ecológicos de espécies

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INTRODUCTION

In the Amazon region, height-diameter at breast height (H:DBH) models are important because dense forest understory makes it difficult and time-consuming to view the top of the canopy to measure the tree heights. Several H:DBH models have been proposed for old-growth tropical forests for that purpose (Feldpausch *et al.* 2011; 2012; Hunter *et al.* 2013), however, they are scarce for secondary forests (Lucas *et al.* 2002; Neeff and Santos 2005). For instance, Lucas *et al.* (2002) used genus-specific nonlinear models to estimate tree height based on diameter for the most common species from a secondary forest in Manaus (central Amazon). Conversely, Neeff and Santos (2005) estimated tree height, and its increments, at stand-level age based on the Bertalanffy–Chapman–Richards model in a secondary forest in Santarém (eastern Amazon). Other models related to H:DBH include the logistic, Weibull, and Richards models (Fang and Bailey 1998; Huang *et al.* 2000).

The choice of the best model, however, depends on the relation between tree height and DBH, which, in turn, can be associated with physical and biological factors at tree- and stand-level (Poorter and Bongers 2006; Weiskittel *et al.* 2011). At tree level, H:DBH scaling may be represented by the stem-form factor, which can be indicative of the tree's position within the forest stand (Weiskittel *et al.* 2011). The stem-form factor is defined as the ratio of the volume of a tree, or its part, to the volume of a cylinder with the same size (height) and cross section (DBH). Therefore, the tree may present a conical or cylindrical shape depending on its stem-form factor. For example, dominant trees often have a DBH greater than 30 cm, enjoy favorable light conditions, and have cylindrical shapes (Assmann 1970). In these trees, the scaling exponent between H and DBH is equal or similar to two-thirds, and the allometry assumes an elastic similarity model (Norberg 1988). Meanwhile, most sub-dominant and pioneer species follow a geometric similarity model (H:DBH scaling = 1.0), *i.e.*, the trunk diameter will scale in direct proportion to the tree height (Sposito and Santos 2001). However, when H:DBH scaling ~2.0 there is a constant stress model, which is commonly caused by wind or other stresses (Sposito and Santos 2001).

At stand level, tree growth depends on forest structure, dominance type, tree density, species composition, and site environmental conditions (Weiskittel *et al.* 2011). Therefore, tree growth rate and H:DBH scaling are influenced by environmental conditions and functional traits at both tree and stand levels (Selaya *et al.* 2008; Chazdon 2014). Sites with nutrient-rich soils and favorable climate conditions promote fast tree growth; pioneer species seek these resources in order to quickly colonize newly deforested areas (Chazdon 2014). The tree-height growth is highest at sites with better quality of environmental conditions, even though the maximum increase could be reached at the same age in poor sites (Weiskittel *et al.* 2011). Several studies have been carried out to develop site-based H:DBH models exploring these different environmental conditions in varying forest types (Pillsbury *et al.* 1995; Huang *et al.* 2000; Feldpausch *et al.* 2011). Huang *et al.* (2000) noted that the application of H:DBH models from one region to another may result in an average bias of 29%.

Different species make use of distinct strategies to reach sunlight, promoting fast or slow growth, depending on resource availability and plant physiology (Poorter *et al.* 2012). In Amazonian secondary forests dominated by *Cecropia* sp. and *Vismia* sp., the pioneer species showed fast growth and aboveground biomass (AGB) accumulation, reaching 110–115 Mg ha^{-1} during the first 10–15 years (Lucas *et al.* 2002). As a strategy, these pioneer species intercept more light per unit leaf mass to support their fast growth than late successional species, contributing to the efficient conversion of mass to height (Selaya *et al.* 2008). To maintain rapid growth, pioneer species also present high leaf turnover in the upper-canopy, forming a monolayer leaf arrangement that covers bare soil. In contrast, these species need to form slender stems with low wood density to support such accelerated tree growth, which inevitably reduces their life span (Poorter and Bongers 2006; Selaya *et al.* 2008).

Late successional tree species are characterized by lower growth rates, resulting in the requirement for greater wood densities to support larger canopies and to reduce the risk of hollow stem formation (Poorter and Bongers 2006). These species are generally taller and long-lived when compared to pioneer species, although the photosynthetic rate by leaf mass is smaller (Chazdon 2014). Therefore, carbon assimilation by long-lived late successional species is lower and more persistent compared with short-lived pioneer species (Santiago *et al.* 2004). Such differences in vertical growth among species have significant implications for AGB accumulation in tropical forests (Feldpausch *et al.* 2011; Feldpausch *et al.* 2012). Tree height is highly variable in the Amazon forest, therefore it is important that this parameter is included in equations to estimate tree AGB more accurately (Lefsky *et al.* 2010; Chave *et al.* 2014; Sawada *et al.* 2015). Feldpausch *et al.* (2011) observed a tree height gradient from northeast to southwest Amazon, with the tallest trees in the Guiana Shield and the shortest in the southern Amazon. By including tree height in the AGB models, biomass estimates errors were consistently reduced from 66 to 48 Mg ha^{-1} from the eastern-central to the western Amazon, respectively (Feldpausch *et al.* 2012). Furthermore, the AGB of the Brazilian Amazon is often estimated by applying allometric equations generated from only primary or old-growth forest species, which may lead to overestimation (by 10–60%) when applied for AGB secondary forest trees (Nelson *et al.* 1999).

In this study, we hypothesized that there are significant differences in H:DBH relationships among ecological species groups, *i.e.*, pioneer, early, and late secondary species. We also expected to find significant differences between groups of ecological species across the study sites owing to different environmental and climate conditions. It has been reported that maximum tree heights at stand level vary among primary forests across the Amazon (Feldpausch *et al.* 2011, 2012; Lefsky *et al.* 2010); however, it is unclear whether these differences also occur over secondary forests. For this investigation, we evaluated five commonly used H:DBH models adjusted to different ecological species groups occurring in two sites, with the aim of improving tree height estimation in secondary forests in the Brazilian Amazon.

MATERIAL AND METHODS

Study area and data

This study was carried out at two sites in the Brazilian Amazon: Manaus (Amazonas State) in the central Amazon region, and Santarém (Pará State) in the eastern Amazon region. At the Manaus site, the sampling plots were chosen on either side of the BR-174 highway, 70 km to the north of the city of Manaus. At the Santarém site, the sampling plots were chosen close to the Tapajós National Forest (FLONA Tapajós) on either side of the BR-163 highway, 100 km to the south of the city of Santarém (Figure 1).

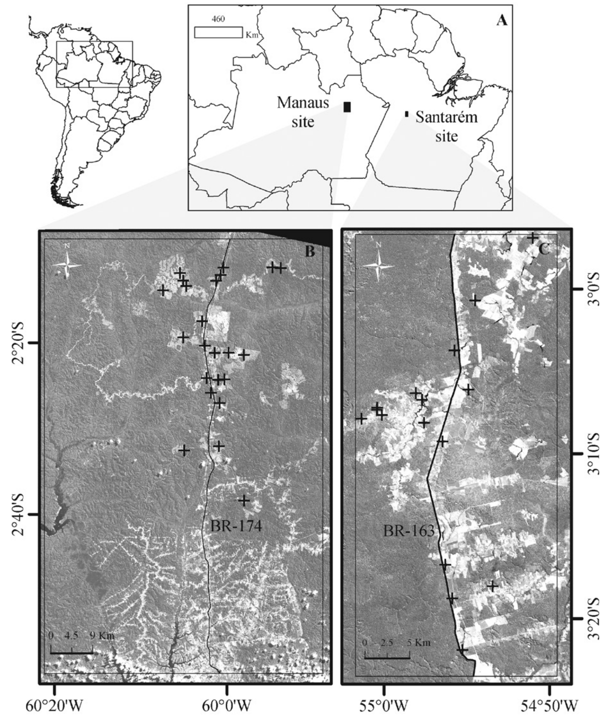

Figure 1. Geographical distribution of the study sites. A. Map of South America detailing the geographical position of study sites of the REGROWTH-BR project (rectangles) in Amazonas and Pará states, Brazil. B. Distribution of plots in the Manaus site (triangles) on either side of the BR-174 highway, 70 km to the north of the city of Manaus. C. Distribution of plots in the Santarém site (triangles) on either side of the BR-163 highway, 100 km to the south of the city of Santarém.

According to Chave *et al.* (2005), both study sites are classified as 'moist forest', with less than 5 months averaging < 100 mm month^{-1} of rainfall during the dry season. The dry season length is shorter in Manaus (3.1 months) than in Santarém (4.5 months) (Malhi *et al.* 2004). Manaus receives an average annual rainfall of 2,200 mm, which is slightly higher than that received at Santarém (2,000 mm) (Asner *et al.* 2003). The mean annual temperature at both sites is approximately 26 °C. Soils are predominantly nutrient-poor clay oxisols with some sandy ultisols (Silver *et al.* 2000).

Secondary forests in Manaus and Santarém occur in a region dominated by *terra firme* old-growth dense forests, which have a similar average canopy height (26 and 28 m, respectively), but very different height distributions (Hunter *et al.* 2015). Santarém primary forests present a bi-modal distribution of tree-canopy heights, one comprised of emergent trees (average 35–40 m heights) and the other comprised of sub-dominant trees (average 15–30 m), while Manaus primary forests show a near unimodal Gaussian distribution, with an average 26 m canopy height (Hunter *et al.* 2015). Additionally, open tropical forests occur in the east side of FLONA Tapajos, with these being widely dominated by palm trees such as *babaçú* (*Attalea speciosa* Mart.) and *inajá* (*A. maripa* (Aubl.) Mart.) on sandy soils (Prates-Clark *et al.* 2009; personal observation).

In both study sites, only advanced secondary forests (age > 16 years) were measured in a 60 × 100 m nested plot. All sampling plots were randomly selected based on the age of the secondary forest and on land-use history (period of active land use and frequency of land clearance), assessed through the analysis of extensive Landsat sensor time-series data (Carreiras *et al.* 2014). Field measurements were conducted during August 2014 in Manaus (23 plots) and September 2015 in Santarém (16 plots) (Figure 1) as part of the REGROWTH-BR project (Carreiras *et al.* 2014).

All trees with a DBH (at 1.3 m height) greater than or equal to 5 cm were measured within a 10 × 100 m plot. Trees with a DBH $\geq$ 10 cm were measured within a 20 × 100 m plot, and trees with a DBH $\geq$ 20 cm were measured within a 60 × 100 m plot. All trees were identified botanically to species level or marked as unknown (three cases; see Supplementary Material, Table S1).

Trees were randomly selected and heights were measured at each nested plot (*circa* 25 measurements per plot) with a laser hypsometer (True Pulse 200$^{\text{TM}}$, LaserInc Technology, Denver, CO, USA), whereas DBH was measured with a girth tape. All trees with broken or damaged crowns, and all palms, were excluded from the analysis.

The individuals were assigned to an ecological species group (ESG): pioneers (P), early secondary stage (ES), or late secondary stage (LS). This was based on the information collected from the literature and from the Global Wood Density Database (Zanne *et al.* 2009, see Supplementary

Material, Table S1). The formal Mann-Whitney U test was used to compare differences between wood densities among the three ESGs. The Bonferroni correction for pair-wise Mann-Whitney U test alpha was $\alpha/3 = \sim 0.0167$. Therefore, we used median wood density thresholds to assign a species to a specific ESG when the previous classification was not found in the literature, e.g., pioneers ≤ 0.5 g cm^{-3}, 0.5 g cm^{-3} < early secondary ≤ 0.59 g cm^{-3}, and late secondary < 0.74 g cm^{-3}.

Height and DBH data from 1,178 individual trees ranging from 5-70 cm in diameter, corresponding to 188 species and 52 families, were collected during the field campaign: 529 individuals in Manaus and 649 in Santarém. Before adjusting H:DBH models, the data were stratified by ecological species and study site, and then split into two subsets: the training subset (80%) for model fitting, and the remainder (testing subset) for model validation (Table 1). The H:DBH ratio was evaluated by study site using the Mann-Whitney U test to support *a priori* any difference in tree architecture (Feldpausch *et al.* 2011). The Mann-Whitney U *test* was performed using the R statistical program (R Development Core Team 2008).

Model selection and comparison of fitted models

Several linear and nonlinear allometric models have been proposed to describe the relationship between tree height and diameter (Fang and Bailey 1998; Huang *et al.* 2000). In this study, we tested five widely used H:DBH models (Fang and Bailey 1998; Huang *et al.* 2000; Feldpausch *et al.* 2011) (Table 2). Only H:DBH models with up to three parameters were selected in order to avoid problems with over-parameterization in nonlinear regression estimation, as reported by Fang and Bailey (1998).

To select the most suitable model, we compared the ability of these five allometric models to predict tree height at each ESG by study site. The nonlinear least squares (*nls*) command from R was used to estimate the parameters in all nonlinear models (Bates and Watts 1990), and the ordinary least squares (*lm*) command in the case of the log-linear model (m1).

The following statistics were used to select the best models in terms of goodness-of-fit using the training subset (Motulsky and Christopoulos 2003): (i) absolute and relative root mean square error (RMSE); and (ii) Akaike information criterion (AIC) weights (Wagenmakers and Farrel 2004). The relationship between standardized residuals and predicted height was evaluated visually through scatterplots in each model to account for heteroskedasticity. Additionally, a formal Breusch-Pagan test against heteroskedasticity (Neter *et al.* 1996) was performed using the lmtest package in R.

Model validation and presence of outliers

Prediction bias was calculated by subtracting the predicted height from the observed height (measured) using the testing subset. A null hypothesis, whereby the bias is equal to zero, was tested by *t-test*, with $\alpha = 0.05$ significance level. Therefore, the root mean square error of prediction (RMSEP) was calculated by Eq. (1) (Hastie *et al.* 2009): $\text{RMSEP} = (\text{bias}^2 + \text{variance})^{1/2}$. The first term in Eq. (1) is relative to the average prediction bias and the second term refers to the variance-bias, which in turn, is related to the spread of points around the mean prediction.

The presence of outliers was evaluated in both training and testing subsets using *outlier* in the "outliers" package of R program. The presence of outliers was verified by observing the spread of the residuals. If confirmed, the model selection and validation were iteratively repeated to improve model fitting. This process was performed twice with removal of 19 outliers from the analysis, including the training and testing subsets.

We arbitrary attributed a descending rank order to choose only one model based on highest AIC weight: value 5 for the best model (highest), and 1, for the worst (lowest). The best ranked fitted model (sum of rank values) was then used to analyze differences between ESG and study sites using an indicator regression approach.

Table 1. Summary of the training and validation datasets (in parentheses) by study area and ecological species groups (ESG). N = number of trees, min = minimum, max = maximum, SD = standard deviation, DBH = diameter at breast height, P – pioneers, ES – early secondary, LS – late secondary.

Study area	ESG	N	DBH (cm)				Total height (m)			
			min	max	mean	SD	min	max	mean	SD
Manaus	P	253 (65)	5.0 (5.1)	56.0 (40.3)	20.9 (20.2)	8.9 (8.3)	2.0 (7.6)	28.3 (23.7)	16.8 (16.5)	4.4 (4.1)
	ES	96 (24)	5.0 (5.5)	34.0 (26.5)	15.4 (14.3)	7.8 (6.7)	5.2 (6.7)	28.6 (27.4)	15.0 (14.2)	5.6 (5.5)
	LS	73 (18)	5.1 (5.0)	42.4 (32.3)	15.8 (17.3)	10.5 (9.7)	5.1 (3.0)	31.7 (27.1)	13.9 (15.4)	6.6 (7.6)
	All	422 (107)	5.0 (5.0)	56.0 (40.3)	18.8 (18.3)	9.3 (8.5)	2.0 (3.0)	31.7 (27.4)	15.9 (15.7)	5.2 (5.1)
Santarém	P	208 (50)	5.0 (5.0)	57.0 (47.8)	18.0 (19.2)	10.8 (10.2)	3.4 (7.0)	28.0 (28.0)	15.8 (16.1)	5.9 (5.8)
	ES	172 (42)	5.0 (5.2)	56.0 (26.6)	12.4 (11.3)	8.9 (5.9)	5.5 (7.2)	28.7 (24.7)	12.5 (12.3)	4.9 (4.4)
	LS	142 (35)	5.0 (5.2)	70.0 (64.2)	15.2 (16.6)	12.4 (12.8)	5.3 (5.4)	29.0 (26.0)	13.2 (14.1)	5.2 (5.3)
	All	521 (128)	5.0 (5.0)	70.0 (64.2)	15.4 (15.9)	10.9 (10.4)	3.4 (5.4)	29.0 (28.0)	14.0 (14.3)	5.6 (5.5)

Table 2. Height-diameter models selected for analysis. H = total height (m); DBH = diameter at breast height (1.3 m above ground).

Model number	Model form	Model type
m1	$H = a + b.\log.DBH$	Log-Linear
m2	$\log H = a + b.\log.DBH$	Log-Log
m3	$H = a.DBH/(b+DBH)$	Hyperbolic
m4	$H = a.(1 - c.\exp^{(-\boldsymbol{b}.DBH)})$	Monomolecular
m5	$H = a.(1 - \exp(b.DBH)^{c})$	Chapman-Richards

Comparison of H:DBH models by ecological species group and study site

The indicator regression approach was used to evaluate full and reduced nested models with a simple ANOVA F-test (Bates and Watts 1990; Neter *et al.* 1996). The indicator variable, or dummy variable, is an artificial variable created to represent an attribute with two or more distinct categories/levels, which, in our case, was represented by a study site or a specific ESG (Neter *et al.* 1996).

In the full model, the indicator variable could only take the values 0 and 1, corresponding to each study site or ESG, and the reduced model was fitted using the whole dataset without the indicator variable. However, to avoid over-parametrization of the full models, the ANOVA F-test was performed to compare each pair of ESGs per study site, because the difference in parameter estimation may be caused by only two or more indicator variables involved in the analysis, and this method reduces the number of parameters whilst retaining validation of the nested approach (Huang *et al.* 2000).

For instance, if the response function was modeled by the log-linear model between pioneers and early secondary forest species, the full-model of H:DBH would have three parameters (Neter *et al.* 1996) [Eq. (2): $h = a+b\log(\text{DBH})+c\,G1\log(\text{DBH})+\varepsilon$; where a and b are log-linear parameters, c represents the parameters related to indicator variable, and ε is the regression error; G1 refers to the indicator variable of a specific ESG (pioneer or early secondary)]. In this case, the reduced model has only two parameters (a and b). Considering that the response function (2) is for pioneers for which $G1 = 0$, then the model would take the form: $h=a+b\log(\text{DBH})$. If the response function is for early secondary species for which $G1 = 1$, then Eq. (2) would take the form: $h = a+b\log(\text{DBH})+c\,G2\log(\text{DBH})$, and so on. Similarly, the analysis can be performed with all nonlinear models described in Table 1, and with all other ESG pairs or study sites.

The equality of the two models was tested by considering the null hypothesis, H_0, whereby indicator parameters in the full model are equal to zero, against the alternative hypothesis, H_1, whereby at least one parameter differs from zero using the F-test according to Motulsky and Christopoulos (2003). ANOVA F-test was performed in R (R Core Team 2008) with a 0.95 confidence level.

Finally, we estimated the relative growth height rate (HGR) by taking the derivative of the selected model by its diameter. The fitted curves for relationships between HGR and H:DBH were provided.

RESULTS

Ecological species groups

Median differences in wood density between ESG pairs differed from zero (Mann-Whitney U test: $W = 64$, $p < 0.016$), suggesting that wood density values could be used to separate species groups. Then, we used median wood density to assign species into an ESG when these were not available in the literature (in this case 22 of 323 species collected, Supplementary Material, Table S1).

Wood density outliers, marked with an open circle in Figure 2, indicate the low wood density of *Hevea brasiliensis* (Willd. ex A. Juss.) Müll.Arg. (0.40 g cm^{-3}, late secondary species) in Manaus. In Santarém, outliers were represented by high wood density of *Neea oppositifolia* Ruiz & Pav. (0.89 g cm^{-3}, pioneer species) and *Sloanea nitida* G. Don. (0.96 g cm^{-3}, early secondary species), and low wood density of *Jacaratia spinosa* (Aubl.) A.DC. (0.14 g cm^{-3}, early secondary species).

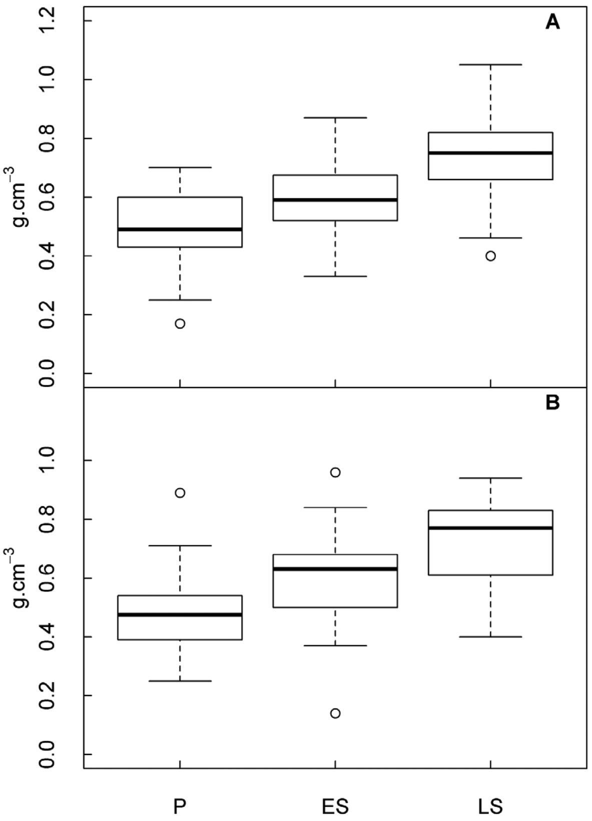

Figure 2. Distribution of wood density (g cm^{-3}) by ecological species groups: (P) pioneer, (ES) early secondary, and (LS) late secondary species in secondary forests. A - Wood density values from Manaus species; B - Wood density values from Santarém species.

The simple ratio H:DBH of the secondary forest trees was significantly different between study sites, as determined by the Mann-Whitney U test: W = 133246, $p < 0.001$ (Manaus = 0.9037; Santarém = 1.0588). Tree diameters from secondary forests in Manaus (median 19.8 cm) were significantly different from those in Santarém (median 12.2 cm), and the same was observed for tree heights in Manaus (median 16.7 m) and Santarém (median 12.8 m), $p < 0.001$. This indicates that the H:DBH relationship followed a different distribution at each study site, considering that forests at both study sites are of similar average age (*circa* 23 years after clear cut).

Models' goodness-of-fit

Two-parameter models showed the best goodness-of-fit given by the sum ranked order of the lowest AIC (Table 3): hyperbolic model (sum of 21 points) and log-log model (19 points). The monomolecular model (18 points) also had a low AIC among the three-parameter models. All regression parameters were significant at $\alpha = 0.05$ for all models, with the exception of the Weibull model for early secondary species in Manaus, the Chapman-Richards model for early secondary species in Santarém, and for late secondary species in Manaus (Table 3).

Table 3. Fitting statistics of the tested H:DBH models by ecological species groups and study area. RMSE and RMSE are the absolute and relative root mean square error, respectively. RMSEP is the RMSE of prediction. R is the value of the rank order based on the lowest wiAIC (in bold). wiAIC – weights of Akaike information criterion; BP - Breusch-Pagan test. *Non-significant parameters for alpha = 0.05. NC – do not converge.

Model	Regression parameter			RMSE (m)	RMSE (%)	AIC	wi AIC	RMSEP (m)	R	p-value BP
	a	b	c							
Manaus	Ecological Species Group = 1 (Pioneers) train. n = 255 test n = 63									
m1	-3.67	6.97		**2.61**	**15.55**	**1207.36**	**0.618**	**2.62**	**5**	**0.41**
m3	29.12	13.65		2.62	15.58	1208.68	0.319	2.59	4	0.64
m5	23.74	0.05	0.76	2.63	15.62	1212.89	0.039	2.58	3	0.76
m4	22.73	0.92	0.07	2.64	15.72	1213.95	0.023	2.56	2	0.24
m2	0.66	0.44		2.68	15.92	1219.99	0.001	2.73	1	0.68
Manaus	Ecological Species Group = 2 (Early Secondary) train. n = 96 test n = 24									
m2	0.44	0.64		**2.52**	**16.78**	**444.61**	**0.672**	**3.07**	**5**	**0.19**
m4	55.16*	0.93	0.016*	2.54	16.89	446.80	0.225	3.09	4	0.65
m3	43.97	27.21		2.57	17.18	448.48	0.097	3.03	3	0.88
m1	-8.18	8.95		2.65	17.65	454.20	0.006	3.07	2	0.25
m5	NC	NC		NC	NC	NC	NC	NC	1	NC
Manaus	Ecological Species Group = 3 (Late Secondary) train. n = 73 test n = 18									
m2	0.41	0.63		**2.96**	**21.25**	**359.68**	**0.456**	**2.93**	**5**	**0.14**
m3	43.08	28.84		2.98	21.50	360.65	0.282	2.80	4	0.07
m4	37.60	0.93	0.03	2.97	21.29	360.91	0.247	2.87	3	0.04
m1	-8.30	8.75		3.11	22.29	366.43	0.016	2.95	2	0.05
m5	32.22	0.031*	0.81	3.15	22.48	379.58	0.000	2.94	1	0.01
Santarém	Ecological Species Group = 1 (Pioneers) train. n = 208 test n = 50									
m4	30.90	0.94	0.04	**2.52**	**15.99**	**965.94**	**0.446**	**3.09**	**5**	**0.16**
m3	40.95	25.21		2.53	16.08	966.78	0.293	3.11	4	0.38
m5	31.46	0.04	0.84	2.53	16.04	967.02	0.260	3.14	3	0.63
m1	-8.78	9.02		2.61	16.52	978.35	0.001	3.17	2	0.62
m2	0.53	0.55		2.61	16.52	979.29	0.001	3.07	1	0.25
Santarém	Ecological Species Group = 2 (Early Secondary) train. n = 172 test n = 42									
m2	0.53	0.53		**2.34**	**18.74**	**780.48**	**0.371**	**1.86**	**5**	**0.42**
m5	37.22	0.02*	0.62	2.34	18.72	780.77	0.321	1.80	4	0.49
m4	30.28	0.88	0.04	2.34	18.77	781.80	0.192	1.77	3	0.26
m3	33.66	18.16		2.36	18.98	783.36	0.088	1.75	2	0.78
m1	-5.08	7.53		2.38	19.04	785.59	0.029	1.83	1	0.79
Santarém	Ecological Species Group = 3 (Late Secondary) train. n = 142 test n = 35									
m1	-3.46	6.74		**2.38**	**18.03**	**643.95**	**0.699**	**2.32**	**5**	**0.14**
m3	29.19	14.50		2.41	18.27	647.21	0.137	2.30	4	0.32
m5	28.78	0.02	0.59	2.40	18.21	647.83	0.101	2.37	3	0.16
m2	0.61	0.46		2.43	18.39	649.91	0.036	2.49	2	0.21
m4	25.79	0.85	0.04	2.43	18.40	650.50	0.027	2.37	1	0.04

The visualization of standardized residuals against predicted height showed the absence of heteroskedasticity (Figure 3), which further supports the non-significant results of the Breusch-Pagan test (Table 3). The residuals were drawn only for the selected hyperbolic model.

Based on the ranked model (Table 3), the hyperbolic model (m3) presented satisfactory results for all ESGs without being the best for a specific ESG. The prediction error of the hyperbolic model extended from RMSEP = 1.75 to 3.11 m (Table 3). Considering that bias is close to zero by the null hypothesis, we did not reject H_0 in any of the ESG cases, meaning that the average bias was equal to zero with d_{fF} (n-1) degrees of freedom. Because the mean bias was not significantly different from zero in all models fitted by a one sample t-test (p > 0.05), variance of prediction was a large source of error. In general, the hyperbolic model performed well, although it overestimated tree height above 20 m, independent of age, as this seems to be the height at which this model begins to consistently underestimate values (Figure 4).

Comparison of H-DBH models by study site and ESG

The null hypothesis was not rejected for the ESG 2–3 pair (early secondary and late secondary species) at both study sites (Table 4), suggesting that parameters *c* and *d* from the full models were different from zero in these cases (p > 0.05). Based on the results of the paired F-test, and the estimated parameters of the full model, we concluded that secondary species (early and late) had a similar H:DBH relationship in both study sites, hereafter grouped into one class, while pioneer species belonged to another class.

We compared the differences in the H:DBH relationships of these new groups (pioneers and secondary species) by study site, in order to determine whether tree growth was also influenced by geographic location. A clear difference in the H:DBH relationship between pioneer and secondary species from Manaus and Santarém by statistical inference (Table 5) was strengthened by the low p-value obtained by the F-test. H:DBH models for the pioneer species took the form: h = 29.12 DBH/(13.65+DBH) for Manaus, and h = 40.94 DBH/(25.21+DBH) for Santarém (Table 5). Similarly, secondary species took the form: h = 42.84 DBH/(27.05+DBH) for Manaus, and h = 30.83 DBH/(15.81+DBH) for Santarém. Model adjustments for pioneer and secondary species for Manaus and Santarém are provided in Figure 5.

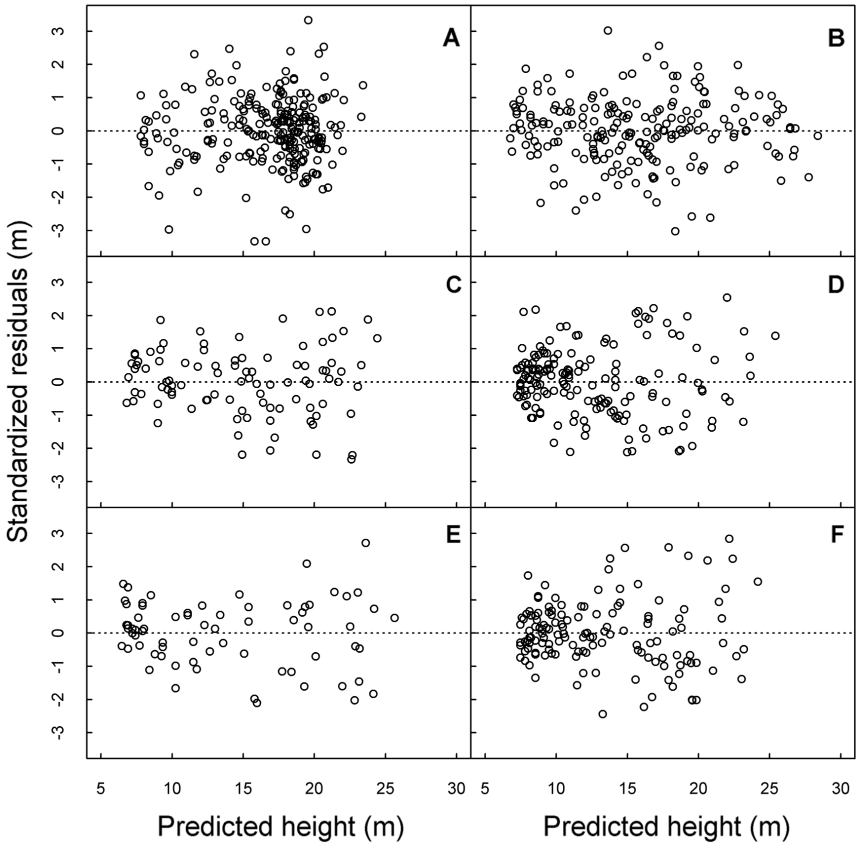

Figure 3. Plots of standardized residuals against predicted height using nonlinear least squares fitting of the hyperbolic model for pioneer (A), early secondary (C), and late secondary (E) species in Manaus and Santarém (B, D, and F), respectively.

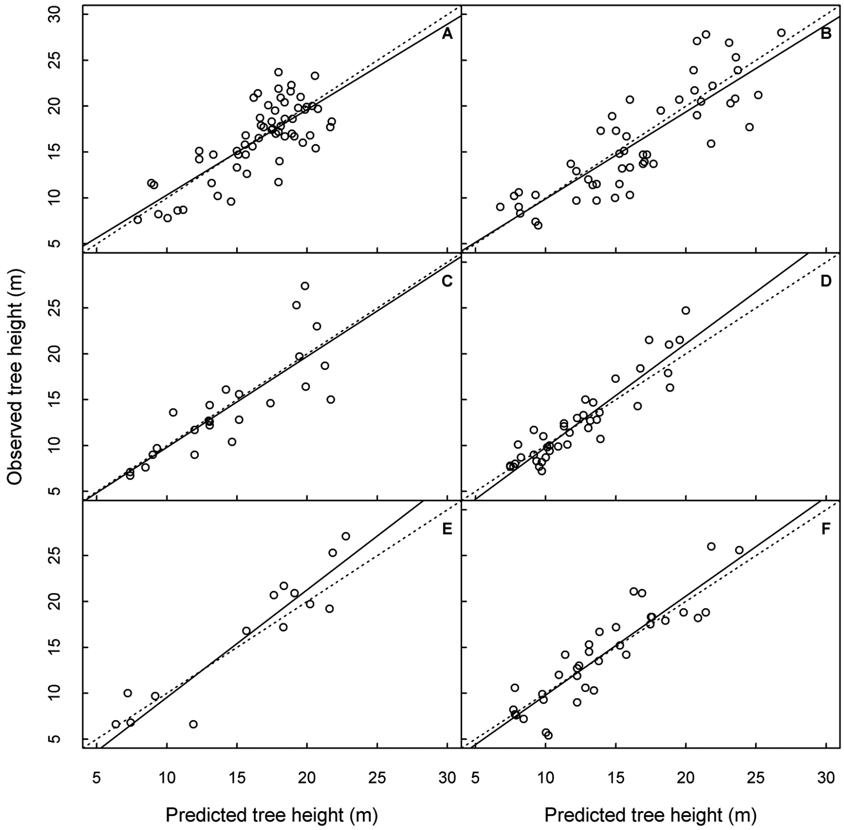

Figure 4. Scatterplot of observed vs. predicted tree heights using the validation subset for pioneer (A, B), early secondary (C, D) and late secondary (E, F) species from Manaus (A, C, and E) and Santarém (B, D, and F). Observed vs. predicted height is fitted using a continuous line; the dashed line refers to the perfect agreement (1:1).

Table 4. Fitted parameters of the full (F) and reduced (R) hyperbolic model by ESG pairs. CI = 95% confidence interval, as shown in parentheses. SSE (F) and SSE (R) are the sum of square error for full and reduced models, respectively. *a*, *b*, *c*, and *d* are the parameters. ESG-Pair (ecological species group pairs): 1–2 (pioneers-early secondary species), 1–3 (pioneers-late secondary species), 2–3 (early-late secondary species).

Manaus								
ESG pair	a (CI)	b (CI)	c (CI)	d (CI)	SSE (F)/ SSE (R)	n	F_0	p-value (>F)
1–2 F	29.12 (2.58)	13.65 (3.12)	14.84 (12.24)	13.56 (12.93)	2328.00	347	11.36	<0.001
1–2 R	30.92 (2.45)	15.34 (2.87)			2482.30			
1–3 F	29.12 (2.68)	13.65 (3.24)	13.96 (11.31)	15.19 (13.37)	2332.40	324	7.84	<0.001
1–3 R	31.88 (2.76)	16.88 (3.33)			2446.70			
2–3 F	43.97 (13.05)	27.21 (13.76)	-0.88 (14.02)	1.63 (15.90)	1223.40	163	1.84	0.161
2–3 R	42.84 (7.42)	27.05 (8.14)			1251.50			
Santarém								
ESG pair	a (CI)	b (CI)	c (CI)	d (CI)	SSE (F)/ SSE (R)	n	F0	p-value (>F)
1–2 F	40.95 (3.99)	25.21 (4.54)	-7.29 (5.28)	-7.05 (5.52)	2245.90	376	3.71	0.025
1–2 R	38.31 (2.79)	22.47 (3.02)			2290.80			
1–3 F	40.95 (4.04)	25.21 (4.60)	-11.76 (4.43)	-10.71 (4.88)	2101.70	345	17.04	<0.001
1–3 R	35.44 (2.46)	19.94 (2.76)			2311.70			
2–3 F	33.66 (3.91)	18.16 (3.89)	-4.47 (4.25)	-3.66 (4.31)	1743.00	311	2.69	0.069
2–3 R	30.83 (2.14)	15.81 (2.20)			1773.60			

Table 5. Fitted parameters of full (F) and reduced (R) hyperbolic models by study area for pioneer and secondary species. CI = 95% confidence interval, as shown in parentheses. SSE (F) and SSE (R) are the sum of square error for full and reduced models, respectively. *a*, *b*, *c*, and d are the parameters.

Groups	*a* (*CI*)	*b* (*CI*)	*c* (*CI*)	*d* (*CI*)	*SSE* (*F*)/ *SSE* (*R*)	*n*	F_0	*p-value* (>*F*)
Pioneers F	29.12 (2.54)	13.65 (3.08)	11.82 (4.72)	11.56 (5.42)	3020.80	458	19.105	p<0.001
Pioneers R	34.15 (2.40)	18.89 (2.83)			3275.00			
Secondary F	42.84 (6.64)	27.05 (7.28)	-12.01 (5.55)	-11.24 (5.90)	3025.10	476	12.463	p<0.001
Secondary R	34.00 (2.19)	18.56 (2.30)			3184.80			

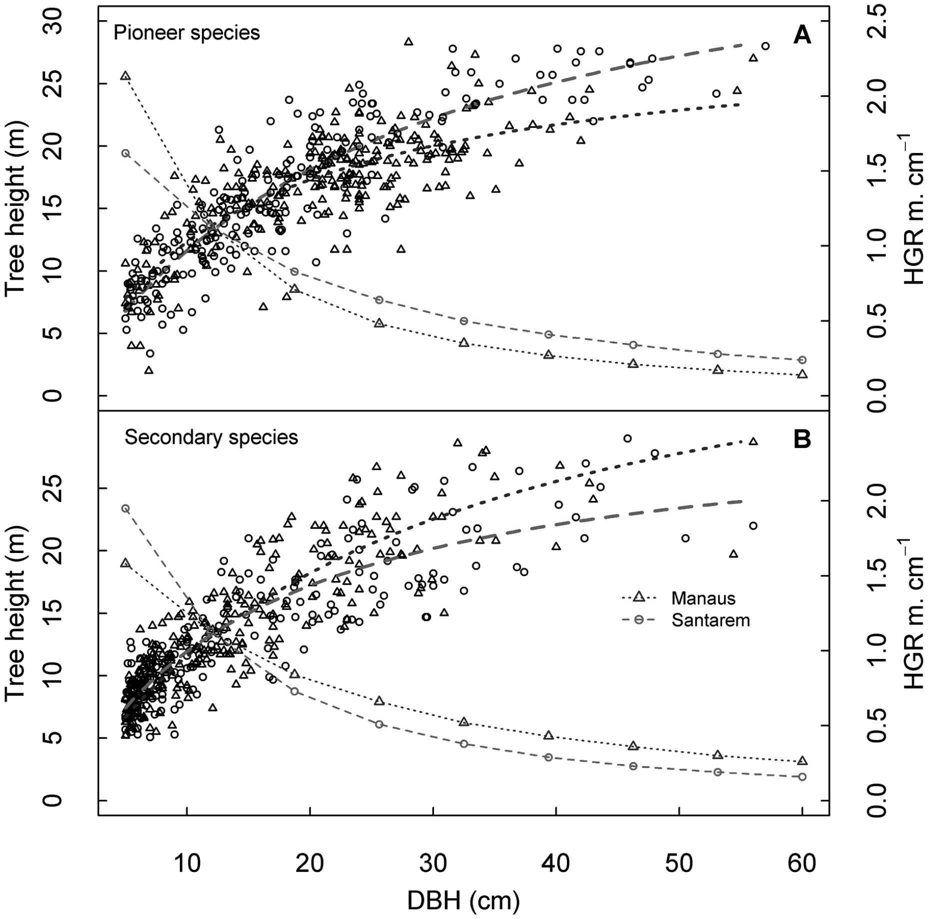

Figure 5. Scatterplot of the hyperbolic model adjustment between diameter and tree height on the primary y-axis, and between DBH and tree height growth rate on the secondary y-axis.

Height growth by site and species groups

The hyperbolic model was relatively easy to fit, achieved good validation results, and was meaningful in terms of the biological interpretation of its parameters. In this function, *a* represents total height at maximum DBH (asymptote), and *b* is the DBH when tree height reaches half the asymptote. Thus, a first derivative of the hyperbolic model allows us to obtain the absolute rate of height growth by DBH unit [Eq. (3): $dy/dx = ab/(b+x)^2$]. Therefore, when DBH approaches zero, a/b represents the maximum height increment by DBH unit (m cm^{-1}). Disregarding other underlying dynamic processes of H:DBH relationships, we observed that pioneers in Manaus had the highest HGR. The HGR in pioneer species from Manaus was 2.13 m cm^{-1}, meaning that for every centimeter in diameter increment, height increased more than 2 m. Santarém pioneers had a HGR = 1.62 m cm^{-1} (Figure 5). Conversely, secondary species in Santarém had a greater HGR than those in Manaus, HGR = 1.95 and 1.58 m cm^{-1}, respectively.

Pioneer species had high initial HGR in Manaus compared with secondary species, and this decreased with increasing diameter. Compared with Manaus, pioneer species in Santarém showed a greater HGR for large trees (Figure 5). The increase in height growth fell below 0.20 m cm^{-1} at DBH > 40 cm. This decline can be expected to continue until the regenerating forest becomes structurally similar to the average canopy heights of the mature forest, which is reported to be 26 m in Manaus and 28 m in Santarém (Hunter *et al.* 2015). Based on height modelling of secondary forests in Santarém, height initially increases by a maximum of 2 m per year, and then falls below 0.25 m per year at age 30 (Neeff and Santos 2005). Pioneer species in Manaus exhibited fast growth in the first years; this was around 30% higher than that observed in Santarém (Figure 5). However, later in life, they had about 50% smaller HGR than pioneers in Santarém (DBH = ~40 cm).

DISCUSSION

The hyperbolic model presented the best validation results among the most common models. We found statistical differences between pioneer and secondary species for H:DBH relationships, but not between early and late secondary species. These differences were consistent across sites, probably due to environmental and climate conditions. The HGR presented distinct behavior among ESGs and between sites.

Model selection for goodness-of-fit comparison

According to Fang and Bailey (1998), different H:DBH models with the same number of parameters usually result in similar goodness-of-fit when the nonlinear least square method is used on the same data set. Feldpausch *et al.* (2011) observed that log-log models (two parameters) were the most suitable for estimating tree height in dry and wet forests, with no trend observed in their residuals by diameter class. Asymptotic functions with three parameters, such as the Weibull model, provided good estimates of ecologically meaningful H max in moist forests (Feldpausch *et al.* 2011). Conversely, when one or two parameters are introduced in the model (e.g., three or four parameters instead of two), biological interpretation of parameters may be lost (Fang and Bailey 1998). Convergence could not be attained as easily as when using the Weibull and Chapman-Richards models (Table 3).

In this study, the hyperbolic model was found to produce the most satisfactory fit among the tested models, which was consistent with previous studies that also satisfactorily tested this model for adjusting H:DBH relationships (Fang and Bailey 1998; Huang *et al.* 2000). Nevertheless, due to the adjusted asymptote being close to 40 m for secondary forest trees, the hyperbolic model tended to underestimate the height of large trees, therefore its application in old growth forest should be avoided.

Separating H:DBH models by study site and ESG

Statistical differences were found between study sites in H:DBH relationships. Considering that the secondary forest plots were at a similar age (~23 years), the most important local factors influencing H:DBH relationships are the stand density, basal area, and species composition (Gómez-García *et al.* 2016). Basal area and stand density are the first parameters to reach similarity in mature forests (within 20–40 years), while similarity in species composition can take longer (Feldpausch *et al.* 2005; Neeff and Santos 2005).

Owing to resource competition, trees of the same DBH usually have greater height in denser stands. We estimated average stand basal area as 22.3 and 23.7 m² ha^{-1} in secondary forest plots in Santarém and Manaus, respectively, which may be indicative of greater average tree height in Manaus. Hunter *et al.* (2013) reported a greater average basal area of primary forests in FLONA Tapajós (31 m² ha^{-1}), with average canopy height taller than that in Reserva Ducke, near Manaus site (28.7 m² ha^{-1}). Such differences are probably due to primary forests from Santarém having larger trees with DBH > 60 cm than Manaus primary forests (Vieira *et al.* 2005), increasing both the average basal area and the mean canopy height, which is not observed in secondary forests.

Some climatic variables, such as greater annual precipitation, shorter dry season length, and greater mean annual air temperature, could be drivers of greater relative tree growth in central Amazon secondary forests (Malhi *et al.* 2004). From a hydraulic perspective, it would be expected that, for a given DBH, trees would be shorter with increasing water deficit. Hence, the application of H:DBH models from the moderately seasonal central Amazon may overestimate tree height in the dry forest, and underestimate it in the wet regions (Malhi *et al.* 2004).

Regarding ESG-specific H:DBH models, pioneer and secondary species may be regarded as different groups at our study sites. Although pioneer species grow faster than late successional species (Selaya *et al.* 2008), we found a different behavior in pioneer species in Santarém. In this study site, pioneer species showed similar behavior to early secondary species, which can be supported by interpretation of the magnitude of the confidence intervals of the regression parameters in Table 4.

Pioneer species were prevalent in Manaus with regard to their importance in species composition (% of total species number), and their relative coverage (by summing relative density and dominance in the stand level). In Manaus, pioneer species comprised 33% of species richness, and 52% of the total stand trees, while in Santarém, they represented 29% and 39%, respectively. The monodominance of pioneer species such as *Cecropia* spp. and *Vismia* spp., which form a monolayer canopy arrangement, may prevent the recruitment of taller and later secondary species in Manaus (Lucas *et al.* 2002).

It is probable that pioneer species from Santarém are still competing for resources with other secondary trees, while in Manaus, short-lived species are being replaced by other long-lived secondary species. The most important pioneer species in Manaus, *Vismia* spp., *Cecropia* spp., and *Bellucia* spp., are short-lived (20–30 years), and are virtually absent from old growth forest (Lucas *et al.* 2002). Secondary forests in Santarém are dominated almost exclusively by *Guatteria poeppigiana* Mart., a pioneer species with a lifespan of 54 years (Holm *et al.* 2014). The high growth rate of large trees (DBH > 60 cm) of late secondary species may be a major cause of faster carbon assimilation in the eastern Amazon than in the central Amazon (Vieira *et al.* 2005).

CONCLUSIONS

Among the models tested, the hyperbolic model presented the best performance for estimating tree height through diameter measured for secondary forests located near the cities of Manaus (central Amazon) and Santarém (eastern Amazon). In addition, we presented an alternative method of analyzing the height-diameter (H:DBH) relation of secondary forests species, separating them by ESGs. The results suggest that pioneer and secondary species belong to distinct groups in terms of H:DBH relationships, and that tree height growth differs between both study sites. Pioneer species from Manaus showed rapid tree height growth at low DBH compared with secondary species, while in Santarém the opposite trend was observed. We showed that separate H:DBH models are required to achieve more accurate predictions of tree height in secondary forests in Manaus and Santarém. These new H:DBH models are essential to provide improved estimation of tree height in secondary forests, as required for carbon stock estimation (Chave *et al.* 2014; Poorter *et al.* 2016).

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SUPPLEMENTARY MATERIAL (only available in the electronic version)

CASSOL *et al*. Improved tree height estimation of secondary forests in the Brazilian Amazon

Table S1. List of species and their respective botanical families recorded in this study. Scientific names according to http://www.theplantlist.org/; WD – wood density in gcm^{-3}; ESG – ecological species group: 1 – Pioneers, 2 – Early secondary, 3 – Late secondary/Climax, 4 – Exotic, 5 – Dead/Unknown; OCC – occurrence: 1 – Manaus, 2 – Santarem, 3 – Both; WD Ref – reference for wood density value; ESG Ref – reference for ecological species group.

Nº	Family	Species	WD gcm^{-3}	ESG	OCC	WD Ref	ESG Ref
1	ACHARIACEAE	*Lindackeria paludosa* (Benth.) Gilg	0.56	2	2	40	62
2	ANACARDIACEAE	*Astronium lecointei* Ducke	0.79	3	2	40	43,17
3		*Spondias mombin* L.	0.39	1	2	40	43
4		*Tapirira guianensis* Aubl.	0.46	1	3	40	74
5		*Thyrsodium spruceanum* Benth.	0.64	1	1	40	73
6	ANNONACEAE	*Annona amazonica* R.E.Fr.	0.46	1	1	40	
7		*Annona ambotay* Subl.	0.46	2	1	40	68
8		*Annona foetida* Mart.	0.57	2	1	21	68
9		*Bocageopsis multiflora* (Mart.) R.E.Fr.	0.64	2	1	40	17
10		*Duguetia echinophora* R.E.Fr.	0.80	3	2	16	17
11		*Duguetia surinamensis* R.E.Fr.	0.80	3	1	40	17
12		*Ephedranthus amazonicus* R.E.Fr.	0.82	3	1	40	62
13		*Guatteria foliosa* Benth.	0.49	2	1	20	67
14		*Guatteria olivacea* R.E.Fr.	0.46	1	1	40	17
15		*Guatteria poeppigiana* Mart.	0.41	1	3	6,30,31	43
16		*Guatteria scytophylla* Diels	0.52	2	1	40	67
17		*Rollinia insignis* R.E. Fr.	0.43	1	1	40	84
18		*Rollinia exsucca* (DC. ex Dunal) A. DC.	0.38	2	2	40	43
19		*Xylopia amazonica* R.E.Fr.	0.79	3	1	40	
20		*Xylopia nitida* Dunal	0.55	2	3	40	43,17
21	APOCYNACEAE	*Ambelania acida* Aubl.	0.52	2	1	40	74
22		*Aspidosperma album* (Vahl) Benoist ex Pichon	0.77	3	2	40	75
23		*Aspidosperma nitidum* Benth. ex Müll.Arg.	0.76	3	3	40	43
24		*Aspidosperma schultesii* Woodson	0.78	3	1	9,38,40	
25		*Geissospermum argenteum* R.	0.79	2	1	37	56,17
26		*Geissospermum sericeum* Miers	0.78	3	2	40	89
27		*Himatanthus stenophyllus* Plumel	0.53	2	1	40	
28		*Lacmellea aculeata* (Ducke) Monach.	0.48	3	2	40	43
29		*Lacmellea arborescens* (Müll.Arg.) Markgr.	0.48	2	1	40	31
30		*Rauvolfia sprucei Müll.Arg.*	0.54	2	1	38,40	79
31	ARALIACEAE	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin	0.43	1	3	40	17
32	ARECACEAE	*Astrocaryum aculeatum* G.Mey.	0.40	2	2	13	43,56
33		*Astrocaryum vulgare* Mart.	0.45	1	2	40	43,97
34		*Attalea maripa* (Aubl.) Mart.	0.42	1	3	40,12	43
35		*Attalea speciosa* Mart.	0.52	1	2	12	77
36		*Elaeis oleifera* (Kunth) Cortés	0.64	4	1	35	
37		*Euterpe precatoria* Mart.	0.40	2	1	13	63
38		*Oenocarpus bacaba* Mart.	0.47	1	3	40	43
39		*Oenocarpus minor* Mart.	0.68	3	1	40	43
40		*Syagrus coccoides* Mart.	0.60	2	2	40	43
41		*Syagrus inajai* (Spruce) Becc.	0.66	2	1	40	43
42	BIGNONIACEAE	*Handroanthus serratifolius* (Vahl) S.O.Grose	0.94	3	3	40	43
43		*Handroanthus impetiginosus* (Mart. ex DC.) Mattos	0.90	3	2	40	43
44		*Jacaranda copaia* (Aubl.) D.Don	0.35	1	3	40	43,17
45	BIXACEAE	*Bixa arborea* Huber	0.37	1	2	40	64

Nº	Family	Species	WD gcm^{-3}	ESG	OCC	WD Ref	ESG Ref
46	BORAGINACEAE	*Cordia alliodora* (Ruiz & Pav.) Oken	0.52	2	2	40	52,29
47		*Cordia bicolor* A.DC.	0.48	2	2	40	43,29
48		*Cordia exaltata* Lam.	0.40	1	1	40	43,75
49		*Cordia goeldiana* Huber	0.50	2	2	40	43,75
50		*Cordia nodosa* Lam.	0.39	2	1	40	31
51	BURSERACEAE	*Protium altsonii* Sandwith	0.68	3	1	40	43
52		*Protium hebetatum* D.C. Daly	0.58	3	1	17	48
53		*Protium heptaphyllum* (Aubl.) Marchand	0.71	2	1	40	69,43
54		*Protium paniculatum* Engl.	0.65	3	2	40	47
55		*Protium puncticulatum* J.F. Macbr.	0.64	2	2	34	46
56		*Protium robustum* (Swart) D.M.Porter	0.68	2	2	16	56
57		*Protium nitidifolium* (Cuatrec.) D.C. Daly	0.62	2	1	20	
58		*Tetragastris altissima* (Aubl.) Swart	0.71	2	2	40	65
59		*Tetragastris panamensis* (Engl.) Kuntze	0.73	3	1	40	43
60		*Trattinnickia burserifolia* Mart.	0.46	3	3	40	43
61	CANNABACEAE	*Trema micrantha* (L.) Blume	0.25	1	3	40	51
62	CARICACEAE	*Jacaratia spinosa* (Aubl.) A.DC.	0.14	2	2	31	88
63	CARYOCARACEAE	*Caryocar pallidum* A.C.Sm.	0.84	3	1	40	17
64		*Caryocar villosum* (Aubl.) Pers	0.76	3	3	40	43
65	CHRYSOBALANACEAE	*Licania incana* Aubl.	0.86	3	2	40	43
66		*Licania micrantha* Miq.	0.84	3	1	40	43
67		*Licania oblongifolia* Standl.	0.80	3	1	40	17
68		*Licania prismatocarpa* Spruce ex Hook.f.	0.84	3	1	9,38,40	67
69	CLUSIACEAE	*Symphonia globulifera* L.f.	0.62	3	2	40	43
70		*Tovomita brasiliensis* (Mart.) Walp.	0.71	2	1	20	17
71	COMBRETACEAE	*Buchenavia macrophylla* Spruce ex Eichler	0.82	3	1	38,40	17
72	CONNARACEAE	*Connarus perrottetii* (DC.) Planch.	0.57	1	1	18	17
73	EBENACEAE	*Diospyros manausensis* Cavalcante	0.72	3	1	38,40	31
74	ELAEOCARPACEAE	*Sloanea nitida* G. Don	0.96	2	2	40	43
75		*Sloanea laurifolia* (Willd.) Benth.	0.82	2	1	40	43
76	EUPHORBIACEAE	*Aparisthmium cordatum* (A.Juss.) Baill.	0.39	1	3	40	43
77		*Croton* sp.	0.47	1	2	40	17
78		*Croton matourensis* Aubl.	0.62	1	1	40	43
79		*Glycydendron amazonicum* Ducke	0.68	2	3	40	43
80		*Hevea guianensis* Aubl.	0.57	3	1	40	17
81		*Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg.	0.40	3	3	40	43
82		*Joannesia heveoides* Ducke	0.39	2	2	40	78,47
83		*Mabea angularis* Hollander	0.61	2	1	38,40	17
84		*Mabea speciosa* Müll.Arg.	0.64	1	1	40	43
85		*Mabea subsessilis* Pax & K.Hoffm.	0.60	2	1	40	45
86		*Maprounea guianensis* Aubl.	0.59	1	1	40	43
87		*Micrandra siphonioides* Benth.	0.58	2	1	40	57,99
88		*Nealchornea yapurensis* Huber	0.61	3	1	40	76
89		*Pausandra macropetala* Ducke	0.59	2	1	37	79
90		*Pogonophora schomburgkiana* Miers ex Benth.	0.74	3	1	40	74,101,17
91		*Sapium marmieri* Huber	0.41	2	2	40	55
92		*Sapium glandulosum* (L.) Morong	0.47	2	1	40	93

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93	FABACEAE CAESALPINIOIDEAE	*Apuleia leiocarpa* (Vogel) J.F.Macbr.	0.80	3	2	40	31
94		*Cassia leiandra* Benth.	0.64	2	2	7	43,70
95		*Chamaecrista xinguensis* (Ducke) H.S.Irwin & Barneby	0.90	3	2	16	
96		*Crudia glaberrima* (Steud.) J.F.Macbr.	0.79	2	2	40	43
97		*Dimorphandra pennigera* Tul.	0.75	3	1	40	
98		*Hymenaea courbaril* L.	0.81	3	3	40	43
99		*Hymenaea parvifolia* Huber	0.88	3	2	40	43
100		*Platymiscium duckei* Huber	0.78	3	1	40	90
101		*Schizolobium amazonicum* Ducke	0.49	1	3	40	43
102		*Tachigali paniculata* var. *alba* (Ducke) Dwyer	0.55	1	2	31	43
103		*Tachigali myrmecophila* (Ducke) Ducke	0.48	3	2	40	43
104		*Tachigali paniculata* Aubl.	0.55	3	3	40	43
105		*Tachigali setifera* (Ducke) Zarucchi & Herend.	0.67	1	1	40	96
106		*Tachigali venusta* Dwyer	0.57	1	1	23	96
107	FABACEAE FABOIDEAE	*Andira parvifolia* Benth.	0.92	3	1	40	17
108		*Bowdichia nitida* Benth.	0.80	3	2	40	43
109		*Diplotropis martiusii* Benth.	0.63	2	1	40	43
110		*Diplotropis purpurea* (Rich.) Amshoff	0.78	3	2	40	82
111		*Diplotropis triloba* Gleason	0.78	3	1	40	43
112		*Dipteryx odorata* (Aubl.) Willd.	0.92	3	3	40	43
113		*Dipteryx punctata* (S.F.Blake) Amshoff	0.92	3	1	40	89,102
114		*Hymenolobium sericeum* Ducke	0.72	3	1	20	43
115		*Monopteryx inpae* W.A.Rodrigues	0.74	3	1	40	
116		*Ormosia discolor* Benth.	0.61	3	2	40	56
117		*Ormosia flava* (Ducke) Rudd	0.58	2	2	40	43
118		*Ormosia nobilis* var. *santaremnensis* (Ducke) Rudd	0.58	3	2	40	43
119		*Ormosia paraensis* Ducke	0.63	3	3	40	43
120		*Poecilanthe parviflora* Benth.	0.85	3	1	10, 4	80
121		*Pterocarpus rohrii* Vahl	0.46	2	1	40	17
122		*Swartzia arborescens* (Aubl.) Pittier	0.83	3	2	40	43
123		*Swartzia cuspidata* Benth.	0.68	3	1	40	67
124		*Swartzia laevicarpa* Amshoff	0.61	3	2	40	70
125		*Swartzia polyphylla* DC.	0.69	2	2	40	43
126		*Swartzia recurva* Poepp.	0.89	3	1	40	95
127		*Swartzia schomburgkii* Benth.	0.97	3	1	9	67
128		*Sweetia nitens* (Vogel) Yakovlev	0.80	3	2	40	59,47
129	FABACEAE MIMOSOIDEAE	*Abarema jupunba* (Willd.) Britton & Killip	0.59	2	1	40	74,43
130		*Alexa grandiflora* Ducke	0.66	2	2	40	88
131		*Dinizia excelsa* Ducke	0.94	3	1	40	89
132		*Enterolobium maximum* Ducke	0.41	1	2	40	14
133		*Enterolobium schomburgkii* (Benth.) Benth.	0.72	3	3	40	64
134		*Inga alba* (Sw.) Willd.	0.59	2	3	40	29,74,56
135		*Inga cayennensis* Benth.	0.53	2	1	40	74
136		*Inga gracilifolia* Ducke	0.66	3	1	38,40	43
137		*Inga macrophylla* Willd.	0.68	3	1	2	43
138		*Inga paraensis* Ducke	0.82	3	1	40	74
139		*Inga pilosula* (Rich.) J.F.Macbr.	0.61	2	1	39	64
140		*Inga rubiginosa* (Rich.) DC.	0.66	3	2	40	43
141		*Inga stipularis* DC.	0.53	2	1	40	43

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142	FABACEAE MIMOSOIDEAE	*Inga thibaudiana* DC.	0.66	2	3	20	86,74,17
143		*Marmaroxylon racemosum* (Ducke) Record	0.84	3	2	40	47
144		*Parkia gigantocarpa* Ducke	0.26	1	2	40	85
145		*Parkia multijuga* Benth.	0.65	2	3	40	43
146		*Parkia panurensis* H.C.Hopkins	0.65	3	1	27	94
147		*Parkia pendula* (Willd.) Walp.	0.52	2	1	40	43,56
148		*Pseudopiptadenia psilostachya* (DC.) G.P.Lewis & M.P.Lima	0.61	3	3	16	43
149		*Stryphnodendron pulcherrimum* (Willd.) Hochr.	0.48	1	3	40	43
150		*Stryphnodendron racemiferum* (Ducke) W.A.Rodrigues	0.75	3	1	40	
151		*Stryphnodendron guianense* (Aubl.) Benth.	0.57	2	1	40	17
152		*Zygia racemosa* (Ducke) Barneby & J.W. Grimes	0.75	3	1	40	17
153	GOUPIACEAE	*Goupia glabra* Aubl.	0.73	2	3	40	43,56,17
154	HUMIRIACEAE	*Endopleura uchi* (Huber) Cuatrec.	0.79	3	2	40	17
155		*Sacoglottis mattogrossensis* Malme	0.77	3	1	40	41
156	HYPERICACEAE	*Vismia cayennensis* (Jacq.) Pers.	0.49	1	3	40	74
157		*Vismia guianensis* (Aubl.) Pers.	0.48	1	3	40	17
158		*Vismia japurensis* Rchb.f.	0.56	1	3	19	51
159		*Vismia gracilis* Hieron.	0.49	1	1	40	51
160		*Vismia sandwithii* Ewan	0.49	1	1	40	51
161	ICACINACEAE	*Emmotum acuminatum* (Benth.) Miers	0.79	2	1	40	43
162		*Poraqueiba sericea* Tul.	0.91	3	1	8	8
163	LACISTEMACEAE	*Lacistema aggregatum* (P.J.Bergius) Rusby	0.51	1	1	40	74
164		*Lacistema grandifolium* Schnizl.	0.52	1	1	40	74
165	LAMIACAEAE	*Vitex triflora* Vahl	0.56	2	1	9	31
166	LAURACEAE	*Aniba burchellii* Kosterm.	0.52	3	1	40	43
167		*Aniba ferrea* Kubitzki	0.52	3	1	9,38,40	17
168		*Aniba panurensis* (Meisn.) Mez	0.61	3	1	40	31
169		*Aniba paraense* Mez.	0.59	3	2	40	43,17,31
170		*Dicypellium manausense* W.A.Rodrigues	0.53	3	1	14	53
171		*Endlicheria bracteata* Mez	0.50	2	1	40	45
172		*Licaria chrysophylla* (Meisn.) Kosterm.	0.79	2	2	40	56
173		*Mezilaurus ita-uba* (Meisn.) Taub. ex Mez	0.74	3	2	40	43
174		*Mezilaurus lindaviana* Schwacke & Mez	0.68	2	2	40	71
175		*Nectandra cuspidata* Nees & Mart.	0.52	3	1	40	43
176		*Ocotea baturitensis* Vattimo-Gil	0.56	2	2	40	
177		*Ocotea canaliculata* (Rich.) Mez	0.48	1	2	40	73
178		*Ocotea cujumary* Mart.	0.70	3	1	20	43
179		*Ocotea glomerata* (Nees) Mez	0.51	1	2	40	73
180		*Ocotea guianensis* Aubl.	0.53	3	1	40	43
181		*Sextonia rubra* (Mez) van der Werff	0.55	3	3	40	43
182	LECYTHIDACEAE	*Bertholletia excelsa* Bonpl.	0.64	2	2	40	64
183		*Corythophora rimosa* W.A.Rodrigues	0.81	3	1	4	60
184		*Couratari guianensis* Aubl.	0.51	3	2	40	43
185		*Eschweilera amazonica* R.Knuth	0.90	3	2	40	43
186		*Eschweilera atropetiolata* S.A.Mori	0.75	3	1	40	17
187		*Eschweilera bracteosa* (Poepp. ex O.Berg) Miers	0.88	3	1	9	56
188		*Eschweilera coriacea* (DC.) S.A.Mori	0.85	3	3	40	43
189		*Eschweilera obversa* (O.Berg) Miers	0.83	3	2	40	82,43
190		*Eschweilera wachenheimii* (Benoist) Sandwith	0.81	3	1	40	82,43
191		*Lecythis lurida* (Miers) S.A.Mori	0.86	3	2	40	43
192		*Lecythis pisonis* Cambess.	0.86	3	2	40	43
193		*Lecythis prancei* S.A.Mori	0.88	3	1	40	43
194		*Lecythis zabucajo* Aubl.	0.85	3	1	40	43

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195	LINACEAE	*Roucheria columbiana* Hallier f.	0.77	2	1	40	43
196	MALPIGHIACEAE	*Byrsonima chrysophylla* Kunth	0.69	1	1	38,40	43
197		*Byrsonima crispa* A.Juss.	0.58	3	3	40	43
198		*Byrsonima duckeana* W.R.Anderson	0.69	3	1	38,40	84,17
199	MALVACEAE	*Apeiba echinata* Gaertn.	0.36	1	3	31	88
200		*Eriotheca globosa* (Aubl.) A.Robyns	0.41	2	3	40	49
201		*Luehea speciosa* Willd.	0.52	2	2	25	43
202		*Lueheopsis rosea* (Ducke) Burret	0.33	2	1	40	56
203		*Pachira glabra* Pasq.	0.37	2	2	24	42
204		*Quararibea ochrocalyx* (K.Schum.) Vischer	0.56	2	1	20	88
205		*Sterculia frondosa* Rich.	0.47	1	1	40	
206		*Theobroma speciosum* Willd. ex Spreng.	0.63	2	2	40	43
207		*Theobroma sylvestre* Aubl. ex Mart. in Buchner	0.67	2	1	40	17
208	MELASTOMATACEAE	*Bellucia dichotoma* Cogn.	0.54	1	3	17	17
209		*Bellucia grossularioides* (L.) Triana	0.60	1	3	40	51
210		*Miconia argyrophylla* DC.	0.54	1	3	23	74,17
211		*Miconia cuspidata* Mart. ex Naudin	0.87	2	1	5	43
212		*Miconia eriodonta* DC.	0.63	1	1	2	74
213		*Miconia poeppigii* Triana	0.60	1	1	40	74
214		*Miconia regelii* Cogn.	0.60	2	1	38,40	68
215		*Miconia serialis* DC.	0.60	2	1	38,40	43
216		*Miconia tetraspermoides* Wurdack	0.60	2	1	38,40	31
217		*Miconia tomentosa* (Rich.) D.Don.	0.71	2	1	40	68
218	MELIACEAE	*Carapa procera* DC.	0.68	2	2	40	74
219		*Cedrela fissilis* Vell.	0.47	2	2	40	14
220		*Cedrela odorata* L.	0.46	3	2	40	43
221		*Guarea scabra* A.Juss.	0.74	3	1	40	43,93
222		*Trichilia septentrionalis* C.DC.	0.53	3	1	29	43
223	MORACEAE	*Bagassa guianensis* Aubl.	0.71	1	2	40	74,100
224		*Brosimum rubescens* Taub.	0.83	3	1	40	17
225		*Brosimum acutifolium* Huber	0.64	2	2	40	43
226		*Brosimum guianense* (Aubl.) Huber ex Ducke	0.84	2	2	40	69,29
227		*Brosimum lactescens* (S.Moore) C.C.Berg	0.66	2	2	40	29,75
228		*Brosimum parinarioides* Ducke	0.63	2	3	40	69
229		*Clarisia racemosa* Ruiz & Pav.	0.59	3	3	40	31
230		*Ficus gomelleira Kunth* & C.D.Bouché	0.39	2	1	22	31
231		*Ficus nymphaeifolia* Mill.	0.59	1	3	38,40,4	74
232		*Ficus* sp.	0.41	2	3	40	75
233		*Helicostylis scabra* (J.F.Macbr.) C.C.Berg	0.74	3	1	40	31
234		*Helicostylis tomentosa* (Poepp. & Endl.) J.F.Macbr.	0.63	2	1	40	43
235		*Maquira sclerophylla* (Ducke) C.C.Berg	0.51	1	3	40	43
236		*Naucleopsis caloneura* (Huber) Ducke	0.55	2	1	20,37	56
237		*Perebea mollis* (Poepp. & Endl.) Huber	0.37	2	2	40	82
238	MYRISTICACEAE	*Iryanthera grandis* Ducke	0.63	3	2	40	31
239		*Iryanthera juruensis* Warb.	0.63	2	1	40	69,17
240		*Osteophloeum platyspermum* (Spruce ex A.DC.) Warb.	0.47	3	1	40	43
241		*Virola multinervia* Ducke	0.45	2	1	15	15
242		*Virola michelii* Heckel	0.47	2	3	40	17

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243	MYRTACEAE	*Calyptranthes crebra* McVaugh	0.78	2	1	40	56
244		*Eugenia patrisii* Vahl	0.83	3	1	40	70
245		*Eugenia* sp.	0.76	3	3	40	17
246		*Myrcia fallax* (Rich.) DC.	0.82	3	1	40	74
247		*Myrcia guianensis* (Aubl.) DC.	0.74	2	1	1	61
248		*Myrcia magnoliifolia* DC.	0.77	3	1	40	
249		*Myrcia paivae* O.Berg	0.77	2	2	40	55
250		*Myrcia sylvatica* (G.Mey.) DC.	0.76	3	1	6	31
251		*Myrciaria floribunda* (H.West ex Willd.) O.Berg	0.79	3	3	40	88
252	NA	Dead tree	0.34	5	3	3	
253	NYCTAGINACEAE	*Neea madeirana* Standl.	0.55	2	1	40	67
254		*Neea oppositifolia* Ruiz & Pav.	0.89	1	2	40	43,75
255	OLACACEAE	*Chaunochiton kappleri* (Sagot ex Engl.) Ducke	0.52	2	1	40	43
256		*Dulacia guianensis* (Engl.) Kuntze	0.57	3	1	40	49
257		*Minquartia guianensis* Aubl.	0.80	3	1	40	43
258	OPILIACEAE	*Agonandra silvatica* Ducke	0.83	3	1	40	62
259	PERACEAE	*Pera glabrata* (Schott) Poepp. ex Baill.	0.67	1	1	40	43
260	PHYLLANTHACEAE	*Margaritaria nobilis* L.f.	0.48	2	2	40	72
261	POLYGONACEAE	*Coccoloba latifolia* Poir.	0.58	1	2	40	43
262	PROTEACEAE	*Roupala montana* Aubl.	0.73	3	1	40	44,98
263	QUIINACEAE	*Lacunaria jenmanii* (Oliv.) Ducke	0.92	3	1	38,40	56
264		*Touroulia guianensis* Aubl.	0.76	3	1	40	
265	RUBIACEAE	*Capirona decorticans* Spruce	0.59	2	2	40	96
266		*Chimarrhis barbata* (Ducke) Bremek.	0.71	2	1	40	62
267		*Chimarrhis turbinata* DC.	0.72	2	2	40	74
268		*Coussarea ampla* Müll.Arg.	0.48	2	1	40	83
269		*Duroia longiflora* Ducke	0.81	3	1	38	82,70
270		*Genipa americana* L.	0.62	1	2	40	43
271		*Isertia hypoleuca* Benth.	0.61	1	1	40	50
272		*Palicourea corymbifera* (Müll.Arg.) Standl.	0.66	1	1	38,40	92
273		*Palicourea guianensis* Aubl.	0.54	1	1	40	74
274		*Fagara* sp.	0.56	2	2	40	66
275		*Zanthoxylum rhoifolium* Lam.	0.57	2	3	40	43,56,17
276	SALICACEAE	*Casearia grandiflora* Cambess.	0.77	2	1	40	31
277		*Casearia javitensis* Kunth	0.75	2	2	40	74
278		*Casearia pitumba* Sleumer	0.73	2	1	40	74,63
279		*Casearia spruceana* Benth. ex Eichler	0.68	2	2	40	75
280		*Casearia ulmifolia* Vahl ex Vent.	0.68	2	1	33,40	74,63,75
281		*Laetia procera* (Poepp.) Eichl.	0.63	2	3	40	74,51,17
282		*Ryania speciosa* Vahl	0.49	1	1	36	
283	SAPINDACEAE	*Cupania hispida* Radlk.	0.64	1	1	40	43
284		*Matayba arborescens* (Aubl.) Radlk.	0.70	1	1	40	43
285		*Talisia carinata* Radlk.	0.86	3	2	30	
286		*Talisia longifolia* (Benth.) Radlk.	0.93	3	2	6	81
287		*Talisia praealta* Radlk.	1.05	3	1	38	

Nº	Family	Species	WD gcm^{-3}	ESG	OCC	WD Ref	ESG Ref
288	SAPOTACEAE	*Manilkara bidentata* (A.DC.) A.Chev.	0.87	3	1	40	43
289		*Manilkara huberi* (Ducke) Standl.	0.92	3	2	40	43
290		*Micropholis casiquiarensis* Aubrév.	0.71	3	1	40	
291		*Micropholis venulosa* (Mart. & Eichler ex Miq.) Pierre	0.67	3	1	40	43
292		*Pouteria bilocularis* (H.J.P.Winkl.) Baehni	0.71	3	2	40	43
293		*Pouteria gongrijpii* Eyma	0.80	3	2	40	43
294		*Pouteria guianensis* Aubl.	0.93	3	1	40	43
295		*Pouteria macrophylla* (Lam.) Eyma	0.74	3	2	40	43
296		*Pouteria oblanceolata* Pires	0.79	3	1	40	17
297		*Pouteria opposita* (Ducke) T.D.Penn.	0.65	3	1	9	43
298		*Pouteria petiolata* T.D.Penn.	0.68	3	1	20	91
299		*Pouteria platyphylla* (A.C.Sm.) Baehni	0.80	3	1	28	43,70
300		*Pouteria* sp.	0.78	3	2	40	43,70
301		*Pouteria torta* (Mart.) Radlk.	0.77	2	2	40	87
302		*Pouteria manaosensis* Aubrév. & Pellegr.	0.64	3	1	15	17
303	SIMAROUBACEAE	*Simaba cedron* Planch.	0.47	2	1	40	43
304		*Simaba polyphylla* (Cavalcante) W.W. Thomas	0.45	2	1	38	54
305		*Simarouba amara* Aubl.	0.38	2	1	40	74,17,56
306	SIPARUNACEAE	*Siparuna guianensis* Aubl.	0.56	2	1	11	17
307	STRELITZIACEAE	*Phenakospermum guyannense* (A.Rich.) Endl.	0.17	1	1	32	58
308	ULMACEAE	*Ampelocera edentula* Kuhlm.	0.70	2	1	40	43
309	URTICACEAE	*Cecropia palmata* Willd.	0.39	1	2	26	43
310		*Cecropia purpurascens* C.C.Berg	0.31	1	1	17	51,17
311		*Cecropia sciadophylla* Mart.	0.39	1	3	40	17
312		*Pourouma guianensis* Aubl.	0.38	1	3	40	74,43
313		*Pourouma villosa* Trécul	0.34	1	1	40	74,43
314	VIOLACEAE	*Rinorea guianensis* Aubl.	0.78	2	3	40	17
315		*Rinorea racemosa* (Mart.) Kuntze	0.68	2	1	40	17
316		*Rinorea pubiflora* (Benth.) Sprague & Sandwith	0.75	3	2	40	55
317	VOCHYSIACEAE	*Erisma bicolor* Ducke	0.70	3	1	27	75
318		*Qualea paraensis* Ducke	0.69	3	1	40	43
319		*Qualea albiflora* Warm.	0.57	3	1	40	43
320		*Vochysia vismiifolia* Spruce ex Warm.	0.75	3	1	27	43
321		Unknown	0.62	5	2		
322		Unknown	0.62	5	2		
323		Unknown	0.62	5	2		

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