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Modeling Tree Diameter Distributions in Natural Forests: An Evaluation of 10 Statistical Models

Renato Augusto Ferreira de Lima, João Luís Ferreira Batista, and Paulo Inácio Prado

In forestry, the description of tree sizes is commonly performed by fitting statistical models to diameter distributions. However, there is little agreement on which models are more flexible to this end, especially in tropical forests. Here we provide the simultaneous evaluation at species and subplot levels of 10 models using large data sets from four representative forest types in Brazil. We aimed to detect which models provide best fits and under which sample properties (size, median, variance, skewness, and kurtosis). We show that the combination of the logit-logistic, odd Weibull, Weibull, and Johnson's special bounded models provided reasonable descriptions for nearly all species (94.8%) and subplots (99.6%). However, there was little overlap between these four models, meaning that single models were rarely appropriate to describe the majority of cases. This complementarity was evident between the odd Weibull (better performance for more symmetrical, bimodal, or rotated-sigmoid patterns) and logit-logistic models (typical right-skewed and heavy-tailed patterns). The performance of all models was significantly related to forest type or sample properties. Models with more than three parameters had more problems related to optimization convergence, confidence interval estimation, and unrealistic fits. Finally, we discuss some theoretical issues related to the choice of appropriate models.

Keywords: diameter modeling, forest structure, model selection, size structure, tropical forest

Tree size distributions are a simple yet effective tool to describe tree populations and forest stands. They are used to value forests, plan harvest activities, predict forest growth, and thus enhance forest productivity (Bailey and Dell 1973, Hyink and Moser 1983, Burkhart and Tomé 2012, p. 261–297). Size distributions can also be used to infer past disturbance events, forest successional status, and aboveground biomass stocks (Coomes and Allen 2007). When assessed at the species level, they can be used to provide information on species-specific regeneration strategies, demographic rates, and population trends (Knight 1975, Wright et al. 2003).

Traditionally, tree size is assessed through stem dbh, and its frequency distribution is described using probability distributions, hereafter referred to as models. At least from the 1950s on, foresters started to search for models to describe dbh distributions (e.g., Meyer 1952), which are typically right-skewed. Classic models used to this end are the exponential, log-normal, Weibull, and gamma

models (Bliss and Reinker 1964, Hafley and Schreuder 1977). Also known as lifetime distributions, these models are often used to model the survival of machines, processes, or organisms (Lawless 2003, p. 1–8). In forestry, however, the use of such models is nearly always phenomenological (Leak 1965). A nonphenomenological use of such models would rely on a known relationship between tree size and age, which is rarely available, with the exception of even-aged stands (Bailey and Dell 1973).

Since the 1970s, new models have been derived, with some of them being recently applied to model dbh distributions (Wang and Rennolls 2005, Podlaski 2008). Amid the numerous models available, criteria are needed to choose appropriate candidate models. The simplest criterion is model fit to data. This assessment has been conducted using different combinations of models and using dbh data from natural or managed forests (Hafley and Schreuder 1977, Li et al. 2002, Palahí et al. 2007). Although a model capable of describing all possible shapes of dbh distributions probably does not

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This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft; hectares (ha): 1 ha = 2.47 ac.

Table 1. Main properties of the 10 candidate distributions used to model tree diameter distributions.

Model	Parameters	Bounded	$f(x)^*$	$h(x)^*$
Log-normal	shape (σ), scale (μ)	No	dec, modal	dec, modal
Exponential	scale (= 1/rate)	No	dec	cte
Weibull	shape, scale	No	dec, modal	cte, inc, dec
Odd Weibull	shape ₁ , shape ₂ , scale	No	dec, modal, S	cte, inc, dec, modal, U
Mod. Weibull	shape ₁ , shape ₂ , scale	No	dec, modal, S	cte, inc, dec, U
Gamma	shape, scale	No	dec, modal	cte, inc, dec
B.-Saunders	shape, scale	No	dec, modal	dec, modal, S
Beta	shape ₁ , shape ₂ , range	Yes	cte, inc, dec, modal, U, S	cte, inc, dec, modal, U, S
Johnson's SB	shape ₁ , shape ₂ , range	Yes	dec, modal, U	dec, inc, modal, U, S†
Logit-logistic	shape ₁ , shape ₂ , range	Yes	dec, modal, U	dec, inc, modal, U, S†

All distributions have an additional location parameter, which can be set to any desired value depending on the diameter cutoff criteria. The density function [$f(x)$] defines the probability of having dbh x , and the hazard function [$h(x)$] defines the probability of death/failure in dbh x .

* Types of shapes: cte, constant; dec, decreasing; inc, increasing; modal, unimodal; U, bathtub (U-shaped); S, sinuous or rotated sigmoid (S-shaped).

† For these models, we were not able to obtain the hazard functions, so the assignment of shapes for this function may not be complete.

exist, there is still little agreement on what is the amount of flexibility needed for a given model to appropriately describe this type of data. Previous studies generally compared a restricted set of candidate models or used dbh data from very specific forest types. In addition, the selection of appropriate models should not be based solely on fit to data. Other important criteria are the number and interpretability of the parameters and the existence of proper methods of parameter estimation and model comparison (Cox and Oakes 1984, p. 13–28).

Aiming to help the choice of flexible models to describe dbh distributions, we evaluate the performance of a representative set of models using empirical dbh data. To cover a wide range of possible applications, we perform this evaluation at species and subplot levels using data obtained from structurally different but representative types of natural forests in southeastern Brazil. We ask the following questions: Which models provide better fits to the observed dbh distributions? What properties of the samples (sample size, median, variance, skewness, and kurtosis) influence model fit? Which models have fewer analytical drawbacks during parameter estimation? Finally, we discuss other practical or theoretical properties that may help in the choice of proper candidate models.

Materials and Methods

Study Sites and Data Collection

Dbh measurements were conducted in four types of forests: savanna, white-sand, seasonal, and rainforests. These forests are markedly different in their composition, structure, and diversity. In each forest type, a 10.24-ha forest plot was placed in different protected areas of southeastern Brazil (plot coordinates vary between 22°24' and 25°04' S and 47°55' to 50°22' W). Each plot has 320 × 320 m, resulting in a total sampled area of 40.96 ha. Within each plot, all trees with dbh ≥ 4.8 cm were measured and identified to species. In cases of multiple stems, if at least one stem met the dbh cutoff criterion, measurements were taken for all stems. In cases of buttresses and bent trees, measurements were taken following the recommendations of Condit (1998, p. 46–54). Tree ferns or palm species, except for *Euterpe edulis*, were not included because they have limited or no secondary stem growth. Dbh data refer to the 2004/2005 surveys of the plots that resulted in densities of 2,142, 1,492, 1,176, and 1,135 trees ha⁻¹ for the savanna, white-sand, seasonal, and rainforest plots, respectively. Correspondingly, maximum dbh measurements were 45.2, 85.4, 216.5, and 151.2 cm.

Statistical Analyses

The evaluation of candidate models was carried out at the species and subplot levels. We only modeled species with ≥ 30 stems in each plot. When the same species presented ≥ 30 stems in two or more plots simultaneously, the populations of each plot were modeled separately. This resulted in 232 populations of 214 different tree species and a total of 95.1% of the 64,187 stems measured in the four plots (range, 31–4,927 stems per population; mean ± SD, 263 ± 568). Hereafter, these 239 populations are referred to as species. Then, we modeled the dbh distribution of 40 × 40 m subplots (0.16 ha), resulting in a total of 256 subplots evaluated (range, 37–517 stems per subplot; mean ± SD, 251 ± 90). This subplot dimension was chosen with the aim of avoid possible spatial autocorrelation between subplots in their stem density and total basal area, which had an average range of ~20–30 m (R.A.F. Lima and P.I. Prado, Laboratório de Ecologia Teórica, Departamento de Ecologia, Universidade de São Paulo, unpubl. results, 2013). All stems with dbh ≥ 4.8 cm from each population or subplot were used to obtain the dbh distributions. The analysis using equivalent dbh for the multitemmed trees (i.e., the dbh equivalent to the total basal area of all stems together) instead of all stems resulted in similar results (not shown). For all dbh distributions, we calculated sample size, variance, standardized L-skewness, and standardized L-kurtosis, hereafter referred to simply as sample and skewness. We used L-moments instead of C-moments because the first are less dependent on sample size and less susceptible to the presence of outliers (Hosking 1990). Because maximum dbh was strongly correlated to variance and skewness, the analyses including this variable were omitted.

We evaluated 10 models: log-normal (LN), exponential (EXP), Weibull, gamma, Johnson's special bounded (JSB), generalized beta (beta), Birnbaum-Saunders (BS), logit-logistic (LL), new modified Weibull (MW), and odd Weibull (OW) models. The first five are commonly used to model empirical dbh distribution (Hafley and Schreuder 1977), whereas the beta, BS, and LL models have been applied to this end only recently (Li et al. 2002, Wang and Rennolls 2005, Podlaski 2008). As far as we know, this is the first time that the MW (Lai et al. 2003) and OW (Cooray 2006) are being used to model dbh distributions. Both are modifications of the Weibull model and have the EXP and Weibull models as special cases. General properties of the 10 models are given in Table 1. We tried to select a representative set of models that have up to four parameters and that have been suggested as good descriptors of dbh distribution

in previous studies. We did not attempt to fit models with more than four parameters, which are often difficult to estimate and to interpret biologically. Moreover, we have not evaluated finite mixtures (Liu et al. 2002) that would add subjectivity related to the arbitrary definition of the models to be mixed.

Parameter estimation was performed using maximum likelihood techniques (Bolker 2008, p. 227–291) and the probability density functions (PDFs) of the 10 models (Supplemental File S1[■]). The negative log-likelihood function of each PDF was minimized using numerical optimization to find the parameters that best fit the data, the maximum likelihood estimates (MLEs). MLEs have many desirable statistical properties, such as invariance to reparameterization, consistency, and asymptotic normality (Royle and Dorazio 2008, p. 43–50). In addition, studies have reported MLEs as being superior or comparable to other parameter estimation methods, such as moments and percentile methods (Zhou and McTague 1996, Zhang et al. 2003). Because dbh distributions are left truncated, we used location-free versions of the PDFs to build the likelihood functions, and we fixed the location parameter at minimum dbh $- c$, a constant that simply is half of the dbh measurement precision. Although arbitrary, fixing the location parameter avoids convergence problems and biased estimates (Cousineau 2008). An exception to this rule was the BS model that had the location parameter fixed at minimum dbh $- 2c$. The LN and BS models were very sensitive to the definition of the location, so that when it was fixed at values close to minimum dbh, both models had much worse performance (results not shown). Ideally, all 10 PDFs should have been truncated using the accumulated probability at the location. However, cumulative distribution functions were not available or did not have a closed form for all models, which greatly complicates the numerical estimation of the parameters.

Three of the 10 models (beta, JSB, and LL models) are bounded, meaning that they only vary within a finite interval of values. For these models, the range parameter was kept free during optimizations, and the maximum minus minimum dbh was used as the starting value in the optimization routine. For other parameters and for unbounded models, starting values for the parameters were defined using the method of moments, whenever available for a given model. All fits were visually inspected by superimposing them to density histograms. In cases of bad fits, we varied the start parameters, the maximum number of iterations, or the optimization method (e.g., Nelder-Mead, quasi-Newton, or simulated annealing [Bolker 2008, p. 293–346]). This was particularly true for bounded models that often resulted in unreasonable fits, such as U-shaped fits when the distribution was clearly not U-shaped.

The comparison of candidate models was based on the Akaike information criterion ($AIC = -2 \ln(L) \pm 2k$, where L is likelihood and k is number of parameters) that measures the distance of a candidate model relative to an unknown true model, taking into account the number of parameters in the model (Burnham and Anderson 2002, p. 60–64). The difference in AIC from the model with the lowest AIC (ΔAIC) was used here as a measure of “goodness of fit,” allowing simultaneous comparison of models with different numbers of parameters. The performance of the 10 candidate models to describe each dbh distribution was classified into plausible or nonplausible according to their ΔAIC . We used three different ΔAIC thresholds (two, four, and seven) to rank models. If ΔAIC was

smaller than the threshold, than the model was ranked as “plausible.” The use of larger thresholds avoids models providing good descriptions to data being discarded due to small sample sizes (when n is small, models with fewer parameters tend to perform better [Richards 2005]). We are aware that the ΔAIC of each model is conditioned on the set of candidate models. Therefore, we also present an evaluation of the models based on the general shapes that they can assume, which is described here in terms of their coverage in the skewness-kurtosis space, sometimes referred to as the β_1 - β_2 plane (Hafley and Schreuder 1977, Wang and Rennolls 2005). However, instead of the skewness-kurtosis space based on C-moments, here we also used standardized L-moments. Each model covers an amount of area in the skewness-kurtosis space, and the comparison of these areas can be used to select appropriate candidate models for specific situations.

The effect of sample properties on model performance was evaluated by regressing the performance of each model on sample size, median, variance, skewness, kurtosis, and forest type. A separate regression was applied to each combination of models and sample properties. Because the performance of the models was binary (plausible and not plausible), analysis was performed using mixed-effects logistic regressions (Pinheiro and Bates 2000, p. 337–347), in which the sample properties were the fixed effects and the evaluation level (species or subplots) was the random effect. Thus, although the performance of models at species and subplot levels was lumped together ($n = 488$), we controlled for the variations in model performance between levels of evaluation. The overall effect of the sample property on the regression model was assessed by comparing the AIC of regression models with and without the sample property as a covariate. The difference between forest types was assessed based on the overlap of likelihood profiles of their coefficient estimates. The same procedures were used to perform a direct comparison between the two models with the best fit to the data, aiming to assess under which sample properties each model performed better. In practice, we assessed whether the means of sample properties were different for dbh distributions that were well fitted by the first or second model, by both models, or by neither of the two models. Analyses were performed using R version 2.14 and the packages *bbmle* (Bolker 2010) and *lme4* (Bates et al. 2012).

Results

The evaluation of the 10 models in terms of their fit to dbh data resulted in the following best-to-worst ranking: LL, OW, Weibull, gamma, beta, JSB, MW, EXP, LN, and BS. This outcome varied little among species and subplot levels and between ranking using different ΔAIC thresholds (Table 2). The main difference was that the OW performed better at the species level, whereas the LL performed better at the subplot level. It should be noted, however, that single candidate models were rarely appropriate for describing the majority of dbh distributions. The models with the best fit to the data, the OW and LL, provided plausible fits for 51 and 60% of the species and subplots at an ΔAIC threshold of 2, respectively. The top three models provided plausible fits for 87.5% of species and 94.5% of subplots at the same threshold level. The JSB was the model with the least overlap with the top three models in cases for which it provided reasonable descriptions for dbh data (Figure 1), raising these proportions to 94.8 and 99.6%. The gamma model, which outperformed the JSB, had a large overlap with the Weibull

[■] Supplementary data are available with this article at <http://dx.doi.org/10.5849/forsci.14-070>.

Table 2. Performance of the 10 candidate models used to describe species and subplot level diameter distributions.

Model	Species (<i>n</i> = 232)				Subplots (<i>n</i> = 256)			
	<2	<4	<7	M[ΔAIC]	<2	<4	<7	M[ΔAIC]
Log-normal	8.6	13.6	18.7	18.5	5.1	9.7	16.9	20.3
Exponential	24.6	33.2	50.4	6.7	13.3	18.4	25.0	15.9
Weibull	44.4	59.1	73.3	3.2	34.0	44.1	56.3	5.3
Odd Weibull	50.9	77.2	89.7	1.9	48.1	71.5	87.5	2.3
Mod. Weibull	28.0	63.7	77.6	3.3	10.6	36.7	48.8	7.1
Gamma	34.1	48.3	68.5	4.3	26.6	35.6	44.1	8.5
B.-Saunders	10.4	17.4	25.5	19.8	2.8	6.6	7.7	37.1
Beta	30.2	60.4	77.6	3.4	11.3	28.5	39.4	10.1
Johnson's SB	25.4	43.5	56.5	4.4	13.3	21.9	35.2	8.9
Logit-logistic	46.3	64.1	73.7	2.5	60.2	71.9	84.8	0.6

Values represent the percentage of times when the distribution provided a plausible fit among the set of candidate models. Model ranking was done using three different thresholds of ΔAIC (i.e., 2, 4, and 7). M[ΔAIC] is the median of the ΔAIC values for each model; lower M[ΔAIC] values indicate better performances of the models.

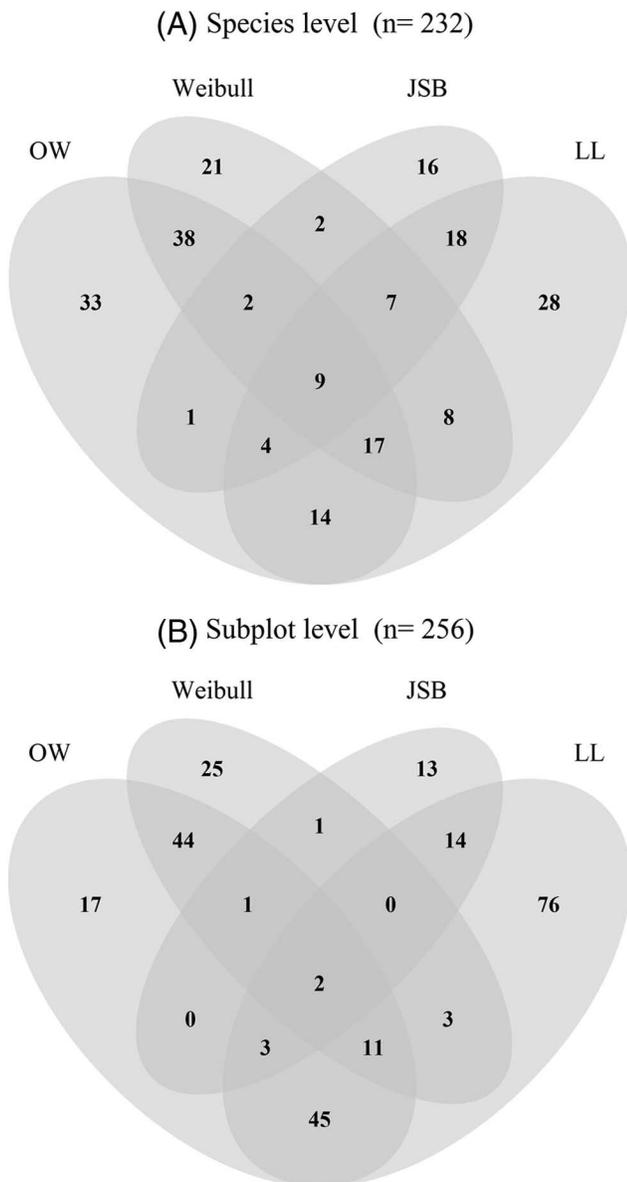


Figure 1. Venn diagrams of the four distributions with the best fit to species and subplot diameter distributions. The numbers represent the cases in which a model provided plausible descriptions for dbh data, exclusively or simultaneously with other models.

(72.9% at ΔAIC threshold of 2). There was also a large overlap of the Weibull and MW with the OW (66.5 and 86.7%, respectively) and of the JSB with the LL (62.3%). The one-parameter EXP provided good fits for only 19% of the distributions, and out of this proportion only 11% did not overlap with the Weibull or OW, which have the EXP as a special case [shape parameter(s) ≈ 1].

The overall results presented above are well illustrated by the comparison between the sample skewness and kurtosis of the observed dbh distributions and the theoretical skewness-kurtosis space that the candidate models cover (Figure 2). In this graph, the two-, three-, and four-parameter models are represented by points, lines, and planes, respectively. The two best models in terms of fit, the LL and OW, were the ones with the largest coverage of the skewness-kurtosis space. However, the Weibull (upper limit line of the MW) and gamma (upper limit line of the beta) represented by lines outperformed much more flexible models such as the beta, MW, and JSB. Thus, it seems that the position of the upper limit line of the four-parameter models and not that of their lower limit line was crucial to their ability to fit the observed dbh distributions. The LN line (upper limit line of the JSB) passes above or below the majority of the values of skewness and kurtosis observed for species and subplots, respectively, which may explain its poor performance in this study. The same was true for the line of the BS (not shown in the graph for clarity), a model that was only appropriate for distributions with a well-defined mode at values away from the location. As expected, the one-parameter EXP represented by a single point (Figure 2) was not very flexible to fit the variety range of observed skewness and kurtosis.

The performance of models was significantly related to sample properties and forest type. In general, their performance worsened as size, total basal area, variance, skewness, and kurtosis of the sample increased (Table 3). Exceptions were the positive relationships of the OW with sample size and of the LL with sample variance, skewness, and kurtosis. The absence of a relationship between the JSB with variance and skewness and between the OW with basal area, kurtosis, and forest type was remarkable as well. The direct comparison between the LL and OW performances revealed that the OW was more appropriate for distributions with larger medians and smaller variances, skewness, and kurtosis (i.e., more symmetric distributions) than the LL (Table 4). The OW also performed better for fitting unimodal distributions and distributions with tendencies for bimodality. The visual inspection of model fits revealed some of these trends (Figure 3).

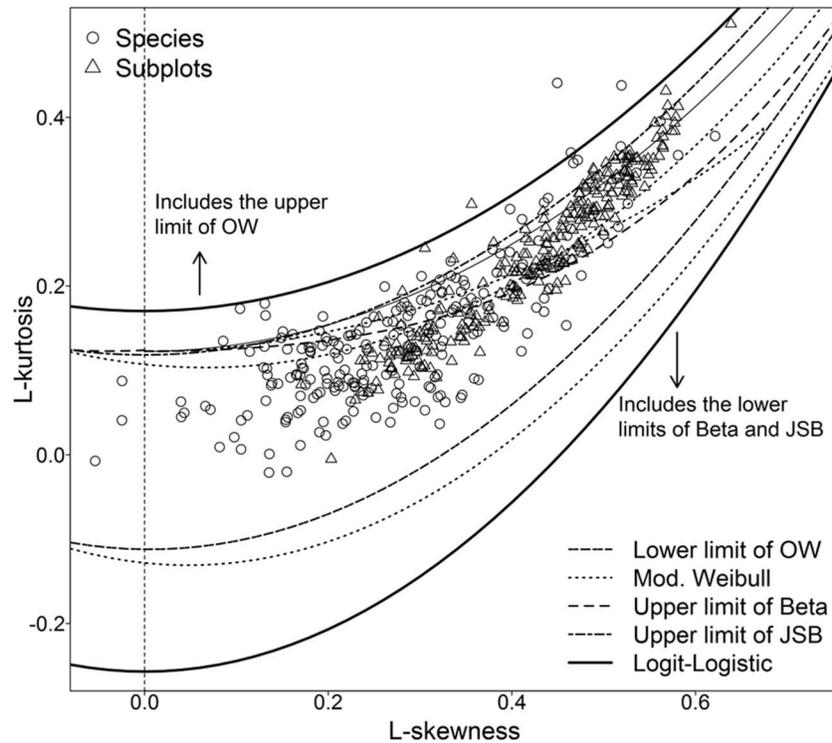


Figure 2. Coverage of the models evaluated in the L-skewness versus L-kurtosis space and the values of the two sample L-moments for the observed species (○) and subplots (△) dbh distributions. Here, the EXP model is represented by the point (L-skewness, L-kurtosis) = (1/3, 1/6), whereas the LN, Weibull, and gamma models coincide with the upper limits of the JSB, MW, and beta models, respectively. The BS is not presented for clarity. The vertical dashed line is the line of perfectly symmetrical distributions (i.e., L-skewness = 0).

Table 3. Results of the simple mixed-effects logistic regressions used to assess the effects of different sample properties and forest types on the performance of the 10 models evaluated here.

Model	<i>n</i>	BA	Med	var	Skew	Kurt	Forest type
Log-normal	14.6*	2.1*	0.6	3.9†	31.9†	21.8†	8.5: Rf ≥ Ws = Sv = Sf
Exponential	12.8*	32.9*	-1.5	0.1	-1.9	0.9	2.5: Rf > Sf = Ws = Sf
Weibull	-1.4	30.9*	3.2*	47.1*	26.4*	11.3*	17.5: Sv = Sf > Rf = Ws
Odd Weibull	3.7†	-1.2	-1.2	6.8*	8.4*	-1.2	1.9: not significant
Mod. Weibull	-0.2	1.2	4.7†	17.0*	131.4*	80.2*	17.9: Sv = Ws = Sf ≥ Rf
Gamma	3.1*	45.0*	5.5*	39.6*	10.5*	10.0*	10.9: Sv > Sf = Rf = Ws
B.-Saunders	17.1*	1.8	1.9	1.9	12.3†	3.7†	4.7: Rf ≥ Sv = Sf = Ws
Beta	-1.8	11.4*	-0.1	20.0*	112.3*	98.3*	11.1: Sv > Ws = Sf = Rf
Johnson's SB	27.6*	12.5*	-1.9	-0.8	-0.5	27.5*	18.5: Rf = Sv = Ws > Sf
Logit-logistic	34.4*	-1.9	-1.8	36.3†	69.9†	44.3†	29.7: Rf = Ws = Sf > Sv

Values correspond to the Δ AIC between the model without the covariate (constant model) and the model with the covariate. If the Δ AIC value is positive, the model with the covariate was a better fit than the constant model; if the Δ AIC value is negative, the model with the covariate was a worst fit. Absolute Δ AIC values <2 are not strong evidence of a difference between the fit of models. Regressions were constructed separately for each combination of model and sample property. The results for forest type are given in decreasing order of performance from left to right and \geq means that one forest type has mean performance equal to that of the adjacent one, but different from that of the others. *n*, sample size; BA, basal area; Med, median; Var, variance; Skew, L-skewness; Kurt, L-kurtosis; Sv, = savanna; Ws = white-sand; Sf = seasonal forest; Rf = rainforest.

* Negative/decreasing relationship between model performance and the covariate.

† Positive/increasing relationship between model performance and the covariate.

Table 4. Comparison of the sample properties of observed dbh distributions for which the Logit-logistic, Odd Weibull, both, or other distributions were plausible fits.

	Logit-logistic (154)	Odd Weibull (136)	Both (105)	Others (93)
<i>n</i>	197.9 ± 117.7A	398.3 ± 573.2B	169.7 ± 105.1A	244.8 ± 519.4A
Median	9.5 ± 2.9A	10.3 ± 4.1B	9.7 ± 3.5AB	9.8 ± 2.8AB
Variance	122.2 ± 136.5A	57.4 ± 67.2B	112.6 ± 125.8A	63.9 ± 76.3B
Skewness	0.412 ± 0.107A	0.293 ± 0.118B	0.392 ± 0.158A	0.313 ± 0.103B
Kurtosis	0.210 ± 0.091A	0.162 ± 0.092B	0.243 ± 0.121C	0.154 ± 0.073B

The same letters indicate that the means were not different between groups. The addition of the grouping variable in the model greatly improved the overall fit for all sample properties (i.e., Δ AIC between models with and without the grouping variable was always >4). The number of distributions in each group is given in parenthesis. *n*, sample size; Skewness, standardized L-skewness; Kurtosis, L-kurtosis.

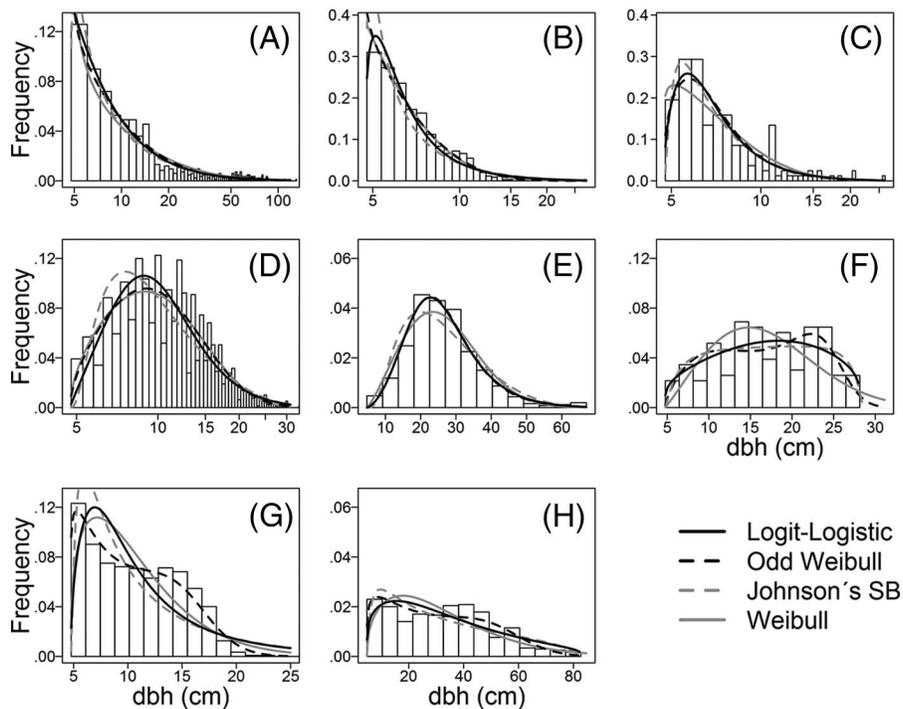


Figure 3. Examples of the observed dbh-frequency distributions and their respective fits by the four models with best fit to data: (A) *Aspidosperma polyneuron* (seasonal forest); (B) *Trichilia catigua* (seasonal forest); (C) *Maprounea guianensis* (savanna); (D) *Ocotea corymbosa* (savanna); (E) *Ocotea pulchella* (white-sand forest); (F) *Myrcia ilheosensis* (White-sand forest); (G) *Euterpe edulis* (rainforest); (H) *Calophyllum brasiliensis* (white-sand forest). Note that the x-axis is presented in log scale in panels A–D but not in panels E–H.

The two- and three-parameter models presented no problems of convergence in the numerical optimization and fits were very robust to changes in the start parameters. For other models, namely OW, MW, beta, JSB, and LL, parameter estimation generated optimization problems (nonconvergences using the initial starts were 9, 1, 4, 2, and 62, respectively). Most of the convergence problems occurred at the species level and were solved by changing the start parameters. For the LL, however, convergence was not attained at all in 11 cases. In general, the OW and MW were much less sensitive than the beta, JSB, and LL to bad start parameters. The flexibility of the beta, JSB, and especially the LL resulted in some U-shaped fits, i.e., fits that predicted increasing probabilities of having larger dbh values. Very large range estimates such as values >500 were also common for the beta model. The inversion of the Hessian matrix to find the confidence intervals of the parameters (Bolker 2008, p. 262–263) frequently failed for the four-parameter models, mainly the bounded ones. And when these intervals were attainable, they often were so broad that they became meaningless.

Discussion

At the species and subplot levels, we described dbh distributions obtained from four 10-ha plots placed in contrasting types of natural tropical forests. In terms of fit, the overall result was straightforward: the joint use of the LL, OW, Weibull, and JSB models provided good descriptions for nearly all species and subplot dbh distributions. Good performances of the LL, Weibull, and JSB have been demonstrated before in natural (Podlaski 2006, Palahí et al. 2007) and planted forests (Nanang 1998, Wang and Rennolls 2005). Our results place the OW among models with better performances for the description of dbh data. Overall, the LL and OW models often provided good descriptions regardless of the ΔAIC threshold ad-

opted, meaning that even when they were not the best fit, their fit was generally plausible.

Although the LL and OW models covered wide ranges of skewness and kurtosis, they performed better under different circumstances. The OW described better, more symmetrical distributions or distributions with trends toward bimodal or rotated sigmoid shapes (Goff and West 1975). This may be the case for early-successional species (Wright et al. 2003), species or stands presenting peaks of growth and/or mortality (Leak 2002), even-aged stands (Schmelz and Lindsey 1965), and forests under thinning (Maltamo et al. 2000) or harvesting focused on specific tree sizes. This last suggestion was evident for *Euterpe edulis* (Figure 3G), a palm species that is illegally harvested in the rainforest plot. Moreover, the OW was able to deal with such irregular distributions using fewer parameters than finite mixtures (Zhang et al. 2001, Liu et al. 2002). In addition, the OW performed better for larger sample sizes, which might suggest that the best fit of the LL and other models over the OW could be a matter of sample size. Conversely, the LL is indicated for typical right-skewed patterns, which was probably the reason that the LL performed even better at the subplot level. In particular, the LL described well species with large contributions of small and extreme values at the same time (Figure 3B). This may be the case for large-sized species with low growth and/or high survival of juveniles (shade-tolerant species [Knight 1975]) or with massive recruitment followed by high juvenile mortality (emergent species [Swaine and Hall 1988]).

The beta model, although being fairly flexible in shape (Figure 2), performed worse than the two-parameter Weibull and gamma models. In addition, we found little difference between the performance of the beta and JSB models at either level, somewhat contradicting the results found by Li et al. (2002) and by Wang and

Rennolls (2005) and those that would be expected solely by the assessment of the skewness-kurtosis space coverage of the candidate models. Moreover, we found better performance of the Weibull than of the MW, an unexpected result based on Lai et al. (2003). This shows that the flexibility given by the extra parameter of the beta, JSB, and MW models was not enough to overcome the penalty imposed by the AIC on these less parsimonious models, at least for this type of data. Besides providing poorer fits than the best performance models, the gamma and MW had great overlap with them, so the decision of selecting these models to describe similar forests should be based on criteria other than fit (see below). The EXP, LN, and BS models clearly performed worse, suggesting that they may provide better descriptions in temperate or managed forests, as found by Bliss and Reinker (1964), Nanang (1998), and Podlaski (2008).

A good fit to data, however, should not be the sole criterion to select one model over another. One may choose models with equally good or poorer fits if there are theoretical or practical reasons to do so (Burnham and Anderson 2002, p. 15–19). Each model has its own theoretical assumptions on the processes generating the observed patterns, and if these processes make sense to a given population or forest, a model can serve as a hypothesis of underlying mechanisms. For instance, an exponential pattern is expected when individual mortality and growth are independent of tree size (Muller-Landau et al. 2006), meaning that tree growth and death are related to random events independent of the individual (Cox and Oakes 1984, p. 13–28), such as disturbances. A Weibull distribution is expected when mortality is constant, but growth is a power-law function of tree size (Muller-Landau et al. 2006). The LN assumes a multiplicative degradation process (Leiva et al. 2009, p. 35–37). The gamma assumes mortality as a wear-out process generated by the accumulation of independent but consecutive damage or stress events (Leiva et al. 2009, p. 35–37). Unfortunately, there is no such clear interpretation of the theoretical assumptions for all models. Some of them have been derived from transformations of other models, such as the MW, OW, LL, and JSB (Lai et al. 2003, Wang and Rennolls 2005, Cooray 2006), making them more phenomenological than theoretical descriptions of diameter distributions. Moreover, the above-cited assumptions of the models may only be valid under the assumption that populations are at demographic equilibrium (Harcombe 1987, Muller-Landau et al. 2006). And because different processes may result in similar patterns, there is always the risk of a model describing well a pattern that has been generated by processes different from those assumed in the original formulation of such a model (Lawless 2003, p. 38).

In addition to theory, the selection of models can be judged by the existence of meaningful parameters. Models with two shape parameters such as the LL, OW, MW, beta, and JSB are more flexible, but they are also more difficult to interpret biologically. In addition, one may give preference to models that have the EXP as a special case (e.g., gamma and Weibull, and its generalizations), so that deviations from the well-known exponential pattern can be easily assessed (Schmelz and Lindsey 1965). Moreover, one should ask whether bounded models (e.g., LL, Beta, and JSB) make sense for the data in hand. Their fit is quite sensitive to the definition of upper and lower bounds, which are generally defined arbitrarily, vary with sample size, or change over time in planted forests (Palahí et al. 2007, Taubert et al. 2013). Although the range parameter could provide extra information on tree maximum sizes, in this

study it often worked purely as a phenomenological parameter with unrealistic estimates, such as dbh ranges larger than 500 cm.

We showed that the performance of some models was less influenced by sample properties than others. For instance, the lack of relationship of model performance with forest type was a positive feature of the OW over other models. In addition, technical or computational convenience, such as the frequency of convergence problems and sensibility to start parameters in optimization procedures, can be taken into account as well (Cox and Oakes 1984, p. 1–11). Optimization procedures for four-parameter models often result in convergence problems. Unfortunately, the definition of an appropriate set of candidate models based on criteria other than fit is much more subjective and greatly relies on the researcher's previous knowledge of the models and on the system being modeled (Burnham and Anderson 2002, p. 15–19).

Although the evaluation presented here ended in straightforward results, the performance of the 10 candidate models should be interpreted with care. We could have had different outcomes if dbh data had come from managed forests (Nanang 1998, Li et al. 2002) or from even-aged stands (Bliss and Reinker 1964, Nord-Larsen and Cao 2006), had different cutoff criteria (Goff and West 1975), or had different development stages (Podlaski 2006). Moreover, other aspects not covered here can be addressed in future research. What would be the effect of different criteria to define the location or range parameters? Another promising approach is the assessment of the LL and OW to model bivariate distributions such as tree dbh and height (Li et al. 2002) or distributions in time (Knoebel and Burkhardt 1991). It seems unlikely that the use of parameter estimators other than maximum likelihood would lead to different outcomes in terms of model performance. However, it would be interesting to explore maximum likelihood methods that could account for dbh measurement errors (Taubert et al. 2013) or that could give greater weight to larger dbh values (Cousineau 2008), which are much less frequent but greatly contribute to forest structure and biomass (Chave et al. 2003). Thus, although there were clear indications of flexible candidate models to describe very different forest types, there still are many opportunities to broaden the use of such models to describe tree diameter distributions.

Literature Cited

- BAILEY, R.L., AND T.R. DELL. 1973. Quantifying diameter distributions with the Weibull function. *For. Sci.* 19:97–104.
- BATES, D., M. MAECHLER, AND B. BOLKER. 2012. *lme4: Linear mixed-effects models using Eigen and S4 classes*. R package version 0.999999-0. Available online at CRAN.R-project.org/package=lme4; last accessed Mar. 30, 2014.
- BLISS, C.I., AND K.A. REINKER. 1964. A lognormal approach to diameter distributions in even-aged stands. *For. Sci.* 10:350–360.
- BOLKER, B.M. 2008. *Ecological models and data in R*. Princeton Univ. Press, Princeton, NJ. 396 p.
- BOLKER, B.M. 2010. *bbmle: Tools for general maximum likelihood estimation*. R package version 0.9.5.1. Available online at CRAN.R-project.org/package=bbmle; last accessed Mar. 30, 2014.
- BURKHART, H.E., AND M. TOMÉ. 2012. *Modeling forest trees and stands*. Springer, New York. 459 p.
- BURNHAM, K.P., AND D.R. ANDERSON. 2002. *Model selection and multi-model inference: A practical information—Theoretic approach*, 2nd ed. Springer, New York. 488 p.
- CHAVE, J., R. CONDIT, S. LAO, J.P. CASPERSEN, R.B. FOSTER, AND S.P. HUBBELL. 2003. Spatial and temporal variation of biomass in a tropical forest: Results from a large census plot in Panama. *J. Ecol.* 91:240–252.

- CONDIT, R. 1998. *Tropical forest census plots: Methods and results from Barro Colorado Island, Panama and a comparison with other plots*. Springer-Verlag, Berlin, Germany. 211 p.
- COOMES, D.A., AND R.B. ALLEN. 2007. Mortality and tree-size distributions in natural mixed-age forests. *J. Ecol.* 95:27–40.
- COORAY, K. 2006. Generalization of the Weibull distribution: The odd Weibull family. *Stat. Model.* 6:265–277.
- COUSINEAU, D. 2008. Fitting the three-parameter Weibull distribution: Review and evaluation of existing and new methods. *IEEE Trans. Dielectr. Electr. Insul.* 16:281–288.
- COX, D.R., AND D. OAKES. 1984. *Analysis of survival data*. Monographs on Statistics and Applied Probability. Chapman and Hall, London, UK. 201 p.
- GOFF, F.G., AND D. WEST. 1975. Canopy-understory interaction effects on forest population structure. *For. Sci.* 21:98–108.
- HAFLEY, W.L., AND H.T. SCHREUDER. 1977. Statistical distributions for fitting diameter and height data in even-aged stands. *Can. J. For. Res.* 7:481–487.
- HARCOMBE, P.A. 1987. Tree life tables. *Bioscience* 37:557–568.
- HOSKING, J.R.M. 1990. L-moments: Analysis and estimation of distributions using linear combinations of order statistics. *J. R. Stat. Soc. Ser. B* 52:105–124.
- HYINK, D.M., AND J.W. MOSER JR. 1983. A generalized framework for projecting forest yield and stand structure using diameter distributions. *For. Sci.* 29: 85–95.
- KNIGHT, D.H. 1975. A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. *Ecol. Monogr.* 45:259–284.
- KNOEBEL, B.R., AND H.E. BURKHART. 1991. A bivariate distribution approach to modeling forest diameter distributions at two points in time. *Biometrics* 47:241–253.
- LAI, C.D., M. XIE, AND D.N.P. MURTHY. 2003. A modified Weibull distribution. *IEEE Trans. Reliability* 52:33–37.
- LAWLESS, J.F. 2003. *Statistical models and methods for lifetime data*, 2nd ed. John Wiley & Sons, New York. 630 p.
- LEAK, W.B. 1965. The J-shaped probability distribution. *For. Sci.* 11:405–409.
- LEAK, W.B. 2002. *Origin of sigmoid diameter distributions*. USDA For. Serv., Res. Pap. NE-178, Northeastern Research Station, Newtown Square, PA. 10 p.
- LEIVA, V., M. BARROS, AND G.A. PAULA. 2009. *Generalized Birnbaum-Saunders models using R*. Brazilian Statistical Association, São Paulo, Brazil. 329 p.
- LI, F., L. ZHANG, AND C.J. DAVIS. 2002. Modeling the joint distribution of tree diameters and heights by bivariate generalized beta distribution. *For. Sci.* 48:47–58.
- LIU, C., L. ZHANG, C.J. DAVIS, D.S. SOLOMON, AND J.H. GOVE. 2002. A finite mixture model for characterizing the diameter distributions of mixed-species forest stands. *For. Sci.* 48:653–661.
- MALTAMO, M., A. KANGAS, J. UUTTERA, T. TORNIAINEN, AND J. SARAMAKI. 2000. Comparison of percentile based prediction methods and the Weibull distribution in describing the diameter distribution of heterogeneous Scots pine stands. *For. Ecol. Manage.* 133:263–274.
- MEYER, H.A. 1952. Structure, growth, and drain in balanced uneven-aged forests. *J. For.* 50:85–92.
- MULLER-LANDAU, H.C., R. CONDIT, K.E. HARMS, C.O. MARKS, S.C. THOMAS, S. BUNYAVEJCHEWIN, G. CHUYONG, ET AL. 2006. Comparing tropical forest tree size distributions with the predictions of metabolic ecology and equilibrium models. *Ecol. Lett.* 9:589–602.
- NANANG, D.M. 1998. Suitability of the normal, log-normal and Weibull distributions for fitting diameter distributions of Neem plantations in Northern Ghana. *For. Ecol. Manage.* 103:1–7.
- NORD-LARSEN, T., AND Q.V. CAO. 2006. A diameter distribution model for even-aged beech in Denmark. *For. Ecol. Manage.* 231:218–225.
- PALAHÍ, M., T. PUKKALA, E. BLASCO, AND A. TRASOBARES. 2007. Comparison of beta, Johnson's SB, Weibull and truncated Weibull functions for modeling the diameter distribution of forest stands in Catalonia (north-east of Spain). *Eur. J. For. Res.* 126:563–571.
- PINHEIRO, J., AND D. BATES. 2000. *Mixed-effects models in S and S-PLUS*. Springer, New York. 528 p.
- PODLASKI, R. 2006. Suitability of the selected statistical distributions for fitting diameter data in distinguished development stages and phases of near-natural mixed forests in the Swietokrzyski National Park (Poland). *For. Ecol. Manage.* 236:393–402.
- PODLASKI, R. 2008. Characterization of diameter distribution data in near-natural forests using the Birnbaum-Saunders distribution. *Can. J. For. Res.* 38:518–527.
- RICHARDS, S.A. 2005. Testing ecological theory using the information-theoretic approach: Examples and cautionary results. *Ecology* 86: 2805–2814.
- ROYLE, J.A., AND R.M. DORAZIO. 2008. *Hierarchical modeling and inference in ecology: The analysis of data from populations, metapopulations and communities*. Academic Press, San Diego, CA. 444 p.
- SCHMELZ, D.V., AND A.A. LINDSEY. 1965. Size-class structure of old-growth forests in Indiana. *For. Sci.* 11:258–264.
- SWAINE, M.D., AND J.B. HALL. 1988. The mosaic theory of forest regeneration and the determination of forest composition in Ghana. *J. Trop. Ecol.* 4:253–269.
- TAUBERT, F., F. HARTIG, H.-J. DOBNER, AND A. HUTH. 2013. On the challenge of fitting tree size distributions in ecology. *PLoS One* 8:e58036.
- WANG, M., AND K. RENNOLLS. 2005. Tree diameter distribution modeling: Introducing the logit-logistic distribution. *Can. J. For. Res.* 35:1305–1313.
- WRIGHT, S.J., H.C. MULLER-LANDAU, R. CONDIT, AND S.P. HUBBELL. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84:3174–3185.
- ZHANG, L., K.C. PACKARD, AND C. LIU. 2003. A comparison of estimation methods for fitting Weibull and Johnson's SB distributions to mixed spruce-fir stands in northeastern North America. *Can. J. For. Res.* 33:1340–1347.
- ZHANG, L., J.H. GOVE, C.A. LIU, AND W.B. LEAK. 2001. A finite mixture of two Weibull distributions for modeling the diameter distributions of rotated-sigmoid, uneven-aged stands. *Can. J. For. Res.* 31:1654–1659.
- ZHOU, B., AND J.P. MCTAGUE. 1996. Comparison and evaluation of five methods of estimation of the Johnson system parameters. *Can. J. For. Res.* 26(6):928–935.