

FORUM

Response to Coomes & Allen (2009) ‘Testing the metabolic scaling theory of tree growth’

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Summary

1. Coomes & Allen (2009) propose a new statistical method to test the Metabolic Scaling Theory prediction for tree growth rate size scaling (scaling constant $\alpha = 1/3$) presented in Enquist *et al.* (1999). This method finds values of the scaling constant that yield standardized major axis (SMA) slopes of one in a comparison of allometrically transformed diameter census data. This SMA ‘slope-of-one’ method produces results that contrast with those generated by maximum-likelihood estimation (MLE; Russo, Wiser & Coomes 2007; Coomes & Allen 2009).

2. We hypothesize that the SMA slope-of-one method is inappropriate for this application because it assumes, unrealistically, that there is no biological or error variance in tree growth size scaling. To test our hypothesis, we simulate ‘allometric’ tree growth with biological and error variance in parameters and measurements. We find that the SMA slope-of-one method is sensitive to the amount of biological and error variance and consistently returns biased parameter estimates, while the MLE method displays relatively little bias, particularly at larger sample sizes.

3. *Synthesis.* The conclusions of Coomes & Allen (2009) should be reconsidered in the light of our findings. Investigations of tree growth rate size scaling must consider the influence of biological and error variance in model-fitting procedures to ultimately unravel the effects of tree architecture and ecological factors on patterns of size-dependent growth.

Key-words: Costa Rica, forests, growth rate size scaling, light competition, maximum-likelihood estimation, metabolic scaling theory, plant development and life-history traits, San Emilio, SMA line-fitting

Assessing the scaling of tree growth from discrete diameter measures

In 1999, Enquist *et al.* proposed a theoretical extension of Metabolic Scaling Theory (MST) that predicted the scaling of tropical tree growth under ‘optimized tree architecture and resource transport’ (West, Brown & Enquist 1997, 1999). In this model, $dD/dt = \beta D^\alpha$, where D is trunk or stem diameter at breast height, α is a scaling exponent that relates the rate of stem diameter growth to tree size and β is an allometric normalization constant. While β is hypothesized to be determined by several specific physiological and allocation traits of the tree and thus can vary (Enquist *et al.* 1999, 2007), the optimized ‘idealized’ tree architecture version of MST predicts that α is constant (West, Brown & Enquist 1999). More specifically, $\alpha = 1/3$ within species and between species at the ‘interspecific mean’ community level (Enquist *et al.* 1999). To test their model framework, Enquist *et al.* (1999)

proposed a novel regression method using temporal stem diameter measurements and applied this method to a tree growth data set (20-year interval of 2277 individuals from 45 species) from about 20 hectares of tropical dry forest in San Emilio, Costa Rica.

In a recent paper, Coomes & Allen (2009) proposed a new statistical methodology for assessing the scaling of tree growth and re-analysing the San Emilio data set. They concluded that their new methodology calls into question the findings of Enquist *et al.* (1999). Specifically, Coomes & Allen argue that Enquist *et al.* used methodology and a data set that had insufficient power to falsify the hypothesis that α is $1/3$, since the methodology used in Enquist *et al.* does not directly produce α estimates with confidence intervals (CIs). Using their method, Coomes & Allen find that the estimated interspecific mean value of α is significantly *greater* than $1/3$ (observed mean of species’ α -values = 0.44). They argue that this is consistent with a signal of asymmetric competition that would reduce growth rate in smaller individuals and thus tilt the allometric slope up (higher α -value; see Coomes & Allen 2007).

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Comparing differing methodological approaches to estimate the scaling of tree growth

Coomes & Allen (2009) and Enquist *et al.* (1999) both seek to test the prediction that α is 1/3 by investigating the time-course of allometric growth, given by the equation

$$D_2^{1-\alpha} = D_1^{1-\alpha} + \beta(1-\alpha)\tau \quad \text{eqn 1}$$

where τ is the census interval – in this case 20 years – and subscripts denote diameter measurements at times ‘one’ and ‘two.’ Enquist *et al.* (1999) set out to falsify the ‘optimized’ MST prediction that $D_2^{2/3}$ and $D_1^{2/3}$ have a slope of 1 in a regression model, as predicted by eqn 1 (below, we return to ask whether this is a strong prediction). In contrast, Coomes & Allen (2009) took a different approach and searched for the value of α that corresponds to the slope of the SMA regression between $D_2^{1-\alpha}$ and $D_1^{1-\alpha}$ equal to 1. Next, Coomes & Allen generated regions they refer to as CIs by finding different values of α where the upper and lower bound of the SMA slope CI correspond to 1. They then ask whether the CIs surrounding α exclude the value 1/3 predicted by MST. In doing so, Coomes & Allen propose a new method (hereafter referred to as SMA slope-of-one method) for parameter estimates for α – and by extension β – that best fit the data.

It is important to underscore that the central findings of Coomes & Allen, and associated conclusions, are strongly at odds with a nonlinear regression (or the equivalent Maximum-Likelihood Estimation, MLE) approach—introduced in Russo, Wisser & Coomes (2007) (see also Muller-Landau *et al.* 2006 for an earlier similar method). In their supplemental document (see Table S2 in Supporting Information), Coomes & Allen (2009) compare both results and show that the MLE method produces an interspecific mean of $\alpha = 0.004$ – significantly lower than the estimate produced by either Enquist *et al.* (1999) or SMA slope-of-one. Coomes & Allen (2009) state that “the two sets of estimates (MLE and SMA slope-of-one) are significantly correlated ($r = 0.47$, $P < 0.00001$) but the correspondence is not close (see Fig. S1 in Supporting Information)... [s]eeking an explanation for the systematic differences is beyond the scope of this paper, but certainly deserves attention.” We agree that this difference deserves attention, however, we disagree that it is the beyond the scope of a study aimed at testing a MST prediction for the value of α . Providing a strong test of MST requires that we resolve the difference between these parameter estimation methods and choose the most statistically appropriate and biologically relevant approach.

Deconstructing methods to estimate scaling parameters of interest

The MLE method returns α and β values that maximize the probability of the following equation

$$D_2 = (D_1^{1-\alpha} + \beta(1-\alpha)\tau)^{1/1-\alpha} + \varepsilon_{\text{model}} \quad \text{eqn 2}$$

where $\varepsilon_{\text{model}}$ is model error. In contrast, the ‘SMA-slope-of-one’ method proposed by Coomes & Allen (2009) adjusts variance and covariance terms in the equation for the SMA slope ($\text{covar}(f(D_1), f(D_2)) \text{var}(f(D_2)) / \text{var}(f(D_1))$ where $f(x) = x^{(1-\alpha)}$; Warton *et al.* 2006) until the slope equals 1. It is important to note that the ‘SMA-slope-of-one’ method is not a standard application of SMA to fit a linear relationship to correlated variables that have been measured with error. Typically, in its common application to biological allometry, SMA produces slope and intercept parameter estimates that realistically represent underlying biological relationships (Warton *et al.* 2006). Here, the SMA-slope-of-one method adds an additional step in order to estimate a nonlinear model parameter (α in $f(x) = x^{(1-\alpha)}$). This added step is based upon the slope-of-one constraint, and is not directly linked to standard SMA slope or intercept estimates. Furthermore, to the best of our knowledge, the connection between the SMA-slope-of-one method and the likelihood of the model or the probability of observing the data given the model has not been described. As such, we cannot be certain if the statistical criteria for CIs are met for SMA slope-of-one parameter estimates. The CIs described by Coomes & Allen (2009) may, therefore, not be appropriate for hypothesis testing. On the other hand, MLE has the probabilistic interpretation that parameter estimates maximize model likelihood and thus parameter estimates can be used in hypothesis testing (Clark 2007).

We hypothesize that MLE is not only the most statistically appropriate method, but also the most biologically relevant approach to analysing these types of data for two reasons:

First, the MLE method incorporates an error term that relates to biological variability and measurement error. On the other hand, the SMA slope of $D_2^{1-\alpha}$ on $D_1^{1-\alpha}$ is only expected to be one in the absence of diameter measurement error and individual-level biological variability in α or in β ; these sources of variability combine with model nonlinearity to cause deviations from this basic prediction for allometric growth because of Jensen’s inequality (Ruel & Ayres 1999). In other words, the SMA slope-of-one method assumes there is neither measurement error nor variability in α and β . Note that this assumption applies to β – not just to α as a first glance might suggest – because D_2 is a nonlinear function of β (eqn 2). While empirical patterns of individual-level variability in α are not well known, general models now exist to explain individual- (and species-) level variability in α (Price, Enquist & Savage 2007), and variability is plausible if different forest shade environments influence plasticity in growth form (e.g. diameter radius relationships; Dietze, Wolosin & Clark 2008). Diameter measurement error, on the other hand, is a well-known and ubiquitous component of tree censuses (Chave *et al.* 2004; Metcalf, Clark & Clark 2009).

Second, MLE maximizes model goodness-of-fit while the SMA slope-of-one method places more importance on the slope-of-one constraint by requiring this constraint to be strictly satisfied. These different priorities are reflected in the way parameters are fit: MLE simultaneously varies α and β parameters to find the best model fit (values that maximize the model likelihood function). In contrast, the SMA slope-of-one

method first varies α to find the value that satisfies the slope-of-one constraint and then calculates β using this α value and eqn 1 (SMA intercept = $\beta(1-\alpha)\tau$). This two-step approach does not effectively explore the contribution of uncertainty and biological variability in β to the confidence interval on α and *vice versa*; to properly take uncertainty and biological variability in both parameters into account while describing CIs, α and β must be varied simultaneously (Russo, Wiser & Coomes 2008). By this logic, we expect approaches that focus on satisfying constraints like SMA slope-of-one to generate parameters that are further from a realistic characterization of the underlying biological relationship. While most attention has focused on solely evaluating and generating estimates for α when applying MST to tree growth size scaling (e.g. Coomes & Allen 2009; Muller-Landau *et al.* 2006; Russo, Wiser & Coomes 2007), accurate estimates of β are equally crucial, since β is linked to key plant functional traits and physiological processes such as wood density and photosynthesis (Enquist *et al.* 1999, 2007). A shortfall of both the SMA slope-of-one and the MLE approach is that neither allows direct estimation of biological variability associated with α or β .

A simulation to evaluate model performance

To test the hypothesis that MLE is the most biologically relevant of these methods, we compared the performance of both methods in estimating α and β parameters from simulated tree growth data. Using the statistical and computational platform R (R Development Core Team 2009), we simulated tree growth data sets that included the same number of species, distribution of individuals between species (pattern of relative abundance), distribution of starting tree sizes, and total number of individuals (2277) as found in the original Enquist *et al.* (1999) San Emilio data set. To estimate the effects of biological variability and measurement error, we simulated data sets with different amounts of variability – moderate and low – in intraspecific (within species or ‘population-level’) α and β distributions and stem diameter measurement error.

More specifically, to simulate realistic data sets of allometric tree growth, we first established interspecific (between species) parameter sampling distributions that were characterized by the same means and standard deviations as the empirical distribution of MLE α and β estimates presented in see Table S2 in Coomes & Allen (2009). This choice should not bias the comparison of fitting methods since the performance of each method is gauged by its accuracy returning parameter estimates close to values chosen to simulate each species. Since the interspecific MLE distribution of β was found to be lognormal, while α was better characterized as a normal distribution, simulation distributions were set as such. The geometric mean and standard deviation of β were 0.31 and 3.69, respectively, and the arithmetic mean and standard deviation for α were 0.004 and 0.38, respectively. Next, values for intraspecific variation in α and β were chosen to follow either a moderate or a low-variability case. Since the model fit is on a species-by-species basis, it is these parameter distributions (not interspecific distributions) that introduce the biological variation (in this case,

simulated) that may be implicated in creating biases in the parameter estimation methods. MST predicts a strong ‘basin of attraction’ at 1/3 for the allometric slope α (Price, Enquist & Savage 2007; Coomes & Allen 2009), while the value of β likely varies due to the effects of local resource environments and plant trait variation on plant growth (Enquist *et al.* 2007; see also Enquist *et al.* 1999). Nonetheless, patterns of intraspecific variation in α and β are, to our knowledge, unknown. Since the intraspecific distribution of β is expected to be characterized best by a lognormal distribution – as in the interspecific case – because the factors affecting individual growth are largely multiplicative in effect (Hunt 1978; Enquist *et al.* 2007), a lognormal intraspecific β distribution was set as the ‘base-line’ simulation scenario. We noted that standard deviations one-half those of the interspecific values – for both α and β – generated a raw diameter growth distribution roughly comparable to the empirical data; we chose this to be the ‘moderate’ – or perhaps ‘realistic’ – variability case. We also considered the case in which within-species variation in β followed a normal probability density function (distribution). Here, we found that standard deviations for α and β needed to be reduced to one-tenth the interspecific (arithmetic) levels to generate realistic distributions of raw simulated tree growth.

Regardless of the β distribution used in this ‘moderate’ scenario, we set the standard deviation of diameter measurement error to 0.1 cm, an estimate based upon statistical modelling of tropical tree growth at La Selva Biological Station in Costa Rica (Metcalfe, Clark & Clark 2009). For the low-variability case, we reduced the standard deviation of both α and β to just one percent of interspecific values and decreased diameter measurement error until it was negligible (standard deviation of just 0.001 with a mean of zero). We expect this biological parameter variability and measurement error to be unrealistically low; however, this case serves as a valuable control as both methods are expected to perform well in the absence of these sources of model uncertainty.

Finally, we tested the performance of SMA slope-of-one and MLE by comparing the α and β estimates from each method (‘predicted’) to the *actual* (‘true’) means of simulation parameter distributions for each species. We iterated the procedure for 100 communities for the moderate and low-variation cases, making a total of 4500 species simulated for each case. Since the simulated number of individuals per species matched the San Emilio data set, we treated each species as a replicate to study the influence of sample size on parameter estimation.

MLE α and β parameter estimates are closer to ‘true’ values when simulated data include realistic levels of biological variation and measurement error

When we simulated tree growth with low biological variability and measurement error (according to the ‘low’ case described above) both the MLE and SMA slope-of-one methods returned parameter estimates (predictions) very close to simulated (true) values. To compare estimated and true values quantitatively, we considered the distributions created by

subtracting true parameters from model estimates for each species; we call these ' $\Delta\alpha$ and $\Delta\beta$ distributions.' Mean $\Delta\alpha$ and $\Delta\beta$ distribution values that differ from zero reflect significant differences and potential biases in estimation techniques; values significantly less than zero represent underestimates, while values significantly larger than zero represent overestimates. We used t -tests that were Bonferroni corrected for multiple comparisons for significance testing. Table 1 shows that differences between predicted and true parameter values under the low variation and error scenario tend to be consistently small (small interspecific means and standard deviations), particularly for the SMA slope-of-one method. We note that these differences are small relative to the interspecific variability in α and β suggested by applying MLE to the San Emilio data set (Coomes & Allen 2009; see Table S2) – and tree growth in New Zealand (Russo, Wiser & Coomes 2007) – where α ranges approximately from -1 to 1 and β from 0.02 to 5 . However, these small differences may reflect real biases. Considering the proportions of species that differ from zero (Table 1), we find significant differences for over 50% of species for $\Delta\alpha$ and $\Delta\beta$ distributions under MLE, while this portion is 10% or less under SMA slope-of-one. These results indicate that MLE may be biased towards underestimates of α and overestimates of β ; however, the magnitudes of these biases are quite small. In sum, both methods generate *reasonably unbiased* parameter estimates when growth is neither variable nor measured with error.

When we simulated tree growth with more realistic biological variability and measurement error (according to the 'moderate' case described above), only the MLE method returned unbiased parameter estimates when species were represented by more than c. 50 individuals (Fig. 1a–b and 2a–b). The SMA slope-of-one $\Delta\alpha$ distribution displayed the greatest potential bias with a mean well above zero and nearly all species signifi-

cantly overestimating the parameter (Table 1). The pattern of potential bias is different for the β parameter. In this case, considering all species, the mean difference from zero for $\Delta\beta$ distributions was highest for MLE not SMA slope-of-one (0.55 vs. -0.05). However, as Fig. 2a–b reveals increasing sample size decreases potential bias in the MLE estimate for β . If we only consider species represented by 50 or more individuals, this pattern reverses with the SMA slope-of-one method predicting less accurate parameter estimates and more significant differences from zero (Table 1).

Basic results were similar for the 'moderate' variation and sampling error case in which trees had normally (*not* lognormally) distributed intraspecific β -values. Again, the SMA slope-of-one method strongly overestimated α , while β estimates showed a putatively large bias at low sample sizes for the MLE method, but this bias decreased once species included at least 50 individuals (Table 1). For species with more than 50 individuals, however, both MLE and SMA slope-of-one methods produced β estimates that were consistently biased; the absolute magnitude of bias was similar (c. 0.1) but differed in direction between methods (Table 1).

The best statistical method most closely matches the structure of the underlying process, its biological variability and measurement error

When we simulated 'allometrically ideal' tree growth with little biological variation in parameters and little diameter measurement error, we found that both the MLE and SMA slope-of-one parameter fitting methods performed well, returning parameters that were on average very close to the 'true' simulation values. However, we were able to detect a consistent bias of MLE parameter values. In this low-variability case, MLE

Table 1. Summary of simulation results for all biological variation and error scenarios

	Mean (SD) $\Delta\alpha$		Mean (SD) $\Delta\beta$		Proportion species (Over, Under) - Estimating $\Delta\alpha^*$		Proportion species (Over, Under) - Estimating $\Delta\beta^*$	
	MLE	SMA slope-of-one	MLE	SMA slope-of-one	MLE	SMA slope-of-one	MLE	SMA slope-of-one
Low variation/error	-0.013 (0.009)	0.000 (0.002)	0.018 (0.011)	0.000 (0.004)	(0, 0.56)	(0.11, 0.04)	(0.51, 0)	(0.04, 0.02)
Moderate variation/error (lognormal β)	-0.003 (0.052)	0.34 (0.21)	0.13 (0.11)†	-0.28 (0.10)†	(0.11, 0.04)	(0.91, 0)	(0.5, 0)†	(0, 1)†
Moderate variation/error (normal β)	-0.05 (0.04)	0.26 (0.18)	0.10 (0.05)†	-0.09 (0.06)†	(0, 0.36)	(0.91, 0)	(0.92, 0)†	(0, 1)†

MLE, maximum-likelihood estimation; SMA, standardized major axis.

*The proportion of species over and underestimating the parameter is defined as the proportion of species found to have mean Δ -parameter values significantly different from zero at the 0.05-level using t -tests with Bonferroni correction for multiple comparisons. The adjusted significance level is $0.05/45$ where 45 is the total number of t -tests (species). The total proportion of species significantly different from zero is the sum of over and underestimate proportions.

†Only the 12 species represented by 50 or more individuals are considered (see text for more detail).

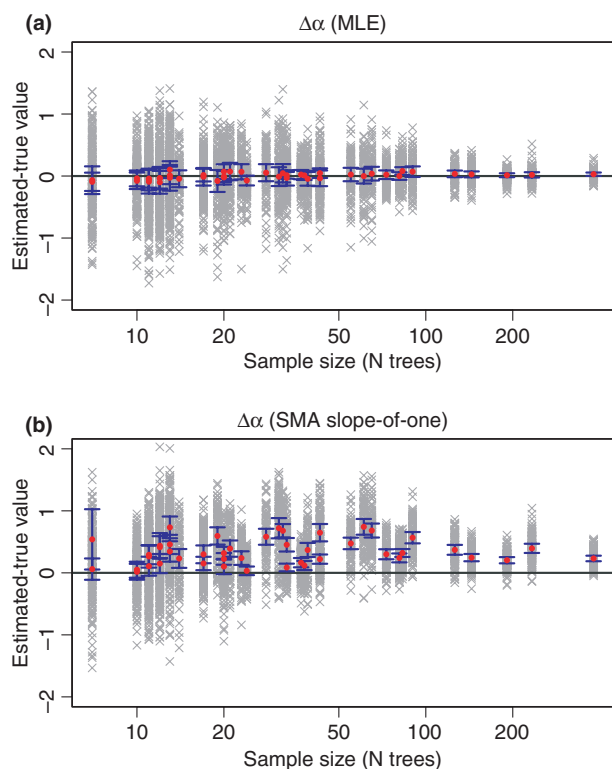


Fig. 1. (a–b) True (simulation) α values, ‘scaling exponents’, subtracted from values estimated by a fitting method ($\Delta\alpha$ distributions) vs. sample size for all replicate species. Results of (a) maximum-likelihood estimation (MLE; Russo, Wiser & Coomes 2007) and (b) standardized major axis regression subject to a slope-of-one constraint (SMA slope-of-one; Coomes & Allen 2009) applied to replicate simulations of tree growth that incorporate moderate levels of biological variation in parameter values and measurement error (see text for details). We replicated each of 45 simulated species 100 times while fitting growth parameters individually to each replicate species. Levels of variation were chosen for this moderate case to generate distributions of simulated tree growth similar to the Costa Rican dry forest San Emilio data set (Enquist *et al.* 1999) while the level of diameter measurement error match estimates from another study of tropical tree growth (Metcalf, Clark & Clark 2009). Blue bars are confidence intervals around means (red dots) while grey ‘x’s are $\Delta\alpha$ values for each simulated species. Unbiased parameter estimation results in a $\Delta\alpha$ mean of zero (horizontal line) while negative values are underestimates and positive values are overestimates.

parameter values tended to be more variable and less accurate than those produced by the SMA slope-of-one method. This could reflect (i) underlying data-model mismatch, or (ii) the effect of fitting three parameters instead of just two – as is the case for SMA slope-of-one (MLE requires that the standard deviation of model error also be fit).

When we considered realistic levels of biological parameter variation and measurement error, the relative performance of the two methods switched. In this case, MLE α estimates were unbiased while the SMA slope-of-one method overestimated α by *c.* 0.3 units. The differences between α estimates from the SMA slope-of-one and MLE methods are consistent across simulated and empirical data (San Emilio); the SMA slope-of-one estimate is higher. If the simulation correctly represents

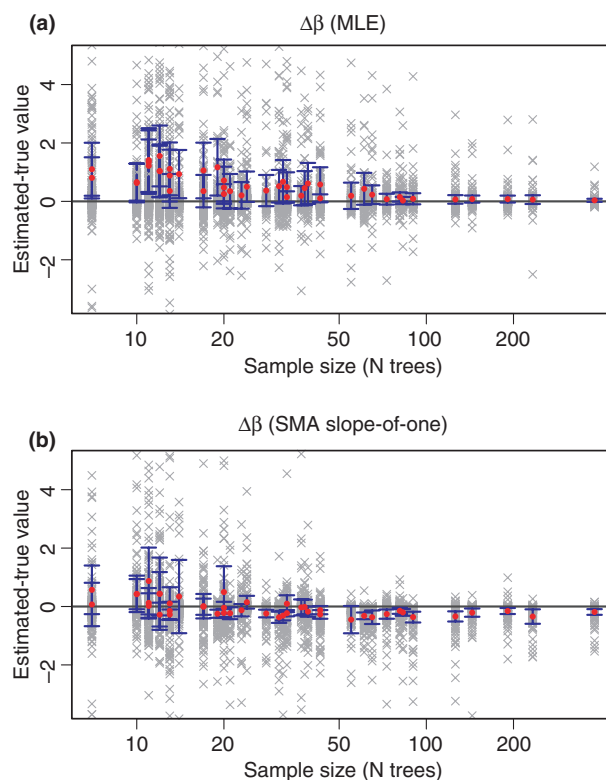


Fig. 2. (a–b) True (simulation) β values, ‘scaling normalizations’, subtracted from values estimated by a fitting method ($\Delta\beta$ distributions) vs. sample size for all replicate species. Results of (a) maximum-likelihood estimation (MLE; Russo, Wiser & Coomes 2007) and (b) standard major axis regression subject to a slope-of-one constraint (SMA slope-of-one; Coomes & Allen 2009) applied to replicate simulations of tree growth (see legend for Fig. 1a–b and text for details). Blue bars are confidence intervals around means (red dots) while grey ‘x’s are $\Delta\beta$ values for each simulated species. Unbiased parameter estimation results in a $\Delta\beta$ mean of zero (horizontal line) while negative values are underestimates and positive values are overestimates.

bias in the empirical application then the SMA slope-of-one putatively overestimates α by about 0.4 units (0.44 vs. *c.* 0).

When simulated β distributions were lognormal, (normal) MLE produced more accurate (similarly accurate) β estimates only when species contained more than 50 individuals. We cannot easily explain MLE bias for species with fewer than 50 individuals; the reasons listed above may again be implicated. Since species represented by few individuals tended to be overestimated by MLE, we predict that species with less than 50 individuals will have relatively large MLE β values in the San Emilio data set. However, this is not the case; geometric means of β are similar for both groups, *c.* 0.7. We conclude that either (i) the simulation does not accurately represent patterns of bias in β in the San Emilio data set or (ii) that the pattern of bias is accurate but abundant species tend to have higher β values. We note that the comparison between the MLE and SMA slope-of-one interspecific mean β values is consistent with simulation results; the MLE value, *c.* 0.7, is higher than the SMA slope-of-one value, *c.* 0.4.

We conclude that under the most biologically realistic simulation scenarios the MLE method most accurately estimates growth model parameters. Since tree growth varies intraspecifically and diameter census data likely include measurement error, we expect that MLE is also more accurate than SMA slope-of-one in application to real-world data sets. MLE likely out-performs the SMA slope-of-one method because it better represents the effects of biological variability and measurement error on the growth process in its error structure. This MLE method relies on a single model error term that accounts for a combined effect of measurement error and biological parameter variability while fitting the model to the data. However, we note that the first term on the right-hand side of eqn 2 combines biological variability in parameters and measurement error in a nonlinear form. Thus, we expect a single model error term to *incorrectly* capture how variation and error propagate through model structure to relate model likelihood to parameters – and ultimately to the biological processes underlying size-dependent tree growth – again because of Jensen's inequality. The best model-fitting method would match the statistical model to the true structure of variability and error; to achieve this, a maximum-likelihood or Bayesian approach is required that incorporates multiple sources of variability and error (Clark 2007). Nonetheless, our simulation results suggest that, for moderate to large sample sizes, MLE does a good job of estimating growth parameters with little bias.

Due to likely bias in the SMA slope-of-one method, we disagree with Coomes & Allen (2009) that true values of α for the San Emilio data set are likely *greater* than the optimal value predicted by MST. However, given the small sample sizes for many species in the San Emilio data set (see Table 1 in Enquist *et al.* 1999) and the wide CIs associated with nonlinear regression α estimates (see Table S2 in Coomes & Allen 2009) it seems likely that, as suggested by Coomes & Allen (2009), the signal-to-noise ratio in this data set is low. Therefore, using the MLE method on the San Emilio data set, there is not enough power to detect differences between estimated and predicted allometric slopes. From this we infer that interspecific mean estimates of α and β from the MLE method must be interpreted with caution for data sets with small sample sizes. Importantly, these results indicate that, using the MLE method, we cannot argue for or against the 'optimized' MST predictions or the importance of asymmetric competition for the tree community in the San Emilio data set.

We note that one study utilizing the MLE method with larger sample sizes of individuals, Russo, Wiser & Coomes (2007), finds high variability in α (and β). While Russo, Wiser & Coomes (2007) conclude that their study finds no support for MST because individual species, specific size ranges, and growth forms differ from the MST 1/3 prediction, it is interesting to note that the broadest interspecific mean for the α parameter is very close to this prediction, 0.31 (data in Russo, Wiser & Coomes 2007, see their Fig. 3 and Table S2, one outlier at $\alpha = -1.61$ removed). We suggest that more work is needed to quantify patterns in growth rate size scaling relationships and to test the predictions of MST at multiple hierarchi-

cal levels of ecological organization, e.g. for individual trees, tree species and groups of species.

Parameter estimation methods should produce accurate estimates of both α and β under differing levels of biological variability and measurement error. Our simulation results show that MLE is the most appropriate of the methods we considered, particularly for trees represented by more than 50 individuals. Indeed, our results indicate that in order to better test macroscopic theories for diameter size scaling – including the Enquist *et al.* (1999) tree growth model – future studies should (i) explicitly assess intraspecific variation in α and β ; (ii) incorporate realistic error structures including errors in all measured variables; (iii) consider larger sample sizes; and (iv) employ hierarchical MLE or Bayesian methods (Clark 2007; Dietze, Wolosin & Clark 2008; Price *et al.* 2009) that allow for confidence interval estimation on intraspecific and interspecific mean parameter estimates.

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