

Testing metabolic theory with models of tree growth that include light competition

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Summary

1. Metabolic scaling theory predicts that diameter growth rates of tree species are related to tree diameter by a universal scaling law. This model has been criticised because it ignores the influence of competition for resources such as light on the scaling of demographic rates with size.

2. We here test whether scaling exponents of abundant tropical tree species comply with the prediction of metabolic scaling theory and evaluate whether the scaling of growth with size depends on light availability. Light reaching each individual tree was estimated from yearly vertical censuses of canopy density, and a hierarchical Bayesian approach allowed quantifying confidence intervals for scaling exponents and accounting for different sources of error.

3. We found no universal scaling relationship, and 50–70% of the species had scaling exponents that significantly differed from the predicted value of 1/3. As would be expected if competition for light were important, scaling exponents were $> 1/3$ for the majority of species when all trees were combined. However, the community average of scaling exponents was not significantly different from the predicted value of 1/3 when only considering individuals that grew under high-light conditions.

4. These results support the hypothesis that the prediction of metabolic ecology for the scaling of tree growth with size is only valid when competition for light is unimportant.

Key-words: allometric scaling, Barro Colorado Island, hierarchical Bayesian model, light competition, metabolic scaling theory, Panama, tropical rainforest

Introduction

Metabolic theory of ecology combines principles of physics, chemistry and biology to link metabolism and allometry of individuals to population, community and ecosystem properties (West, Brown & Enquist 1997, 1999; Brown *et al.* 2004). Proponents of metabolic ecology theory claim that its predictions apply equally to animals and plants, and recent extensions of the theory have sought to explain forest structure and dynamics from individual tree metabolism and allometry (e.g. Enquist, West & Brown 2009; West, Enquist & Brown 2009). It is debated, however, whether this theory that neglects competition for light can be predictive for structure and dynamics in uneven-aged closed-canopy forests where light is a limiting environmental resource (e.g. Muller-Landau *et al.* 2006; Coomes & Allen 2007; Coomes, Lines & Allen 2011).

The core prediction of metabolic ecology theory is that metabolic rate, or gross photosynthetic rate (P) for plants,

scales with biomass (M) as $P \propto M^{3/4}$ (West, Brown & Enquist 1999). This prediction is based on the assumptions about the structure of plants' vascular networks and their hydraulic resistance, which in turn leads to a scaling relationship of $D \propto M^{1/3}$ between stem diameter at breast height (D) and M (West, Brown & Enquist 1999). Enquist *et al.* (1999) further assume that biomass growth rate is proportional to photosynthetic rate, and it follows that tree diameter growth scales with diameter as $\frac{dD}{dt} \propto D^{1/3}$.

Empirical support for this prediction is lacking because in previous studies sample sizes were small (< 100 individuals) for the majority of tree species (Enquist *et al.* 1999; Coomes & Allen 2009; Stark, Bentley & Enquist 2011). In the one case where 56 species with > 100 individuals were analysed, scaling exponents were significantly different from 1/3 for the majority of species (Russo, Wiser & Coomes 2007).

Muller-Landau *et al.* (2006) and Coomes & Allen (2009) hypothesised that when competition for light is important, scaling exponents should be $> 1/3$ because trees receive more light as they grow taller. This hypothesis has been confirmed in a recent indirect test using site productivity as a proxy for

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the intensity of light competition. Scaling exponents of mountain beech (*Nothofagus solandri* var. *cliffortioides*) were close to the prediction in low-productivity environments, where competition for light is assumed to be weak, and $> 1/3$ in sites with higher productivity, where competition for light is assumed to be intense (Coomes, Lines & Allen 2011). However, no study to date has directly assessed whether scaling exponents depend on light availability within multiple species.

We use data for tropical tree species at Barro Colorado Island (BCI), Panama, to test the prediction of metabolic ecology for the scaling of growth with size within species as well as the distribution of scaling exponents across the species. We explicitly assess whether the scaling depends on light availability. Light availability is a key limiting resource in moist tropical forests (e.g. Denslow 1987; Denslow *et al.* 1990; King *et al.* 2005), and we use light estimates from yearly censuses of vegetation in six height layers to compare scaling exponents in low, intermediate and high light environments. We further explicitly include light availability as a predictor of tree growth, together with tree size, to assess the scaling of growth separately for both covariates. In a previous study, we demonstrated the effectiveness of a hierarchical Bayesian model in quantifying species differences in the response of growth to light (Rüger *et al.* 2011a). Here, we employ the same approach to study growth-diameter allometry and predictions of metabolic theory.

Growth may slow down when allocation of resources to reproduction starts (Enquist *et al.* 1999). Therefore, we assessed growth scaling separately for trees below their estimated reproductive threshold as well as for all trees pooled irrespective of reproductive status. The Bayesian approach allows quantifying confidence intervals for scaling exponents and accounting for different sources of error (Ellison 2004; Clark 2005; Clark *et al.* 2007). However, to assure strongest results, we included only common species with ≥ 100 individuals because parameter estimates for rare species would be more strongly affected by parameter estimates for the other species in the community.

Thus, we address all issues identified by Stark, Bentley & Enquist (2011) as desirable for future evaluations of metabolic ecology theory for demographic rates, namely the incorporation of realistic error structures, consideration of larger sample sizes and the application of hierarchical Bayesian methods that allow for confidence interval estimation on intraspecific and interspecific mean parameter estimates.

Materials and methods

STUDY AREA

We analysed data from a 50-ha forest census plot on BCI, Panama (9°9'N, 79°51'W). BCI is a 1567-ha island in the Panama Canal covered with tropical lowland moist forest. The plot consists of 48 ha of undisturbed old-growth forest and 2 ha of secondary forest about 100 years old (Foster & Brokaw 1982). The climate on BCI is warm throughout the year, but rainfall is seasonal with most of the 2500 mm falling during the wet season from April to November

(Windsor 1990; Windsor, Rand & Rand 1990). Elevation of the plot is 120–155 m a.s.l. (Hubbell & Foster 1983). Detailed descriptions of flora, fauna, geology and climate can be found in Croat (1978), Leigh, Rand & Windsor (1982) and Leigh (1999).

GROWTH DATA

All free-standing woody individuals ≥ 1 cm diameter at breast height (dbh) were mapped, identified to species and measured in 1981–1983, 1985, and every 5 years thereafter (<http://ctfs.arnarb.harvard.edu/webatlas/datasets/bci/>; Condit 1998; Hubbell & Foster 1983). Here, we use the census intervals from 1985 to 1990 and 1990 to 1995 (because these are the only census intervals with consistent canopy census data) and determined annual dbh growth rate (mm year^{-1}).

We discarded cases where a tree survived but its stem was measured at a different height, or where one stem broke, so a resprouted stem of the same tree was measured. We excluded extreme outliers: stems that grew $> 75 \text{ mm year}^{-1}$ or shrunk $> 25\%$ of their initial dbh. Smaller negative growth observations because of dbh measurement error were included (see Estimation of Measurement Error). Owing to their lack of secondary growth, we excluded palm species. Because dbh values were rounded down to the nearest 5 mm for all stems < 55 mm in 1985 but not in 1990, it was necessary to round 1990 dbh values below 55 mm down as well before calculating growth rates for the first census interval. Rounding down may bias growth estimates of small stems, but Condit, Hubbell & Foster (1993) showed that the bias was minimal. To avoid edge effects of the light availability calculation (see below), we excluded all individuals within 20 m of any edge of the plot.

Although the prediction of metabolic scaling applies to instantaneous growth, we used annualised growth rates from a 5-year census interval to calculate scaling exponents. We checked for a potential bias this may introduce by numerical integration of the growth model using species' parameters estimated from the hierarchical Bayesian model (see below). Scaling exponents calculated from 5-year intervals of simulated growth differed by an average (across species) of 0.005 from the true (instantaneous) scaling exponents; no species had a difference > 0.02 . These small differences indicate that using growth rates from 5-year intervals instead of instantaneous growth rates does not considerably bias our results.

We evaluated the prediction of metabolic ecology for two subsets of the data: (i) for trees smaller than the reproductive threshold (non-reproductive) and (ii) for all individuals pooled irrespective of reproductive status. We attempted the analyses when only trees larger than the reproductive threshold were included, but few species had large enough sample sizes to draw conclusions, so we do not present results (see Table S1, Appendix S1 in Supporting Information). Reproductive size was estimated after many years of observation by R. B. Foster (personal communication) and later confirmed by quantitative evaluation in a subset of the species (Wright *et al.* 2005). To cover a reasonable dbh range (Coomes, Lines & Allen 2011), we only included species that become reproductive at a dbh ≥ 15 cm in the subset of non-reproductive trees and species with a maximum dbh ≥ 15 cm when all trees were analysed.

We included only species with ≥ 100 individuals that met the size criteria. The non-reproductive subset had 47 species (42 234 trees) and 46 species (43 588 trees) in the two census intervals, respectively, and when all trees were pooled, there were 86 species (92 138 and 96 511 trees). Sample sizes and dbh ranges of all data subsets (including the subset of reproductive trees) are given in the Supporting Information (see Table S1).

ESTIMATION OF LIGHT AVAILABILITY

We used annual canopy census data to produce an index of the amount of light reaching any point in the forest. The censuses were conducted from 1983 to 1996, except for 1994. The canopy census recorded the presence/absence of vegetation in six height intervals (0–2, 2–5, 5–10, 10–20, 20–30 and ≥ 30 m) every 5 m across the 50 ha. If vegetation was present in a height interval, we assume that it casts shade below exactly as would a flat circle of diameter 5 m placed at the vertical midpoint of the height interval. For each tree, we calculated a shade index as a weighted sum of vegetation located above the tree and ≤ 20 m away. Weighting was proportional to the section of sky that is obscured by the vegetation accounting for distance from focal tree and angle (Rüger *et al.* 2011b). The height of each tree was estimated based on species-specific allometric equations for about 2/3 of the species; for the remaining species, an overall equation was used (Chave *et al.* 2003). We converted this measure of shading to an estimate of light availability by comparing the distribution of shading at 2 m height to a published distribution of irradiance measured 1 m above the ground (see Wirth, Weber & Ryel 2001; Rüger *et al.* 2011b).

Even though dbh and the light estimate are strongly correlated ($r^2 = 0.67$), there are many observations of small trees receiving high light and of larger trees receiving low light (see Fig. S1 in Supporting Information). This allows us to separate the effects of the two variables. When Akaike Information Criterion (AIC) was used to compare models including only dbh or dbh and light as predictors of growth, for 40 of 46 species, the model including dbh and light performed better (lower AIC) than the model only including dbh (for 35 species, ΔAIC was ≥ 2 ; for 25 species, it was ≥ 10).

ESTIMATION OF MEASUREMENT ERROR

To estimate the error of dbh measurements, in 1995, 2000 and 2005 double-blind remeasurements of 1562 randomly chosen trees (dbh range 1–96 cm) were performed less than 30 days apart. We modelled the discrepancy assuming there are two types of error: routine error caused by slightly different placement of the callipers or tape measure, and large error caused by missing a decimal place or recording a number with the wrong tree. A Bayesian approach allows an estimate of the 'true' dbh (truedbh) of those 1562 trees given two observed dbhs (obsdbh), assuming no growth between measurements:

$$\text{obsdbh} - \text{truedbh} \sim (1-f)N(\mu=0, \sigma=SD_1) + fN(\mu=0, \sigma=SD_2)$$

(Chave *et al.* 2004). The first Gaussian describes routine errors, assuming they are proportional to the dbh of the tree, $SD_1 = \text{sda} + \text{sdb} \times \text{dbh}$. The second Gaussian (SD_2) covers large errors that are independent of dbh and occur a fraction f of the time.

Errors were best fit with $\text{sda} = 0.927$ mm (SD of the posterior distribution was 0.024 mm), $\text{sdb} = 0.0038$ mm⁻¹ (SD = 0.00036 mm⁻¹), $SD_2 = 25.6$ mm (SD = 2.49 mm) and $f = 2.76\%$ (SD = 0.39%). This means that a 100-mm tree is subject to 1.3-mm routine error, while 2.76% of the time, it will be badly mismeasured, with an error of 26 mm. Growth calculations involve two dbh measurements; thus, the variance of growth error is twice the variance of measurement error. The posterior distributions of error parameters sda , sdb , SD_2 and f enter as fixed priors in the hierarchical Bayesian model.

GROWTH MODEL

To determine the scaling of growth with dbh, we modelled growth as a power function (linear log–log relationship) of dbh for all subsets of

the data (see Growth Data). We assessed whether the scaling of growth with dbh depends on light availability in two ways. First, we controlled for light availability by including light as a second predictor. Second, we calculated growth-dbh scaling separately for individuals growing in different light environments. We split individuals into three light classes that approximately correspond to terciles of light availability ($< 4\%$, $4\text{--}8\%$, $\geq 8\%$ of above-canopy irradiance). In these light-class analyses, we only included species that had at least 50 individuals in each light class.

In a hierarchical Bayesian model (Gelman & Hill 2007), we predicted growth of individual i (pred_i) as a power function given dbh or dbh and light,

$$\log(\text{pred}_i) = a_j + b_j \log(\text{dbh}_i),$$

or

$$\log(\text{pred}_i) = a_j + b_j \log(\text{dbh}_i) + c_j \log(\text{light}_i),$$

where parameter a_j describes the mean growth rate, b_j the size effect on growth and c_j the light effect on growth of species j (Rüger *et al.* 2011a).

Variation of growth at a given dbh and light availability was modelled using a lognormal distribution (process error, σ_p)

$$\text{true}_i \sim \log N(\text{pred}_i, \sigma_p).$$

where true_i is the estimated true growth rate of tree i . The process error (σ_p) is estimated for each species. Using a lognormal distribution, the process error automatically scales linearly with predicted growth (e.g. Kerkhoff & Enquist 2009).

Data enter our model as the observed annual dbh growth of individual i (obs_i , mm year⁻¹), which is assumed to be subject to measurement error as described above. The likelihood to observe obs_i is determined as:

$$P(\text{obs}_i) = (1-f)N\left(\mu = \text{true}_i, \sigma = \frac{SD_1}{\text{int}_i}\right) \times fN\left(\mu = \text{true}_i, \sigma = \frac{SD_2}{\text{int}_i}\right),$$

with SD_1 describing the size-dependent error component and SD_2 the size-independent error component. Standard deviations have to be adjusted to the time period elapsed between the two dbh measurements of the tree (int_i) from which the annual growth rate has been calculated.

To describe the variation of a_j , b_j and c_j across the species, we defined a hyperdistribution for each parameter. The specific type of distribution was chosen based on model runs without hyperdistributions (i.e. estimation of the posterior distributions for each species independently of the other species), which revealed that all model parameters were approximately normally distributed across the community. Thus, we used normal hyperdistributions for a , b and c , with hyperparameters μ_a , μ_b and μ_c describing the community-wide means and σ_a , σ_b and σ_c measuring the between-species variation. As we did not have prior knowledge, we used non-informative flat priors for these parameters:

$$\begin{aligned} \mu_a, \mu_b, \mu_c &\sim \text{Uniform}(-10, 10), \\ \sigma_a, \sigma_b, \sigma_c &\sim \text{Uniform}(0, 2). \end{aligned}$$

The process error (σ_p) was assumed to vary lognormally across the community with hyperparameters μ_h and σ_h . Priors for both parameters were

$$\mu_h, \sigma_h \sim \text{Uniform}(0.001, 100).$$

The runs without hyperdistributions also revealed that estimates of all parameters were largely determined by the data because we did not include species with < 100 individuals.

MODEL IMPLEMENTATION AND DIAGNOSTICS

Posterior distributions of the parameters of the growth models, true growth of each individual tree and process error were obtained using a Markov chain Monte Carlo (MCMC) method that is a hybrid of the Metropolis–Hastings algorithm and the Gibbs sampler (Gelman *et al.* 1995; Condit *et al.* 2006). Parameter values are sequentially updated as in the Gibbs sampler, and acceptance depends on the likelihood ratios as in the Metropolis–Hastings algorithm. The proposal distribution is a normal distribution centred on the current value of the given parameter. The step width for each parameter, that is, the standard deviation of the proposal distribution, is constantly adjusted during the burn-in period in such a way that acceptance rate is kept around 0.25 (Gelman *et al.* 1995). To speed up the convergence of the Gibbs sampler, we weakened the correlation of intercepts and coefficients by centring the dbh data on mean log(dbh) for each species and the light data on 5% light.

We monitored convergence by running two chains with different initial values and used the Gelman and Rubin's convergence diagnostics and a value of 1.1 to detect convergence of individual parameter estimates (Gelman & Rubin 1992; Gelman *et al.* 1995). We used a burn-in period of 5000 iterations, and an additional 10 000 iterations were used for analysis. From the posterior distributions, we computed the mean and 95% credible intervals (CI) of all model parameters. All analyses were carried out using the software package R version 2.11.1 (R Development Core Team 2010).

Results

Based on visual inspection, the power function was a reasonable description of size dependence of growth, except for a few species where growth showed a hump-shaped pattern when all individuals were analysed irrespective of reproductive status (see Fig. S2 in Supporting Information).

When only dbh was used as a predictor of growth, the community-wide average of the distribution of scaling exponents (μ_b) was significantly > 1/3 for non-reproductive trees and when all trees were combined (Table 1, Fig. 1a, Appendix S1). Species-level scaling ranged from –0.2 to 1.5 (Fig. 1a, Table S1). In both census intervals and for both data subsets, fewer than half the species had scaling exponents consistent with the prediction (Table 2).

When light was included as an additional predictor of growth, μ_b was significantly less than 1/3 for both subsets of trees (Table 1, Fig. 1b). The number of species that conformed to the prediction increased for the non-reproductive trees but decreased when all trees were analysed (Table 2). Comparing the coefficients of the models with and without light, the dbh exponent of the model without light approximately equals the sum of the exponents of dbh and light of the model including light (Fig. 2, Appendix S1). Parameter estimates of all growth models and data subsets are given in the Supporting Information (Table S1).

When individuals were split into classes of low, intermediate and high light availability, the scaling exponent was highest at high-light availability (Fig. 3). The 95% CIs of the community average of the scaling exponent included 1/3 only in the high-light category (> 8% light) for non-reproductive trees in the first census interval and when all trees were analysed in both census intervals (Table 1).

Discussion

By studying a large number of species with a rigorous modelling approach to account for species variation and measurement error, we conclude first that species vary significantly in growth-size scaling, so there is clearly not yet a universal theory to account for every species (e.g. Russo, Wiser & Coomes 2007). Moreover, we find that the predicted exponent of 1/3 is supported in fewer than half of the species and that the

Table 1. Community-wide mean (μ_b) and SD (σ_b) of the scaling exponent of dbh (b) for different data sets and growth models (–L, model not including light; +L, model including light)

Model	Light class	1985–1990		1990–1995	
		Mean*	SD	Mean*	SD
Non-reproductive trees					
–L	All	0.52 (0.43, 0.60)	0.29 (0.22, 0.36)	0.62 (0.52, 0.72)	0.31 (0.25, 0.39)
–L	< 4%	0.07 (–0.03, 0.16)	0.20 (0.11, 0.31)	0.12 (0.04, 0.20)	0.18 (0.10, 0.27)
–L	4–8%	0.14 (0.01, 0.26)	0.27 (0.18, 0.39)	0.16 (0.03, 0.28)	0.32 (0.21, 0.43)
–L	> 8%	0.44 (0.31, 0.57)	0.35 (0.24, 0.46)	0.55 (0.40, 0.71)	0.39 (0.29, 0.52)
+L	All	0.07 (–0.04, 0.17)	0.33 (0.25, 0.41)	0.18 (0.07, 0.28)	0.34 (0.26, 0.43)
All trees					
–L	All	0.42 (0.37, 0.48)	0.25 (0.21, 0.29)	0.47 (0.41, 0.52)	0.27 (0.23, 0.32)
–L	< 4%	0.10 (0.04, 0.17)	0.20 (0.14, 0.26)	0.15 (0.08, 0.22)	0.22 (0.16, 0.29)
–L	4–8%	0.10 (0.03, 0.20)	0.27 (0.20, 0.34)	0.17 (0.08, 0.26)	0.30 (0.22, 0.37)
–L	> 8%	0.27 (0.17, 0.39)	0.37 (0.31, 0.45)	0.32 (0.22, 0.43)	0.39 (0.31, 0.47)
+L	All	0.02 (–0.05, 0.09)	0.30 (0.25, 0.36)	0.07 (0.00, 0.15)	0.32 (0.27, 0.38)

Values in brackets indicate 95% credible intervals of parameter estimates.

*Means that are not significantly different from the predicted value of 1/3 are highlighted in bold.

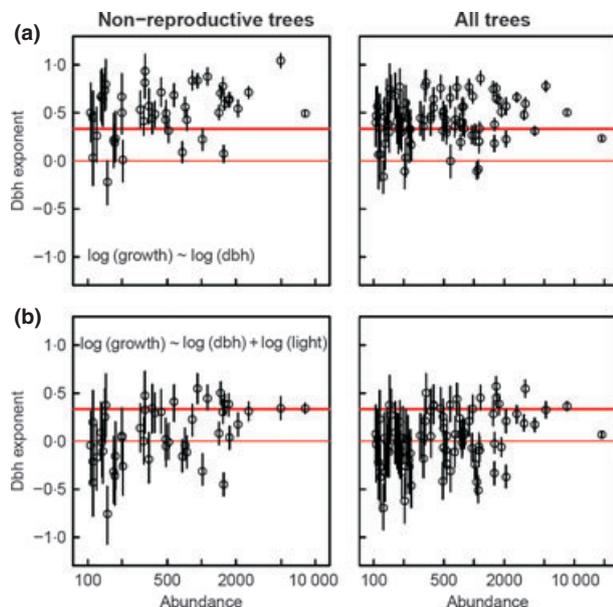


Fig. 1. Relationship between abundance and scaling exponents of dbh in growth models for tree species on Barro Colorado Island, Panama, with ≥ 100 individuals. 95% credible intervals are shown as vertical lines. (a) Model with only dbh as predictor of growth and (b) model with dbh and light as predictors of growth. The thick horizontal line indicates the predicted value of $1/3$; the thin line indicates an exponent of zero.

Table 2. Number and percentage of species for which scaling exponents were consistent with the predicted value of $1/3$ based on 95% credible intervals of parameter estimates

Model	-L		+L	
Data subset	1985–1990	1990–1995	1985–1990	1990–1995
Non-reproductive trees	13 (28%)	12 (26%)	21 (45%)	24 (52%)
All trees	41 (48%)	33 (38%)	26 (30%)	31 (36%)

-L, model not including light; +L: model including light.

discrepancy is partly accounted for by changes in light availability (see below).

The subsets of the data best conforming to the prediction of metabolic ecology included individuals least affected by

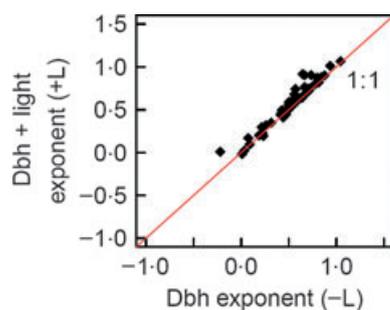


Fig. 2. Scaling exponent of dbh in the model including only dbh as predictor (-L) vs. the sum of scaling exponents of dbh and light in the model including light as additional predictor (+L).

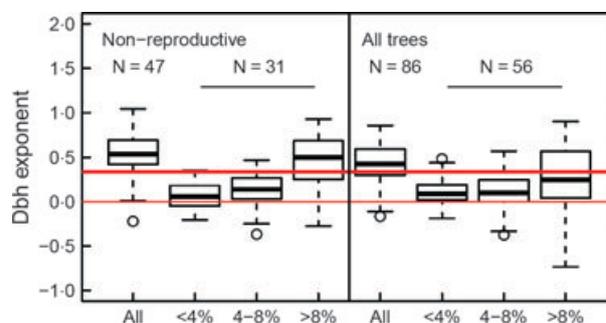


Fig. 3. Scaling exponents of dbh for tree species with ≥ 100 individuals on Barro Colorado Island, Panama, for different subsets of the data and light availability classes and the growth model using only dbh as predictor. N is the number of species that were included in the analysis. The thick horizontal line indicates the predicted value of $1/3$; the thin line indicates an exponent of zero.

competition for light (e.g. Coomes & Allen 2007): trees that grow in relatively high light. This supports a recent analysis of Coomes, Lines & Allen (2011) reporting that scaling exponents were close to the prediction of metabolic ecology in low-productivity sites, where competition for light is thought to be unimportant, and greater than the prediction of metabolic ecology in high-productivity sites.

As hypothesised by Muller-Landau *et al.* (2006) and Coomes & Allen (2009), we also find that scaling exponents were $> 1/3$ in the model without light. One explanation offered by those authors is that trees gradually gain access to more light when growing larger and hence may grow faster (Rüger *et al.* 2011a). Thus, the growth-size scaling should be steeper than the scaling predicted under the assumption that tree growth is independent of access to resources (West, Brown & Enquist 1999).

To test this explanation, Muller-Landau *et al.* (2006) incorporated the scaling of light availability with tree height (H) as H^{S_L} into the original prediction (Enquist *et al.* 1999). They assumed that biomass (M), height and crown area (C) scale with diameter (D) as D^{S_M} , D^{S_H} , and D^{S_C} , respectively. Further assuming that a tree's gross photosynthetic rate is proportional to its crown area D^{S_C} times the light reaching its crown $D^{S_H \times S_L}$, and that that biomass growth is proportional to gross photosynthetic rate (Enquist *et al.* 1999), leads to $\frac{dM}{dt} \propto D^{S_C + S_H \times S_L}$. Thus, the scaling of diameter growth with diameter (S_G) is predicted by $S_G = S_C + S_H \times S_L - S_M + 1$ because $\frac{dD}{dt} = \frac{dM/dt}{dM/dD} \propto \frac{D^{S_C + S_H \times S_L}}{D^{S_M - 1}}$.

Using canopy openness derived from canopy census data at BCI, Muller-Landau *et al.* (2006) estimated that for trees < 20 cm dbh, the light-height scaling exponent was $S_L = 1.64$. Using data on allometry as well as biomass from a pantropical compilation (Chave *et al.* 2005; Bohlman & O'Brien 2006), they estimated $S_C = 1.39$, $S_H = 0.65$ and $S_M = 2.65$ (which is consistent with the $8/3$ scaling predicted by metabolic ecology theory; Niklas 1994; West, Brown & Enquist 1999). Hence, they arrived at a predicted growth-size scaling for small trees of $S_G = 0.81$.

When we used our light estimate instead of canopy openness for non-reproductive trees, the scaling of light with dbh was 0.93 in the first census interval and 1.0 in the second, as compared to 1.1 ($S_H \times S_L$). Thus, the prediction of Muller-Landau *et al.* (2006) would be modified to $S_G = 0.67$ and $S_G = 0.74$ for the first and second census interval, respectively. Our results are closer to these values than to 1/3 (first interval: $\mu_b = 0.52$, second interval: $\mu_b = 0.62$), although the confidence intervals of the means do not overlap with these predictions either. However, at the species level, scaling exponents were consistent with these predictions in 40% and 48% of the species in the two census intervals as compared to 28% and 26% for the prediction of metabolic ecology.

Thus, the fact that metabolic ecology theory ignores competition for light may at least partly explain the divergence between observed and predicted scaling (Kerkhoff & Enquist 2006; Muller-Landau *et al.* 2006; Coomes & Allen 2007). However, several issues complicate a rigorous testing of this prediction. First, our light estimate may not correctly capture the scaling of light availability with tree size, and second, interspecific and/or ontogenetic variation in plant physiology (e.g. Peng *et al.* 2010), allometry (e.g. Poorter *et al.* 2003; Bohlman & O'Brien 2006) or wood density (Williamson & Wiemann 2010) may hamper the comparison of universal scaling predictions with species-level estimates.

An alternative, albeit unlikely, explanation of scaling exponents $> 1/3$ involves violations of secondary assumptions of metabolic ecology: complete space-filling and/or minimised hydrodynamic resistance (Price, Enquist & Savage 2007; Price *et al.* 2009). For small plants with few branching levels and where gravity is less important, such as seedlings and saplings, the scaling of gross photosynthesis or biomass growth with plant biomass (θ) approaches 1 as compared to 3/4 for 'optimised' plants (Enquist *et al.* 2007). Translated into growth-size scaling, the predicted scaling exponents would vary from 1 for seedlings ($\theta = 1$) to 1/3 for optimised plants ($\theta = 3/4$). However, θ is shown to be close to 3/4 already for plants with a biomass > 0.1 kg (Enquist *et al.* 2007). Thus, all our trees should be considered 'optimised', and according to the prediction of metabolic ecology, scaling exponents should be 1/3.

When we explicitly accounted for increased light availability when trees grow, growth-size scaling exponents were $< 1/3$, on average and for the majority of single species. This indicates that observed faster growth at larger size is to a large degree caused by greater access to light. In the model without light, the size exponent picked up both effects: the change in growth with size and the increase in growth with light. This is because light scales nearly linearly with dbh. And indeed, the scaling exponent of growth in the analysis without light ($\mu_b = 0.52$) is close to the sum of the scaling of diameter ($\mu_b = 0.07$) and light ($\mu_c = 0.50$) (Fig. 2).

In summary, there is not yet a universal theory that explains growth-size scaling, neither on average nor for single species. If metabolic ecology theory shall facilitate the parameterisation of models of forest dynamics as tools to predict carbon stocks and sequestration of natural forests when environmental conditions change (Phillips *et al.* 2004; Purves &

Pacala 2008), competition for light needs to be incorporated and the deviations of single species from mean scaling need to be better understood. Future studies should include also rare species and explore whether species' differences in crown allometry, shade tolerance or functional traits, such as wood density or maximum height, can explain differences in the growth-size relationship.

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Supporting Information

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Figure S1. Light estimate vs. tree diameter.

Figure S2. Model fits.

Table S1. Sample sizes, dbh ranges and parameter estimates.

Appendix S1. Results for reproductive trees and the census interval 1990–1995.

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