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LETTER

Comparing tropical forest tree size distributions with the predictions of metabolic ecology and equilibrium models

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Abstract

Tropical forests vary substantially in the densities of trees of different sizes and thus in above-ground biomass and carbon stores. However, these tree size distributions show fundamental similarities suggestive of underlying general principles. The theory of metabolic ecology predicts that tree abundances will scale as the −2 power of diameter. Demographic equilibrium theory explains tree abundances in terms of the scaling of growth and mortality. We use demographic equilibrium theory to derive analytic predictions for tree size distributions corresponding to different growth and mortality functions. We test both sets of predictions using data from 14 large-scale tropical forest plots encompassing censuses of 473 ha and > 2 million trees. The data are uniformly inconsistent with the predictions of metabolic ecology. In most forests, size distributions are much closer to the predictions of demographic equilibrium, and thus, intersite variation in size distributions is explained partly by intersite variation in growth and mortality.

Keywords

Demographic rates, forest structure, large-scale disturbance, metabolic theory of ecology, old-growth forests, tree diameter distributions.

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INTRODUCTION

Tropical forests vary widely in their structure and aboveground biomass (Ashton & Hall 1992; Ter Steege *et al.* 2003), differences attributable mainly to wide variation in the density of large trees (Chave *et al.* 2001). However, their tree size distributions show fundamental similarities that suggest general underlying principles (Coomes *et al.* 2003). Given that tropical forests hold almost half of all aboveground carbon stores in the biosphere (Dixon *et al.* 1994), we cannot hope to understand the terrestrial carbon budget without an understanding of tropical forest tree size distributions. Recently, the theory of metabolic ecology has generated specific predictions about the functional form of this relationship (Enquist & Niklas 2001) and its variation among sites (Niklas *et al.* 2003). Such a general theory could potentially advance fundamental understanding of forest structure and provide a basis for understanding current changes and predicting future changes in forest structure and associated carbon pools (Baker *et al.* 2004; Wright 2005).

The metabolic theory of ecology strives to explain ecological structure by considering how the metabolic rates of organisms vary with body size and environmental conditions because of fundamental physical and chemical constraints (Brown *et al.* 2004). The seminal paper by West *et al.* (1997) derives the scaling of metabolic rates (gross photosynthetic rates in plants) with size from consideration of the limits on maximal rates of resource redistribution through the organism via fractal branching networks. By adding the assumptions that plants grow until they are limited by resources and that resource use is proportional to metabolic rate, Enquist *et al.* (1998) obtain a prediction for the scaling of plant density across plant communities varying in mean plant mass. This is essentially a self-thinning law, albeit one that predicts an exponent of $-4/3$ rather than the traditional $-3/2$ for the relationship between individual plant biomass and the density of plants across plant stands.

Enquist & Niklas (2001) state that this model also applies within stands, and thus turn it into a prediction for plant size distributions within old growth, and presumably equilibrium, communities.

Alternatively, equilibrium plant size distributions can be understood as the simple demographic consequence of size-dependent variation in growth and mortality (Coomes *et al.* 2003; Kohyama *et al.* 2003). Because mortality removes trees from size classes, increasing mortality in a given size class reduces the number of trees in that size class. Because growth moves trees from one size class to another and thus is inversely related to residence time within a size class, an increase in growth in a size class will also reduce the number of trees in that size class and increase the number in the next larger size class (Condit *et al.* 1998; Wright *et al.* 2003). Mathematically, the general relationship between size and age distributions, growth, and mortality is given by the von Foerster equation (Von Foerster 1959; Sinko & Streifer 1967) which has long been an important tool in fisheries management (e.g. Ebert *et al.* 1993; Smith *et al.* 1998). At demographic equilibrium, size distributions are determined completely by the functions relating average growth and mortality to size (Kohyama *et al.* 2003). Thus, for example, exponential size distributions are expected if absolute growth rate and mortality rate are both size independent (Coomes *et al.* 2003).

Tests of the predictions of the metabolic ecology and demographic equilibrium models against whole-community tree size distributions have had mixed results to date. Enquist & Niklas (2001) found support for their metabolic prediction of tree size distribution scaling in a data set from tropical forests. However, their criteria for excluding data bias their analyses, and a reanalysis of the same data set without this bias showed consistent deviations from the prediction at large tree sizes (Coomes *et al.* 2003). Coomes *et al.* (2003) also analysed a large data set from New Zealand temperate forests, again finding consistent deviations from metabolic ecology predictions. In contrast, Coomes *et al.* (2003) found support for the demographic equilibrium model in both tropical and temperate forest data sets.

If forests are at demographic equilibrium, then the equilibrium model makes it possible to precisely link functions describing size-dependent growth and mortality – including those proposed by the theory of metabolic ecology – to functions describing tree size distributions. Foresters regularly use quantitative descriptions of tree diameter distributions as indicators of management impacts and successional status (Goff & West 1975; Goodburn & Lorimer 1999; Schwartz *et al.* 2005). Further, several studies have previously simulated equilibrium diameter distributions in mixed-aged forests on the basis of size-dependent growth and mortality (e.g. Lorimer & Frelich 1984; Kohyama 1991). However, although foresters have long used a variety of statistical models to quantitatively describe tree diameter distributions, including the negative exponential (DeLiocourt 1898; Meyer & Stevenson 1943; Leak 1964; Moser 1972) and the two-parameter Weibull (Bailey & Dell 1973), these and other theoretical diameter distributions have neither previously been derived directly from size-dependent growth and mortality, nor have their parameters been linked quantitatively to parameters describing growth and mortality.

Here, we first concisely state the logic underlying the metabolic ecology prediction for tree size distributions. We then develop the alternative demographic equilibrium model, analytically deriving the size distributions it predicts for different combinations of growth and mortality functions and thereby predicting exactly how the parameters of these size distributions are related to parameters of the growth and mortality functions. We test the metabolic ecology prediction using data on tree size distributions in 14 large (16–52 ha) census plots in tropical forests around the globe. We test the demographic equilibrium model in 10 of those forests (those for which we have growth and mortality data) by numerically integrating over the exact observed changes in growth and mortality with size. Finally, we test the utility of the analytical relationships we derive relating growth, mortality and size distributions at demographic equilibrium by fitting each forest's size distribution using each of the functional forms suggested for different combinations of growth and mortality functions, and evaluating how the best-fit parameters of the size distributions compare quantitatively with the values predicted given the best-fit growth and mortality functions.

METABOLIC ECOLOGY THEORY

West *et al.* (1997, 1999) derive predictions for the scaling of vessel diameters, biomass and metabolic rates of organisms that optimize resource distribution through branching networks of vessels. For plants, their predictions can be stated as follows:

> *M1 – Prediction*: A plant's trunk diameter, D scales with its biomass, M as $M^{3/8}$ (thus $M \propto D^{8/3}$).
>
> *M2 – Prediction*: A plant's gross photosynthetic rate scales with $M^{3/4}$, and thus with D^2 and with its total leaf area and leaf mass, L.

To develop these ideas into predictions for the form of plant size distributions within communities, Enquist & Niklas (2001) make the following key assumption:

> *M3 – Assumption*: The scaling of the density of plants with plant mass within an old-growth (equilibrium) plant community is the same as the scaling across plant communities varying in mean plant mass.

They then make use of prior work by Enquist *et al.* (1998) on plant density variation among communities:

> *M4 – Assumption*: A plant's resource use is proportional to its gross photosynthetic rate.
>
> *M5 – Assumption*: Plants grow until they are limited by resources.
>
> *M6 – Prediction*: A plant's resource use scales with $M^{3/4}$ (based on M2 and M4).
>
> *M7 – Prediction*: Across plant communities of similar total resource availability and varying in mean individual plant biomass, plant density, N scales as $M^{-3/4}$ (based on M4, M5 and M6).

By combining this last result (M7) with the assumption equating scaling within stands to scaling across stands (M3), Enquist & Niklas (2001) derive the following prediction:

> *M8 – Prediction*: In old-growth (equilibrium) plant communities, the density of plants of biomass M scales with $M^{-3/4}$ and the density of plants of diameter D scales with D^{-2} (based on M1, M3 and M7).

Here, we test how well tree diameter distributions in old-growth forests are fit by a power function with exponent −2 (M8). We further evaluate how well these diameter distributions are fit by power functions in general, and whether the best-fit exponents are or are not significantly different from −2.

DEMOGRAPHIC EQUILIBRIUM THEORY

An alternative approach to understanding size distributions of old-growth forests starts from the relationship of size distributions with growth and mortality at demographic equilibrium (Kohyama *et al.* 2003):

> *D1 – Assumption*: In old-growth forests without major long-term temporal variation, stands reach a demographic equilibrium at which mean growth as a function of size, $g(D)$, mortality as a function of size, $m(D)$, and the tree size probability distribution, $p(D)$, are inter-related as
>
> $$p(D) = \frac{1}{K\,g(D)} \exp\left[- \int_{D_0}^{D} \frac{m(\tilde{D})}{g(\tilde{D})} \mathrm{d}\tilde{D} \right], \tag{1}$$
>
> where K is a normalization constant (equal to the total number of individuals divided by the recruitment rate) and D_0 is the size of individuals upon recruitment.

This general relationship has previously been used to numerically calculate what size distributions follow from different growth and mortality functions (e.g. Coomes *et al.* 2003). Here, we show that this relationship also allows us to analytically derive the tree size distributions that follow from various combinations of growth and mortality scaling functions. We thereby derive the following specific predictions (see Appendix S1 for full derivations):

> *D2 – Prediction*: If absolute diameter growth rates and mortality rates are both constant with diameter and take values r and a, respectively (i.e. $g(D) = \mathrm{d}D/\mathrm{d}t = r$ and $m(D) = a$), the diameter distribution is a negative exponential with rate parameter $\lambda = a/r$:
>
> $$p(D) = \frac{1}{K_e} \exp\left(-\frac{a}{r} D\right), \tag{2a}$$
>
> $$p(D) = \frac{1}{K_e} \exp(-\lambda D), \tag{2b}$$
>
> where K_e is a normalization constant whose value depends on λ and on D_0 (see Appendix S1).
>
> *D3 – Prediction*: If growth is a power function of diameter, following
>
> $$g(D) = \frac{\mathrm{d}D}{\mathrm{d}t} = rD^c \tag{3}$$
>
> and mortality is constant at a ($m(D) = a$), the diameter distribution will take the form of a Weibull distribution with shape parameter $\mu = 1 - c$ and scale parameter $v = (r(1 - c)/a)^{1/(1-c)}$:
>
> $$p(D) = \frac{1}{K_w} D^{-c} \exp\left(\frac{-a}{r(1-c)} D^{1-c}\right), \tag{4a}$$
>
> $$p(D) = \frac{1}{K_{w'}} \left(\frac{D}{\beta}\right)^{\mu-1} \exp\left(-\left(\frac{D}{v}\right)^{\mu}\right), \tag{4b}$$
>
> where K_w and $K_{w'}$ are normalization constants.
>
> *D4 – Prediction*: If growth and mortality are both power functions of diameter, with growth following eqn 3 and mortality following
>
> $$m(D) = aD^b \tag{5}$$
>
> and if the scaling exponents are related such that $c - b = 1$ (i.e. mortality is proportional to relative growth rate), the diameter distribution will be a power function with exponent $-\theta = -c - a/r = -1 - b - a/r$:
>
> $$p(D) = \frac{1}{K_p} D^{-c-a/r}, \tag{6a}$$
>
> $$p(D) = \frac{1}{K_p} D^{-1-b-a/r}, \tag{6b}$$
>
> $$p(D) = \frac{1}{K_p} D^{-\theta}, \tag{6c}$$
>
> where K_p is a normalization constant.

Note that metabolic ecology predictions for the scaling exponents of growth (1/3) and mortality (−2/3) are such that the condition $c - b = 1$ is met, and thus, a power function size distribution is predicted – but the exponent will be equal to −2 only if the ratio of the mortality and growth coefficients is such that $a/r = 5/3$, a condition not specified in previous publications (Enquist *et al.* 1999; Brown *et al.* 2004). Note further that when the diameter distribution is a power function, the probability distribution of $\log(D)$ is a truncated exponential distribution with rate parameter $\theta - 1$.

> *D5 – Prediction*: If growth and mortality are both power functions of diameter (eqns 3 and 5) and $c - b \neq 1$, the diameter distribution will take a form similar to a Weibull distribution with quasi-shape parameter $\alpha = 1 - c$, quasi-scale parameter $\beta = (r(1-c)/a)^{1/(1-c)}$, and a third new parameter $\gamma = b$:
>
> $$p(D) = \frac{1}{K_q} D^{-c} \exp\left(\frac{-a}{r(1-c+b)} D^{1-c+b}\right), \qquad (7a)$$
>
> $$p(D) = \frac{1}{K_q} D^{\alpha-1} \exp\left(-\left(\frac{D}{\beta}\right)^{\alpha+\gamma}\right), \qquad (7b)$$
>
> where K_q is a normalization constant.

Here, we first evaluate whether the assumption that size distributions are in demographic equilibrium (D1) is warranted by numerically integrating eqn 1 over exactly interpolated observed growth and mortality functions and comparing the predicted diameter distributions with those observed. We then fit observed size distributions with exponential, power function, Weibull, and quasi-Weibull functions, examine which function produces the best fit, and compare the fitted parameter values with those expected based on growth and mortality parameters (D2–D5). Because it has been shown that growth and mortality functions change as trees reach the canopy at *c.* 18- to 20-cm diameter (Coomes *et al.* 2003; Muller-Landau *et al.* in press), size distributions were fit separately for all individuals combined, for small individuals (< 20 cm in diameter) only, and for large individuals (≥ 20 cm in diameter) only.

METHODS

Data sets

Our study sites are 14 large plots (16–52 ha each) in old-growth tropical forests around the world (see Table 1 and Losos & Leigh 2004). All plots were censused one or more times using the standard methods of the Center for Tropical Forest Science (Condit 1998): all free-standing woody plants with a stem diameter ≥ 1 cm (at 1.3 m above the ground) were mapped, tagged, identified to species, and measured in diameter (with a precision of 0.1 cm – we excluded early censuses in which small stems were measured only to the nearest 0.5 cm). We excluded data for individuals whose diameters were recorded as 1.0 cm to avoid the influence of inconsistencies in the definitions of this smallest size class.

Table 1 The 14 tropical forest dynamics plots used in this study; their sample sizes in area, censuses and trees (with tree number from the most recent census), and their climate

Site	Plot area (ha)	No. censuses	No. trees	Rainfall (mm)	Dry season (months)
Sinharaja Wilderness Area, Sri Lanka	25	2	190 328	5016	0
La Planada Nature Reserve, Colombia	25	2	99 802	4415	0
Luquillo Experimental Forest, Puerto Rico	16	1	64 291	3548	0
Palanan Wilderness Area, Philippines	16	1	63 891	3379	0
Yasuni National Park, Ecuador	25	2	139 566	3081	0
Lambir Hills National Park, Sarawak, Malaysia	52	2	347 236	2664	0
Pasoh Forest Reserve, Malaysia	50	3	291 954	1788	1
Korup National Park, Cameroon	50	1	314 747	5272	3
Khao Chong Wildlife Refuge, Thailand	24	1	96 110	2660	3
Barro Colorado Nature Monument, Panama	50	3	209 097	2551	3
Edoro study area, Ituri Forest, Congo	20*	2	149 045	1785	3
Lenda study area, Ituri Forest, Congo	20*	2	127 038	1674	4
Huai Kha Khaeng Wildlife Sanctuary, Thailand	50	2	70 597	1476	6
Mudumalai Wildlife Sanctuary, India	50	3	18 008	1250	4

Rainfall is the average annual total; dry season length is the number of calendar months with average rainfall < 100 mm. Climate data from Losos & Leigh (2004), except for Yasuni (S. J. Wright, personal communication) and Khao Chong (S. J. Davies, unpublished data). Plots are ordered by increasing dryness.

*The two Congo sites each consist of two 10-ha plots; all other sites are one contiguous rectangle or square.

(At some sites, any stem between 0.95 and 1.05 cm was recorded as a 1.0-cm stem, while in others only stems between 1.00 and 1.05 cm were thus recorded.) In total, we analysed over 4.4-million size measurements on over 2.1-million individuals in 473 ha.

Evaluating the two models

To compare the fits of the metabolic ecology (M8) and demographic equilibrium (D1) predictions to the data, we used likelihood, the preferred approach for comparing fits to continuous probability distributions (Johnson *et al.* 1994). For both models, the predictions were exact, with no fitted parameters. In both cases, we normalized the predicted probability densities so that they summed to exactly one over the total diameter range considered ($D_0 = 1.05$ cm to $D_{\max} = 499.95$ cm). In the case of the theory of metabolic ecology, the prediction can be stated analytically. In a size class i bounded below at $D_{i\min}$ and above at $D_{i\max}$, we should observe a proportion of the total stems equal to

$$p_{i,M\text{pred}} = \frac{1/D_{i\,\min} - 1/D_{i\,\max}}{1/D_0 - 1/D_{\max}}. \tag{8}$$

For the demographic equilibrium theory, numerical methods are necessary. We calculated mean diameter, growth and mortality within wider size classes and then linearly interpolated between these points to obtain complete functions, $g(D)$ and $m(D)$ for growth and mortality (see Appendix S2 and Muller-Landau *et al.* in press). We then used eqn 1 and numerical integration to obtain the predictions for the number of individuals in each diameter class.

Because measurement precision is limited to 0.1 cm and thus the data are essentially binned into classes of this width, the likelihood of the complete data set given a predicted probability distribution is essentially a multinomial distribution, $\prod_i p_i^{N_i}$ (Kulldorff 1961; Johnson *et al.* 1994). The total log likelihood is

$$L = \sum_i N_i \log(p_i). \tag{9}$$

We calculate this log likelihood for each model using the finest size classes possible for our data set: classes evenly 0.1-cm wide from 1.05 to 499.95 cm.

Phenomenological fits and their relationships to growth and mortality

We fitted negative exponential (eqn 2b), Weibull (eqn 4b), power function (eqn 6c), and quasi-Weibull (eqn 7b) probability distributions to the diameter distributions using maximum likelihood methods (Kulldorff 1961); that is, we searched for the parameters that maximized the log likelihood, as given in eqn 9. We used Akaike's Information Criterion to compare the maximum likelihood fits of the different functions (Burnham & Anderson 2002). For each census at each plot, we separately fit distributions for all individuals (bins from 1.05 to 500.05 cm), small individuals only (measured at < 20 cm in diameter, thus encompassing bins from 1.05 to 19.95 cm), and large individuals only (measured at ≥ 20 cm in diameter, thus encompassing bins from 19.95 to 500.05 cm), always using 0.1-cm bins (the limits of measurement precision). We bootstrapped over 50 × 50-m subplots to obtain confidence intervals on parameter estimates. The fitted power-function parameters were compared with the -2 value predicted under metabolic ecology, specifically examining whether the confidence intervals included this prediction.

We calculated predicted parameter values of each phenomenological model of tree size distributions from fitted parameters of growth and mortality (eqns 2a, 4a, 6a, 6b and 7a). The parameters of power functions relating growth and mortality to diameter were obtained from Muller-Landau *et al.* (in press); details of the fitting methods are given in Appendix S2. We calculated mean growth and mean mortality rates for each site for all individuals, small individuals and large individuals. In each case, we calculated weighted mean values, weighing each size class by its width on a log-diameter scale (size classes were chosen to be approximately equal on a log-diameter scale, while also being bounded at round numbers to avoid the influences of measurement biases). We used weighted mean values because unweighted mean values are dominated by the growth and mortality rates of the very abundant small individuals, which are not typical of all size classes. Confidence intervals on all growth and mortality parameters were obtained by bootstrapping over 50 × 50-m subplots. Confidence intervals on the size distribution parameters calculated from the growth and mortality parameters were obtained by bootstrapping over the growth and mortality parameters that went into the calculation (using the confidence intervals of the parameters and assuming errors in the estimates are normally distributed).

To compare predicted and observed size distribution parameters, we first assessed which predicted size distribution model (exponential, power, Weibull or quasi-Weibull) had the highest likelihood of the data across all sites combined. We then used this best model and the most recent census for each site to investigate the degree to which we could explain intersite variation in size distributions in terms of growth and mortality. To do this, we examined the correlations among sites between the size distribution parameters predicted from growth and mortality and the size distribution parameters fitted directly to the tree size data.

RESULTS

Evaluating the two models

In general, tree diameter distributions were qualitatively similar yet quantitatively different across all the closed canopy sites, with a relationship that approximates a power function for small individuals and becomes ever more curvilinear on log–log scales at larger diameters (Fig. 1a–h). The dry, open forest at Mudumalai had a substantially different diameter distribution, with two modes; this site experiences frequent disturbance from fires and elephants (Fig. 1j). The densities of large trees and thus the shape of the size distribution at larger diameters varied widely among the closed canopy sites.

The metabolic ecology prediction of power function size distributions with exponent −2 was a very poor fit for all sites (Fig. 1, Table 2). This is due in large part to large deviations from the power function prediction at large diameters, where there are many fewer individuals than predicted (Table 2). Even at small sizes, however, the metabolic ecology prediction was not a good fit (Table 3), especially at the two more open-canopy forests in the data set, Huai Kha Khaeng and Mudumalai (Fig. 1i,j). The poor fit of the metabolic ecology prediction is further reflected by the phenomenological fits, which show that power functions are never the preferred model for whole-forest distributions, and that their fitted exponents are almost always significantly different from −2 (Table 3).

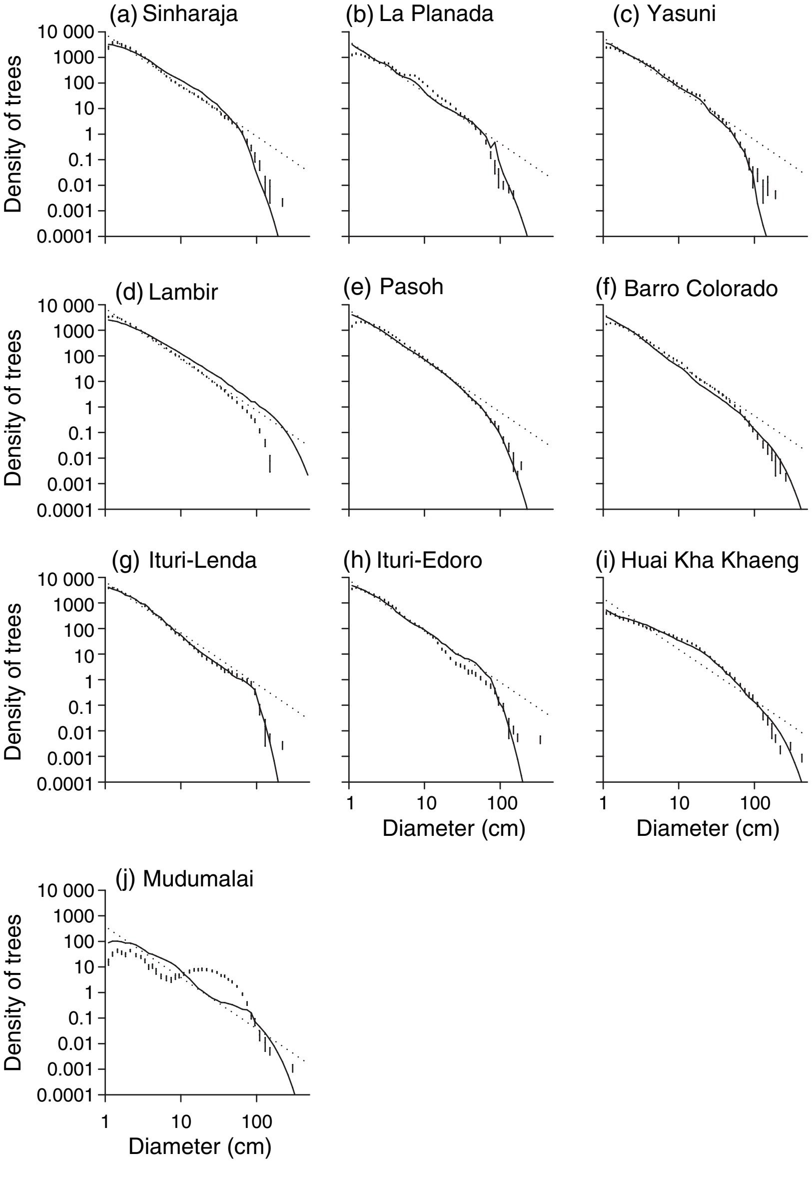

Figure 1 Observed tree size distributions for the most recent censuses of 10 tropical forests (vertical bars) and the predictions of the metabolic ecology (dotted line) and demographic equilibrium (solid line) models. The observed data were grouped into approximately log-even size classes for graphing purposes, and bootstrapping was performed over 50 × 50-m subplots to obtain 95% CI (vertical bars) for the densities of trees per 1-cm diameter interval per ha for each of these size classes. (In some cases the confidence intervals are so small that bars appear as dots.) Predicted size distributions are continuous and plotted as such; the likelihood of the data under each prediction was calculated for the full data set using regular 0.1-cm size classes, the limits of measurement precision (see Table 2 for the likelihoods).

Table 2 The fit of the metabolic ecology and demographic equilibrium models to the diameter distribution data for each census of each site, as reflected in the total log likelihood of the data

Site	Census	Log likelihood		Difference in log likelihoods (ME − DE)
		Metabolic ecology	Demographic equilibrium	
Sinharaja	1995	**−833 722**	−838 183	4461
Sinharaja	2000	−827 307	**−824 867**	−2441
La Planada	1997	−539 709	**−534 125**	−5584
La Planada	2003	−494 607	**−489 056**	−5551
Yasuni	1997	−680 775	**−673 615**	−7160
Yasuni	2004	−651 039	**−643 494**	−7545
Lambir	1992	**−1 479 775**	−1 491 397	11 622
Lambir	1997	**−1 527 610**	−1 540 531	12 921
Pasoh	1990	−1 404 963	**−1 392 765**	−12 198
Pasoh	1995	−1 404 615	**−1 390 759**	−13 857
Pasoh	2000	−1 341 067	**−1 326 366**	−14 700
Barro Colorado	1990	−1 034 347	**−1 032 609**	−1738
Barro Colorado	1995	−984 831	**−983 861**	−970
Barro Colorado	2000	−943 374	**−942 460**	−914
Ituri-Edoro	1995	−643 365	**−639 077**	−4288
Ituri-Edoro	2000	−634 505	**−629 716**	−4789
Ituri-Lenda	1995	−523 558	**−520 162**	−3396
Ituri-Lenda	2000	−522 669	**−518 851**	−3818
Huai Kha Khaeng	1993	−418 929	**−400 087**	−18 842
Huai Kha Khaeng	1999	−401 398	**−380 264**	−21 134
Mudumalai	1992	−138 494	**−133 008**	−5487
Mudumalai	1996	−126 383	**−121 525**	−4858
Mudumalai	2000	−135 178	**−130 692**	−4486

Note that there are no free parameters for either model, and thus the Akaike Information Criterion is equal simply to −2 times the log likelihood. The better score for each site and census combination is highlighted in boldface, and the difference between the two is given in a separate column where positive values indicate a better fit for the metabolic ecology model (higher log likelihoods) and negative values a better fit for the demographic equilibrium model. To put these numbers in perspective, note that a difference in log likelihoods of just 9 indicates that the likelihood of the data under the better model is 10 000 times greater than under the worse model. Sites are ordered by increasing dryness.

The demographic equilibrium prediction, in contrast, was able to capture the fundamental curvature of the size distributions, and thus was generally a better fit to the data. A notable exception was Lambir, where the demographic equilibrium model predicted many more large individuals than were observed (Fig. 1d). The likelihood of the data was much higher under the demographic equilibrium model than under the metabolic ecology model in 20 of 23 data sets; the exceptions were the two censuses at Lambir and the first census at Sinharaja (Table 2).

Phenomenological fits and their relationships to growth and mortality

Of the four phenomenological models that were fitted (eqns 2b, 4b, 6c and 7b), the three-parameter quasi-Weibull distribution proved the best fit for 24 of 27 whole-forest (all-individual) data sets, with the Weibull just barely superior to it in the other three cases (Table 3). These two functions were always the top two in their Akaike Information Criteria; the power and exponential functions were far behind (Table S1). When size distributions of small individuals or large individuals alone were fit, the quasi-Weibull was again the best fit in 48 of 54 cases (Table 3). The power function did better than the exponential among small individuals, and the exponential better than the power function among large individuals, but both were almost always far inferior in their fit to the Weibull and quasi-Weibull (Table S1). The power function was the best fit for only two of 81 data sets: small individuals at Luquillo and in the first census at Huai Kha Khaeng. The exponential function was the best fit for only one of 81 data sets: large individuals at Luquillo.

The shapes of these diameter distributions differed significantly from the power-function prediction of

Table 3 Comparison of the maximum likelihood fits to the size distributions of all individuals, small individuals (< 20-cm diameter), and large individuals (≥ 20-cm diameter) for all sites and censuses

		Best-fit function			Power-function exponent, theta (eqn 6c) (95% CI)		
Site	Census	All	Small	Large	All	Small	Large
Sinharaja	1995	W	Q****	Q****	2.05 (2.02–2.07)	1.96 (1.93–2.00)	3.01 (2.93–3.09)
Sinharaja	2000	Q****	Q****	Q****	1.99 (1.96–2.01)	1.86 (1.82–1.90)	3.01 (2.94–3.07)
La Planada	1997	Q	Q****	Q****	1.78 (1.77–1.79)	1.48 (1.46–1.50)	3.39 (3.33–3.46)
La Planada	2003	Q**	Q****	Q**	1.73 (1.72–1.74)	1.40 (1.38–1.41)	3.39 (3.33–3.46)
Luquillo	1992	Q****	P****	E	1.75 (1.73–1.78)	1.46 (1.41–1.50)	3.16 (3.07–3.25)
Palanan	1998	Q****	Q****	Q****	1.81 (1.80–1.83)	1.61 (1.58–1.64)	2.95 (2.87–3.04)
Yasuni	1997	Q****	Q****	Q*	1.86 (1.85–1.87)	1.62 (1.60–1.64)	3.68 (3.60–3.77)
Yasuni	2004	W	Q****	W	1.84 (1.83–1.85)	1.59 (1.57–1.60)	3.65 (3.57–3.72)
Lambir	1992	Q****	Q****	Q****	1.95 (1.95–1.96)	1.80 (1.79–1.81)	2.91 (2.88–2.94)
Lambir	1997	W	Q****	Q****	1.96 (1.95–1.97)	1.81 (1.80–1.82)	2.91 (2.87–2.94)
Pasoh	1990	Q****	Q****	Q****	1.93 (1.93–1.94)	1.73 (1.71–1.74)	3.15 (3.11–3.19)
Pasoh	1995	Q****	Q****	Q****	1.90 (1.89–1.91)	1.66 (1.65–1.68)	3.19 (3.15–3.23)
Pasoh	2000	Q****	Q****	Q****	1.87 (1.86–1.88)	1.61 (1.60–1.63)	3.18 (3.14–3.22)
Korup	1998	Q****	Q****	Q*	1.96 (1.95–1.97)	1.79 (1.78–1.81)	3.28 (3.23–3.32)
Khao Chong	2001	Q****	Q***	Q	1.84 (1.82–1.86)	1.61 (1.59–1.64)	3.04 (2.97–3.11)
Barro Colorado	1990	Q****	Q****	Q	1.97 (1.96–1.97)	1.81 (1.80–1.82)	2.83 (2.78–2.87)
Barro Colorado	1995	Q****	Q****	W	1.93 (1.93–1.94)	1.76 (1.75–1.77)	2.85 (2.81–2.90)
Barro Colorado	2000	Q****	Q****	Q	1.90 (1.90–1.91)	1.72 (1.71–1.73)	2.84 (2.79–2.88)
Ituri-Edoro	1995	Q****	Q****	Q****	2.07 (2.05–2.08)	1.90 (1.88–1.92)	2.56 (2.50–2.63)
Ituri-Edoro	2000	Q****	Q****	Q	2.04 (2.02–2.05)	1.86 (1.84–1.88)	2.60 (2.54–2.66)
Ituri-Lenda	1995	Q****	Q****	Q****	2.13 (2.12–2.15)	2.05 (2.04–2.07)	2.43 (2.38–2.48)
Ituri-Lenda	2000	Q****	Q****	Q****	2.13 (2.11–2.14)	2.04 (2.02–2.06)	2.42 (2.36–2.47)
Huai Kha Khaeng	1993	Q****	P**	Q***	1.56 (1.54–1.58)	1.17 (1.13–1.21)	2.93 (2.89–2.97)
Huai Kha Khaeng	1999	Q****	W	Q***	1.52 (1.50–1.54)	1.08 (1.04–1.12)	2.95 (2.91–2.99)
Mudumalai	1992	Q****	Q***	Q****	1.08 (1.06–1.10)	−0.06 (−0.22 to 0.10)	2.86 (2.80–2.92)
Mudumalai	1996	Q****	Q****	Q****	1.04 (1.02–1.05)	−0.23 (−0.41 to −0.07)	2.81 (2.75–2.88)
Mudumalai	2000	Q****	Q****	Q****	1.16 (1.14–1.18)	0.75 (0.67–0.83)	2.75 (2.70–2.81)

The best-fit function is the one with the lowest Akaike Information Criterion (AIC): Weibull (W), power function (P), exponential (E) or quasi-Weibull (Q) distribution. Asterisks indicate whether the three inferior models have combined Akaike weights of < 0.05 (*), 0.01(**), 0.001(***) or 0.0001(****) (Burnham & Anderson 2002). For every data set, the best-fit power function exponent with its 95% confidence interval is listed. Confidence intervals were obtained from 1000 bootstraps over 50 × 50-m subplots. Plots are ordered by increasing dryness. The AIC values for all fits are given in Table S1.

metabolic ecology. Moreover, the best-fit power-function exponents for the whole size distribution were significantly different from the predicted slope of −2 in 13 of 14 forests (Table 3). When diameter distributions of small individuals alone were fitted, the exponents were significantly greater than −2 (shallower slopes) at 13 of 14 sites and significantly smaller at the remaining site; for large individuals, they were significantly smaller than −2 (steeper slopes) for all sites. In all cases, the exponents for small and large individuals were highly significantly different, reflecting the strong changes in shape of the size distribution with tree size.

Among the five size probability distributions predicted from growth and mortality (eqn 2a, 4a, 6a, 6b and 7a), the Weibull proved to be the most reliable predictor, as exemplified by having the highest likelihood of the data (Table S2). When examining only data sets for the full diameter distribution (all individuals), the quasi-Weibull and Weibull were each best at four sites, while the power function was best at Lambir and the exponential was best at Mudumalai. When the quasi-Weibull was not the best, it was always much worse than the best fit; in contrast, when the Weibull was not the very best, it generally was the closest second best. The Weibull also was by far the best predictor among the data sets for only small and large individuals (Table S2).

The match to the diameter distributions of the fitted and predicted models is demonstrated graphically in Fig. 2 for one census at one site, and in Fig. S1 for all other censuses and sites. The site shown, Barro Colorado (data available on the web at: http://ctfs.si.edu/datasets/bci/), is typical in the much better fit obtained by the fitted Weibull and

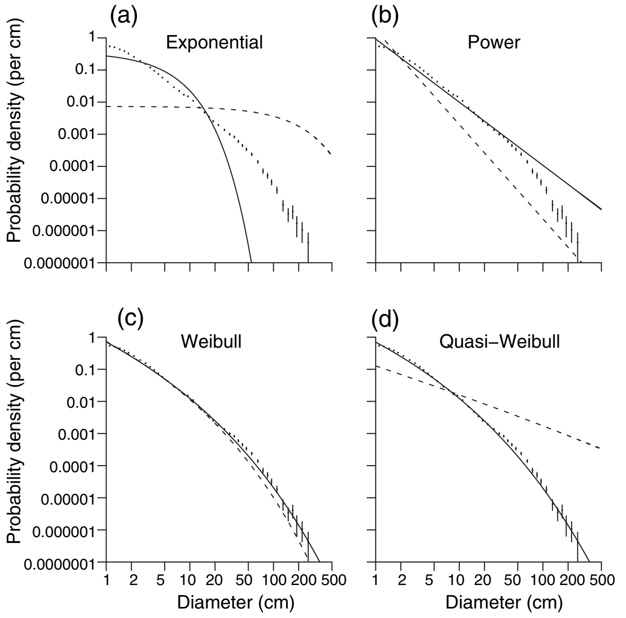

Figure 2 The observed tree size distribution from the 1990 census on Barro Colorado (vertical bars), maximum likelihood fits of various phenomenological models to the size distribution (solid lines), and the corresponding functions predicted by the demographic equilibrium model based on the change in growth and mortality with size (dashed lines). (a) Exponential distribution model, with fits to eqn 2b and predictions based on eqn 2a; (b) power function model, with fits to eqn 6c and predictions based on eqn 6b; (c) Weibull distribution model, with fits to eqn 4b and predictions based on eqn 4a; (d) quasi-Weibull distribution model, with fits to eqn 7b and predictions based on eqn 7a. Again, for graphing purposes only the observed data were grouped into approximately log-even size classes, with 95% CI based on bootstrapping over 50 × 50-m subplots. Fits were carried out to the full data set using regular 0.1-cm size classes (the limits of measurement precision). Fitted parameter values and their bootstrapped CIs are given in Table 3 and Table S1.

quasi-Weibull over the fitted power and exponential distributions. It is also typical in the good match of the predicted Weibull distribution, and in the poor matches for the predicted exponential and power functions. The fit of the predicted quasi-Weibull distribution is highly variable among sites, and is sometimes much better than at Barro Colorado (Table S2).

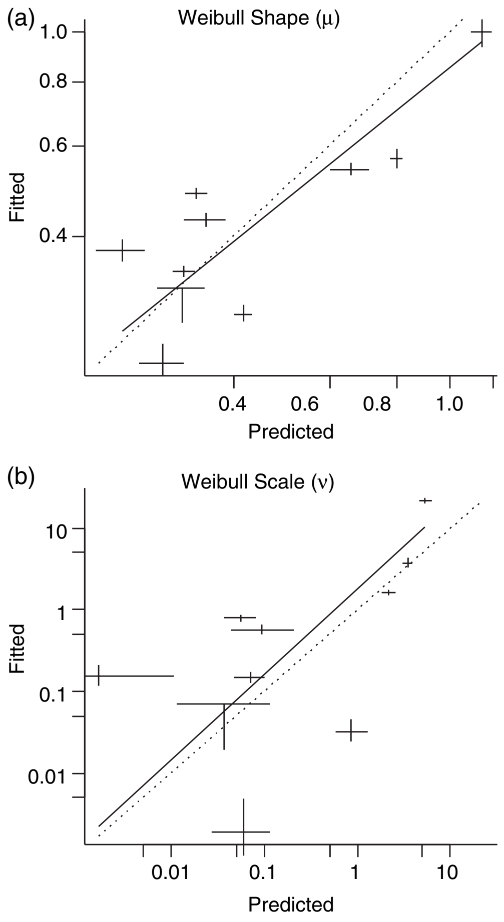

Figure 3 The relationship between the predicted (from growth and mortality) and best-fit (using maximum likelihood) Weibull parameters of the tree diameter distribution across sites. There is one point per site, with only the most recent census represented. Confidence intervals on predicted and fitted parameters are based on bootstrapping over 50 × 50-m subplots. The solid line shows the model 2 regression of the log-transformed parameters; the dotted line is 1 : 1.

Variation among sites in the parameters of the best-fit Weibull to the tree diameter distribution was in part explained by growth and mortality. The Weibull parameters predicted based on growth and mortality (eqn 4) were positively correlated with the fitted parameters, with model 2 regression slopes not significantly different from 1 : 1 (Fig. 3). The shape parameters were significantly correlated ($n = 10$, $r^2 = 0.68$, $P = 0.003$), while the scale parameters were marginally so ($n = 10$, $r^2 = 0.30$, $P = 0.10$).

DISCUSSION

Assessing existing models for tree size distributions

The metabolic ecology prediction for the scaling of tree abundance with diameter in old-growth forests was unequivocally rejected in all 14 tropical forests examined here. We believe the core problem is the assumption that the same logic that determines the densities of plants in thinning even-aged stands applies to the relative abundances of size classes in mixed-aged stands. While different stands of even age and size have access to the same total resources, the same is not true of different size classes of trees within mixed-aged forests. Further, the number of individuals in each size class is not necessarily limited strictly by the energy that reaches that size class, as reflected in competition-induced mortality that thins abundant recruits to a fixed number that use all available energy. Instead, the number of individuals may be limited to a lower level based on the rate at which individuals are removed by mortality unrelated to resource competition, and the rates at which they grow into and out of the size class.

The demographic equilibrium model is based on exactly these considerations of the joint influences of growth and mortality in determining the change in number of individuals with size, and thus it provides both an accurate and useful explanation of the form of tree size distributions in old-growth tropical forests. Under this model, a power-function size distribution emerges as a special case when growth and mortality are themselves both power functions of size, with mortality proportional to the relative growth rate. One way in which this last condition can be met is if both relative growth and mortality are proportional to the mass-specific gross photosynthetic rate, as hypothesized by both metabolic ecology theory (Brown *et al.* 2004) and an alternative incorporating change in resource availability with size (Muller-Landau *et al.* in press). Thus, the approximately power-function size distribution among 'small' individuals informs us of the approximate proportionality of relative growth and mortality in these size classes, consistent with the results of Muller-Landau *et al.* (in press). Such proportionality may in turn reflect the dominant influence of resource availability and competition in determining both growth and mortality below the canopy (Coomes *et al.* 2003). Similarly, the lack of a power-function relationship among large individuals can be interpreted as demonstrating the partial decoupling of growth and mortality in these size classes. As hypothesized by Coomes *et al.* (2003), this may be because mortality is at least partly independent of resource availability and competition among large trees. Differences in growth and mortality scaling between small and large individuals may also in part reflect differences in species composition and thus in life-history strategies and allocation patterns.

The linkage between size distributions, growth and mortality in forests at equilibrium is potentially a useful tool both for estimating one quantity from the other two and for detecting departures from equilibrium. However, despite the fact that predicted and fitted size distribution parameters were positively correlated with slopes not significantly different from one across sites (Fig. 3), these relationships were not sufficiently tight to permit reliable predictions of size distributions from growth and mortality (note the mostly non-overlapping confidence intervals in Table S3). We believe this reflects strong interannual variation in growth and mortality, which means that longer-term data sets are necessary to accurately estimate the long-term average growth and mortality rates that should determine equilibrium size distributions. This temporal variation in growth and mortality also leads to temporal variation in tree size distributions, and thus in itself represents a deviation from homogenous equilibrium assumptions and predictions. Thus, comparisons of predicted and observed size distributions are a very crude tool to detect departures from equilibrium, able only to detect particularly large deviations such as those observed at Lambir. In practice, departures from equilibrium can be better detected by comparing forest structure among the two or more censuses required to calculate growth and mortality.

The failure of the demographic equilibrium model, both in its exact (eqn 1) and approximate (eqns 2a, 4a, 6a, 6b and 7a) forms at Lambir is consistent with other data indicating that this forest was far from steady state. Total above-ground biomass increased dramatically between the 1992 and 1997 censuses. This may reflect recovery from previous large-scale tree mortality. Interannual variation in growth and mortality in Southeast Asia is closely tied to the El Niño Southern Oscillation cycle, with droughts and thus high tree mortality during El Niño events (Salafsky 1998; Potts 2003; van Nieuwstadt & Sheil 2005). The 1992–1997 census interval is notable in not containing an El Niño event, and thus, we might expect a net accrual of tree biomass during such a time period. Further, the lack of an El Niño event during the measurement period implies that our estimates of mortality (and growth) rates at Lambir probably underestimate (and overestimate) long-term average rates, and thus overestimate the long-term equilibrium densities of large trees.

Significance and future directions

The results presented here add to a growing body of evidence demonstrating that there is no site- and size-independent scaling relationship of tree abundance with diameter among trees in old-growth forests, tropical or temperate (Coomes *et al.* 2003). Instead, there are significant quantitative differences in tree size distributions among forests, differences that our work suggests are related proximally to among-site variation in tree growth and mortality. Among-site variation in the scaling of growth and mortality with size in turn reflects variation in tree allometries and the scaling of resource availability with size (Muller-Landau *et al.* in press). The most important resource for determining changes in resource availability with size is almost certainly light, because light is clearly limiting and competition for light is highly size asymmetric. Variation in the scaling of light availability within forests itself depends on the tree size distribution and especially the abundances of large trees (Nicotra *et al.* 1999; Montgomery & Chazdon 2001; Montgomery 2004). Thus, ultimately, variation in tree size distributions and resource availability is interlinked and feeds back upon itself, and a complete explanation requires an understanding of these linkages.

Despite the observed variability, there is considerable consistency in the scaling of size distributions within and among closed canopy forests – indeed, more than would be expected based on growth and mortality alone. This is especially evident for subcanopy individuals and within sites, where the growth and mortality patterns (Muller-Landau *et al.* in press) are more variable among censuses than the size distributions. This consistency indicates the presence of negative feedbacks, such that a decrease in the abundance of trees results in increased growth and decreased mortality until the forest returns to its previous size distribution. Models that explicitly incorporate resource dynamics can capture these types of feedbacks (Pacala *et al.* 1996; Chave 1999), and such models provide the best avenue for understanding the ultimate causes of the similarities and differences among forests observed here.

Muller-Landau *et al.* (in press) hypothesize that the key factor for understanding differences and similarities in growth and mortality functions among forests is the relative degree to which large individuals can monopolize resources vs. the degree to which their abundance and resource monopolization are limited by other factors such as lethal disturbances (Coomes *et al.* 2003) or relatively more symmetric resource competition (Stoll *et al.* 2002). We propose that this same factor is critical for tree size distributions as well. Among-site variation in size distributions is, by definition, greatest between what we refer to as closed and open canopy forests. In open canopy forests, the abundance of large trees is obviously far below its theoretical maximum – in the two forests here because of recurring fire and elephants (Sukumar *et al.* 2005). Even in closed canopy forests, the densities of large trees are limited by the mortality imposed by droughts, wind storms, lightning and disease. In some cases, mortality rates of large trees may be fairly similar across years, reflecting the dominance of frequent small-scale events; in other cases, strong interannual variation may reflect the importance of rare and typically large-scale events (Asner *et al.* 2000; Williamson *et al.* 2000). It will take much longer-term records than we have to date to disentangle the relative influences of different processes in determining large tree mortality rates.

If we are correct, then attempts to understand geographical variation in the above-ground biomass of tropical forests today and to predict future changes to associated carbon stores should focus on the determinants of mortality rates of large trees (Loehle 1988, 2000). The gaps made in the canopy by the deaths of large trees due to disturbances or droughts may quickly be filled by smaller trees, but the gaps in the size class are not. Anthropogenic global change may be increasing the frequency and severity of cyclones and hurricanes (Webster *et al.* 2005), which can cause great increases in tropical tree mortality (Zimmerman *et al.* 1994). These changes may lead to permanently lower long-term average abundances of large trees in many tropical forests, and concomitant decreases in above-ground carbon stores. A better, more mechanistic understanding of tropical forest structure and dynamics will provide insight into both geographical variation today and future forest change.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online from http://www.Blackwell-Synergy.com:

Appendix S1 Derivations of tree size distributions from growth and mortality relationships.

Appendix S2 Details of the methods for fitting growth and mortality.

Table S1 Akaike Information Criteria for the phenomenological fits to the tree size distributions.

Table S2 Log likelihoods of the observed size distributions under the predictions based on growth and mortality parameters.

Table S3 Parameters of the fitted and predicted size distributions.

Figure S1 Observed, predicted and fitted tree size distributions for all sites.

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