1 Supplemental Materials, Methods, Results and Discussion

1.1 LiDAR Acquisition

LiDAR acquisition and the geolocalization of forest plot data relative to LiDAR data is described in greater detail in Stark et al. (2012), which employs the same LiDAR and geolocation datasets. We summarize this report in the following two paragraphs.

Sites were overflown with a discreet-return small footprint LiDAR system—a Leica ALS70-II Airborne LiDAR (Heerbrugg, Switzerland)—in June 2008. Aircraft height was less than 1000m above the ground and aircraft speed was 120-150 knots. The LiDAR operated at a data capture pulse rate of 100 KHz, had a maximum scan angle of 10 degrees with a cross-track scan rate of 50 Hz. LiDAR pulse density averaged ∼50 pulses m$^{-2}$. There were up to 4 distance-measurement ‘returns’ for each laser pulse, which were combined with LiDAR and aircraft positional and geo-positional data to geo-locate each pulse return—sub-meter accuracy was expected. Most pulses only returned a single energy peak (i.e., first return). The LiDAR laser footprint (beam diameter) was between 20 and 40 cm and the ranging laser operated in the near infrared (NIR) range of wavelengths.

Stark et al. (2012) collected GPS data from hand-held and higher accuracy differential GPS measurement systems in forest plots to facilitate comparison with airborne LiDAR data. Ultimately, however, a distance decay correlation analysis was employed to optimize forest plot coordinates to best match LiDAR data. This analysis compared data from tree positions within plots and a ground-based profiling LiDAR (Riegl LD90-3100VHS-FLP; Riegl Laser Measurement Systems, Horn, Austria) with canopy surface height estimates from the Airborne LiDAR dataset. (Additional detail is provided in the Supplementary Materials of Stark et al. (2012).) After plot relative positions were adjusted, original GPS-based estimates we found to fall within 10 meters of adjusted plot coordinates.

1.2 LiDAR-based Leaf Area and Light Estimation

We applied the MacArthur-Horn method to the transmission rate of LiDAR pulses sampling the canopy to estimate surface area—and after calibration leaf area—as a function of height (MacArthur & Horn, 1969). Stark et al. (2012) provides a validation analysis of this method by comparing profiles estimated from coincident airborne and ground-based profiling LiDAR. If the MacArthur-Horn method were biased, profiles collected from nadir (airborne) vs. zenith (ground-based) view angles should produce differing results. However, the profiles strongly corresponded, capturing site differences. Furthermore, the profile from the Ducke forest corresponded with a previous destructive sample (see McWilliam et al., 1993). Work in progress will report a subsequent LiDAR calibration approach that made use of destructive leaf area measurements paired with LiDAR samples at the Tapajós site, providing a direct calibration for the LiDAR devices. Here we employed this calibration, and an adjustment for light-dependency of leaf angles (see Posada et al., 2009), to calculate mean leaf area profiles and average fractional light transmission profiles in both sites. We note that the calibration approach generated site and plot-level profiles very similar to those presented in Stark et al. (2012).

As in Stark et al. (2012), we modeled light penetration from exponential reduction that depended on leaf area density within each canopy voxel (with a 1 m vertical dimension). We also, as in this previous article, adjusted the exponential extinction constant to generate predicted understory light conditions that matched observations. Specifically, the leaf area transmittance constant was derived by requiring light transmission to produce a global geometric average of 3.4% at a 2 m height, matching site data. This approach maintained
we calculated absorption as the change in average light availability over the profile.

1.3 Fitting Standard Parametric Size Distributions to Site Data

We fit Pareto and Weibull distributions to stem diameter observations (Muller-Landau et al., 2006). The Weibull appeared to be a better fit overall and particularly in the Ducke site (Fig. S1; ΔAIC >2). The Pareto did not capture the observed log-log concave-down curvilinearity of the size distribution in either site. The Tapajós, however, uniquely displayed a large approximately log-log linear region of the size distribution—consistent with the Pareto form—spanning from ≈10 to 95 cm DBH. Truncated Pareto distributions were fit to avoid the regions of clearest non-power law like behavior of the upper ranges of the empirical size distributions (trees below 94 and 65 cm DBH, corresponding with 99th lower diameter quantiles at the Tapajós and Ducke sites respectively; White et al., 2008). Fit scaling exponents for the Tapajós and Ducke sites respectively were -2.6 and -2.2, somewhat lower than the expectation of -2 based on optimal three-dimensional space filling, but consistent with the expectation for a regenerating forest in the case of the Tapajós (Enquist & Niklas, 2002; West et al., 2009). Weibull distributions were fit to all tree data greater than 10 cm DBH at both sites—shape and scale parameters were 0.315 & 0.0841 and 0.805 & 7.396 for the Tapajós and Ducke respectively.

1.4 Forest Structure Model I (start of ‘Step A’)

We constructed parallel analytical and computational approaches to explicitly predict the vertical structure of leaf area in the canopy from stem diameter distributions. In the case of the analytical approach, our objective was to describe exact quantitative predictions for vertical leaf area profiles corresponding with the ideal metabolic scaling theory prediction for the diameter distribution, i.e., a Pareto distribution with a -2 scaling exponent (West et al., 2009; Enquist et al., 2009; Enquist & Niklas, 2001; Muller-Landau et al., 2006). For both analytical and computational approaches we employed a set of scaling relationships that linked the vertical position and extent of tree crowns with tree diameter. Following the notation of Enquist et al. (2009), we defined the key canopy scaling relationships:

\[ a_k^L = c_1 \cdot r_k^\beta \]  
\[ a_k^L \propto v_{can}^k = c_2 \cdot r_k^\beta \]

where \( r_k \) is the stem radius (diameter/2) of trees in the size group \( k \), \( a_k^L \) is the leaf area, while \( v_{can}^k \) is the canopy volume and \( \alpha \) and \( \beta \) are scaling exponents, and \( c_1 - c_2 \) are normalization constants. Next, consider a discrete power-law distribution (Pareto distribution, in the continuous case) of individual number \( N_k \) over size groups, i.e.,

\[ N_k = c_3 \cdot r_k^\theta \]

where \( \theta \) is a new scaling constant. And, the height-diameter relationship referenced to the center of the tree crown was:

\[ H_k = \kappa \cdot r_k^\phi \]

LiDAR leaf area density profiles (see Stark et al., 2012) correspond conceptually to a 3D sample of the canopy, though in the case of this study the sample was elongated in one horizontal direction. Our objective was to predict these profiles. We first predicted profiles from ideal size distributions and individual tree-level
canopy scaling before then predicting profiles for a community with any empirical size distribution. We began by assuming that individual tree crowns could be approximated by a rectangular solid (though the arguments presented here should generalize to any Euclidean solid). In this case, the volume was the length times the width times the height of the canopy, \( v_k = lwh = 2^{\frac{3}{2}}u_k^3 \), where we assumed \( u_k \) is one-half the length, width and height. From this relationship and Equation 3 above we found:

\[
u_k = c_4 \cdot r_k^{\frac{3}{2}}
\]  

(5)

Next, we noted that within each crown, the total leaf area of the voxels centered on a particular horizontal strata gives the contribution of that crown to the total leaf area at that height, \( h \), which we defined as \( a_{k,h} = c_5 \cdot r_k^\beta \cdot 2^{\frac{3}{3}k} \). Here \( c_5 \) is \( c_4 \) multiplied by the leaf area density of one unit of canopy volume \((m^3)\). The total leaf area associated with all individuals of that size at that height was then:

\[
a_{k,\text{tot}} = N_k \cdot c_5 \cdot r_k^\beta \cdot 2^{\frac{3}{3}k},
\]  

(6)

where \( c_6 = c_3 \cdot c_5 \). The leaf area density can now be found by dividing \( a_{k,\text{tot}} \) by the plot area, \( A_{\text{tot}} \). Next, we describe the overlapping contributions of different size groups at all heights in the profile.

By assuming that each crown was a Euclidean solid (cylinder) we also effectively assumed that the vertical overlap between crowns increases with increasing tree diameter and thus crown volume because the crown then expands in all directions with increasing size. To quantify the overlap we first asked the question: where is the top and bottom of the crown for each size group? (Note that we switch here to continuous notation for clarity.) The lower and upper bounds of these crowns are:

\[
H_{\text{low}} = \kappa \cdot r_\phi - c_4 \cdot r_k^\beta \quad \text{and} \quad H_{\text{high}} = \kappa \cdot r_\phi + c_4 \cdot r_k^\beta,
\]

respectively. Under ideal expectations \( \phi = 2/3 \) and \( \beta = 2 \) (Enquist et al., 1999); thus, we simplified the upper and lower height boundary equations by imputing these expectations to:

\[
H_{\text{low}} = (\kappa - c_4) \cdot r_2^{\frac{3}{2}} \quad \text{and} \quad H_{\text{high}} = (\kappa + c_4) \cdot r_2^{\frac{3}{2}}.
\]

We found trunk radius boundaries for the largest and smallest individuals with crowns overlapping at any height by setting \( H_{\text{high}} = H_{\text{low}} = H_x \) to get \( r_1 = \left(\frac{H_x}{\kappa + c_4}\right)^{\frac{3}{2}} \) and \( r_2 = \left(\frac{H_x}{\kappa - c_4}\right)^{\frac{3}{2}} \). Next, we defined leaf area density as a function of height by superimposing the contributions from all size groups with overlapping crowns at each height:

\[
\text{LAD}(H) = c_7 \int_{r_1(H)}^{r_2(H)} \hat{r}^{\frac{3}{2} + \theta} \, d\hat{r}
\]  

(7)

where \( c_7 = c_6 / A_{\text{tot}} \), and integrating

\[
\text{LAD}(H) = \frac{c_7}{\frac{3}{2} + \theta + 1} \left[ \hat{r}^{\frac{3}{2} + \theta + 1} \right]_{r_1(H)}^{r_2(H)}
\]  

(8)

and substituting the ideal expectations of tree radius boundaries from above,

\[
\text{LAD}(H) = \frac{c_7}{\frac{3}{2} + \theta + 1} \cdot \left( \left( \frac{H}{\kappa - c_4} \right)^{\frac{3}{2}} \right)^{\frac{3}{2} + \theta + 1} - \left( \left( \frac{H}{\kappa + c_4} \right)^{\frac{3}{2}} \right)^{\frac{3}{2} + \theta + 1}
\]  

(9)

and then collecting constants and simplifying we found

\[
\text{LAD}(H) = K \cdot H^{2 + \frac{3}{2}(\theta + 1)}
\]  

(10)
Finally, setting the Pareto diameter distribution exponent $\theta$ to the ideal expectation -2 generated the following prediction for the ideal leaf area density profile, an increasing function with height in the canopy:

$$LAD(H) = K \cdot H^{1/2}$$  \hspace{1cm} (11)

**Computational version of Model I.** The same scaling relationships—Equations 1 - 5—underlie a parallel computational approach to Model I. By simulating the contribution of individual trees based upon crown scaling relationships we were able to investigate the effect of a finite maximum tree size on the otherwise theoretically ideal expectation. We were also able to make explicit predictions for leaf area profiles that did not arise from ideal tree size distributions, but instead arose from plot observations of trunk diameter distributions. In this later case, we were able to optimize crown scaling parameters, using the observed size distributions of the two sites as inputs and the observed LiDAR-estimated leaf area density profiles as the training data for the model fit.

Evaluating the computational model against theoretical predictions, but including a finite maximum height corresponding to the field observation, we found that leaf area density indeed scales with height to the one-half power, at least initially moving up through the canopy (Fig. S2). However, the effect of the truncation of the size distribution at the upper size limit influences much of the height profile, leading the profile to decrease in the region spanning the lowest to the highest extent of the crowns of trees in the largest size group. Given the particular parameters detailed in Fig. S2, approximately half of the canopy profile was found to decline with height because of this upper size cut-off.

**Fitting Model I to Leaf Area Profiles.** We next adjusted scaling parameters to best predict LiDAR-estimated canopy profiles from observed stem size distributions data. In this supplement we present fit parameters while goodness of fit statistics are found in the main text ‘Results’ section. Fig. S3 presents the comparison of fit vs. LiDAR-estimated leaf area density profiles for Model I and Model II (next section). The model parameters of the best fit Model I were in the following ordered vector $(\phi, \kappa, c_1/c_2, c_1): (0.6297, 2.3335, 5.2362, 0.1178)$. Note that $\beta$ was set to the predicted value of 2 to increase the identifiability of other parameters. There was no model comparison employed to develop Model I, in contrast to Model II.

1.5 Forest Structure Model II

The structure of the second more detailed Model is specified both in the article main text and in this supplement. Main text Fig. 1 provides a comprehensive graphical overview and detailed caption summarizing Model II structure. Here, we define the analytical-computational rules for the inclusion of crown geometrical dependencies on light or secondary diameter relationships, which are also summarized in main text Table 1. (Note that the term ‘secondary diameter relationships’ indicates diameter relationships in addition to the primary allometries described above in Equations 1 - 5.) Detailed visualization of Model II output is found in Figs. 2 & 3 and Figs. S5 & S6.

Model II included a set of rules governing the responses of crown geometry to either light environments—light availability at the top of tree crowns or, in one case, light transmission and absorption profiles—or stem diameter. Model II ‘versions’ were different combinations of these rules and predictor variables. Model II allowed LiDAR-based estimates of light transmission or absorption, or stem diameter, to be associated with variation between plots and sites in the vertical position of the leaf area associated with particular size groups (Fig. 1). These rules were: *(Rule I)* that the maximum tree height was related to light, *(Rule II)* that the moments of the vertical leaf area distribution depended on light, *(Rule III)* that the position of leaf area within size groups directly responded to light profiles, and finally *(Rule IV)* that the size group allocation to leaf area was influenced by light environments. The mathematical-computational specifications of these rules are summarized in main text Table 1 and detailed below. In sum, model versions that included between
0 and 4 of these rules to introduce crown scaling dependency on one, the other, or both light metrics—or, alternatively, stem diameter—were fit to data with the maximum likelihood methods, 288 combinations were considered.

**Rule I. Maximum tree height related to light.** In this case, we adjusted maximum individual crown-top height, given a particular size group median diameter, according to a light response. If the height–diameter allometry is $H = \kappa' \cdot D^\phi$, we specified the light response in the parameter $\kappa'$, specifically $\kappa' = b' + aI + d' \Delta I$. Note that $\kappa'' = \kappa' \cdot 2$ from Equation 4 above. We assumed that values of light metrics associated with crown-top positions influenced height. Since maxim height determined crown-top positions, we estimated maximum tree height—and found corresponding light metric values—using a standard allometry, specifically the Feldpausch et al. (2010) relationship for this region. Subsequent rules relied on light estimates at the tops of crowns as defined by Rule I, or just the fit height-diameter allometry in the case that $\kappa'$ is a constant with no additional dependencies.

**Rule II. Parameters of vertical leaf area origin point distribution related to light.** Gamma distributions were used to model either size group leaf area profiles or the positions of leaf area origin points (i.e., crown or branch bases) if Rule III was active. These distributions were determined by two parameters, i.e., $\gamma(\kappa, \theta)$, where $\kappa$ and $\theta$ were shape and scale parameters respectively. We then determined shape and scale parameters for each size group from the following models incorporating light and (or) diameter dependence: $\kappa = c'_0 + c'_1 v'_1 + c'_2 v'_2$ and $\theta = d_0 + d_1 v_1 + d_2 v_2$, where $c'_0$ and $d_0$ were particular fit constants and $v_1$ and $v_2$ were light metrics and (or) size group diameter. Light metric values for each size group were taken from canopy strata that corresponded with expected maximum tree height (Rule I). The same two variables were simultaneously considered in the equations for the shape and scale parameters.

**Rule III. Leaf deployment directly related to light.** Light metrics over the vertical profile determined where leaf area was deployed directly within each size group sub-profile. In this case, height was interpreted not as the maximum individual height, but instead as the maximum height of the crown base, the lowest position with leaf area for an individual in a given size group. The gamma distribution was then the relative vertical leaf area profile in terms of the heights of the crown base positions comprising a size group. A rule to distribute leaf area vertically as a function of light metrics was applied to all crown base starting positions; the rule was defined as, $\text{LAD}_{z,i} = \mu_0 + \mu_1 I_z + \mu_2 \Delta I_z$, where $\mu_2$ were fit constants and $z$ indexed the vertical positions while $i$ indexed crown base starting points. This function was applied stepping upwards from the base of the crown. The size group vertical leaf area profile was then the sum over the crown-base starting positions, stratified by height.

**Rule IV. Leaf area vs. basal area relationship related to light.** The leaf area vs. basal area relationship was directly proportional within light environments, i.e., $\text{BA} = \eta \cdot \text{LAI}$, where $\eta$ was a proportionality constant and LAI and BA were the size group total leaf area and basal area respectively. Light metrics could influence the proportionality constant as $\eta = \eta' \cdot (1 + \rho V^\alpha)$ where $\alpha$ and $\rho$ were maximum likelihood fit constants while $V$ was one of the light metrics $I$ or $\Delta I$. The exponent $\alpha$ allowed light dependency to be nonlinear. The parameter $\eta'$ was not fit with maximum likelihood because as a normalization, it did not contribute to defining stem probabilities over diameter; this parameter was instead adjusted to minimize the least-squares residuals of observed vs. expected stem counts in size groups.

**Variable by Rule Combinations.** Model versions including one or more of these rules employed as light or size metrics the mean light transmission and absorption estimated from LiDAR (light variables), as well as in the case of Rule II the stem diameter of size groups. Under Rule I, one or both light variables influenced maximum size group height in addition to a stem diameter dependence. Rule II considered one or two of diameter and light variables in determining changes of gamma leaf area, or leaf area origin point, distribution shape and scale parameters. In this case, the variables considered for the scale parameter response were always the same as those considered for the shape parameter and vice versa. Rule III allocated leaf area in
response to one or both light variables. Finally, Rule IV only considered a single light variable—transmission or absorption.

**Model Fitting.** We first determined the relative vertical distribution of leaf area for each model and set of parameters. Next, total LAI values were estimated for each size group by creating a linear combination of size group profiles at each height and equating this combination to the observed LiDAR-estimated leaf area profile. We then solved the system of equations for size group weightings, i.e., size group LAI values. Models with between 6 and 15 parameters were considered; the 6 parameter model corresponded with the absence of light rules, while the 15 parameter models corresponded with the inclusion of Rules I through IV and the full inclusion of predictor variables (Table 1). We fit the model to a subset of plots from the Tapajós and Ducke sites. Eight plots were randomly selected from each site to be considered simultaneously in model fitting such that 16 of 38 total plots were employed.

We optimized parameters of all Forest Structure Model II versions—employing maximum likelihood—against both tree plot size distribution and LiDAR-based leaf area profile observations while roughly equivalently weighting likelihoods. Likelihood weighting allowed canopy leaf area profiles and diameter observations to have similar numerical contributions to the overall likelihood—initial testing found this approach superior in rapidly identifying biologically realistic MLE parameter optima. Furthermore, we expect that the most realistic model would find high likelihood predictions for size and canopy leaf area structure, which was also critical to ensure that the best models approximated the assumption that size group leaf area profiles were a linear combination of the total profile. Finally, roughly equivalently weighting the likelihoods of these data (given the model) was important because we observed a trade-off in how well models fit size structure vs. the canopy profile predictions and our objective was to generate a model that fit both canopy and size structure well. Model selection considered these likelihoods separately in distinct steps to allow comparison of model version rankings in terms of both predictions.

Maximum heights estimated with LiDAR served to facilitate the upper bound truncation of estimated size distributions, to prevent unrealistically large trees from being sampled from the expected distribution. To find the largest size group that could be considered in the model, we used the Feldpausch et al. (2010) height-diameter relationship to estimate the largest diameter tree corresponding to the tallest point in the plot, which we then increased by 20% to allow for height–diameter variability.

**Scaling Diameter Distributions to One Hectare Plot Tree Densities.** One parameter was not fit by maximum likelihood: the normalization of the size distribution, \( \eta' \), which set the numbers of individuals in size groups and hence tree density. This parameter was instead adjusted to create the maximum correspondence between the number of individuals observed and expected over the size range for the 16 model training plots (8 from each site)—i.e., least squares minimization was used. The sizes considered ranged from 10 to 82 cm, corresponding with the upper \( \approx 99^{th} \) percentile of the site combined size distribution. The full size range for this fitting step was, thus, truncated slightly because we chose to reduce the influence of size groups with expectations of less than one individual—computationally, we excluded the two adjacent groups falling immediately below the largest size group that empirically did not include a single individual. Because we adjusted the individual density normalization constant (\( \eta' \)) over both sites simultaneously, if there had been strong site differences in the parameter, they would manifest as visible offsets in site-level individual frequency predictions vs. plot observations of individual frequencies. We did not observe any such offsets (Fig. 3, second column of panels).

### 1.6 The best models & model structure

**Results: Model II, Forest Structure with Plasticity of Crown Architecture.** Using \( \Delta \text{AIC} \) analysis we identified the most parsimonious version of Model II predicting (1) size distributions alone and (2) size distributions and leaf area profiles together—the best 'size distribution model’ and the best ‘combined
model,' respectively. The best combined model was selected as the model with the lowest combined ∆AIC rank (Table S1). The best size distribution model was ranked with the worst for leaf area profile predictions (82nd, rankings normalized to 100)—failing completely to predict the peak in upper canopy leaf area at the Ducke site. We focus additional results and discussion on the best combined rank model and this is the model referred to as the best Model II in the main text.

The best size distribution model failed to predict the peak in leaf area observed in the upper canopy of the Ducke site, while combined model was able to predict this peak, though underestimating it while overestimating the leaf area density just below (Fig. 3). We found, in general, that there was a negative correlation between the ∆AIC ranks of the size distribution and the leaf area profile predictions. Given the advantages of the combined model—i.e., the successful prediction of conspicuous site scale variation in vertical canopy leaf area profiles and 3rd from the best size distribution prediction—we focus the presentation of results and the discussion on the best combined rank model. The model that included no rules based on light metrics or additional diameter dependencies was ranked 15th in the size distribution prediction but 81st in the profile prediction.

The best combined model included light Rules II - IV while the best size distribution model included only light Rule IV (parameters in Table S1). The combined model incorporated 11 maximum likelihood fit parameters: Gamma distribution shape and scale parameters depended on light transmission, decreasing with increasing light (Rule II). There was a direct influence of light metrics on size group profiles (Rule III): Absorption was strongly positively related to profile leaf area density; light transmission had a negative direct effect on leaf area density that was about two orders of magnitude weaker than the absorption effect. Leaf area increased relative to basal area in higher light environments (Rule IV). Averaging within size groups, we found that leaf area per basal area was up to ≈10 times higher in the largest size groups than the smallest (Fig. S7c). However, leaf area per basal area less than doubled on average over the size range spanning the lower 99% of the diameter distribution (ranges: Tapajós, 10 cm <= tree DBH < 94 cm; Ducke, 10 cm <= tree DBH < 65 cm), suggesting that allocation differences were not typically as large as 10 times higher in sunny vs. shady environments. Additional size dependency of canopy structure on tree diameter—i.e., dependency beyond basic underlaying scaling relationships—was not supported.

The best size distribution version of Model II included only light Rule IV and had 8 (instead of 11) fit parameters. In this case, parameters associated with the gamma distribution do not represent a second light rule because the predictor variable was diameter, instead of a light metric. While the gamma distribution in this case was influenced by diameter, instead of a light metric, the qualitative behavior of size group profiles over variation in light availability was similar. Specifically, profiles appeared more peaked in higher average light environments. However, this model provided a leaf area profile prediction of comparable quality to that of the best combined model only in the Tapajós site, while failing to predict the peak in upper canopy leaf area density associated with the developed canopy found in the Ducke site (Fig. S3).

The best size distribution and combined models did not include light as a factor influencing height–diameter relationships (Rule I). The parameters that governed the height–diameter relationships, emerging from model fitting, were very similar to those reported for the Eastern Amazon from the comprehensive Feldpausch et al. (2010) study (Normalization = 3.1789, Exponent = 0.5072 vs. this study, best size distribution model N = 3.4949, E = 0.5110 and best combined model N = 2.7992, E = 0.5526, where the normalization in this second case is lower presumably because the allometry corresponds with crown base not crown top height).

**Results: Predicting Site and Plot-scale Differences with the Best Model II.** The best combined model significantly predicted site and plot level differences in size distributions (see main text). Considering all tree data, the plot-level model did not have a lower AIC value than the site-mean model, which was surprising given the apparent correspondence between observed and predicted relationships within one-hectare plots revealed by data visualization (Figs. S5 & S6). Thus, we truncated size distributions at
upper size limits and recalculated AIC values, finding that the plot-level prediction was significant when we
considered just trees below below the upper 98.5th diameter quantiles at each site (diameter ranges below
86 and 59 cm DBH at the Tapajós and Ducke sites, respectively). Thus, the largest individuals—with
large effects on likelihoods—were poorly predicted within plots. A potential explanation is that the largest
individuals have highly variable geometries and fall in size classes with low expected numbers of individuals
(i.e., less than one), conditions where model error and poor fits in particular plots may have large effects on
overall likelihoods. The best combined model was not a better predictor of size distributions within sites
than fit parametric models (Weibull distributions; see Fig. S1; note that this is not an equivalent comparison
since parametric distribution models do not predict the structure of leaf area in the canopy).

1.7 Size group leaf area profiles in relation to light environments

We analyzed model output to understand the combined effect of parameters that described relationships
between light at the tops of tree canopies and the model-predicted leaf area profiles of size groups. First, we
calculated the heights associated with particular quantiles of size group LAD profiles—after inspection we
chose the upper 75th quantile of profiles, as this corresponded approximately with the region of highest leaf
area. Next, we related height of the 75th upper profile leaf area quantile with diameter and with canopy top
light transmission estimates (Fig. S4). We found high heteroscedasticity in the relationship between 75th
quantile height and diameter; there was greater variance in the upper, higher light, portions of the canopy.
We fit 75th quantile height vs. diameter allometries to the lower 99% quantiles of the size range in each
site—and extended the model over the whole size ranges—using a Weibull height diameter relationship to
capture apparent log-log scale curvilinearity as proposed in Feldpausch et al. (2012) (Fig. S4; model was
\[ H_{75\text{th Quant.}} = a \cdot (1 - e^{-b \cdot D^c}) \]
with Tapajós parameters \(a=159.6902, b=0.007788\) and \(c=0.6605\), and Ducke
parameters \(a=101.304, b=0.01810\) and \(c=0.5431\)).

We investigated the relationship between light variation and leaf area profile height by taking the residuals
from the fit 75th quantile height vs. diameter relationships and the light transmission vs. diameter relation-
ships (in this case, residuals from size class means). As shown in Fig. S4c, the residuals were significantly
correlated (\(P < 0.0001, R^2=0.095\) pooled over sites), suggesting that higher than average crown-top light
transmission was associated with a greater vertical extent of leaf area profiles.

We also considered the relationships between leaf area profile peakedness and diameter and crown-top light
transmission. We standardized the range of size group leaf area frequency profiles to avoid artifacts due
to mean-variance correlation and then calculated the kurtosis for each standardized size group leaf area
profile as \(E[(X - \mu)^4]/(E[(X - \mu)^2])^2 - 3\). We found that peakedness—as reflected by this kurtosis metric—
increased drastically in the upper canopies of both sites as suggested by the relationships between kurtosis
and diameter (Fig. S4d). To further investigate the role of light in leaf area profile peakedness, we also looked
at the relationships between light and kurtosis within each size class within each site. Of 76 possible size
class correlations, 26 were significant at the \(P < 0.05\) level, and of these 22 were positive relationships,
which is significantly different from the null model of a even probability of positive or negative relationships (sign
test, \(P < 0.001\)). This suggested strongly, that even within size classes, increasing crown-top light created
leaf area profiles that were relatively more peaked. Again, we note that the results of this section are a
reanalysis of the output of Model II applied to LiDAR canopy observations.

1.8 Estimating size group absorption, & other size-group properties

We estimated size group absorption from LiDAR vertically incident light transmission—and absorption—
estimates and the best combined Forest Structure Model II. (For additional detail on LiDAR light estimation
see supplement of Stark et al. 2012.) We began by discounting leaf area density values associated with
particular size groups that fell below a particular value (\(LAD_{\text{critical}} = 0.0025\) m²/m³; e.g., one 5X5 cm leaf
in a meter-cubed of canopy space). We took this step because initial inspection showed that many size
group leaf area profiles displayed a long tail of very low leaf areas that trailed upwards in the canopy, a likely byproduct of minor mismatch between the structure of our process model and the actual biological allometries and canopy plasticity underlying the model (i.e., the true process). These unrealistic long tails were found mostly in larger size groups and contributed to a small but consistent overestimation of leaf area density profiles in the extreme upper canopy. This minimum leaf area density cut-off also favored the exclusion of large size groups where we expect to find less than one individual tree on average at the one-hectare plot scale. In these size classes, the total leaf area estimate would be less than that associated with a single tree. This would effectively spread a total leaf area expectation for large trees, that in reality would belong to one or a few individuals, over too many size classes. Discounting these size groups from analysis increased absorption estimates in the remaining size groups, suggesting that a method to include estimates for low probability size groups should be found to improve future work. We note that the relative relationships between site absorption patterns—critical for demographic analysis—was not sensitive to changing this cut-off parameter. To estimate light absorption, we next assumed that size group associated leaf area was randomly distributed over horizontal variation in light availability at each vertical position in the canopy. This assumption then allowed the partitioning of total light absorption estimates at each vertical position into constituent values associated with each size group. Summing light absorption over each size group profile and then dividing by the total leaf area yielded estimates of light absorption per unit leaf area of each size group. Because total leaf area varied by size group and varied vertically within size groups, we chose to investigate the role of light in size group demographic dynamics using light absorption per unit leaf area—we assumed that this served as a unified metric for the effective light environment experienced by each size group over relevant variation.

Fig. S7 reports additional size group—and mean size group, i.e., size class—expectations for total leaf area (LAI), basal area, basal area specific LAI, total size group light absorption, leaf area specific size group absorption, and basal area specific absorption. We note that the minimum leaf area density cut-off approach for absorption estimation discussed in the paragraph above influenced only the relationships involving absorption (e.g., size group leaf area estimates were the raw total values).

1.9 Demography and Canopy Light Environments (investigation ‘Step B’)

Our objective in this section was to first derive predictions for the influence of canopy status (light environments) on size distributions by elaborating on forest demographic theory (Kohyama, 1993; Muller-Landau et al., 2006). We then present an analysis showing that the model we derived is consistent with observed differences between between sites in light absorption patterns, the ratio of mortality to relative growth rates, and the shape of the size distributions. This analysis (1) assumed based on preliminary analysis that the ratio of tree mortality to relative growth rate—the demographic ratio—was directly related to absorption, (2) predicted parameters governing light absorption over tree size relationships from observed size distributions at each site, (3) fit unconstrained parameters from the relationships of estimated light absorption and tree size and (4) compared observed and predicted differences in light absorption between sites graphically based on steps 1 through 3. If we were able to predict site differences in absorption from size distributions we concluded that our simple model relating demographic processes to light environments was consistent with the data. We anticipate future work that can provide more rigorous and detailed tests of this hypothesis by elaborating and extending the empirical approach that we have developed.

Muller-Landau et al. (2006) presented a solution to the demographic flux equation that relates growth and mortality—under the assumption of stable demographic structure—to the stem diameter probability density distribution, \( p(D) \):

\[
p(D) = \frac{1}{K \cdot g(D)} \cdot e^{-\int_{D_{\text{min}}}^{D_{\text{max}}} \frac{m(D)}{g(D)} dD}
\]  

(12)
where \( g(D) \) and \( m(D) \) are growth and mortality as functions of stem diameter, \( D \), and \( K \) is a constant that normalizes the function to a total probability of 1 in the diameter range of \( D_{\text{min}} \) to \( D_{\text{max}} \). Growth and mortality functions may both be influenced by—or associated with—the availability of light for photosynthetic production (Hubbell, 2001; Metcalf et al., 2009; Kobe, 1999). Fig. S8a—and also main text Fig. 5a—present site patterns of estimated leaf area specific absorption over tree size. Before our next step—incorporating specific assumptions about the role of light absorption environments on demography—we consider how leaf area specific light absorption may be related to diameter. We chose the following equation to represent this relationship:

\[
A(D) = \psi + \zeta \cdot D \cdot (1 + \ln(D))
\]  

(13)

where \( \psi \) and \( \zeta \) were fit constants. This equation captured general differences in the light absorption relationships and allowed for analytical model solutions in the following steps.

After preliminary analysis (Figs. 4 & 5) we related the ratio of mortality to relative growth (e.g., \( (m(D) \cdot D)/g(D) \)) to light absorption. This assumption corresponds with growth and mortality being coordinated over light in such a way that the observed concave-down log-log curvilinearity would correspond with an increasing relative importance of mortality over increasing light (consistent with observation, Fig. 5a). Under this assumption and the additional assumptions—corresponding with those of metabolic scaling theory—that growth and mortality are \( g(D) = \gamma \cdot D^\lambda \) and \( m(D) = \delta \cdot D^\nu \) we have:

\[
p(D) = \frac{1}{K \cdot \gamma \cdot D^\lambda} \cdot e^{-f_{D_{\text{min}}}^D \xi \cdot A(D) \cdot D^{\nu - \lambda} dD}
\]  

(14)

Next we replace the ratio of the mortality to growth normalization constants, \( \delta/\gamma \), with the equation for absorption, with an additional scaling constant that adjusts for components of growth and mortality that are not influenced by leaf level absorption, \( \xi \cdot A(D) \)

\[
p(D) = \frac{1}{K \cdot \gamma \cdot D^\lambda} \cdot e^{-f_{D_{\text{min}}}^D \xi \cdot A(D) \cdot D^{\nu - \lambda} dD}
\]  

(15)

If we assume that \( \nu - \lambda = -1 \) so that in the absence of light limitation growth and mortality may balance to produce a -2 ‘space filling’ power-law size distribution (\( \delta \) must also be 5/3 of \( \gamma \) for the ‘-2’ prediction; Muller-Landau et al. 2006) we get

\[
p(D) = \frac{1}{K \cdot \gamma \cdot D^\lambda} \cdot e^{-f_{D_{\text{min}}}^D \xi \cdot A(D) \cdot D^{-1} dD}
\]  

(16)

such that \( A(D) \propto m(\hat{D}) \cdot \hat{D}/g(\hat{D}) \), i.e., the demographic ratio—see ‘Methods’ in the main text. Substituting and simplifying, we get:

\[
p(D) = \frac{1}{K' \cdot D^\lambda} \cdot e^{-\xi (\psi \cdot \ln(D) + \zeta \cdot D \cdot \ln(D))}
\]  

(17)

where \( K' \) groups all constants (including those resulting from integration in the exponential term), and finally:

\[
p(D) = \frac{1}{K' \cdot D^{-\xi (\psi + \zeta \cdot D) - \lambda}}
\]  

(18)
Thus, the final simplified relationship includes the expectation of linear dependence of the scaling exponent on diameter. While this relationship may represent a simplified version of reality, it fits size distributions well and predicts qualitative differences between sites in absorption estimates over tree size groups (Fig. S1; next section).

**Fitting demographic theory to data.** The parameters of Equation 20 are not fully identifiable by fitting the equation to observed size distributions. Instead, we fit the following simplified equation to size distributions:

\[ p(D) = \frac{1}{K'} D^{-(A+B \cdot D)} \]  

(19)

where \( A = \xi \cdot \psi + \lambda \) and \( B = \xi \cdot \zeta \). Furthermore, the parameters of the absorption function (Equation 13) are then given as \( \psi = (A - \lambda) / \xi \) and \( \zeta = B / \xi \). Thus, we find all parameters in a two step approach. First, we find \( A \) and \( B \) by fitting Equation 19 to size distributions in each site. Second, we fit \( \lambda \) and \( \xi \) as parameters with one value for both sites using these substitutions for \( \psi \) and \( \zeta \), while inputing values of \( A \) and \( B \) from the first step. We predicted that this forest demographic theory approach will predict site differences in leaf area specific absorption patterns—in effect from the shape of site size distributions—under the assumptions that light environments (level-level absorption estimates) are related to the demographic ratio, and that the model is a sufficiently good representation of size structured dynamics.

**Results: The Link Between Canopy Light Environments, Demography and Size Distributions.** Figs. 4 & 5 in the main text present results of the analysis of demographic rates over canopy light environments, where light environments were estimated as leaf area specific absorption derived from the best forest structure model (‘best combined’ Model II). We evaluated the hypothesis of light environment feedbacks to size distributions by fitting demographic theory to size distributions and then predicting relative site differences in light absorption. We found general agreement between predicted and estimated size group absorption (Fig. S8). Here, we expand on results of fitting demographic theory to the data. In summary, demographic ratios and size distributions appeared to be related to light absorption.

An assumption of our approach was that the (leaf area specific) light absorption was linearly related to the demographic ratio. The demographic metric was not directly proportional to the absorption estimates over the full range of trunk diameter but was approximately so between 10 and 70 cm DBH (evidenced by parallel relationships on the log-log plot of Fig. 5a). Furthermore, we found that Ducke had a greater mortality per relative growth at the same absorption level above 20cm DBH than the Tapajós—on average 2 times more mortality per growth—likely the result of dramatically higher growth rates evidenced in the Tapajós (see Fig. 4).

**Additional parameter fitting results.** Fig. S1 shows the fit of the size distribution Equation 19 to Tapajós and Ducke size distributions (second column of panels) based on non-linear least squares minimization. The parameters fit with common values in both sites were: \( \xi = 22.494 \) and \( \lambda = -0.326 \). In the Tapajós \( A = 1.8661 \) and \( B = 0.003940 \), while in Ducke \( A = 1.7277 \) and \( B = 0.008887 \). Main text Fig. 4 shows observed demographic patterns over tree size in sites. Here, we report the maximum likelihood fit mortality functions: The function was \( P_{\text{mortality}} = c_{\text{on}1} \cdot D^{c_{\text{on}2}} + c_{\text{on}3} \cdot D^2 \). Tapajós and Ducke constant vectors \( (c_{\text{on}1}, \ c_{\text{on}2}, \ c_{\text{on}3}) \) were then, respectively, \( (5.198e-02, \ -2.981e-01, \ 2.557e-07) \) and \( (1.764e-02, \ -1.301e-01, \ 1.616e-06) \).

2 Supplemental Discussion and Conclusions

**On light rules & crown plasticity & architectural variation.** Rules to incorporate light into the model were consistent with the plasticity hypothesis. First, light influenced size group vertical leaf area origin point
distributions and, directly, vertical positions of leaf area within crowns (Rules II & III, respectively). We hypothesized that both light transmission and the rate of change in light transmission could influence leaf deployment—leaves may be expected to preferentially deploy in higher light, but may avoid areas of rapidly declining light in favor of growing upwards (Rule III). Thus, the size group vertical leaf area profiles that emerged from these rules appeared to respond to canopy light environments. In both Ducke and the Tapajós, size group profiles became increasingly peaked in higher light environments, consistent with optimal leaf allocation to minimize shading (and self-shading) in the upper canopy (Coomes et al., 2012). The broader vertical distribution of leaf area in lower, more shaded, size groups may be consistent with leaf arrangement exploring more space to capture light in distributed favorable micro-sites in the understory (Sterck & Bongers, 2001). Furthermore, some individuals in smaller size groups may be allocating preferentially to vertical growth to escape light limitation, creating greater vertical heterogeneity (see Poorter et al., 2003).

Mean light transmission and light absorption estimates were both retained in the best combined model, supporting the hypothesis that these aspects of light environment directly influence vertical leaf area profiles. Absorption had the strongest influence—increasing absorption increased leaf area estimates. Absorption is the light variable most closely related to leaf area density, though with significant unexplained variation (Stark et al., 2012). This light rule led to size group profiles—and plot mean leaf area profile predictions—that matched the leaf area profiles estimated with LiDAR much more closely, including fine scale vertical variation and thus likely enhancing overall model accuracy.

On the finding that total leaf area vs. basal area may be influenced by light. Chambers et al. (2001) find that damage to the crowns of larger individuals may significantly reduce the biomass (and likely leaf area) relative to the diameter-based expectation. In contrast to this finding, our model predicted a modest increase in leaf area per basal area—less than doubling on average over the lower 99th quantile of the diameter distribution—over most of the range of tree size variation. This increase in leaf area allocation with tree size was the result the retention of Rule IV in the best forest structure model, with leaf area allocation increasing with crown top light transmittance estimates. More work is needed to test whether this model finding corresponds with real patterns of leaf allocation, however, this may be expected if trees allocate preferentially to leaf area in higher light environments. Specifically, this is consistent with an economic model that predicts greater leaf growth into high light environments and with preferential allocation towards growth (leaf area) relative to survival (stem support, leaf longevity) in higher light environments (Coomes et al., 2012; Wright et al., 2010). Wright et al. (2010) similarly found preferential allocation towards growth associated leaf traits in high light environments. While some empirical evidence from harvested trees, and the expectation of metabolic scaling theory, suggest consistency of leaf area relative to basal area over tree size and perhaps light environments (Shinozaki et al., 1964; Fownes & Harrington, 1992; Enquist & Niklas, 2002), there is very little information on whole tree allocation over light environments available to evaluate our finding, particularly among larger individuals (reviewed in Valladares & Niinemets 2008). Given the expectation of branch loss (Chambers et al., 2001) in the largest individuals, future work should consider relationships between basal area and leaf area that may have an internal mode over light availability.

Stark et al. (2012) showed that size group basal area specific biomass growth rates were consistent over light environments. In this study site patterns of basal area specific absorption were not clearly consistent with this previously reported finding, with the Ducke particularly showing a strong interior mode in contrast to the prediction of consistency (Fig. S7). However, we note that absorption is not necessarily directly related to biomass production and can be influenced by processes such as allocation that may vary over the tree size-range or light environments. Future improvements will shed additional light on size group patterns of light absorption and production, important for testing metabolic scaling theory, which posits energetic equivalence between size classes (West et al., 2009; Enquist et al., 2009).
References


**Table S1:** Best Fit Models Connecting Canopy Structure with Size Distributions

<table>
<thead>
<tr>
<th>Model</th>
<th>Height–Diameter</th>
<th>Rule II</th>
<th>Rule III</th>
<th>Rule IV</th>
<th>Size Dist.</th>
<th>Leaf Area</th>
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<tr>
<td></td>
<td></td>
<td>Gamma Dist.</td>
<td>Direct Effect</td>
<td>LAI vs. BA Dist. Profile</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>shape=$c_0 + c_1 v_1$</td>
<td>$\mu_0 + \mu_1 I_z$</td>
<td>$\eta' (1 + \rho I_0)$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>scale=$d_0 + d_1 v_1$</td>
<td>$+\mu_2 \Delta I_z$</td>
<td>$(\eta', \rho, \alpha) \dagger$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Best</td>
<td>(0.5526, 2.7992)</td>
<td>2.5664, -1.0643</td>
<td>2.6841e-2, -5.894e-3, 5.6083</td>
<td>1.4686</td>
<td>3/100</td>
<td>32/100</td>
</tr>
<tr>
<td>Comb.</td>
<td>(0.5110, 3.4949)</td>
<td>1.3471, -6.991e-3</td>
<td>(D)</td>
<td>-</td>
<td>6/100</td>
<td>82/100</td>
</tr>
</tbody>
</table>

* In this case, the ‘best combined’ and the ‘best size distribution’ models included different variables $v_1$—light transmittance ($I$) in the case of the combined model and trunk diameter ($D$) in the case of the size distribution model.

† All parameters here were maximum likelihood estimates except $\eta'$, which influenced individual density but not frequency estimates, and thus not likelihood calculations. See Supplementary Information 1.5 for $\eta'$ estimation.

‡ While 288 model combinations were considered, ranks presented here were normalized to 100—i.e., x/100—for ease of comparison.
Fig. S1. Parametric descriptive and mechanistic model fits to size distributions. Rows of panels correspond with the Tapajós and Ducke sites (labeled at left). The left column of panels shows descriptive model maximum likelihood fits of Pareto and Weibull distributions (straight and curved solid lines respectively) to site-scale tree plot observations. The expectation for -2 power function scaling for the size distribution is also shown as the light dashed line (not fit). Parametric distribution models were scaled to exactly predict the number of individuals in the first size group used in model fitting (10–13 1/3 cm). Truncated Pareto distributions—darkest lines—were fit to the lower 99th quantile for each site (10–94 cm Tapajós; 10–65 cm Ducke). Red circles are mean one-hectare tree counts in size classes. The right hand column of panels shows our extended demographic model (lines) fit by minimizing least-squares to probability density estimates in size groups (red circles). These best-fit models were used to predict differences between sites in patterns of leaf area specific absorption (Fig. S8; SI 1.8).
Fig. S2. Forest Structure Model I. Theoretical and analytical simulation of vertical vegetation profiles under ideal individual crown scaling and size distributions predicted by metabolic scaling theory. The solid line is the computational model, showing the effects of upper and lower tree size truncation (trees 5-200cm) as deviation from the purple expected relationship. The parameters selected for this plot were $\phi = 2/3$, $\kappa = 1.6$, $c_1/c_2 = 0.15$, $c_1 = 2$ $\beta = 0.1$ (see Equations 1-4 in SI 1.4), corresponding with ideal metabolic theory expectations for the scaling exponents.
Fig. S3. Leaf area profiles estimated with LiDAR compared with profiles predicted from forest structure models. Plot panels correspond to study sites such that profiles are site means of one-hectare plot profiles (see Figs. 2 & 3). LiDAR-estimated leaf area profiles are thick red lines while dashed blue lines are the predictions of Model I optimized to site-scale observations above 12m. Thin black lines are Model II predictions (best combined model) after optimizing to predict size distributions and leaf area profiles ($R^2=0.95$, p-value <0.0001 for both sites). Model II was a significantly better predictor of LiDAR-estimated canopy structure than Model I (comparing predictions between 12 and 55m height; Model II was favored by $\Delta AIC = 51.40$, taking parameter number differences into account; SI 1.6).
**Fig. S4.** How the vertical extent and peakedness of size group leaf area profiles from the best Forest Structure Model II are related to light environment estimates. Size groups from the Tapajós are **green** while those from Ducke are **blue**. Panel ‘a’ shows 75th quantile height vs. size class diameter relationships. Curves are Weibull type height diameter allometries (SI 1.7). Panel ‘b’ shows crown top light transmission vs. size class diameter relationships. In this case, curves are effectively size class mean values fit with a loess function in R with a span value of 0.1. Panel ‘c’ shows the significant regression of residuals from the relationships in panels ‘a’ & ‘b’ (P < 0.0001, R²=0.095 pooled over sites), which suggests that higher crown top light is related to taller leaf area profiles. Finally, panel ‘d’ shows a metric of peakedness of leaf area profiles (kurtosis) plotted against diameter; the apparent pattern is of drastic increases in profile peakedness in the upper canopies of both sites.
Fig. S5. Tapajós site plot-level size distributions. Heavy black lines are LiDAR-based model predictions from the best Forest Structure Model II, while red circles show empirical data plotted as counts in size bins. Thin grey lines represent a decomposition of the size distribution estimate; each line corresponds with a different canopy height and shows the distribution of individuals of different sizes contributing to leaf area at that position in the canopy. Four of these lines have been color coded with respect to the heights that they represent: 12m = dark blue, 21m = light blue, 31m = yellow, 40m = red. The eight plots employed in model fitting are shown with a light grey background.
Fig. S6. As in Fig. S5 but showing the Ducke site ∼600km West near Manaus.
Fig. S7. Size group level properties predicted by the best Forest Structure Model II, driven with LiDAR data. Small symbols are predictions for size groups at each site, while solid lines are size group means—i.e., size class predictions (Green is the Tapajós, blue is the Ducke site). The bottom row of figures are derived from a reanalysis of model output that combined size group leaf area profile estimates with LiDAR derived estimates of vertical light penetration (SI 1.8). Here large size classes are discounted from the absorption analysis. Leaf area specific absorption—panel e—is essential for comparison with the extended demographic theory developed in this study (see Fig. 4). Finally, note that optimal metabolic scaling theory arguments predict that basal area ∝ total leaf area ∝ total absorption (and production) and that total leaf area, and these other quantities, are expected to be constant over size groups. Thus, MST predicts constant relationships in all panels of this figure, generally in disagreement with Model II output.
Fig. S8. Results of analysis suggesting a link between light absorption over tree size with demographic rates and the size distribution (Green is the Tapajós, blue is the Ducke site). The small points in the left panel are light absorption estimates of size groups in all plots from the best Forest Structure Model II (see Fig. 4). Solid lines are fit functions (SI 1.9; Equation 13), while dashed lines show predicted relative differences in absorption that have been generated by fitting the demographic theory to observed size distributions (see Fig. S1; site-independent parameters were also fit to scale the relationship for visualization, see SI 1.9). The right panel shows the demographic ratio vs. size class diameter in both sites; we have hypothesized that the demographic ratio is directly proportional to light absorption over size classes. The demographic ratio (lines) is calculated from fit growth and mortality curves (Fig. 4). The general agreement of slope and rank between predicted and observed absorption relationships, and the demographic ratio relationships, supported the hypothesis that light absorption may influence demographic processes and thus the shape of size distributions. In this case, the greater log-log curvilinearity of the Ducke size distribution (Fig. S1) may be attributed to a more rapid reduction in light with depth in the canopy.