



Capturing diversity and interspecific variability in allometries: A hierarchical approach

Michael C. Dietze^{1,*}, Michael S. Wolosin, James S. Clark

Nicholas School of the Environment and Department of Biology, Duke University, Durham, NC 27708, USA

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ABSTRACT

There is growing recognition of the role of mechanistic scaling laws in shaping ecological pattern and process. While such theoretical relationships explain much of the variation across large scales, at any particular scale there is important residual variation that is left unexplained among species, among individuals within a species, and within individuals themselves. Key questions remain on what explains this variability and how we can apply this information in practice, in particular to produce estimates in high-diversity systems with many rare and under-sampled species. We apply hierarchical Bayes statistical techniques to data on crown geometry from diverse temperate forests in order to simultaneously model the differences within and among species. We find that tree height, canopy depth, and canopy radius are affected by both successional stage and wood mechanical strength, while tree height conforms to the predicted 2/3 power relationship. Furthermore, we show that hierarchical modeling allows us to constrain the allometries of rare species much more than traditional methods. Finally, crown radius was shown to vary substantially more within individuals than among individuals or species, suggesting that the capacity for local light foraging and crown plasticity exerts the dominant control on tree crowns.

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1. Introduction

The need to produce forecasts of ecosystem services is a growing imperative for ecologists (J.S. Clark et al., 2001a). Toward this end allometric scaling relationships are used frequently in ecology. Ecosystem ecologists use biomass allometries to estimate forest carbon storage and net primary productivity (NPP) from measurements of stem diameter and diameter increment (e.g. D.A. Clark et al., 2001b,c; Martin et al., 1998). More recently the remote sensing community has used estimates of canopy height derived from lidar or radar to calculate forest stand biomass from allometric relations (Hurtt et al., 2004; Drake et al., 2003, 2002; Lefsky et al., 2001, 1999; Kasischke et al., 1994). Allometric models of canopy geometry are used to estimate the light exposure of trees as well as understory light conditions, which are used to drive models of forest community dynamics (Dietze, 2006; Courbaud et al., 2003; Cescatti, 1997a,b; Pacala et al., 1996; Canham et al., 1994).

What lies beneath allometries are labor intensive measurements and simple statistical models that are *species and site specific*. Going to a new site or encountering a new species necessitates the construction of new allometric models. This can be particularly problematic in areas of high-diversity, such as tropical forests, where collecting sufficient data on rare species can be prohibitively difficult and the odds of encountering new species are always high.

One potential way around this challenge of diversity, and its need to continually construct new allometries, is to develop “universal” allometries, either based on phenomenological relationships (e.g. Chave et al., 2005; Lefsky et al., 2002) or through mechanistic theory (e.g. Enquist et al., 1999; West et al., 1999). However, simply fitting one phenomenological relationship across all the data available requires the assumption that there are no differences among species or sites. If this is not true, which is likely for most systems, we end up misinterpreting interspecific differences as random variability. This is not merely a difference in interpretation, but one of practical importance: while measurement error and random individual variability average out in large samples, species differences are not independently distributed and can produce systematic biases (Clark, 2005).

Mechanistic scaling laws, on the other hand, are appealing because they appear to provide a theoretical basis for universal allometries. However, it is often unclear how to employ these theories in empirical studies. Unless one makes the assumption

* Corresponding author at: 265 Morrill Hall, 505 S. Goodwin Avenue, Champaign, IL, 61801. Tel.: +1 217 333 9396; fax: +1 617 244 1224.

E-mail addresses: mdietze@life.uiuc.edu (M.C. Dietze), mw10@duke.edu (M.S. Wolosin), jimclark@duke.edu (J.S. Clark).

¹ Present address: Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA.

that the slope and intercept predicted by a theoretical model are exactly correct, there is no clear way in classical statistics to combine this information with empirical data. Mechanistic relationships are also usually verified with data sets that span many orders of magnitude; while on a large scale species are more alike than different, at any particular scale there may be a large amount of unexplained variation. Indeed, one of the short comings of the search for universal allometries is that most research has given less attention to explaining why species are different and what factors, whether they be driven by life-history, mechanical limits, or phylogenetic constraint, predict the variation among species; research that accounts for the variability among species and sites in scaling is still in early development (e.g. [Enquist et al., 2007](#); [Price et al., 2007](#)). While not directly applicable to empirical studies themselves, these theories do have the potential to increase the efficiency of developing relationships for new species and sites if they can be combined effectively with data.

Fortunately, modern statistical methods provide an alternative, Bayesian hierarchical models, that can accommodate the challenges of diversity—the theoretical need to account for inter- and intraspecific variation and the empirical need to make predictions for rare species. Essentially, hierarchical models enable us to fit one relationship for each species, just as the species-specific approach would, while simultaneously fitting a “universal” relationship across species that constrains the species-specific relationships. How much constraint to provide is determined automatically by the data. If species are similar, the across-species relationship provides stronger constraint, which then strengthens the fit of rare species where data are limited. The hierarchical model can even be used to predict the sampling distribution of allometric relationships for unobserved species. While measuring new species directly is always preferable, extrapolation across species is often necessary, especially in hyperdiverse regions, and the hierarchical modeling framework provides both constraints on this extrapolation and an estimate of the uncertainty this introduces, rather than simply applying equations developed for other species as if this introduced no additional error. Essentially, Bayesian hierarchical models provide an intermediate between the two extremes (species-specific vs. universal allometries) that preserves the strengths of both approaches while reducing both their limitations. The hierarchical approach achieves this because it acknowledges that the growth forms of trees are generally similar across species, but that they are not the same.

In addition to handling rare and novel species, there are a number of aspects of the Bayesian hierarchical framework that allow us to make greater use of the data and improve our ecological understanding: the incorporation of information from mechanistic scaling laws, the dependence of interspecific variability on life-history, biomechanics, and phylogenetic constraint, and the ability to model missing or indirectly observed data. In Bayesian hierarchical models the constraints provided by mechanistic scaling theory enter seamlessly as a prior on the across-species allometry. Similarly, we can explore the effects of species-level differences, such as differences in life-history, mechanics, or phylogeny, by including these as covariates in the across-species model. This is the same idea that underlies the current interest in tying biomass allometries to wood density (e.g. [Chave et al., 2005](#)), but in a more rigorous framework. Finally, the quantities of interest are not always directly observed or observable. For example, we infer the shape and structure of tree canopies based on proxies such as ground measurements of crown extent or LIDAR profiles. Hierarchical Bayesian methods provide a straightforward means of estimating such “latent” variables by decomposing a complex problem into simple conditional probabilities that can be sampled over, defining the

statistical relationship between the observed and unobserved quantities. In a similar way Bayesian methods can sample over the distributions of missing data, reducing the necessity of throwing out useful information because of the occasional missing measurement or covariate. Most importantly, these approaches can lead to a greater ecological understanding of the underlying processes. For example, below we model canopy radius as a latent variable and are thus able to partition residual variability to within-crown and between-crown components. This analysis points to the dominant role of individual-level dynamics, such as crown light foraging, rather than size-dependant scaling, in controlling crown shape and size, but would have been impossible if we had simply worked with sample-mean canopy radius.

For the goal of ecological forecasting, perhaps the greatest strength of the hierarchical Bayes framework is that it provides a unified rigorous framework for inference and prediction. Current allometric models are often applied assuming the parameters with the highest likelihood are “true” and ignoring uncertainty. However, the propagation of uncertainty through forecasts is critical to assessing their accuracy and their usefulness to managers and policy makers; ignoring uncertainty leads to overconfident prediction. Forecasting in a Bayesian framework is no more complicated than sampling over the posterior parameter and error distributions to generate predictive distributions. Propagating this error through further analyses is as simple as sampling from the predictive distributions and performing whatever calculations are needed, whether it be a simple summation of stand biomass or a complex nonlinear simulation model.

In this paper we present an analysis of an allometric model of tree height and crown geometry using a hierarchical Bayes approach. This model is a complex multivariate analysis with species-level covariates that estimates allometric relationships while addressing a wide range of issues encountered with real data. The model is fit to field measurements made in the Carolina Piedmont and the Southern Appalachians. Below we outline the field methods used and derive our statistical models step by step, addressing specific issues and explaining how we improve upon previous approaches. The West, Brown, and Enquist (WBE) metabolic scaling theory is incorporated as a moderately informative prior to constrain the across-species scaling of tree height ([West et al., 1999](#); [Enquist et al., 1999](#)). This analysis shows that hierarchical Bayes methods can provide biologically more reasonable estimates for rare species or species with a narrow observed size range. Furthermore, we find that shade tolerance and wood mechanical strength affect canopy geometry, with shade-tolerant species producing thick trunks with wide and deep canopies. Canopy depth also increases with wood strength. Overall, we find that the tree height allometry is consistent with the predicted $2/3$ scaling law across a wide range of priors, but that canopy radius departs considerably from the predicted $2/3$ scaling ([West et al., 1999](#); [Enquist et al., 1999](#)). Canopy radius is shown to have greater variability within individuals than among, highlighting the importance of individual-level dynamics such as light foraging by tree crowns.

2. Methods

2.1. Field methods

Total tree height, height to base of crown, and crown radius were measured with a laser range finder (Impulse 2000, Lasers Technology Inc., Englewood, Colorado) for a subset of trees from two mapped stands in the southeastern US. The first stand (~4.3 ha) is located in the Blackwood Division of Duke Forest, in

Chapel Hill, NC (35°59'N latitude, 79°06'W longitude) in the Carolina Piedmont. Half of the stand is oak-hickory forest, while the other half is ~80-year-old loblolly pine (*Pinus taeda*) with significant hardwood ingrowth. The second stand (~4.8 ha) is located at the Coweeta LTER site in Otto, NC (35°03'N latitude, 83°27'W longitude) in mixed hardwood forest. Detailed site descriptions can be found at <http://www.env.duke.edu/forest> and <http://coweeta.ecology.uga.edu> for Duke Forest and Coweeta respectively while detailed stand information is in Dietze (2006). In 2000 all trees over 2 m tall were identified, mapped, and measured for diameter at breast height (DBH). For some taxa proper identification to species was difficult and individuals were recorded at the genus level. All unidentified *Quercus* were among the red oaks (*Quercus* section *Lobatae*), which are particularly prone to hybridization making species-level identification occasionally difficult. Taxonomy follows Radford et al. (1968) with the exceptions of *Quercus montana* (chestnut oak, was *Quercus prinus*) and *Frangula caroliniana* (Carolina buckthorn, was *Rhamnus caroliniana*).

Crown geometry data are drawn from two sampling efforts for a combined sample size of 1691 trees measured for 53 species. In the first sample (2001 data), designed specifically to estimate allometries, trees were selected from the stand database in a stratified random manner to insure maximal coverage of all species and sizes. For each tree we measured DBH, height, height to base of crown, and maximum and minimum crown radius. The base of the crown was taken to be the lowest foliage on the lowest major branch and thus excluded young epicormic branches. The second sampling effort (2003 and 2004) was collected to compare canopy measurements made on the ground to those from aerial videography (Wolosin, 2007) and consists of tree height, height to base of crown, and canopy radius in the eight cardinal compass directions. Heights and radii were measured using a laser range finder (Impulse 2000, Lasers Technology Inc., Englewood, Colorado) with a build-in digital clinometer that was custom modified with a mirrored vertical sight to enable accurate identification of the crown edge. Since crown radii are measured as vectors from the trunk, it is possible for radii to have negative values for irregularly shaped crowns.

The species-level covariates that we consider in the crown geometry model include phylum, shade tolerance, and wood strength. Shade-tolerance classification is based on estimates from the U.S. Forest Service (USFS) Silvics Manual (Burns and Honkala, 1990) and the USFS Fire Effects Information System (FEIS) database (<http://www.fs.fed.us/database/feis/>), both of which rely heavily on Baker (1948). The shade-tolerance classes were converted into an ordinal ranking (very tolerant = 1, very intolerant = 5). Mechanical properties were taken from the USFS Forest Products Lab database (<http://www2.fpl.fs.fed.us/>) and Wood Handbook (Forest Products Laboratory 1999). For this analysis we use the compressive strength of green wood parallel to the grain (kPa), which is more likely to be directly related to overall tree strength than more common surrogates such as wood density (Woodcock, 2003; Chave et al., 2005). In this analysis phylum enters as a gymnosperm/angiosperm indicator variable, though more sophisticated approaches using greater taxonomic resolution or phylogenetic distance could easily be developed. The complete list of species, covariates, and sample sizes is given in Table S1.

2.2. Bayesian hierarchical allometries

In this section we describe the Hierarchical Bayes model we use to fit crown allometries. We begin by explaining the simplest possible allometric model and then progress through the steps of

model specification, explaining what each new part does, until we reach the full model. The allometric model that serves as the base of our analysis is the traditional power-law relationship,

$$y = b_0 x^{b_1},$$

which is commonly used to assess scaling rules in many scientific disciplines. Power-law relationships produce a straight line on a log-log graph and are usually fit by either Ordinary Least Squares (OLS) or Reduced Major Axis (RMA) linear regression $Y_{ij} = X_{ij}\beta_j + \varepsilon_{ij}$ where $Y_{ij} = \log(y_{ij})$, $X_{ij} = \{1, \log(x_{ij})\}$, $\beta_j = \{\log(b_0), b_1\}$, and $\varepsilon_{ij} \sim N(0, \sigma_j^2)$ is normally distributed residual error. Throughout this manuscript we use subscripts i and j to denote individual and species, respectively; here the j subscripts denote that each species is being fit separately. A complete Bayesian specification requires that we provide prior distributions on the parameters β_j and σ . The prior on β_j is normal, $\beta_j \sim N(B_j, \Phi_j)$, where B_j and Φ_j are the prior mean and variance. An inverse-gamma distribution, $\sigma^2 \sim \text{Inverse} - \text{Gamma}(\alpha, \gamma)$, is the standard choice of prior on the variance because of its conjugacy and because the parameters α and γ are interpretable as the prior contribution to the sample size and sum-of-squares respectively. Finally, we assume that measurement error in our x variable, tree diameter, is negligible compared to error in the crown measurement, though incorporating this error is straightforward in the Bayesian framework.

Fitting each species separately ignores the fact that the growth forms of trees are generally similar across species. An alternative to this is to treat all individuals as being drawn from one universal allometry, $Y_i \sim N(X_i\beta, \sigma^2)$, that drops species effects (subscript j). These two cases form the bounding extremes: all species are different vs. all species are the same. The intermediate approach is to model each species' parameters as being drawn from a common pool:

$$\beta_j \sim N(B, \Phi) \quad (1)$$

where B is the across-species universal allometry from which species-specific allometric coefficients, β_j , are drawn and Φ is the "global" covariance matrix. If the global allometric parameters (B, Φ) are set to fixed values determined *a priori*, Eq. (1) is the same as the by-species approach above but with all species having the same prior.

It is through the use of priors that we formally include the predictions of mechanistic scaling models into our statistical analysis. However, this method only allows the prior, not the data, to inform the universal allometry. We can improve upon this by allowing B and Φ to be fit parameters, making this a hierarchical Bayes model. When we do this we need to construct hyperpriors on B and Φ rather than priors on β_j ; to do this we use the mechanistic prior to be the constraint on the across-species allometric model:

$$\begin{aligned} B &\sim N(B_0, V_0) \\ \Phi &\sim \text{Inv} - \text{Wishart}(w, w\Psi) \end{aligned} \quad (2)$$

where the inverse-Wishart distribution in the multivariate generalization of the inverse-gamma described earlier. This approach allows the universal allometry to be informed both by data and prior information. The degree to which the allometric relationships are similar across species controls the variance in B and Φ and thus the strength of the hierarchical universal allometry in constraining the species-level fits. Rare species are constrained by the hierarchical structure to be "tree like," while for common species the data will dominate the fit unless the hierarchical constraint is very strong. The hierarchical structure also allows us to formally define the predictive distribution for unobserved species.

2.3. Canopy geometry model

Field-measured tree crowns are defined by three measurements: tree height, height to base of canopy, and canopy radius. We therefore expand the basic allometric model to the multivariate case

$$\begin{aligned} Y_{ij} &\sim N(X_{ij}\beta_j, \Sigma) \\ Y_{ij} &= [H_{ij}, \theta_{ij}, R_{ij}]^T \\ X_{ij} &= [1, D_{ij}]^T \end{aligned} \quad (3)$$

where $H = \log(\text{tree height})$, $\theta = \text{logit}(\text{relative canopy depth})$, $R = \log(\text{canopy radius})$, $D = \log(\text{DBH})$, Σ is a 3x3 covariance matrix, and relative canopy depth is defined as $1 - (\text{height to base of crown}) / (\text{tree height})$. The decision to fit all three-response variables simultaneously using a full covariance matrix, rather than to fit each variable separately, acknowledges the fact that response variables are likely related to each other. The use of logit transformed relative canopy depth, rather than a direct power-law fit to canopy depth, is a simple way to constrain the bottom of the canopy to be between the top of the tree and the ground at all diameters. The alternative of fitting a power-law to the canopy base height requires constraining the slope to be the same as that of total tree height, meaning that relative canopy depth is always constant for a given species. The logit transform of relative canopy allows canopy depth to vary with tree size and allows us to easily incorporate the transformed values in a regression framework.

To include species-level covariates we simply modify Eq. (1) to

$$\beta_j \sim N(ZB, \Phi) \quad (4)$$

where Z is the matrix of species-level covariates. By including species-level covariates at this higher level of the hierarchical model, we are formally including these variables in the model in a way that includes the uncertainty we have in the β_j 's when trying to explain patterns among species. This is in contrast with post-hoc methods which treat the β_j 's as fixed and regress them against the species-level covariates. Such an approach is not only overconfident in its predictions, since it fails to propagate uncertainty in the regression parameters, but also falsely treats each species as representing the same amount of information. Furthermore, by modeling the process in a hierarchical manner with covariates, we are able to reduce the uncertainty we have in predictions of rare and unobserved species when we know their covariates.

An added complication for this model is that we do not observe canopy radius directly, but rather observe 2–8 samples of the canopy radius from which we infer radius. Rather than average these samples beforehand, and thus discard the large within-individual variability in canopy radius, we formally incorporate it. If we let R_i^* be a latent variable for the “unobserved true” canopy radius of individual i and $DBH_i \cdot \sigma_R^2$ be the size-dependent within-individual variance in canopy radius, then we model canopy radius as

$$r_{i,k} \sim N(r_i^*, DBH_i \cdot \sigma_R^2),$$

where $r_{i,k}$ is the k th radius measurement of individual i . r^* can be thought of as either the average canopy radius or the radius of a circular crown with area equivalent to the crown area, both definitions being equivalent in the limit. The linear scaling of the radius variance with diameter was done in order to make the residuals homoskedastic after exploratory analyses revealed unsurprisingly that large trees had greater within-crown variability in radius. A single σ_R was used for the two sampling campaigns because initial analyses suggested they had similar variance, though fitting variances separately for each data set is straightforward in this framework.

The Bayesian framework allows us to formally account for the fact that we are missing species-level covariates, Z_{mis} , for some species (Table S1). We assume the missing data to be missing at random and that the missing-data mechanism is ignorable, in the formal sense that parameters controlling the allometries and those controlling the missing-data imputation are independent in the prior distribution. For simplicity we treat the Z variables as having a multivariate normal distribution, $p(Z|\mu_Z, \sigma_Z) \sim N(\mu_Z, \sigma_Z)$, from which Z_{mis} can be drawn. When one or more of the covariates is known, the remaining can be drawn from the appropriate marginal distribution conditioned on the known values.

To fully specify the model in a Bayesian context we make use of standard conjugate priors wherever possible. The model was fit making use of standard MCMC methods (Clark, 2007; Gelman et al., 1995). For most of the parameters we are able to use a Gibbs sampler to sample directly from the conditional distributions. In order to incorporate existing predictions into the across-species allometry prior (B_0 , Eq. (2)), we used the slope predicted from WBE (West et al., 1999; Enquist et al., 1999) for tree height (2/3) and set the intercept to 1/4 in order to produce reasonable heights. Logit crown depth priors were set to have 0 slope and a 0 intercept (which gives a crown depth of 50% irrespective of DBH) based on the fixed crown depths in Pacala et al. (1996). Crown radius priors were set at a slope of 1/2, based on the assumption that crown area would scale linearly, and an intercept of -0.3 to produce reasonable radii. The prior variance (V_0) was set to a moderately informative but not strong value (10). The remaining priors and conditional sampling distributions are provided in the appendix. Model fitting was done on a Linux workstation using R 2.1.1 (R Development Core Team, 2005).

To determine the importance of the species-level covariates we compared models using predictive loss with a squared error loss function (Gelfand and Ghosh, 1998). Predictive loss was chosen over other model selection criteria, such as DIC or Bayes factors, primarily because of its emphasis on predictive distributions since allometries are most often used for predictive purposes. The predictive loss metric, D , aims to balance model residual sum-of-squares error (G), which tends to decrease with model complexity, and model predictive variance (P), which tends to increase with model complexity due to high parameter uncertainty, by selecting the model which minimizes their sum, $D = G + P$. For the purpose of calculating predictive loss, as well as all other posterior means, moments, and credible intervals, we discarded the initial 20% of the MCMC to reduce burn-in effects and 50% of the remaining sample to reduce autocorrelation. Model selection was based on 30,000 MCMC steps, and then the best fitting model was run for a total of 50,000 MCMC steps. Initially, five versions of the model were compared: the full hierarchical model with all covariates (FULL), the hierarchical model without any covariates (INT), the FULL and INT models with the universal variance T being drawn from inverse-Gamma distributions rather than the joint inverse-Wishart (IG FULL, IG INT), and a non-hierarchical implementation where each species is fit independently (BYSP). The IG models, which only estimate the diagonal of the covariance matrix T , were added after initial runs suggested that there may not be enough information at the hierarchical level (53 species) to constrain the full covariance matrix (21 parameters in the full model versus 6 in the IG). This was supported by model selection which ranked the IG INT and IG FULL models first and second respectively. Following this we ran the IG model for all permutations of species-level covariates in order to select the most parsimonious parameters, again using predictive loss.

3. Results

Model selection showed that the model with inverse-gamma variance and shade-tolerance class and mechanical strength as hierarchical covariates had the lowest predictive loss (Table S2). Models with inverse-gamma hierarchical variance (i.e. diagonal variance structure) were supported over those with an inverse-Wishart variance (i.e. full covariance matrix), suggesting that the full matrix was overfitting the data and that there was insufficient information in 53 species to identify all 15 terms in the 6x6 matrix. Overall, model selection suggested that there were no significant differences in crown allometry between angiosperms and gymnosperms once shade tolerance and wood strength were included and that there was little covariance across species in the three measures of crown shape (tree height, crown depth, and crown radius).

3.1. Species relationships

Looking at the species-level, Fig. 1 shows examples of the log–log fit of the tree height–diameter relationship with 95% credible intervals in comparison to the traditional linear regression fit. It is immediately apparent that for species with a large sample size, and where samples are well distributed across sizes, the two methods of analysis produced essentially the same fit (Fig. 1 left column). This is to be expected because the species data appropriately overwhelm the hierarchical prior. However, for rare or poorly distributed species the hierarchical model and linear regression

can differ considerably. In these cases the ability of the hierarchical model to borrow strength across species produced much more biologically realistic relationships. For example, only large individuals of black walnut (*Juglans nigra*, JUni), unclassified red oaks (QUun), and Virginia pine (*Pinus virginiana*, Pivi) were found in the study area and the classical regression model produced a spurious negative correlation between diameter and height for the first two and too shallow a slope for the third (Fig. 1 center column). Similarly for rare understory tree species (*Frangula caroliniana*, FRca, *Halesia carolina*, HAca, and *Viburnum rufidulum*, VViru), the classical regression fits were either considerably too flat or too steep (Fig. 1 right column). While the sample sizes for the rare species in this study are small, they often represent a complete census of the available stems and the sample sizes found here are for the most part not uncommon in the literature. Thus, while the poor frequentist fits may appear a bit of a strawman, they do represent the only option available in the classical framework other than arbitrarily applying the allometry of a different species. Plots of height, canopy depth, and canopy radius for an example species (*Quercus rubra*) are in Fig. 2 while plots for all species are in Figs. S1–S4 and posterior mean parameter estimates are given in Table S3.

The error covariance matrix (S) suggests that there was a positive correlation in the residuals between log tree height and logit canopy depth, such that trees that were taller than average for their diameter also had deeper canopies (Table 1). The residuals of canopy radius, on the other hand, were not correlated with tree height or canopy depth. There was little residual variance in canopy height

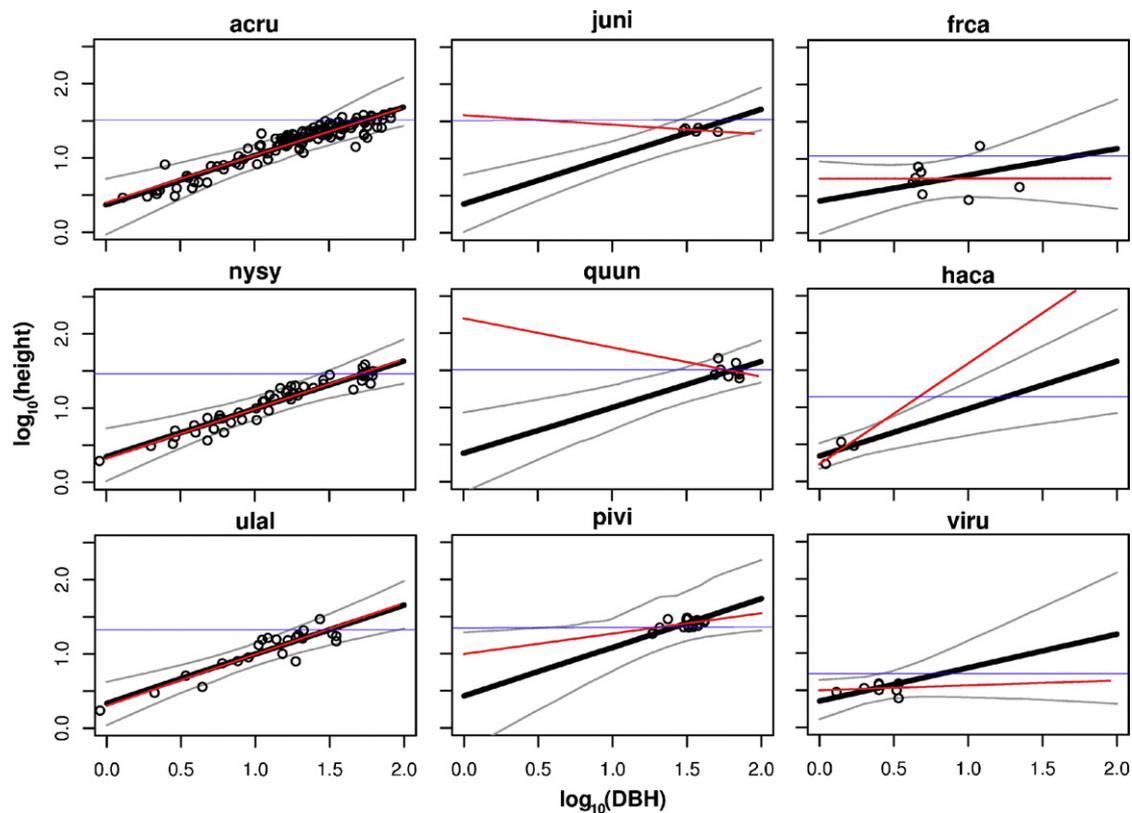


Fig. 1. Height versus diameter log–log allometry model fits for example species. Posterior median model fit is depicted in the solid black lines while the posterior credible intervals (95%) are shown in grey lines. Data are given in open black circles while the frequentist linear regression fit is given by a red line. Horizontal blue lines indicate the “mature height” of each species as reported in the USDA Plants Database (<http://plants.usda.gov>). For species with adequate data the Hierarchical Bayes model and the linear regression model are very similar (acru = *Acer rubrum*, nysy = *Nyssa sylvatica*, ulal = *Ulmus alata*), while for species with limited data, and/or with data for only small (frca = *Frangula caroliniana*, haca = *Halesia carolina*, viru = *Viburnum rufidulum*) or large trees (juni = *Juglans nigra*, quun = *Quercus* section Lobatae, pivi = *Pinus virginiana*), the hierarchical fit constrains these species to more biologically realistic portions of the parameter space. All panels are on the same scale and have log10 diameter breast height on the x-axis (1–100 cm) and log10 total tree height (meters) on the y-axis.

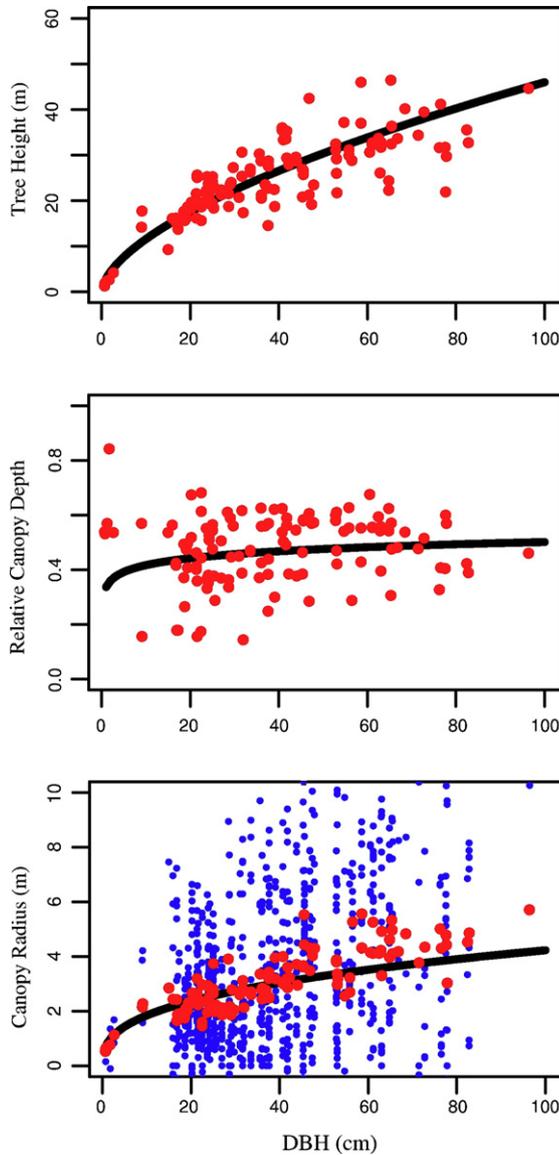


Fig. 2. Canopy allometry of red oak (*Quercus rubra*). The fits of total tree height (m), relative canopy depth, and canopy radius (m) versus diameter. The solid red dots show the observed data for tree height and canopy depth and the posterior means of the “true” canopy radius latent variable for canopy radius, while the smaller blue dots show all the radius measurements. A small portion of observed radii are less than 0 m or greater than 10 m. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

(0.0095), with the allometric model explaining 93% of the height variance in the log scale and 85% in the linear scale. By comparison, the canopy depth model had higher variance (0.57). However, on a linear scale this model still explains 81% of the variance in canopy depth. The variance in canopy radius is more complicated to assess because it was treated as a latent variable.

Table 1
Allometry species-level error covariance matrix (S)

	Height	Depth	Radius
Height	0.0095 (0.0088, 0.0101)		
Depth		0.011 (0.0075, 0.0153)	
Radius			1.5e-5 (-2.4e-4, 2.8e-4)
		0.57 (0.53, 0.61)	1.6e-4 (-1.8e-3, 2.2e-3)
			0.0018 (0.0013, 0.0025))

Values are reported as posterior means and 95% posterior credible intervals. The off diagonal covariance elements show that residual variability in canopy geometry is not correlated.

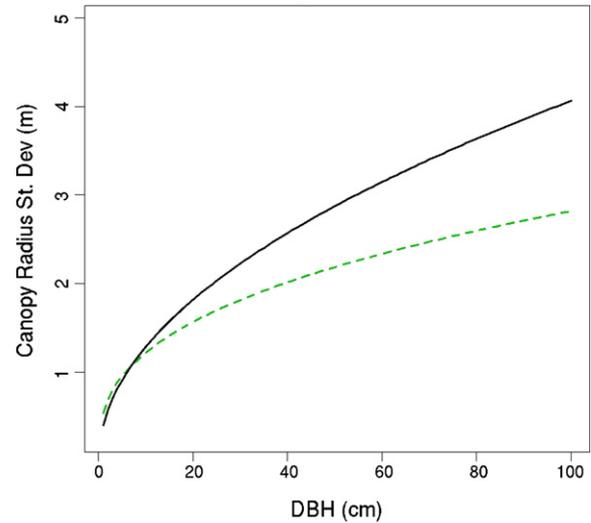


Fig. 3. Within individual (solid line) and among individual (dashed line) variability in tree canopy radius as a function of DBH.

3.2. Canopy radius

Fig. 2 (bottom) shows both the raw canopy radius data (blue) and the posterior means of the canopy radius latent variables (red). These plots show a large amount of variability in the individual measurements of canopy radius compared to the variability in the latent mean radius. The method of treating canopy radius as a latent variable not only allowed us to propagate uncertainty in the canopy radius, which was informed by the samples of each tree’s radius, but it also allowed us to partition the variance in canopy radius. Fig. 3 shows that there was clearly more variance in canopy radius within individual trees than among trees. It should be noted that this is not obvious *a priori*. If the crowns of individual trees were generally round but varied a lot in average radius, for example, due to local neighborhood effects, the overall variability in crown radius would be high (as are the blue points in Fig. 2) and would have to be higher than the overall variability in mean radius (red points), but the variability within trees would be low and the variability among trees would be high.

3.3. Across-species model

The hierarchical across-species parameter posterior means and variances of the best fitting model are reported in Table 2 along with their 95% credible intervals. Overall, the effects of shade tolerance tended to be stronger than the effects of mechanical strength (Fig. 4). Shade intolerant trees were taller for a given diameter, which was largely a result of intolerant trees having a larger intercept rather than a different scaling exponent. In terms of canopy depth, shade-tolerant trees had both deeper canopies than shade intolerant trees (larger intercept) and got deeper at a faster rate (larger slope). Shade-tolerant trees also had a larger

Table 2
Species-level effects

	Intercept	Shade tolerance	Wood Strength	Variance
Height intercept	0.32 (0.08, 0.56)	0.03 (−0.02, 0.08)	−0.02 (−0.22, 0.16)	0.054 (0.033, 0.082)
Height slope	0.59 (0.33, 0.85)	0.00 (−0.06, 0.05)	0.01 (−0.18, 0.23)	0.052 (0.032, 0.080)
Depth intercept	0.31 (0.07, 0.59)	−0.05 (−0.10, 0.00)	−0.09 (−0.31, 0.09)	0.023 (0.015, 0.034)
Depth slope	0.33 (0.10, 0.60)	−0.05 (−0.11, 0.00)	−0.03 (−0.23, 0.15)	0.026 (0.017, 0.039)
Radius intercept	−0.03 (−0.26, 0.22)	−0.04 (−0.09, −0.01)	−0.03 (−0.16, 0.24)	0.044 (0.028, 0.068)
Radius slope	0.37 (0.12, 0.63)	0.01 (−0.04, 0.06)	−0.01 (−0.22, 0.19)	0.054 (0.033, 0.085)

Parameters values (B & T in Eq. (4)) are reported with 95% credible intervals given in parentheses. Shade tolerance varies from 1 (very tolerant) to 5 (very intolerant) while wood strength (bending moment) has been normalized by the mean (23900 kPa). The variance term represents the residual variance among species in their slope and intercept parameters (β).

canopy radius, but as with height the difference was more influenced by a difference in intercept than in scaling exponent. In terms of mechanical strength the only discernable effect was on crown depth intercept, such that species with stronger wood had deeper canopies.

4. Discussion

The hierarchical Bayes model performed well at estimating the allometric relationships for the fifty-three species in the study area. While the height and canopy radius show clear agreement between the data and models, the relative canopy depth allometry was much noisier, suggesting that size is not the strongest constraint on this variable. This is not too surprising since the model did not take into account the local neighborhood conditions, which should affect self-pruning. One area for further model refinement would be the incorporation of stand and neighborhood covariates, such as stem density, basal area, or site factor. Adding additional species-level covariates is straightforward in the current modeling framework. Additional across-species covariates, such as growth form and maximum tree height, could easily be explored in this approach and would be particularly beneficial for constraining rare shrubs and understory trees, though if the aim is to understand across-species variation rather than just prediction care must be taken to avoid circularity. In particular, due to the inherent unreliability of extreme value statistics, data on maximum tree height, diameter, and crown size would more appropriately enter as an additional data source rather than as a covariate.

The estimation of canopy radius using a latent variable approach provided novel estimates of canopy radius that accounted for both within and among crown variability and propagated the uncertainty in mean radius into the allometric model in a clear and defensible manner. The fact that within canopy variability is greater than variability among canopies suggests that future work focus on explaining within-individual crown dynamics. Indeed, a more detailed analysis of high-resolution remote imagery from these stands finds that modeling individual-level crown movement and light foraging is critical for predicting both the ground and canopy-level light environment and adult growth rates (Wolosin, 2007). Interestingly, this analysis finds similar life-history and mechanical constraints on foraging as we do on allometries.

Almost all allometric relationships are faced with the general challenge of describing a snapshot of form and from this trying to infer a process of growth that is plastic and the result of an unknown individual history. This was a clear problem for estimating canopy depth and radius, which show significant variability around simple power-law relationships. The most obvious solution to this is to follow and model the process of growth itself. While estimates of tree diameter growth are commonplace, and measurements of height growth are not uncommon, measurements of

canopy growth are much more rare (Clark et al., 2004). However, growth information would allow a much greater understanding of canopy dynamics than just increasing the sample size of canopy allometric models or further increasing the complexity of the current analysis. Indeed, much of the “noise” in the allometries represents true individual-level variability, rather than measurement error or model mismatch. Using such growth data, Bayesian hierarchical models provide a clear and formal method for separating individual effects from measurement error (Clark et al., 2003, 2004).

At the hierarchical across species-level, the model provides a balance between species-specific and universal allometries. For rare species, and species with a limited size range, the hierarchical model is a great improvement over conventional approaches. This analysis successfully demonstrates the ability of this method to deal with the diversity of the southeast US, an area that has high woody plant diversity for the temperate region, and shows that the model has high potential for application in hyperdiverse regions, such as tropical rain forests.

The effects of the across-species covariates were generally intuitive and consistent with the literature (Aiba and Kohyama, 1997; Ackerly and Donoghue, 1998; Kohyama et al., 2003; Poorter et al., 2006; Sterck et al., 2001)—shade-tolerant species are generally shorter with broad and deep crowns. These patterns are consistent across many ecosystems and are generally interpreted from the perspective of successional trade-offs between fast vertical growth of slender stems and crowns, which potentially risk higher self-shading, decreased mechanical stability, and higher respiration and mortality in order to reach the canopy as quickly as possible versus slow growing, broad and deep crowned species with low mortality in low-light conditions (King, 1990; Aiba and Kohyama, 1997; Kohyama et al., 2003). What is novel in this analysis is that we found that there was greater variability in allometric intercepts than in their slopes. This result is consistent with mechanistic scaling laws, such as the West, Brown, and Enquist (WBE) metabolic theory (West et al., 1999), which suggest that there are basic physiological constraints on scaling exponents. To our knowledge, the various extensions to the WBE theory have not made specific predictions about how these largely hydraulic constraints should interact with the energetic considerations and demographic trade-offs along the successional gradient. The additional effects of wood strength are also interesting in that they suggest that there is residual variation to explain beyond both the primarily hydraulic argument presented in WBE’s theory and the successional gradient of shade-tolerance.

Unfortunately, these hierarchical covariate effects were generally weak. Part of the reason for weak effects is that we are propagating the uncertainty in the species-level allometric parameters into the fitting of the across-species model, and thus our results reflect this additional uncertainty and do not create a false precision that would come from fitting to parameter means.

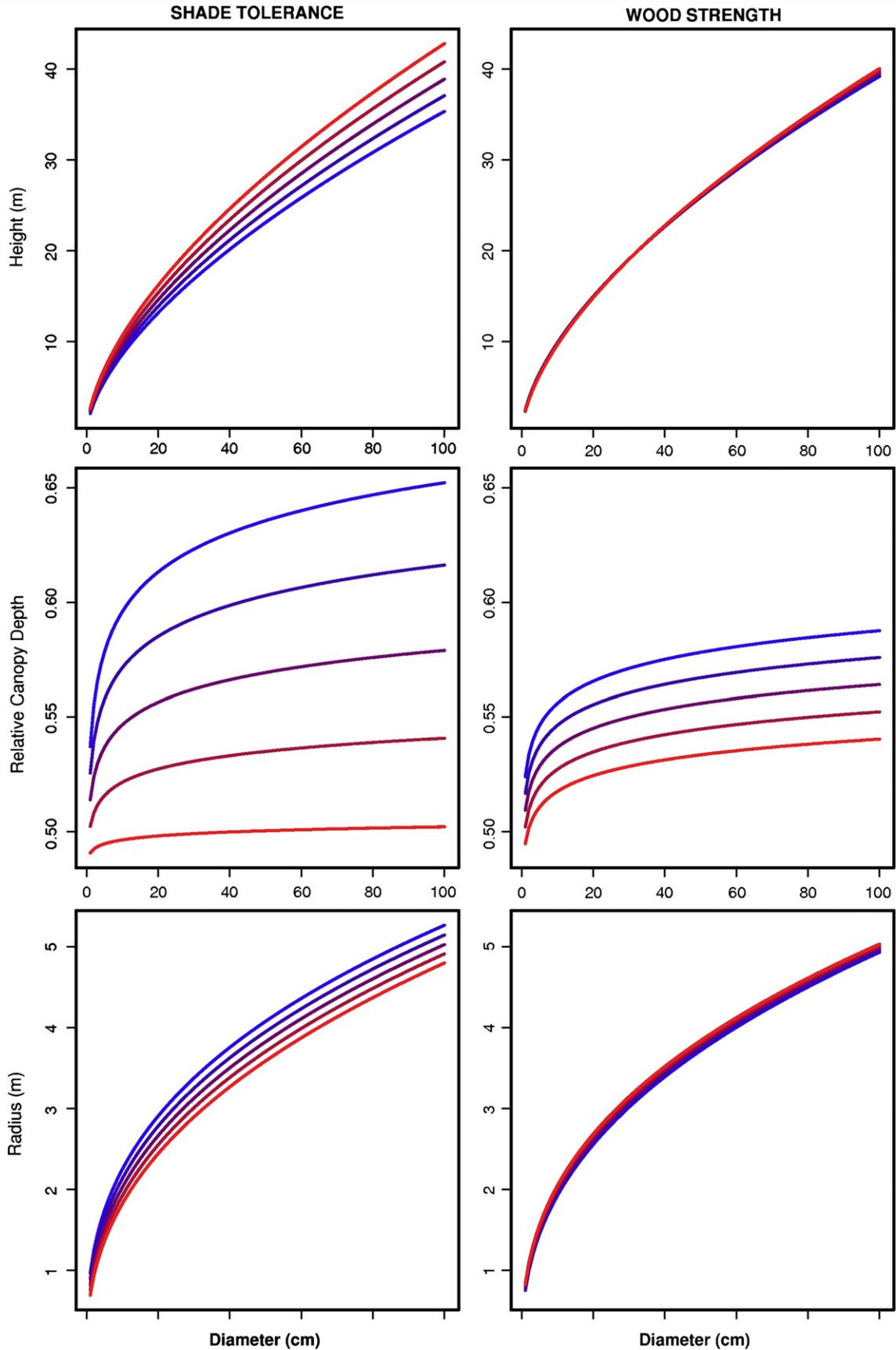


Fig. 4. Effects of species-level covariates on the variation across species in crown allometries. For shade tolerance, curves go from very tolerant (blue) to very intolerant (red), while for wood strength they go from 50% of the mean strength (blue) to 150% (red), which is approximately the range of variability observed. Shade intolerant species tend to be taller for a given diameter, while tolerant species tend to have both deeper and wider crowns. In comparison, the effects of wood strength were much weaker, but suggest that stronger trees tend to be taller and have wider but shallower crowns. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Another part of the reason for weak effects can be attributed to the conservative approach taken to filling in missing data, which draws from the predictive distribution of the observed species-level data, and thus is more “noisy” than drawing values from the joint distribution of the allometric model and the observed species-level data. In the later case, correlations between the species data and the allometries would provide additional constraint to both the missing-data distribution and the allometries. Indeed, the weaker effects of wood strength compared to shade tolerance can in part be attributed to the fact that it had almost twice as much missing data. If the primary interest was in elucidating the across-species constraints, rather than predicting rare species, one could simply limit the analysis to species with the full set of covariates. Likewise, such an analysis could take a more sophisticated approach to accounting for phylogenetic constraint, such as incorporating greater taxonomic resolution or phylogenetic distance. Still, the current analysis does imply the importance of life-history traits and biomechanics in determining the canopy geometry and the patterns observed are consistent with logical expectations and the literature.

One of the advantages put forth in support of the hierarchical Bayes model is the ability to incorporate prior information, such as from prior analyses, biomechanical argument, or expert opinion. For the analysis of tree height we used an informative hyperprior with a 2/3 power–law scaling exponent that comes from the WBE biomechanical model (West et al., 1999; Enquist et al., 1999). The posterior distribution of the across-species scaling exponent was shown to have a posterior mean of 0.61 suggesting that the height of trees in these forests is consistent with the mechanistic scaling (Table 2). Furthermore, the failure to reject the WBE exponent was shown to be independent of the prior strength (Appendix: Sensitivity of across-species allometry to prior strength, Fig. S5). By comparison, other researchers have found the height allometry to be lower than both predicted by WBE and observed in this study. For example, Russo et al. (2007) found an average scaling exponent of 0.45 for forests in New Zealand. On average the New Zealand growth rates are fairly slow (Russo personal communication) while forests in the southeastern US tend to be among the most productive in the temperate region. This difference is thus in many ways consistent with the decline in the scaling exponent with an increase in shade-tolerance observed in this study and points to a need to understand the general principles of how scaling relationships vary across regions and how this relates to differences in energetics and resource constraints among regions versus evolutionary constraints and biogeography.

In contrast to our failure to reject the height allometry, canopy radius scaled as 0.40, which is in clear contrast with the WBE prediction of a 2/3 scaling exponent. Overall the statistical power of these methods to reject the mechanistic prediction may appear weaker than tests performed by other researchers (e.g. Enquist et al., 1998), however since these other methods ignore within-species variation and the inherent uncertainty in species-level allometries they are in many ways overconfident.

Overall, our research represents an important step in unraveling the controls on the dynamics of tree crowns. Understanding crown shape is critical to understanding the forest light environment and thus adult growth and competition. Much of the variation in crown shape is consistent with existing expectations based on scaling laws and life-history traits. We show that the consistency in these traits across species can greatly assist in predicting rare and poorly sampled species. However, much still remains to be understood about the way that the history of an individual and its local competitive environment shape tree crowns.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2008.07.034.

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