

A model-based meta-analysis for estimating species-specific wood density and identifying potential sources of variation

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Summary

1. Plant functional traits are important determinants of survival and fitness, and wood density (WD) is a key trait linked to mechanical stability, growth rates and drought- and shade-tolerance strategies. Thus, rigorous WD estimates are necessary to identify factors affecting tree performance.

2. We obtained 1766 records of WD from the literature for 141 tree species in the United States. We implemented a hierarchical Bayesian (HB) meta-analysis that incorporated sample size, variance, covariate (e.g. moisture content and latewood proportion) and methodological information to obtain standardized estimates of WD for 305 U.S. tree species. The HB framework allowed ‘borrowing of strength’ between species such that WD estimates for data-poor species were informed by data-rich species via taxonomic or phylogenetic relationships.

3. After accounting for important covariates and sampling effects, evaluation of the residual variation revealed the potential importance of environmental factors and evolutionary history. Differential variation in WD between species within genera and between genera within orders suggested that WD is relatively conserved in some genera and orders, but not in others. WD also varied between studies (or sites) indicating the potential influence of edaphic, topographic, or population factors on intraspecific variation in WD.

4. *Synthesis.* Our hierarchical Bayesian approach overcomes many of the limitations of traditional meta-analyses, and the incorporation of phylogenetic or taxonomic information facilitates estimates of trait values for data-poor species. We provide relatively well-constrained WD estimates for 305 tree species, which may be useful for tree growth and forest models, and the uncertainties associated with the estimates may inform future sampling campaigns.

Key-words: borrowing of strength, evolutionary history, hierarchical Bayesian model, meta-analysis, plant development and life-history traits, plant functional traits, wood density, wood specific gravity

Introduction

Plant functional traits describing morphological, physiological and phenological characteristics influence vital rates such as survival, growth, reproduction and ultimately, fitness (Ackerly 2003). Functional traits capture fundamental trade-offs that determine species’ ecological roles and integrate the ecological and evolutionary history of a species, enabling predictions of the conditions under which a species is likely to succeed.

Studies of interspecific variation in plant traits have generated important insights into the occurrence of trait trade-offs (Lambers & Poorter 1992), the classification of plants into functional groups (Grime 2001), and the consequences of these trade-offs and functional groups for ecosystem functioning (Ter Steege & Hammond 2001; Diaz *et al.* 2004). Thus, evaluation of species-specific functional traits is essential to understand how interspecific trait differences mediate community response to perturbations such as climate change and disturbances (Klumpp & Soussana 2009; Bernhardt-Römermann *et al.* 2011).

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Several key functional traits have been proposed as universally important for plant performance and represent relatively independent aspects of ecological strategies (Ackerly 2004). Among these, seed size, specific leaf area, wood density (for woody plants) and maximum plant height at maturity often play a central role in growth or survival (Thomas & Bazzaz 1999; Wright *et al.* 2003, 2007; Poorter *et al.* 2008; Cornwell & Ackerly 2010; Kraft *et al.* 2010; McMahon, Metcalf & Woodall 2011). These traits are also easily measured and thus can be obtained for large numbers of species (Westoby 1998). Wood density (WD) is a particularly important trait for trees, and it represents the biomass invested per unit wood volume. WD plays a central role in tree growth and survival (Martinez-Vilalta *et al.* 2010) via its importance for tree mechanical stability, carbon storage potential, and water relations; thus, WD is often a key parameter in models of tree growth (e.g. King *et al.* 2005; Ogle & Pacala 2009). Hence, it is important to obtain rigorous estimates of species-specific WD for understanding constraints on tree performance and for predicting forest dynamics. Here we provide rigorous estimates of WD for 305 tree species occurring in the United States; importantly, the estimates are standardized for influential covariates (e.g. latewood proportion and moisture content) such that the WD estimates can be compared across species.

Trees with low WD often have relatively fast stem growth rates because greater height and/or diameter (i.e. volume) can be achieved per unit biomass increment when compared with trees with higher WD (King *et al.* 2005). Conversely, high-density wood tends to be constructed from small cells with thick cell walls and limited intercellular space (Castro-Diez *et al.* 1998), making stems with high WD more resistant to breakage (Van Gelder, Poorter & Sterck 2006) and pathogen attack (Augsburger 1984), contributing to enhanced plant survival under such stressors (Muller-Landau 2004). Higher WD may also reduce the likelihood of xylem conduit implosion under low water potentials (Hacke *et al.* 2001), thereby improving survival in water-stressed areas. For a given amount of carbon allocation to wood, low WD may actually convey greater strength and resistance to breakage than high WD (Larjavaara & Muller-Landau 2010, 2012). Nevertheless, high WD species tend to be shade tolerant and have low mortality rates (Kitajima 1994; Wright *et al.* 2003; Poorter *et al.* 2010).

Recent analyses that compiled data from a large number of sites in the northern hemisphere showed correlations between community-averaged WD and environmental variables related to resource availability, and the main influential factors included precipitation, temperature, wind and soil conditions (Swenson & Enquist 2007). WD has also been reported to vary along elevation and latitudinal gradients, which represent proxies for environmental conditions (Chave *et al.* 2009; Dalla-Salda *et al.* 2009). Clearly, variation in WD across species represents a nexus of various physiological, ecological and environmental interactions.

It also appears that evolutionary history is an important determinant of interspecific variation in WD (Zhang & Morgenstern 1995; Swenson & Enquist 2007). That is, WD is conserved at different taxonomic levels, with most of the

variation being explained by genus membership and secondarily by family membership (Chave *et al.* 2006). WD may be considered a composite trait that integrates other more basic anatomical and physiological traits (such as cell size and chemical structure) that may be phylogenetically conserved, thus resulting in conservation of WD. However, intra and interspecific variation in WD may be advantageous, reflecting adaptations to spatial and/or temporal environmental variability. For example, we might expect WD to vary greatly within genera containing species that have radiated into different environments (Lawton 1984). Hence, phylogenetic conservation of WD and the degree to which evolutionary history and environmental variation influence WD may vary by clade association and/or environmental conditions.

Extensive work has been carried out to improve the understanding of ecological and evolutionary influences on WD (Chave *et al.* 2006; Swenson & Enquist 2007; Kraft, Valencia & Ackerly 2008; Flores & Coomes 2011). However, many studies often deal with instances of WD correlations with relatively few environmental variables, within a single study, and typically such data are not available for several species or for multiple individuals or species across different environmental conditions. There is a wealth of information about WD contained in the literature, which could provide species-level WD information across multiple studies and environmental conditions. Compilation of such literature information, however, often results in a sparse data set due to incomplete spatial or temporal representation, and frequently, potentially important covariates may not be measured or reported. Thus, synthesis methods must be able to accommodate such incomplete reporting.

Classical meta-analysis approaches exist for synthesizing information from the literature (Gurevitch & Hedges 1999; Gurevitch, Curtis & Jones 2001; Gates 2002; Lajeunesse & Forbes 2003), but they are generally not appropriate for estimating species-specific traits and to quantify sources of variation affecting such traits. They also do not directly account for non-independence induced by within-study correlations, and they cannot explicitly handle incomplete reporting (or missing data). Until recently, such approaches did not incorporate phylogenetic relationships to account for non-independence between species. Chamberlain *et al.* (2012) showed that the incorporation of phylogenies can significantly change the effect sizes, and the assumption of a common variance (Lajeunesse 2009) is often inappropriate since the rate of speciation—and hence, variation between species—may differ between clades. Although such advances can accommodate evolutionary dependence, the method for doing so is somewhat restrictive because it requires ‘data’ (e.g. effects sizes) at the level of an individual species and estimates of uncertainty must be available (see, Chamberlain *et al.* 2012). Alternatively, Flores & Coomes (2011) described a hierarchical Bayesian (HB) model that incorporates phylogenies using branch lengths to define covariance matrices, which they employed to obtain species-specific WD estimates for hundreds of species. We significantly build-upon Chamberlain *et al.* (2012) and Flores & Coomes (2011) by employing a

new model-based HB meta-analysis approach that has been recently described (Ogle, Barber & Sartor 2013); the approach employs a flexible, probabilistic framework for incorporating species relationships, addressing within study non-independence, accommodating incomplete reporting and quantifying the effects of important covariates.

The objectives of this study were two-fold. First, we sought to obtain rigorous estimates of species-level WD for 305 U.S. tree species that accounted ('standardized') for study-level effects, methodological or sampling artifacts and covariates related to wood properties. Second, we aimed to evaluate the evolutionary and environmental influences on WD in these tree species. We addressed these objectives by extracting 1766 WD values (sample means) from the literature, which we analysed in the context of important covariates (e.g. latewood proportion, moisture content, wood type) and species relationships using an HB meta-analysis approach. We specified a phylogenetically structured hierarchical model for the species-specific, standardized WD values. To further explore the utility of incorporating phylogenetic relationships, we compared this model to ones that used taxonomic relationships and to a model that assumed independence among species. The incorporation of phylogenetic and taxonomic information facilitated the separation of evolutionary and environmental influences, and the approach has the potential to greatly improve trait estimates for data-poor taxa.

Materials and methods

DATA SOURCES

Wood density data base

Wood density information was obtained from published books and journal articles. Relevant journal articles were identified by searching Web of Science using different search terms including: '(wood and (density or volume or mass or structure or properties)) or specific gravity'. The vast majority of the search was completed on/before August 23, 2006. We used sources containing WD data for tree species occurring in the continental U.S. according to the Plants Database (USDA 2008). We specifically focused on the 285 species and

20 subspecies (305 total, which we referred to as simply 'species' as we do not explicitly distinguish between species and subspecies in our analysis) identified by the U.S. Forest Service's Forest Inventory and Analysis (FIA) program (Miles *et al.* 2001). The resulting 1766 records of WD represented 141 species, 55 genera, 20 orders and two divisions (*Magnoliophyta* and *Coniferophyta*) that were synonymous with the major clades *Angiospermae* and *Coniferae* respectively (Cantino *et al.* 2007).

Wood density sample means, standard errors, samples sizes, associated covariates and details of the study location were entered into the TreeTraits data base (Kattge *et al.* 2011; Ogle, Barber & Sartor 2013). When available, covariates extracted from published studies included wood moisture content (%), moisture content type (i.e. categorical description of the moisture content: air dry, green, oven dry, or saturated) associated with the moisture content data and the weight measurement used to compute WD, latewood proportion, sample type (i.e. core, disc, core section, disc section), and whether extractives were removed or not (Table 1 lists the covariates used in the final analyses and their per cent reporting). We also obtained the wood type (ring porous, diffuse porous and softwood) for each species; see Fig. 1 for examples of the three different wood types.

Phylogenetic information

A complete phylogeny for all 305 species was not readily available in the literature, so we used a variety of published sources to compile a phylogeny. We first created a genus-level tree based on the phylogenies available in the Phylocom database (www.phylodiversity.net/phylocom/, version 4.0.1). We then identified families in need of further resolution and performed a literature search for published phylogenies targeted at these taxa. Discrepancies between two published phylogenies were resolved conservatively, often resulting in a polytomy. Molecular-based phylogenies were not available for three families that contained the genera *Pinus*, *Juniperus* and *Ulmus* and genera from these families were grouped by taxonomic subgenera or 'section'. Next, we searched the literature and obtained a phylogeny of the species within each of the 86 genera using similar methods to those described for the genus-level phylogenies. The only exception was *Quercus*, where we used published sequence data in GenBank to create a phylogeny. Sequences were aligned using MEGA (www.megasoftware.net/, version: MEGA 4) and imported to the CIPRES Portal website (www.phylo.org/portal2/login!input.action). The RAxML tool was used to perform phylogenetic tree inference using maximum likelihood with bootstrapping; the 450 bootstrapped trees were

Table 1. Per cent of unreported ('missing') data for the covariates used in this study, and the number of wood density (WD) records (N) by wood type and overall (total records)

Covariate	Wood type			Overall (N = 1766)
	Diffuse porous (N = 404)	Ring porous (N = 360)	Softwood (N = 1002)	
	Per cent unreported data			
Latewood proportion (<i>L</i>)	100.0	99.7	70.7	83.3
Moisture content (<i>W</i>)	29.2	23.6	50.6	40.2
Moisture content type (<i>M</i>)				
For <i>W</i> measurement (<i>M_W</i>)	1.0	0.6	2.2	1.6
For WD mass measurement (<i>M_M</i>)	1.0	1.1	2.2	1.7
Sample size (<i>N</i>)	56.7	63.6	45.2	51.6
Standard error (<i>se</i>)	74.5	70.6	67.2	69.5

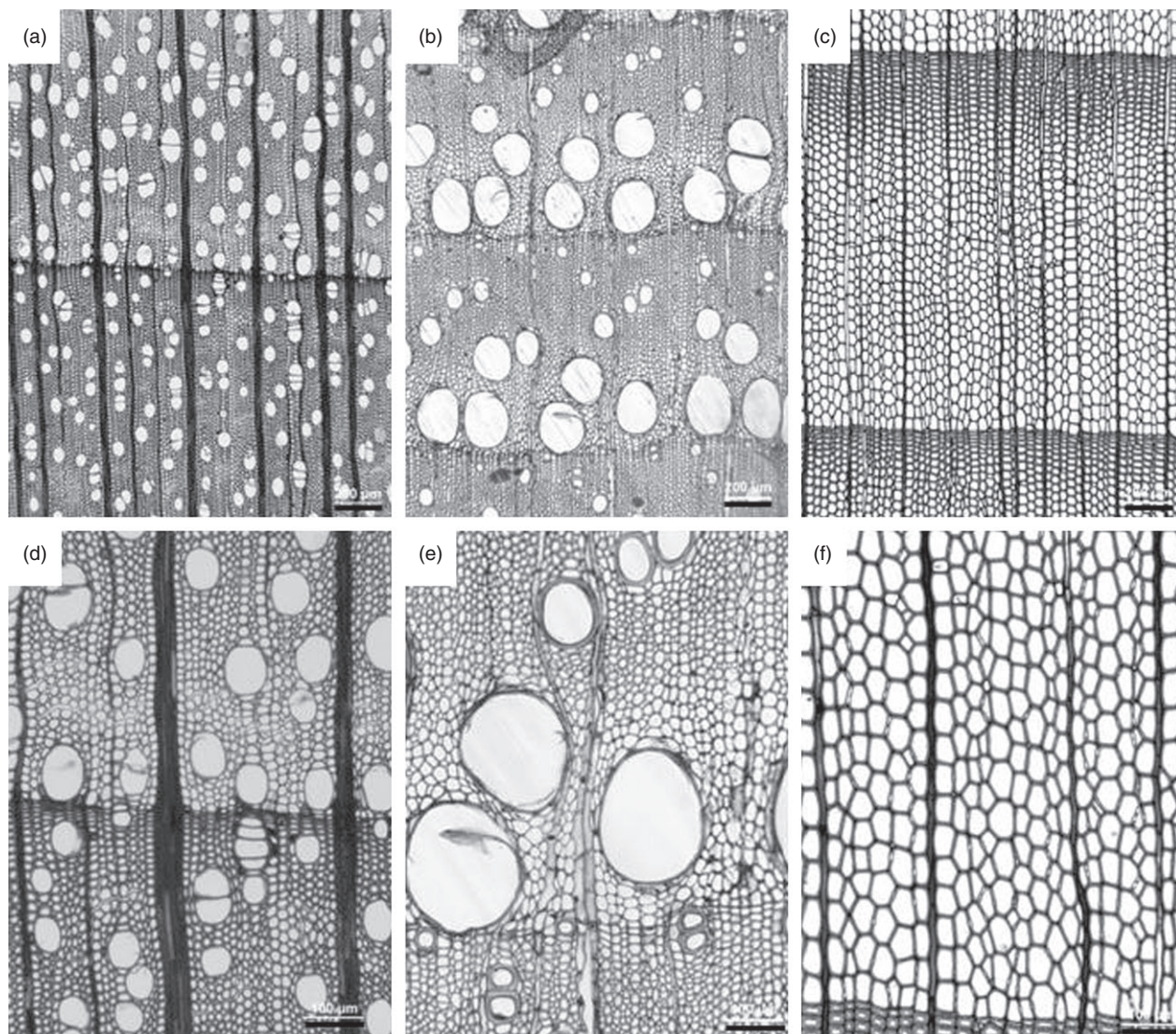


Fig. 1. Example images of wood cross-sections representing different wood types for (a–c) 4× magnification and (d–f) 10× magnification for (a, d) *Acer macrophyllum* (diffuse porous), (b, d) *Fraxinus latifolia* (ring porous) and (c, f) *Taxodium distichum* (softwood). Images were obtained from the InsideWood data base (InsideWood 2004-onwards; Wheeler 2011) and were contributed by Elisabeth Wheeler. The black horizontal bar in the lower right corner of each image gives the scale: (a–c) 200 µm and (d–f) 100 µm.

imported to Phylip (evolution.genetics.washington.edu/phylip.html, version 3.67), and the Consense program was used to create one tree. Although the final phylogeny we developed for all 305 species does not have branch lengths, it does establish the general evolutionary relationships among the species. The genus-level phylogeny that we compiled is given in Appendix S1 in the Supporting Information.

HIERARCHICAL BAYESIAN META-ANALYSIS

We conducted a hierarchical Bayesian (HB) (Clark 2003; Wike 2003; Ogle & Barber 2008) meta-analysis of the published WD information following Ogle, Barber & Sartor (2013). Few studies reported multiple covariates known to affect WD, such as latewood proportion and moisture content (Table 1). A classical meta-analysis approach (e.g. Gurevitch & Hedges 1999) would require that we ignore such covariates or that we delete all records that did not report the covariates. The first option precluded accounting for the effects of covariates that are thought to be important, and the second would substantially reduce the

sample size and taxonomic coverage of the dataset (Table 1). The HB approach, in contrast, enabled the use of all available data by treating missing covariates as unknown parameters wherein values were informed by the covariance structure of the non-missing data (Ogle, Barber & Sartor 2013). For example, Ogle, Barber & Sartor (2013) conducted simulation studies to test the ability of this HB meta-analysis to yield realistic results in the face of similar levels of incomplete reporting; the method was successful in such situations.

The WD data base only provided data for 46% of the 305 species. Thus, we explored four different ways of modeling the species-specific standardized WD values to evaluate the importance of borrowing of strength among species for inferring WD of data-poor species. The phylogeny model (PM) implemented a hierarchical model based on the phylogeny we compiled for the 305 species, allowing borrowing of strength between closely related species (e.g. Figs 2 and 3). The taxonomy model (TM) replaced the phylogenetic relationships with a taxonomic hierarchy such that species were nested within genera, genera within order and orders within major division (e.g. Fig. 2a).

The division-level model (DM) treated species as nested in their respective major division (*Coniferophyta* or *Magnoliophyta*), and additional phylogenetic or taxonomic relationships were not incorporated. In the DM, if we are missing data for a particular oak species, for example, its WD value is informed by the division-level WD for *Magnoliophyta*, which is informed by data on all other species in this division, not just oaks. The independent species model (ISM) treated species as completely independent entities wherein WD values were not related to each other. That is, the ISM treated species as root nodes and no information was borrowed between species such that the WD of data-poor species was not informed by other species. We compared the results of the four models to explore the utility of incorporating phylogenetic or taxonomic information for estimating species-level WD values, and to evaluate the relative importance of study effects (e.g. potential environmental, site, or population effects) vs. evolutionary history.

Below we describe the important aspects of the HB meta-analysis, including: (i) the WD data model, (ii) the process model that incorporated covariate effects to obtain the standardized WD values, (iii) the data models for the covariates that provided a mechanism for estimating missing covariate data, (iv) the four different approaches to model the species-specific standardized WD values and (v) the parameter models

that specified priors for all remaining model parameters. Figure 2 provides a graphical representation of the HB meta-analysis model.

WD data model

The WD data model included the likelihoods of the reported WD sample means, standard errors and sample sizes. We assumed that the WD sample mean (\bar{y}_i) reported for record $i = 1, 2, \dots, 1766$ was normally distributed such that:

$$\bar{y}_i \sim \text{Normal}\left(\mu_i, \frac{\sigma^2}{N_i}\right) \quad \text{eqn 1}$$

The \bar{y}_i were assumed conditionally independent given the record-level 'true' (expected) WD value (μ_i), the population-level variance (σ^2) and the reported sample size (N_i). We explored allowing σ^2 to vary by sample type (i.e. core, disc, core section or disc section), but σ^2 did not differ between sample types, thus we assumed a common σ^2 that quantified uncertainty in the reported WD values due to observation error and intraspecific variability within a site.

The unknown σ^2 was partly informed by the record-level N_i and standard errors (se_i). Not all studies reported N and se , thus we treated these quantities as stochastic, as done for \bar{y}_i , to obtain the posterior distributions of their missing values. Assuming that individual WD measurements were normally distributed, then according to distribution theory, se_i^2 followed a gamma distribution with parameters that depended on N_i and σ^2 (Ogle, Barber & Sartor 2013). For N_i , we assumed that a minimum of two observations were obtained, which would allow for the calculation of an associated se_i , and we assumed that $N_i - 2$ followed a Poisson distribution.

Note, in subsequent text, for ease of presentation, we often dropped subscripts when referring to particular quantities, but we always explicitly indicated subscripts (when relevant) in equations.

Process model

We specified a relatively simple process model for μ_i in Eqn (1) that incorporated the effects of record-level covariates (see Fig. 2b) such as mean latewood proportion (L_i ; $0 \leq L \leq 1$) and mean moisture content (W_i , g water g⁻¹ wood; $W \geq 0$) of the WD mass measurement:

$$\mu_i = \phi_{j(i),s(i)} \cdot (1 + W_i) \cdot (\beta_{T(i)} + L_i \cdot (1 - \beta_{T(i)})) \quad \text{eqn 2}$$

$\phi_{j,s}$ denoted the standardized 'latent' WD value for study (j) and species (s) associated with record i , denoted $j(i)$ and $s(i)$, and it could be thought of as a study random effect. Specifically, ϕ represented the latent WD in terms of grams dry weight (at $W = 0$) per fresh volume (cm³) of latewood (at $L = 1$; for ring-porous and softwood) or bulkwood (for diffuse-porous since $\beta = 1$). The term $(1 + W)$ simply converted from the latent WD to the moisture content (W) associated with the reported WD value for record i . The expression involving β and L adjusted for the observed latewood proportion of record i , and it was derived by assuming that the WD of earlywood was proportional to the WD of latewood, with the constant of proportionality given by β ; if $\beta = 1$, then the WD of latewood was equal to that of earlywood, and if $\beta < 1$, then earlywood was less dense than latewood. We allowed β to vary by wood type (T), where T was a species (s) trait; we set $\beta = 1$ for diffuse-porous species as L was difficult to measure and was never reported for this wood type, and we estimated β for ring-porous and softwood species. We explored incorporating an effect of whether extractives were removed or not, but this effect was not significant and thus was not included in the model for simplicity.

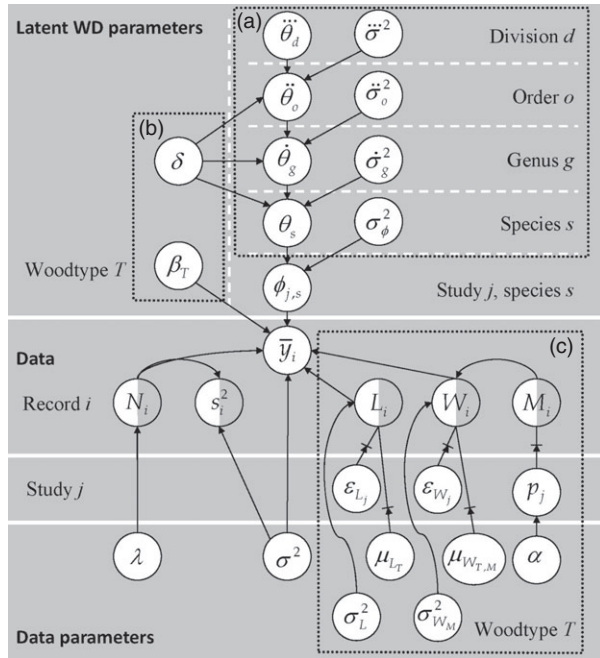


Fig. 2. Graphical representation of the hierarchical Bayesian (HB) meta-analysis model. Each circle is a stochastic node (data or parameters) defined by an underlying distribution. The edges (arrows) indicate conditional relationships between nodes; for example, the distribution of N (sample size) depends on λ , a parameter in the Poisson likelihood for N . Key model components include: (a) model for the species-specific latent wood density (θ_s), where the taxonomy model (TM) version is shown; (b) covariate effects describing the effects of wood type (δ) and latewood proportion (β), where β varies by wood type (T); and (c) covariate models for L , W and M (see Appendix S2 for a detailed description). The valves (\rightarrow) in (c) depict feedback control such that the covariate parameters are only informed by observed covariate data (white region of node), thus missing covariate data (gray region of node) and associated wood density data (\bar{y}) do not influence the covariate parameters.

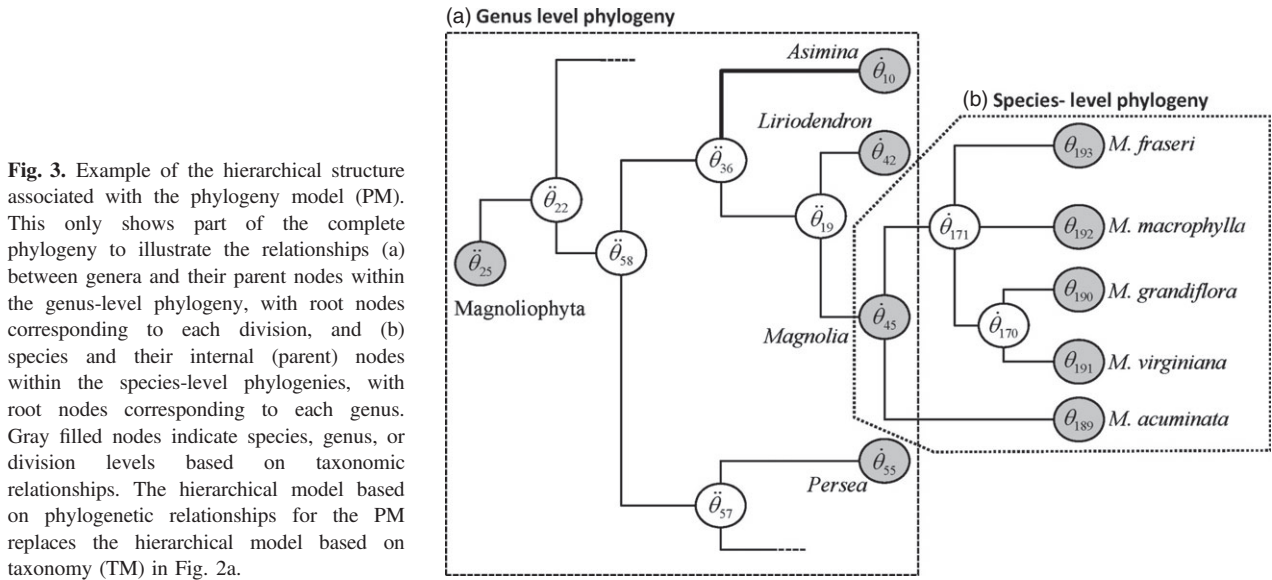


Fig. 3. Example of the hierarchical structure associated with the phylogeny model (PM). This only shows part of the complete phylogeny to illustrate the relationships (a) between genera and their parent nodes within the genus-level phylogeny, with root nodes corresponding to each division, and (b) species and their internal (parent) nodes within the species-level phylogenies, with root nodes corresponding to each genus. Gray filled nodes indicate species, genus, or division levels based on taxonomic relationships. The hierarchical model based on phylogenetic relationships for the PM replaces the hierarchical model based on taxonomy (TM) in Fig. 2a.

Covariate data models

We treated missing covariate values as stochastic and assumed likelihoods for each to obtain posterior predictive distributions for each missing value (Ogle, Barber & Sartor 2013). These stochastic values were generated within the MCMC simulation procedure and subsequently used in the WD process model in Eqn (2). Here we summarized the models for L , W and moisture content type (M) (see Fig. 2c). As wood types differed in their cellular anatomy and wood structure, we assumed that L and W depended on wood type (T). We modelled L on the logit scale and W on the log scale to obey the constraints $0 \leq L \leq 1$ and $W \geq 0$, which was important for estimating missing L and W values. We assumed that $\text{logit}(L)$ and $\log(W + 1)$ followed normal distributions, and the mean of each distribution was decomposed into a fixed effect that varied by T (μ 's in Fig. 2c) plus a random effect for each study (ϵ 's in Fig. 2c). Given data limitations, a common variance was assumed for all L records, but the variance for W was allowed to vary by M . Finally, M could take-on one of four possibilities (air dry, green, oven dry, or saturated), and we assumed that M followed a categorical distribution—analogueous to a multinomial distribution with the total number of ‘trials’ equal to one—with a probability vector (e.g. p , Fig. 2c) whose elements varied by study, which essentially allowed for a study random effect. See Appendix S2 for a detailed description of the covariate data models.

Hierarchical models for species-specific parameters

The study by species latent WD ($\phi_{j,s}$) in Eqn (2) was assumed to vary around a species-level latent WD (θ_s ; g cm^{-3}) according to a normal hierarchical model:

$$\phi_{j,s} \sim \text{Normal}(\theta_s, \sigma_\phi^2)^+ \quad \text{eqn 3}$$

The variance σ_ϕ^2 described study-to-study variation in latent WD within each species, and for simplicity, we assumed that σ_ϕ was the same for all species. We used the superscript $+$ notation, e.g. $x \sim \text{Normal}(a,b)^+$, to indicate that the normal distribution was truncated at zero such that x could only take-on positive values; thus, in Eqn (3) ϕ was restricted to positive values.

Similar to $\phi_{j,s}$, θ_s was interpreted as the species-level latent WD of dry latewood, but we also wished to obtain estimates of the latent WD for dry bulkwood (ω_s , g cm^{-3}). This was done by evaluating Eqn (2) at the mean latewood proportion for each wood type (\bar{L}_T), setting $W = 0$, and replacing $\phi_{j,s}$ with θ_s to obtain the species-level dry bulkwood estimates:

$$\omega_s = \theta_s \cdot (\beta_{T(s)} + \bar{L}_{T(s)} \cdot (1 - \beta_{T(s)})) \quad \text{eqn 4}$$

Note that $\omega_s = \theta_s$ for diffuse-porous species as they had $\beta = 1$. Analogs of Eqn (4) could be applied to obtain the latent bulkwood WD estimates for other taxonomic levels (genus, division, etc.) by replacing θ_s with the appropriate parameter. Next we described the four different approaches to modelling θ_s ; we began with the phylogeny model (PM) and ended with the independent species model (ISM).

Phylogeny model. In the *phylogeny* model (PM), θ_s in Eqn (3) was modelled hierarchically based on the species- and genus-level phylogenies (see Fig. 3 and Appendix S1). Each θ_s was assumed to vary around a mean that depended on its parent (ancestral) node, and the variability among species given their parent node latent WD was allowed to differ according to their genus affiliation (see Fig. 3):

$$\theta_s \sim \text{Normal}(\delta_s^* \cdot \dot{\theta}_{pn(s)}, \dot{\sigma}_{g(s)}^2)^+ \quad \text{eqn 5}$$

δ_s^* (defined below) accounted for evolutionary transitions in wood type (T), and $\dot{\theta}_{pn(s)}$ was the standardized WD for parent node (pn) associated with species (s). The variability among species having the same parent node was captured by $\dot{\sigma}_{g(s)}^2$, which was allowed to differ according to the genus g associated with species s . We allowed for 17 different variances at the genus level; the first 16 were associated with genera containing five or more species, and the mean standard deviation (squared) across these 16 genera defined the 17th variance term, which was applied to the remaining 70 genera.

Let $T(s)$ and $T(pn(s))$ indicate the wood types associated with child node (species) s and its parent node pn , respectively, then δ_s^* in Eqn (5) is defined as:

$$\delta_s^* = \begin{cases} \delta & \text{if } T(s) = RP \text{ and } T(pn(s)) = DP \\ \delta^{-1} & \text{if } T(s) = DP \text{ and } T(pn(s)) = RP \\ 1 & \text{if } T(s) = T(pn(s)) \end{cases} \quad \text{eqn 6}$$

Thus, $\delta^* = \delta$ if the ancestral (parent) node was diffuse porous (DP) but the child node (here, species) was ring porous (RP); $\delta^* = 1/\delta$ if the parent node was RP, but the child node was DP; $\delta^* = 1$ if the wood type of the parent and child nodes were the same. $\delta^* = 1$ for all *Coniferophyta* (softwood), so wood type transitions were only relevant for the *Magnoliophyta*. Within the *Magnoliophyta*, the basal parent node (root node) was defined as being diffuse-porous, and the assignment of wood types to each genus and the internal nodes in the genus-level phylogeny is shown in Appendix S1. Note, δ was a scalar parameter (to be estimated); $\delta < 1$ indicated that ring-porous latewood was less dense than that of diffuse-porous latewood, and $\delta > 1$ indicated the opposite. Based on Eqn (4), the relative difference in bulk-wood WD between ring- vs. diffuse-porous wood (δ_ω) is given by $\delta_\omega = \delta \cdot (\beta_{RP} + \bar{L}_{RP} \cdot (1 - \beta_{RP}))$.

Next, we defined a hierarchical model for the standardized WD values associated with each internal (parent) node (θ_{pn}) of the species-level phylogeny (Fig. 3b) and their corresponding root nodes that defined the genus affiliation. The model for θ_{pn} is analogous to Eqn (5) such that each θ_{pn} is assumed to come from a normal distribution with a mean given by its parent node. Note that pn was simply an indexing variable, and nodes 1, 2, 3, ..., 86 represented the genus-level root nodes of each species-level phylogeny, which we indexed by g , and nodes 87, 88, ..., 179 represented internal nodes, which we indexed by z such that:

$$\theta_z \sim \text{Normal}(\delta_z^* \cdot \theta_{pn(z)}, \hat{\sigma}^2) \quad \text{eqn 7}$$

The variation in latent WD between internal nodes nested in the same parent node was described by $\hat{\sigma}^2$, and we assumed a common variance for the internal nodes. Again, $pn(z)$ indicates the parent node of node z , and δ_z^* is defined in Eqn (6), with z replacing s .

We modelled the genus-level values as varying around a mean given by the parent node associated with each genus (determined by the genus-level phylogenies, Fig. 3a), denoted $\theta_{pn(g)}$, such that for genus $g = 1, 2, 3, \dots, 86$:

$$\theta_g \sim \text{Normal}(\delta_g^* \cdot \theta_{pn(g)}, \hat{\sigma}_{o(g)}^2) \quad \text{eqn 8}$$

The variability between genera given their parent node was captured by $\hat{\sigma}_{o(g)}^2$, which we allowed to differ depending on the order o that genus g was nested in. In total, 11 order-level variance terms corresponded to orders with at least three genera; the 12th was based on the mean standard deviation across the 11 orders, which was applied to all other 15 orders. δ_g^* is defined in Eqn (6), with g replacing s .

Finally, we defined a hierarchical model for the internal nodes of the genus-level phylogeny similar to that for the internal nodes of the species-level phylogenies. The genus-level phylogeny (Fig. 3a) was also associated with one of two root nodes corresponding to the division that each genus belonged. We assigned non-informative normal priors to the division-level root nodes such that for $z = 1, 2, \dots, 70$ nodes were associated with the genus-level phylogeny:

$$\begin{aligned} \theta_z &\sim \text{Normal}(\delta_z^* \cdot \theta_{pn(z)}, \hat{\sigma}^2) \quad \text{for } z \text{ an internal node} \\ \theta_z &\sim \text{Normal}(0, 10000)^+ \quad \text{for } z \text{ a root node} \end{aligned} \quad \text{eqn 9}$$

For simplicity, we assumed a common variance ($\hat{\sigma}^2$) that described the variability between internal nodes. δ_z^* is defined in Eqn (6), with z replacing s .

Taxonomy model. For the taxonomy model (TM), θ_s was modeled similar to the PM, but the hierarchical structure was based on taxonomic relationships (see Fig. 2a). Here, species (s) were nested in genus (g), genera in order (o), order in the division (d), and divisions were again treated as root nodes:

$$\theta_s \sim \text{Normal}(\delta_s^* \cdot \theta_{g(s)}, \hat{\sigma}_{g(s)}^2)^+ \quad \text{eqn 10}$$

$$\theta_g \sim \text{Normal}(\delta_g^* \cdot \theta_{o(g)}, \hat{\sigma}_{o(g)}^2)^+ \quad \text{eqn 11}$$

$$\theta_o \sim \text{Normal}(\delta_o^* \cdot \theta_{d(o)}, \hat{\sigma}_{d(o)}^2)^+ \quad \text{eqn 12}$$

$$\theta_d \sim \text{Normal}(0, 10000)^+ \quad \text{eqn 13}$$

The variances in Eqn (10) and (11) are modeled the same as in the PM such that there were 17 $\hat{\sigma}_g^2$ terms that described variability between species within a genus, and 12 $\hat{\sigma}_o^2$ terms that described variability between genera within an order. We assumed a common variance ($\hat{\sigma}^2$) for the variability between orders, and we bypassed the family level because there were too few families in each order. δ^* is defined in Eqn (6), where the parent node is given by the identity of the higher taxonomic level; for example, for species s , $pn(s) = g(s)$.

Division-level model. For the division-level model (DM), the only information used to construct the hierarchical model for θ_s was the division affiliation; for division d associated with species s :

$$\theta_s \sim \text{Normal}(\delta_s^* \cdot \theta_{d(s)}, \hat{\sigma}_{d(s)}^2)^+ \quad \text{eqn 14}$$

We assumed a division-level variance $\hat{\sigma}_d^2$ that described the variability between species within each division, and we assigned non-informative normal priors to the division-level latent WD (θ_d) analogous to Eqn (13); δ^* is defined in Eqn (6), with $pn(s) = d(s)$.

Independent species model. The independent species model (ISM) treated each θ_s as a root node and assigned each an independent, non-informative normal prior: $\theta_s \sim \text{Normal}(0, 10\,000)^+$. That is, there was no borrowing of strength between species. The ISM was somewhat analogous to treating θ_s as a fixed effect, whereas the PM, TM and DM essentially treated θ_s as a random effect.

Priors for remaining parameters

We defined relatively non-informative priors for the remaining parameters in the above HB meta-analysis model following the approaches employed in Ogle, Barber & Sartor (2013). We provided a detailed description of the priors in Appendix S2.

Implementation

The above model components were combined to obtain the posterior distribution(s) of the standardized latent WD values, covariate effects, covariate parameters, variance terms and missing covariate data. To avoid unrealistic feedback between model parameters and missing data, we modularized (Liu, Bayarri & Berger 2009; Lunn *et al.* 2009a) the covariate models as done in Ogle, Barber & Sartor (2013) (Fig. 2c). The HB meta-analysis was implemented in OpenBUGS (version 3.2.2) (Lunn *et al.* 2009b), and the built-in 'cut' function was used to control unrealistic feedbacks (Lunn *et al.* 2009a) between the covariate parameters and the missing covariate data; the model code for the PM is given in Appendix S3.

OpenBUGS employed Markov chain Monte Carlo (MCMC) to sample from the posterior distribution. The PM, TM, DM and ISM were run with three parallel MCMC chains. The chains were monitored for convergence using the built-in Brooks-Gelman-Rubin (BGR) diagnostic tool. After an initial burn-in period (>10 000 iterations), the chains were run for more than 350 000 iterations, and were thinned every 10th iteration to reduce storage requirements and were within chain autocorrelation. A post burn-in posterior sample size greater than 100 000 was used for computing posterior statistics.

Model comparisons and cross-validation

We employed a combination of graphical and quantitative approaches to compare the four models (PM, TM, DM, ISM) to explore the influence of borrowing of strength between species. For each model, we computed the correlation coefficient (R^2) from a regression of observed vs. predicted WD (to evaluate overall model fit) and the posterior predictive loss (D_∞) (Gelfand & Ghosh 1998). The model with observed vs. predicted values that fell around the 1:1 line had the highest R^2 , and the lowest D_∞ was deemed the 'best' model.

We also conducted cross-validation analyses by removing WD data for a subset of species, thus creating 'reduced' data sets. To create the reduced data sets, we removed WD observations for four 'target' species, including two ring-porous (*Ilex opaca* and *Carpinus caroliniana*) and two softwoods (*Pseudotsuga menziesii* and *Pinus taeda*). These species were selected because they represented both divisions, included both data-rich (*P. taeda*, *P. menziesii*) and comparatively data-poor species (*I. opaca*, *C. caroliniana*), and they belonged to genera that included many species (*Pinus*) or few species (*Pseudotsuga*, *Ilex*, *Carpinus*). For example, *I. opaca* ($n = 4$ records) and *C. caroliniana* ($n = 5$) were the only representatives of their genera amongst our 305 species. Conversely, *P. menziesii* was associated with many observations ($n = 100$), but it occurred in a genus that supported one other species (*P. macrocarpa*) and two subspecies of *P. menziesii*. *P. taeda* was also a data-rich species ($n = 87$), but it occurred in a genus with 41 other species. The 'base-line' standardized bulkwood WD (ω_s) was obtained for each species by running each model with the full data set. Then, ω_s estimates were obtained again by re-running each model four times using the reduced datasets created by removing data for the target species (data were removed for one species at a time). We also compared the ability of each model to predict the data that were removed.

Results

MODEL FITS AND COMPARISONS

The phylogeny model (PM), taxonomy model (TM), division-level model (DM) and independent species model (ISM) fit the observed WD data equally well; regressions of the predicted vs. observed WD data yielded $R^2 = 0.93$ for all four models (Fig. 4). Moreover, the uncertainty associated with the WD predictions was nearly identical among the four models (Fig. S1). The posterior predictive loss (D_∞) (Gelfand & Ghosh 1998) suggested that all four models were equally acceptable given their similar D_∞ values [$D_\infty = 6.078$ (PM), 6.082 (TM), 6.082 (DM) and 5.975 (ISM)]. Thus, R^2 and D_∞ did not provide strong support for one model over the other.

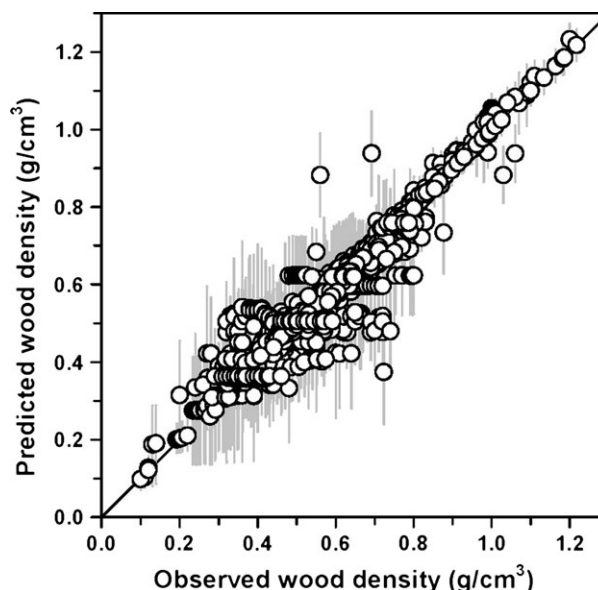


Fig. 4. Predicted vs. observed wood density (WD) for the phylogeny model (PM) ($R^2 = 0.93$, $y = 0.0334 + 0.9362x$). The observed vs. predicted results for the PM are nearly identical to those obtained for the taxonomy model (TM), the division-level model (DM) and the independent species model (ISM). Predicted values are the posterior medians and 95% credible intervals (gray whiskers) of the replicated WD data. The diagonal line represents the 1:1 line.

MODEL CROSS-VALIDATION

Comparison of the base-line (for the complete dataset) posterior estimates of the latent bulkwood WD (ω_s , Eqn (4)) with those obtained from the reduced data sets (created by discarding data for individual target species) indicated that the PM, TM and DM performed better than the ISM (Fig. 5). The ISM yields were highly uncertain and/or biologically unrealistic estimates of ω_s for the species that were removed from the data set; their posterior medians for ω_s spanned 0.47 to 30.66 cm^{-3} and the 95% credible interval (CI) widths ranged from 2.09 to 85.84 g cm^{-3} (see Fig. 5d insert). The posterior distributions for θ_s , and thus ω_s , for species not represented in the data base were strongly influenced by the prior that was specified for θ_s under the ISM.

For the PM, TM and DM, the posterior medians for ω_s for each target species obtained from the reduced data sets were similar to the base-line values (Fig. 5a–c). That is, the 95% CI for the reduced dataset ω_s values contained the corresponding base-line posterior median, and the 95% CI for the base-line ω_s contained the posterior median for the reduced data set for all species except *C. caroliniana* (Fig. 5a–c). Moreover, although the 95% CIs for these models were wider under the reduced data sets when compared with the complete data set, they spanned biologically realistic values and were notably narrower than the ISM CIs. The PM, TM and DM provided nearly identical estimates of ω_s (medians and 95% CIs) for the reduced data set, for all four species; although, the DM tended to slightly underestimate ω_s for *C. caroliniana* and *I. opaca* relative to the base-line. The PM and TM both produced relatively wide CIs for ω_s of *C. caroliniana* and

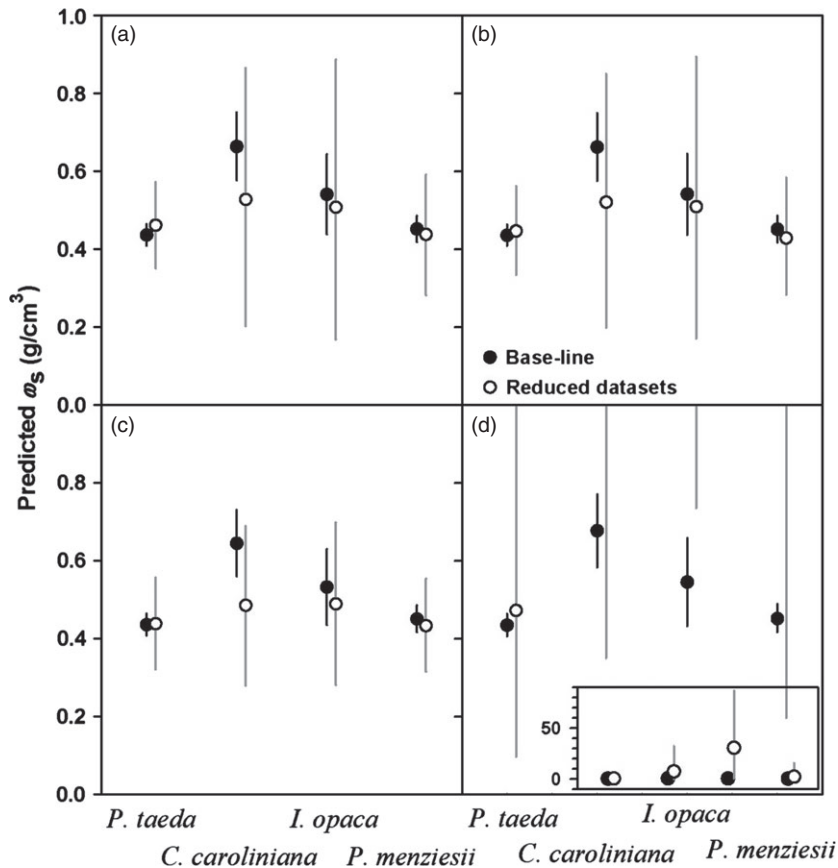


Fig. 5. Posterior medians and 95% credible intervals (CIs) for standardized bulkwood wood density (ω_s ; g cm^{-3}) obtained from the cross-validation analyses that removed records for *Pinus taeda* [data-rich ($n = 124$ records) softwood from a specious genus], *Pseudotsuga menziesii* ($n = 100$, softwood from a genus that contains two species and two subspecies), *Ilex opaca* [relatively data-poor ($n = 4$), diffuse porous], or *Carpinus caroliniana* ($n = 5$, diffuse porous); the latter two are the only species in their genera. Results are shown for (a) the phylogeny model (PM), (b) the taxonomy model (TM), (c) the division-level model (DM) and (d) the independent species model (ISM). The filled circles depict the base-line ω_s values (complete data set); open circles depict the ω_s values when the target species was removed (reduced datasets). The inset in (d) rescales the y-axis to contain the 95% CIs for the reduced data set estimates.

I. opaca when compared with the DM. All four models yielded narrower CIs for the two *Coniferophyta* species when compared with the two *Magnoliophyta* species.

The PM, TM and DM also predicted the removed data equally well. The mean (or median) absolute error (AE)—absolute difference between the observed WD value and the corresponding predicted value—ranged from about 0.07 to 1.42 g cm^{-3} (Table 2). Conversely, with the exception of *P. taeda*, the ISM produced huge AE values, ranging from 3.4 to 81.6 g cm^{-3} for the other three species, thus spanning biologically unrealistic WD values. Similarly, the uncertainty associated with the predicted WD was relatively low for the PM, TM and DM, with the mean (or median) 95% CI widths spanning 0.06 to 1.21 g cm^{-3} , whereas the ISM model produced 95% CI widths that were 1–3 orders of magnitude wider (Table 2).

COVARIATE EFFECTS

The woodtype effect (δ , Eqn (6)) was only relevant to the PM, TM and DM. The posterior median for δ (and δ_{ω} for bulkwood) was consistently greater than one across all three models (Fig. 6a), indicating that within the *Magnoliophyta*, diffuse-porous wood was potentially less dense than ring-porous wood. However, δ (and δ_{ω}) was only significantly greater than one (95% CI did not contain one) for the DM.

Likewise, the estimates of the latewood effect (β Eqn (2)) were generally consistent across all four models, with the

exception of the ISM yielding slightly lower estimates of β for ring-porous species (Fig. 6b). All models indicated that $\beta < 1$, and β of softwoods was significantly lower than that of ring-porous species. In particular, latewood was about 1.9 times denser than earlywood in softwoods ($1/\beta \cong 1/0.52 = 1.9$, Fig. 6b). Although the difference between latewood and earlywood was less pronounced in ring-porous wood, latewood was still about 1.1 times denser than earlywood ($1/\beta \cong 1/0.91 = 1.1$, Fig. 6b). Recall, β was not estimated for diffuse-porous wood given the lack of L data.

SOURCES OF VARIATION

To evaluate the potential role of environmental vs. evolutionary history, we focused on the associated variance terms obtained from the PM and DM (the TM and PM results are nearly identical). The DM suggested that environmental (or site, study, or methodological) factors and evolutionary history explained a comparable amount of the variation in WD (Fig. 7b). That is, the variation between studies within species (posterior median for $\sigma_{\phi} = 0.079 \text{ g cm}^{-3}$; Eqn (3)) was only marginally lower than the variation between species within a division (posterior median for $\sigma = 0.103$ and 0.088 g cm^{-3} for *Magnoliophyta* and *Coniferophyta*, respectively; Eqn (14), Fig. 7b). The PM suggested that the variation between species within a genus ($\hat{\sigma}$, Eqn (5)) and between genera with an order ($\hat{\sigma}$, Eqn (8)) might differ between genera and orders respectively. For example, the posterior medians for $\hat{\sigma}$ spanned

0.017 g cm⁻³ (*Populus*) to 0.108 g cm⁻³ (*Cupressus*), and $\bar{\sigma}$ spanned 0.066 g cm⁻³ (Pinales) to 0.356 g cm⁻³ (Ebenales) (Fig. 7a).

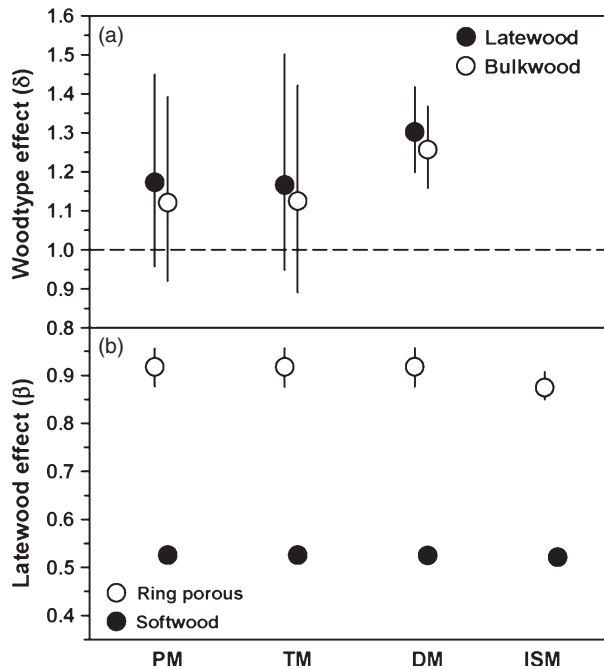


Fig. 6. Posterior medians and 95% credible intervals: (a) the wood type effect that describes the relative difference in wood density (WD) of diffuse- vs. ring-porous wood for latewood (δ , Eqn (6)) and for bulkwood (δ_w) within the *Magnoliophyta* and (b) the latewood effect (β , Eqn (2)) that describes the relative difference in WD of latewood vs. earlywood, which is only relevant for softwoods and ring-porous species. Results are shown for the phylogeny model (PM), taxonomy model (TM), division-level model (DM) and independent species model (ISM). The horizontal dashed line at 1.0 in (a) indicates the lack of an effect. If $\delta < 1$ then ring-porous wood is less dense than diffuse-porous wood; $\delta > 1$ implies the opposite. If $\beta < 1$ then earlywood is less dense than latewood; $\beta > 1$ implies the opposite.

Table 2. Cross-validation statistics for the records that were removed from the wood density (WD) dataset. All data for each of the four species (below) were removed (one species at a time), and the absolute error (AE, g cm⁻³) was computed as the absolute value of the difference between the observed WD value and the posterior median of the corresponding record-level predicted value. The 95% credible interval (CI) width (g cm⁻³) for each predicted value was also recorded. The mean and median AE and CI width were computed across the records that were removed for each species. Results are shown for the phylogeny model (PM), taxonomy model (TM), division-level model (DM), and independent species model (ISM)

	PM		TM		DM		ISM	
	AE	CI width	AE	CI width	AE	CI width	AE	CI width
<i>Pinus taeda</i>								
Mean	0.096	0.413	0.092	0.414	0.089	0.419	0.094	2.205
Median	0.078	0.398	0.078	0.400	0.078	0.404	0.079	2.137
<i>Carpinus caroliniana</i>								
Mean	0.152	1.015	0.157	0.988	0.178	0.734	9.358	46.771
Median	0.194	0.827	0.201	0.800	0.235	0.588	7.916	38.229
<i>Ilex opaca</i>								
Mean	0.203	0.062	1.421	1.212	0.161	0.848	81.570	140.995
Median	0.196	0.064	1.359	1.149	0.158	0.780	80.912	131.463
<i>Pseudotsuga menziesii</i>								
Mean	0.108	0.523	0.104	0.509	0.107	0.464	3.682	19.717
Median	0.070	0.480	0.067	0.465	0.069	0.427	3.428	18.163

Although the variation attributed to study within species (posterior median for $\sigma_\phi = 0.078$ g cm⁻³ for the PM) was higher than the variation among species within a genus ($\bar{\sigma}$) for 12 of the 16 diverse genera (Fig. 7a), the relatively high uncertainty (wide 95% CIs) for most $\bar{\sigma}$ indicated that $\bar{\sigma}$ could potentially be of a similar order of magnitude as σ_ϕ . However, the variation among genera within an order ($\bar{\sigma}$) was significantly greater than σ_ϕ for genera in Ebenales and orders supporting less than three genera (Fig. 7a). Moreover, the widest CIs for $\bar{\sigma}$ tended to occur for genera supporting relatively few species, such as *Cupressus* and *Cercocarpus* (five species each), and the narrowest for diverse genera such as *Pinus* and *Quercus* (42 and 47 species, respectively; see Fig. 7a and Fig. S2 in the Supporting Information). The relationship between the uncertainty in $\bar{\sigma}$ was even more strongly related to clade size (i.e. the number of genera within an order) such that the widest CI for $\bar{\sigma}$ occurred for Ebenales (three genera) and the narrowest for Pinales (14 genera, most diverse) (Fig. 7a and Fig. S2).

SPECIES-SPECIFIC STANDARDIZED WOOD DENSITY ESTIMATES

We focused on the standardized bulkwood WD (ω_s , Eqn (4)) estimates yielded by the PM and DM (results for the PM and TM were very similar). One goal of the HB meta-analysis was to obtain species-specific ω_s estimates for all 305 U.S. tree species, and we provided these estimates in Table S1. Across the 141 species represented in the WD data set (Fig. 8a–c), *Rhizophora mangle* had the least dense wood [posterior median for $\omega_s = 0.164$ g cm⁻³ (PM) and 0.242 g cm⁻³ (DM)] and *Quercus virginiana*, *Maclura pomifera* and *Diospyros virginiana* had the densest wood [posterior medians for ω_s spanned 0.704 to 0.785 g cm⁻³ (PM) and 0.75 to 0.805 g cm⁻³ (DM); Table S1]. Across all models, the softwood species tended to have the lowest ω_s , which ran-

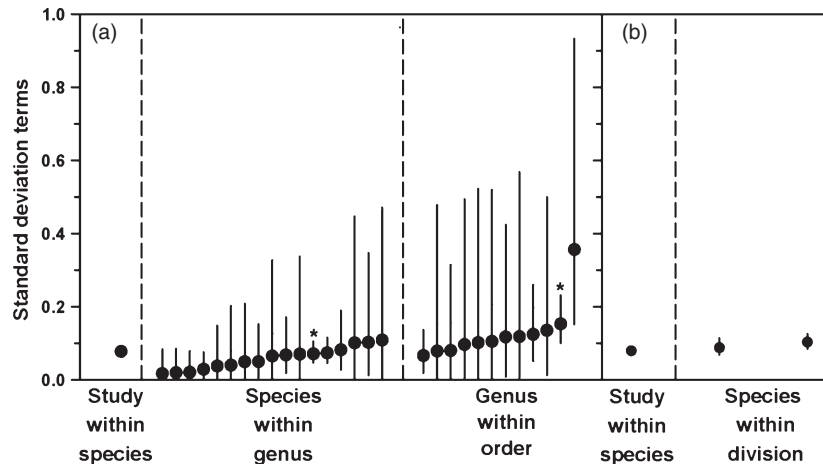


Fig. 7. Posterior medians and 95% credible intervals for standard deviations describing sources of variation affecting wood density (WD) for: (a) the phylogeny model (PM) and (b) the division-level model (DM). Dotted vertical lines separate different sources. The left-most symbol in (a) and (b) represents the variation explained by studies within species (σ_ϕ , Eqn (3)). The middle group of 17 symbols in (a) represent variation among species within a genus (σ , eqn (5)), ordered from lowest to highest σ : *Populus* (lowest), *Abies*, *Carya*, *Quercus*, *Fraxinus*, *Magnolia*, *Betula*, *Ulmus*, *Juniperus*, *Acer*, *Prunus*, mean σ across the 16 genera (with asterisk), *Pinus*, *Picea*, *Cercocarpus*, *Juglans* and *Cupressus* (highest). The right-most group of 12 symbols in (a) represent variation among genera within an order (σ , Eqn (8)), ordered from lowest to highest σ : Pinales, Magnoliales, Fabales, Ericales, Rosales, Laurales, Urticales, Scrophulariales, Fagales, Sapindales, mean σ across the 11 orders (with asterisk) and Ebenales. The right-most group of two symbols in (b) represent variation among species within a division (σ , Eqn (14)), with the lowest for *Coniferophyta* and the highest for *Magnoliophyta*.

ged from 0.329 (*Thuja occidentalis*) to 0.605 g cm⁻³ (*Taxus brevifolia*) (PM; Fig. 8c and Table S1). The ω_s estimates for ring-porous species were generally highest, ranging from 0.429 (*Catalpa speciosa*) to 0.785 g cm⁻³ (*D. virginiana*) (PM; Fig. 8b and Table S1). The diffuse-porous species spanned the widest range in median ω_s values, from 0.164 (*R. mangle*) to 0.668 g cm⁻³ (*Cornus florida*) (PM; Fig. 8a and Table S1). Across all wood types, the PM and DM produced similar estimates (medians and 95% CIs) of the species-specific ω_s (Fig. 8a–c).

Both the PM and DM produced realistic median estimates of ω_s for the 164 data-poor species, which spanned 0.135 to 0.638 g cm⁻³ for the PM and 0.240 to 0.627 g cm⁻³ for the DM (Fig. 8d–f). The DM, however, predicted that all species within a particular wood type had very similar ω_s (see narrow range of ω_s median values, Fig. 8d–f) and the uncertainty in the predicted ω_s was consistent across all species (see CI widths, Fig. 8d–f). Conversely, the PM produced species-specific posterior medians and 95% CI widths for ω_s that were more variable across species (Fig. 8d–f). Additionally, under the PM, the range of median ω_s values was greatest for the diffuse- and ring-porous species (Fig. 8d,e), and was generally lower for the softwoods (Fig. 8f), which paralleled the results obtained for the data-rich species (Fig. 8a–c). The ISM yielded unrealistic estimates for ω_s that reflected the influence of the non-informative priors for $\hat{\theta}$ (results not shown).

Discussion

Wood density (WD) is an important plant functional trait that is a determinant of tree biomass and carbon storage potential (Chave *et al.* 2006, 2009). Species-level WD estimates are

often required by tree growth and survival models, especially physiologically based models (Ogle & Pacala 2009). However, obtaining field-derived estimates of WD may be difficult and logistically restrictive if desired for many species, as might be required by a regional forest simulator. Thus, we draw-upon the large body of published WD values compiled in the Tree-Traits data base (Kattge *et al.* 2011; Ogle, Barber & Sartor 2013), which included 1766 WD sample means ('records') derived from about one million samples (based on a combination of reported and estimated sample sizes). The WD data in the TreeTraits data base is complimented by information on covariates—such as latewood proportion and moisture content—that are important for estimating species-specific WD that is standardized for moisture content and latewood proportion. Below, we highlight the unique and important contributions of the HB meta-analysis that we employed to synthesize these WD data, which leads us to highlight the potential importance of incorporating taxonomic or phylogenetic information into such analyses. We follow this with a discussion of the species-specific patterns in WD revealed by this analysis, and subsequently, the potential roles of evolutionary history vs. environmental drivers of variation in WD.

MODELING FRAMEWORK OVERVIEW

Flores & Coomes (2011) describe a Bayesian analysis that employs a hierarchical parameter model for species-specific WD that is somewhat analogous to our taxonomy model (TM). However, their approach was not intended to address the issues that we encountered when analyzing information extracted from the literature. We implemented a hierarchical Bayesian (HB) meta-analysis that overcomes several limitations

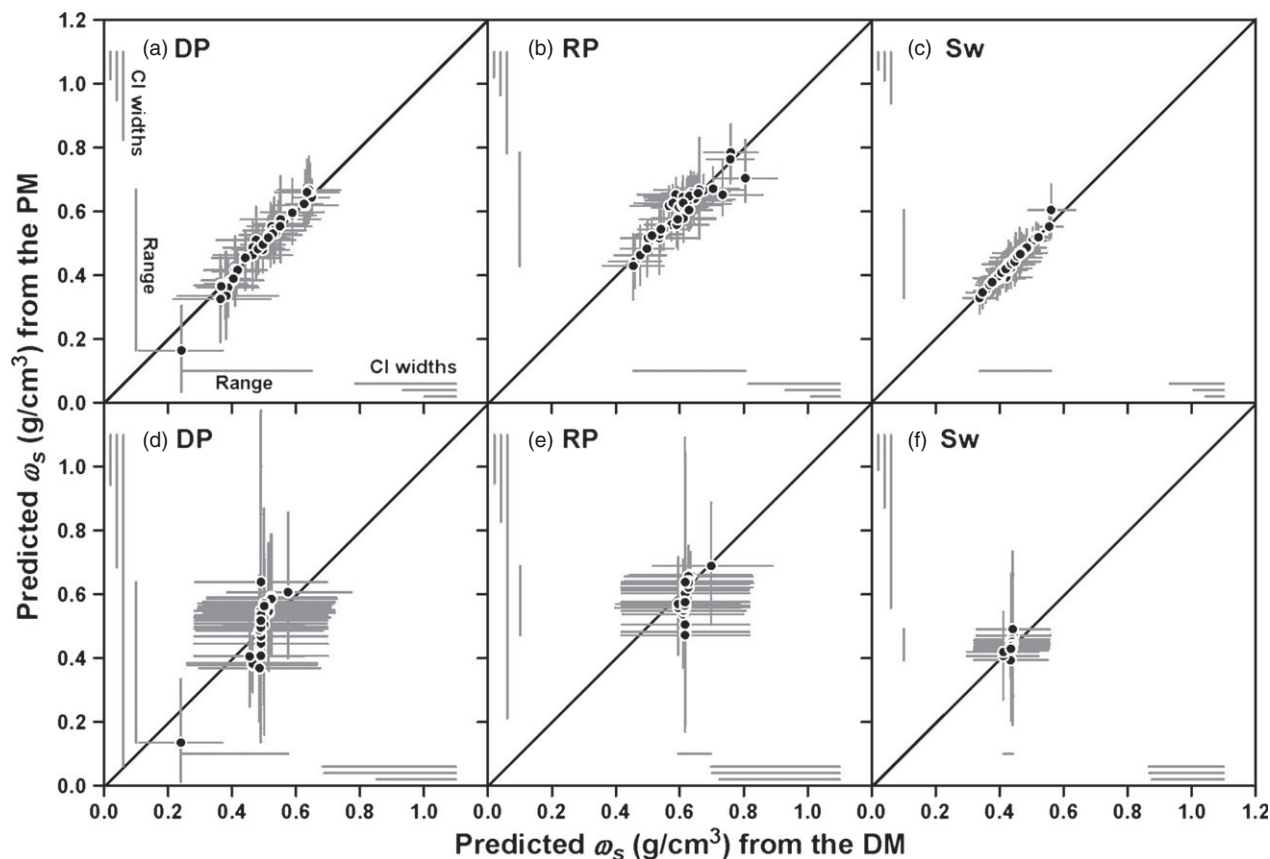


Fig. 8. Posterior medians and 95% credible intervals (CIs) for the species-level standardized bulkwood wood density (WD) (ω_s , g cm^{-3} ; Eqn (4)) estimates obtained from the phylogeny model (PM) and the division-level model (DM). Species are grouped by wood type and representation in the data base: (a, d) diffuse-porous (DP), (b, e) ring-porous (RP), (c, f) softwood (Sw) and (a–c) species for which WD data were reported and (d–f) species lacking WD records in the data base. In each panel, the range of species-level ω_s estimates is depicted for the PM and DM, which represents the difference between the maximum (highest median) and minimum (lowest median) ω_s across the species represented in each panel. Variation in the CI widths, an index of uncertainty, is also depicted such that the group of three bars for the PM (vertical bars, upper right corners) and DM (horizontal bars, lower left corners) denote the narrowest, median and widest CI across the species represented in each panel.

of traditional meta-analysis methods (Rosenberg, Adams & Gurevitch 2000), as discussed in Ogle, Barber & Sartor (2013). Unique to our approach is the ability to simultaneously estimate WD for data-poor species (including ones not represented in the TreeTraits database) and to accommodate missing covariate data. For example, if records with missing data were discarded from our analysis, then the total number of useable records would have dropped from 1766 to 103.

Moreover, WD values used in tree growth or forest simulation models are typically obtained from the literature, from disparate studies that may have employed different approaches to measuring WD. Some studies report WD for green wood and some for oven-dried wood, and factors such as moisture content, wood type and latewood proportion can also influence WD (Zobel & Van Buijtenen 1989; Fromm *et al.* 2001). Hence, it seems problematic to simply average values obtained from the literature to approximate WD of different species or functional types. Our HB approach addresses these issues by (i) integrating methodological and covariate information reported by each study, thus producing standardized WD estimates that account for such factors and (ii) incorporating study random effects such that the likelihood of

reported ('observed') WD values is conditioned on study effects (Ogle, Barber & Sartor 2013).

UNCERTAINTY QUANTIFICATION AND BORROWING OF STRENGTH

Importantly, the HB meta-analysis explicitly quantifies uncertainty in parameters, such as standardized bulkwood WD (ω_s , g cm^{-3})—i.e. WD of dry wood characterized by the mean latewood proportion of a given woodtype—for the 305 species. The uncertainty in the ω_s estimates (Fig. 8 and Table S1) produced by the PM, TM or DM could be propagated to the outputs of tree growth or forest dynamics models or used to prioritize future sampling efforts. For example, it may be unrealistic to obtain sufficient WD data for all 164 species not represented in the TreeTraits data base, and targeted sampling of a subset of species associated with highly uncertain ω_s estimates may be desirable. The PM yields CI widths for ω_s for data-poor species that differ between species such that some are relatively narrow, whereas others are relatively wide (Fig. 8d–f). Thus, the PM may be particularly helpful for identifying particular species, genera, or clades for targeted sampling.

Differences in the CI widths for ω_s reflected different degrees of borrowing of strength within the four different models. That is, borrowing of strength within the PM is affected by relationships between species within a genus; for example, data-poor species occurring in depauperate genera were generally associated with CI widths for ω_s that were up to four times wider than those for data-poor species occurring in diverse genera (see Fig. S3 in the Supporting Information). The ISM treats species as completely independent such that borrowing of strength between species does not occur, resulting in highly uncertain or unrealistic ω_s estimates for data-poor species. Thus, some degree of borrowing of strength—as in the DM, TM or PM—is required to obtain realistic and well-constrained estimates of ω_s for data-poor species. This is further illustrated in the cross-validations (Fig. 5); in the DM, the CI widths for ω_s are more consistent across the four target species, which is expected since borrowing of strength occurs ‘equally’ among all species within a division. Conversely, the 95% CIs obtained from the PM and TM were relatively wide for species from depauperate genera (e.g. *C. caroliniana* and *I. opaca*) when compared with species from diverse genera (e.g. *P. taeda* or *P. menziesii*) (Fig. 5).

IMPORTANCE OF PHYLOGENETIC AND TAXONOMIC INFORMATION

Chamberlain *et al.* (2012) stress the importance of addressing non-independence between species in traditional meta-analyses and suggest that phylogenetic information can help overcome this problem. We explicitly address this issue by specifying hierarchical models for species-specific parameters that are based on phylogenetic or taxonomic relationships. However, Chamberlain *et al.* (2012) also caution against using phylogenetic information in meta-analyses when unbalanced phylogenies are involved; this is not an issue here because our HB framework can explicitly accommodate such unbalanced designs. Importantly, as noted above, incorporation of phylogenetic or taxonomic information can be particularly useful for obtaining trait estimates of data-poor species (Figs 5 and 8d–f) via the borrowing of strength mechanism. Flores & Coomes (2011) come to a similar conclusion by incorporating phylogenetic information indirectly. In contrast to our approach that uses the phylogenies to define the hierarchical model for the mean terms (i.e. latent θ , $\hat{\theta}$, etc.), they used branch lengths, which were unavailable to us, to define the covariances between genus- or family-level latent WD values. A combination of both approaches is worth exploring.

SPECIES-SPECIFIC WOOD DENSITY PATTERNS

The PM and TM produced similar estimates for the species-specific ω_s , and thus, we focus on the PM and DM results (we do not discuss the ISM because the ω_s estimates for the data-poor species are unrealistic). The species-level ω_s estimates differ by about 4.8-fold across the 141 species represented in the TreeTraits database (Fig. 8a–c). Some of this variation in ω_s can be attributed to wood type, whereby

softwoods generally exhibited lower WD when compared with diffuse- and ring-porous species. Lower WD of softwoods may be due to xylem anatomy differences. For example, *Pinus taeda* (loblolly pine; softwood) and *Acer rubrum* (red maple; diffuse porous) stems supported ~62% and ~12% conducting area relative to sapwood area, respectively (Ogle & Pacala 2009). This 5-fold difference in proportion of conducting area may help to explain the 1.2-fold difference in the estimated ω_s of *A. rubrum* (posterior median for $\omega_s = 0.525 \text{ g cm}^{-3}$) vs. *P. taeda* ($\omega_s = 0.410 \text{ g cm}^{-3}$).

The proportion of latewood also contributes to variation in species-level ω_s . Our results indicate that latewood is denser than earlywood (Fig. 6b), which is expected (e.g. Koubaa, Zhang & Makni 2002; Knapic *et al.* 2007) because latewood conducting elements tend to be smaller with thicker cell walls and less lumen area (Domec & Gartner 2002; Woodcock & Shier 2002; Bergès, Nepveu & Franc 2008). Thus, trees with a higher proportion of latewood tend to have denser bulkwood when compared with trees with lower proportions (Zhang & Morgenstern 1995). Based on the PM, the average latewood proportion (\bar{L}_T in Eqn (4)) potentially differed between softwood and ring-porous species given that the posterior medians and 95% CIs for \bar{L}_T were 0.253 (0.193, 0.321) and 0.591 (0.404, 0.760), respectively; \bar{L}_T could not be estimated for diffuse-porous wood given the lack of latewood proportion data. These differences in \bar{L}_T align with the overall lower ω_s estimates for softwoods (lower proportion of latewood) when compared with ring-porous species. The differences in \bar{L}_T between ring-porous and softwood species could be partially explained by difference in their anatomical structure (e.g. Fig. 1), or our results could also be an artifact of the limited amount of L data available on ring-porous species (Table 1), which only represents a single species (*Robinia pseudoacacia*), whereas L data were available for 12 softwood species.

EVOLUTIONARY HISTORY VS. ENVIRONMENTAL INFLUENCES

We explored the degree to which the residual variation in the reported WD can be explained by environmental factors not explicitly included in this analysis (as represented by the study random effects) vs. evolutionary history (as represented by the variability between species and between higher taxonomic levels). Overall, we found that once woody type, latewood proportion and moisture content were accounted for, the study random effects and species identity explained a similar amount of variation (Fig. 7). The study random effects reflected the influence of study-specific environmental, sampling, or population factors that were not explicitly accounted for in the HB model. For example, intraspecific variation in WD has been attributed to site-level differences in soil moisture (Preston, Cornwell & DeNoyer 2006; Fajardo & Piper 2011), tree age or size (Sungpalee *et al.* 2009; Fajardo & Piper 2011) and genetics (Vargashernandez & Adams 1991). Similarly, stand- or community-level mean WD often varies among sites and along gradients in elevation or topographical

complexity, which probably reflects gradients in temperature and water availability (Chave *et al.* 2006; Sungpalee *et al.* 2009). Thus, more refined estimates of ω_s could be obtained by incorporating study- or site-specific indices of ontogeny, temperature and/or water availability. Unfortunately, severe incomplete reporting of candidate variables hampered our ability to include such factors within our HB meta-analysis.

Previous studies suggest that WD is conserved at the genus level (Chave *et al.* 2006; Swenson & Enquist 2007). Our results lend some support for this conclusion because point estimates for the variances among species within genera ($\hat{\sigma}$) tended to be smaller than for the variances among genera with orders ($\hat{\sigma}$) (Fig. 7a). However, our results also imply variability among taxa in the degree of WD conservatism. For example, although WD appears to be relatively conserved within certain genera (e.g. *Populus*, *Abies*, *Carya*, *Quercus*, *Fraxinus*, *Betula*, *Magnolia*, and *Ulmus*; low $\hat{\sigma}$) and orders (e.g. Pinales, Magnoliales, and Fabales; low $\hat{\sigma}$), several of the $\hat{\sigma}$ and $\hat{\sigma}$ estimates are moderately large (e.g. for Ebenales) and/or highly uncertain, indicating that WD may be a variable or labile trait within some clades. Uncertainty in the $\hat{\sigma}$ and $\hat{\sigma}$ estimates tended to decrease with clade size, but the point estimates for $\hat{\sigma}$ and $\hat{\sigma}$ were not clearly related to clade size (Fig. S2). Similarly, Chave *et al.* (2006) reported that genera with highly variable WD may include either few or many species (see their Table 5). This suggests that taxonomic diversification may be largely uncoupled from WD diversification.

The importance of study effects and evolutionary history may reflect the fact that WD is a complex trait that is influenced by other more rudimentary traits—such as xylem anatomy and cellular structure (Hacke *et al.* 2001; Searson, Montagu & Conroy 2004)—some of which may be strongly influenced by the environment, whereas others may be tightly constrained by ancestry. Moreover, the incorporation of evolutionary relationships helped to identify potential species that should be targeted for future WD measurements. On the other hand, the relatively large study effects indicated that estimates of intra-specific variation in WD could be refined by incorporating site-level (e.g. edaphic properties, topography, climate) and tree-level (e.g. age, size, growth rate) information. WD is a key parameter in tree growth and forest simulation models, and more accurate forecasts of forest structure and productivity may be achieved by allowing this parameter to vary among forest stands, reflecting local environmental influences on WD.

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References

Ackerly, D.D. (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences*, **164**, 165–184.
Ackerly, D. (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs*, **74**, 25–44.

Augspurger, C.K. (1984) Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology*, **65**, 1705–1712.
Bergès, L., Nepveu, G. & Franc, A. (2008) Effects of ecological factors on radial growth and wood density components of sessile oak (*Quercus petraea* Liebl.) in Northern France. *Forest Ecology and Management*, **255**, 567–579.
Bernhardt-Römermann, M., Gray, A., Vanbergen, A.J., Bergès, L., Bohner, A., Brooker, R.W. *et al.* (2011) Functional traits and local environment predict vegetation responses to disturbance: a pan-european multi-site experiment. *Journal of Ecology*, **99**, 777–787.
Cantino, P.D., Doyle, J.A., Graham, S.W., Judd, W.S., Olmstead, R.G., Soltis, D.E., Soltis, P.S. & Donoghue, M.J. (2007) Towards a phylogenetic nomenclature of *Tracheophyta*. *Taxon*, **56**, 822–846.
Castro-Díez, P., Puyravaud, J.P., Cornelissen, J.H.C. & Villar-Salvador, P. (1998) Stem anatomy and relative growth rate in seedlings of a wide range of woody plant species and types. *Oecologia*, **116**, 57–66.
Chamberlain, S.A., Hovick, S.M., Dibble, C.J., Rasmussen, N.L., Van Allen, B.G., Maitner, B.S. *et al.* (2012) Does phylogeny matter? Assessing the impact of phylogenetic information in ecological meta-analysis. *Ecology Letters*, **15**, 627–636.
Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Ter Steege, H. & Webb, C.O. (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications*, **16**, 2356–2367.
Chave, J., Coomes, D., Jansen, S., Lewis, L.S., Swenson, N. & Zanne, A. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.
Clark, J.S. (2003) Uncertainty and variability in demography and population growth: a hierarchical approach. *Ecology*, **84**, 1370–1381.
Cornwell, W.K. & Ackerly, D.D. (2010) A link between plant traits and abundance: evidence from coastal California woody plants. *Journal of Ecology*, **98**, 814–821.
Dalla-Salda, G., Martinez-Meier, A., Cochard, H. & Rosenberg, P. (2009) Variation of wood density and hydraulic properties of Douglas fir (*Pseudotsuga menziesii* (Mieb.) Franco) clones related to a heat and drought wave in France. *Forest Ecology and Management*, **257**, 182–189.
Diaz, S.J., Hodgson, J.G., Thompson, K., Cabido, M.J., Cornelissen, J.H.C. & Jalili, A. (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.
Domec, J.-C. & Gartner, B.L. (2002) How do water transport and water storage differ in coniferous earlywood and latewood. *Journal of Experimental Botany*, **53**, 2369–2379.
Fajardo, A. & Piper, F.I. (2011) Intraspecific trait variation and covariation in a widespread tree species (*Nothofagus pumilio*) in southern Chile. *New Phytologist*, **189**, 259–271.
Flores, O. & Coomes, D.A. (2011) Estimating the wood density of species for carbon stock assessments. *Methods in Ecology and Evolution*, **2**, 214–220.
Fromm, J.H., Sautter, I., Matthies, D., Kremer, J., Schumacher, P. & Ganter, C. (2001) Xylem water content and wood density in spruce and oak trees detected by high resolution computed tomography. *Plant Physiology*, **127**, 416–425.
Gates, S. (2002) Review of methodology of quantitative reviews using meta-analysis in ecology. *Journal of Animal Ecology*, **71**, 547–557.
Gelfand, A.E. & Ghosh, S.K. (1998) Model choice: a minimum posterior predictive loss approach. *Biometrika*, **85**, 1–11.
Grime, J.P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. John Wiley and Sons, Chichester, UK.
Gurevitch, J., Curtis, S.P. & Jones, M.H. (2001) Meta-analysis in ecology. *Advances in Ecological Research*, **32**, 199–247.
Gurevitch, J. & Hedges, V.L. (1999) Statistical issues in ecological meta-analyses. *Ecology*, **80**, 1142–1149.
Hacke, U.G., Sperry, S.J., Pockman, W.T., Davis, S.D. & McCulloh, K.A. (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, **126**, 457–461.
InsideWood (2004-onwards). <http://insidewood.lib.ncsu.edu/search/>.
Kattge, J., Ogle, K., Bönsch, G., Döaz, S., Lavorel, S., Madin, J., Nadrowski, K., Nöllert, S., Sartor, K. & Wirth, C. (2011) A generic structure for plant trait databases. *Methods in Ecology and Evolution*, **2**, 202–213.
King, D.A., Davies, S.J., Nur Supardi, M.N. & Tan, S. (2005) Tree growth is related to light interception and wood density in two mixed Dipterocarp forests of Malaysia. *Functional Ecology*, **19**, 445–453.
Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, **98**, 419–428.
Klumpp, K. & Soussana, J.-F. (2009) Using functional traits to predict grassland ecosystem change: a mathematical test of the response and effect trait approach. *Global Change Ecology*, **15**, 2921–2934.

- Knapic, S., Louzada, J.L., Leal, S. & Pereira, H. (2007) Radial variation of wood density components and ring width in cork oak trees. *Annals of Forest Science*, **64**, 211–218.
- Koubaa, A., Zhang, S.Y.T. & Makni, S. (2002) Defining the transition from earlywood to latewood in black spruce based on intra-ring wood density profiles from X-ray densitometry. *Annals of Forest Science*, **59**, 511–518.
- Kraft, N.J., Valencia, R. & Ackerly, D.D. (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, **322**, 580–582.
- Kraft, N.J.B., Metz, M.R., Condit, R.S. & Chave, J. (2010) The relationship between wood density and mortality in a global tropical forest data set. *New Phytologist*, **188**, 1124–1136.
- Lajeunesse, M.J. (2009) Meta-analysis and the comparative phylogenetic method. *American Naturalist*, **174**, 369–381.
- Lajeunesse, M.J. & Forbes, M.R. (2003) Variable reporting and quantitative reviews: a comparison of three meta-analytical techniques. *Ecology Letters*, **6**, 448–454.
- Lambers, H. & Poorter, H. (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research*, **23**, 187–261.
- Larjavaara, M. & Muller-Landau, H.C. (2010) Rethinking the value of high wood density. *Functional Ecology*, **24**, 701–705.
- Larjavaara, M. & Muller-Landau, H.C. (2012) Still rethinking the value of high wood density. *American Journal of Botany*, **99**, 165–168.
- Lawton, R.O. (1984) Ecological constraints on wood density in a tropical montane rain forest. *American Journal of Botany*, **71**, 261–267.
- Liu, F., Bayarri, M.J. & Berger, J.O. (2009) Modularization in Bayesian analysis, with emphasis on analysis of computer models. *Bayesian Analysis*, **4**, 119–150.
- Lunn, D., Best, N., Spiegelhalter, D., Graham, G. & Neuenschwander, B. (2009a) Combining MCMC with 'sequential' PKPD modelling. *Pharmacokinetics and Pharmacodynamics*, **36**, 19–38.
- Lunn, D., Spiegelhalter, D., Thomas, A. & Best, N. (2009b) The BUGS project: Evolution, critique and future directions (with discussion). *Statistics in Medicine*, **28**, 3049–3082.
- Martinez-Vilalta, J., Mencuccini, M., Vayreda, J. & Retana, J. (2010) Interspecific variation in functional traits, not climatic differences among species ranges, determines demographic rates across 44 temperate and Mediterranean tree species. *Journal of Ecology*, **98**, 1462–1475.
- McMahon, S.M., Metcalf, C.J.E. & Woodall, C.W. (2011) High-dimensional coexistence of temperate tree species: functional traits, demographic rates, life-history stages, and their physical context. *PLoS ONE*, **6**, e16253.
- Miles, P.D., Brand, G.J., Alerich, C.L., Bednar, L.F., Woudenberg, S.W., Glover, J.F. & Ezell, E.N. (2001) *The Forest Inventory and Analysis Database Description and Users Manual version 1.0*. U.S. Dept. of Agriculture, Forest Service, North Central Research Station, St. Paul, MN.
- Muller-Landau, H.C. (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica*, **36**, 20–32.
- Ogle, K. & Barber, J.J. (2008) Bayesian data-model integration in plant physiological and ecosystem ecology. *Progress in Botany*, **69**, 281–311.
- Ogle, K., Barber, J.J. & Sartor, K. (2013) Feedback and modularization in a Bayesian meta-analysis of tree traits affecting forest dynamics. *Bayesian Analysis*, **8**, 133–168.
- Ogle, K. & Pacala, S.W. (2009) Modeling framework for inferring tree growth and allocation from physiological, morphological and allometric traits. *Tree Physiology*, **29**, 587–605.
- Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G. et al. (2008) Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology*, **89**, 1908–1920.
- Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J., Peña-Claros, M., Sterck, F., Villegas, Z. & Sass-Klaassen, U. (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytologist*, **185**, 481–492.
- Preston, K.A., Cornwell, W.K. & DeNoyer, J.L. (2006) Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytologist*, **170**, 807–818.
- Rosenberg, M.S., Adams, D.C. & Gurevitch, J. (2000) *MetaWIN: Statistical Software for Meta-Analysis*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Searson, M.D., Montagu, T.K. & Conroy, J. (2004) Wood density and anatomy of water limited eucalyptus. *Tree Physiology*, **24**, 1295–1302.
- Sungpalee, W., Itoh, A., Kanzaki, M., Sri-Ngernyuan, K., Noguchi, H., Mizuno, T. et al. (2009) Intra- and interspecific variation in wood density and fine-scale spatial distribution of stand-level wood density in a northern Thai tropical montane forest. *Journal of Tropical Ecology*, **25**, 359–370.
- Swenson, G.N. & Enquist, B.J. (2007) Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, **94**, 451–459.
- Ter Steege, H. & Hammond, D.S. (2001) Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology*, **82**, 3197–3212.
- Thomas, S.C. & Bazzaz, F.A. (1999) Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest tree. *Ecology*, **80**, 1607–1622.
- USDA (2008) Plant database (<http://www.plants.usda.gov/java/>). National Plant Data Team, Greensboro, NC 27401-4901 USA.
- Van Gelder, H.A., Poorter, L. & Sterck, F.J. (2006) Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytologist*, **171**, 367–378.
- Vargashernandez, J. & Adams, W.T. (1991) Genetic variation of wood density components in young coastal Douglas fir: implications for tree breeding. *Canadian Journal of Forest Research*, **21**, 1801–1807.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.
- Wheeler, E.A. (2011) InsideWood — a web resource for hardwood anatomy. *IWA Journal*, **32**, 199–211.
- Wikle, C.K. (2003) Hierarchical Bayesian models for predicting the spread of ecological processes. *Ecology*, **84**, 1382–1394.
- Woodcock, D. & Shier, A. (2002) Wood specific gravity and its radial variations: the many ways to make a tree. *Trees*, **16**, 437–443.
- Wright, S.J., Muller-Landau, H.C., Condit, R. & Hubbell, S.P. (2003) Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology*, **84**, 3174–3185.
- Wright, J.J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manríquez, G., Martinez-Ramos, M. et al. (2007) Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany*, **99**, 1003–1015.
- Zhang, S.Y. & Morgenstern, E.K. (1995) Genetic variation and inheritance of wood density in black spruce (*Picea mariana*) and its relationship with growth: implications for tree breeding. *Wood Science and Technology*, **30**, 63–75.
- Zobel, B.J. & Van Buijtenen, J.P. (1989) *Wood Variation: Its Causes and Control*. Springer-Verlag, Berlin.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Phylogeny used for the 86 tree genera.

Appendix S2. Detailed description of the covariate data model and prior distributions.

Appendix S3. OpenBUGS model code for the phylogeny model (PM).

Figure S1. Uncertainty estimates associated with the predicted wood density data.

Figure S2. Within clade variability vs. clade size.

Figure S3. Uncertainty in WD predictions for data-poor species vs. clade size.

Table S1. Species- and genus-level standardized wood density estimates.