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REGIONAL AND PHYLOGENETIC VARIATION OF WOOD DENSITY ACROSS 2456 NEOTROPICAL TREE SPECIES

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Abstract. Wood density is a crucial variable in carbon accounting programs of both secondary and old-growth tropical forests. It also is the best single descriptor of wood: it correlates with numerous morphological, mechanical, physiological, and ecological properties. To explore the extent to which wood density could be estimated for rare or poorly censused taxa, and possible sources of variation in this trait, we analyzed regional, taxonomic, and phylogenetic variation in wood density among 2456 tree species from Central and South America. Wood density varied over more than one order of magnitude across species, with an overall mean of 0.645 g/cm^3. Our geographical analysis showed significant decreases in wood density with increasing altitude and significant differences among low-altitude geographical regions: wet forests of Central America and western Amazonia have significantly lower mean wood density than dry forests of Central and South America, eastern and central Amazonian forests, and the Atlantic forests of Brazil; and eastern Amazonian forests have lower wood densities than the dry forests and the Atlantic forest. A nested analysis of variance showed that 74% of the species-level wood density variation was explained at the genus level, 34% at the Angiosperm Phylogeny Group (APG) family level, and 19% at the APG order level. This indicates that genus-level means give reliable approximations of values of species, except in a few hypervariable genera. We also studied which evolutionary shifts in wood density occurred in the phylogeny of seed plants using a composite phylogenetic tree. Major changes were observed at deep nodes (Eurosid 1), and also in more recent divergences (for instance in the Rhamnoids, Simaroubaceae, and Anacardiaceae). Our unprecedented wood density data set yields consistent guidelines for estimating wood densities when species-level information is lacking and should significantly reduce error in Central and South American carbon accounting programs.

Key words: forest biomass estimation; Neotropics; phylogeny; tropical forests; wood density.

Introduction

Wood density has recently emerged as a key variable in carbon cycle research. Reyes et al. (1992) and Fearnside (1997) have highlighted the need to develop wood density databases for tropical biomass estimation, in greenhouse gas emissions mitigation programs. A number of studies have shown that community-level wood density, averaged across all trees in a given locality, varies considerably among Neotropical forests (Wiemann and Williamson 2002, Baker et al. 2004, Muller-Landau 2004; see Plate 1) and should therefore be included as a predictive variable in large-scale tropical biomass estimation protocols (Baker et al. 2004, DeWalt and Chave 2004, Chave et al. 2005). Baker et al. (2004) and Muller-Landau (2004) found that wood density across 59 Amazonian plots and four Neotropical forests, respectively, was negatively associated with soil fertility. At a broader scale Wiemann and Williamson (2002) compared North American and South American communities, and found a positive correlation between wood density and mean annual precipitation. In contrast, ter Steege and Hammond (2001) found that the variation in mean wood density within Guyana was not correlated with either precipitation or soil fertility, whereas in Mexico, Barajas-Morales (1987) found that mean wood density was negatively related to precipitation. All these studies point to contrasting trends in the regional and environmental variability of wood density, although they were based on a limited number of study sites or were restricted to one region of the Neotropics.

These regional patterns are largely driven by ecological processes and wood density should not be consid-

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PLATE 1. Views of two Neotropical forests: (left) tropical understory in French Guiana (Nouragues Research Station); (right) an entangled tropical forest bank along the Rio Madre de Dios, Peru. Photo credits: J. Chave.

ered solely as a predictive parameter for aboveground biomass estimation. One of the major axes of life history variation in self-supporting woody plants separates species that allocate their resources into fast growth and early reproduction from those that are slower growing and better able to withstand environmental hazards (Tilman 1988, Niklas 1992, Wright et al. 2003). The fast-growing species tend to be better colonists and to dominate the early stages of ecological succession, while the slower growing species dominate later successional stages (Uhl and Jordan 1984, Lugo and Scatena 1996). Wood density is a good indicator of where species lie along this continuum: fast-growing species are characterized by low-cost conductive tissues of low wood density (ter Steege and Hammond 2001, Wright et al. 2003, Muller Landau 2004) that allow for fast growth in size because conductive tissue is less expensive to construct (Favrichon 1994, Suzuki 1999, Santiago et al. 2004), while high wood density provides a stronger defense against physical damage, predators, and pathogens (Rowe and Speck 2005), as well as a lower vulnerability to drought stress (Carlquist 1977, Tyree and Sperry 1989, Hacke et al. 2001, Meinzer 2003). The close relationship between wood density and life history traits reflects the fact that wood plays both a physiological role in the transport of sap through vessels and a mechanical role in support and resistance against bending or buckling. Understanding the evolution and current spatial patterns in wood density is therefore important to our understanding of ecological and physiological processes in tropical trees.

Higher wood densities are often found in environments with lower light, higher stress (wind, abundance of wood-rotting fungi, or xylophageous insects), and lower soil fertility (Wilson and Archer 1977, Hillis and Brown 1984, Wiemann and Williamson 1989*a*, *b*, Parolin et al. 1998). Available quantitative genetic studies show high heritability in wood density (Cornelius 1994, Grattapaglia et al. 1996), suggesting that plastic responses to the environment may be limited for this character, and implying that most of this variation in community-averaged wood density is due to ecological sorting of species by habitat. However, community-level wood density variation may also be explained in part by plastic responses to the environment (Koubaa et al. 2000, Woodcock and Shier 2003), within the more fundamental physical/developmental constraints in available lineages due to the fixation of ancestral traits (Webb et al. 2002, Cavender-Bares et al. 2004).

To begin to untangle these myriad influences on species and community wood densities, it is important to quantify how much of the variation in wood density among species is associated with phylogeny and how much with geography. Here, we investigate phylogenetic and regional variation in wood density of Neotropical tree species using the largest compilation of literature values and primary data assembled to date for tree species growing in Central and South America, from Mexico to Argentina. We address the following questions. (1) What are the large-scale regional and altitudinal geographic patterns in the wood density of Neotropical species? (2) To what degree is interspecific variation in wood density explained by genus- and family-level variation? (3) What are the phylogenetic patterns in wood density variation; and specifically, how evolutionarily variable is wood density in seed plants?

METHODS

Principles of wood density measurement

Because wood density varies among trees within species as well as within individual trees, the best wood density estimates are based on samples from multiple individuals, and ideally on large samples from felled trees. Traditionally, forestry studies use large wood samples from felled trees (Sallenave 1955), but an increasing number of recent studies use instead tree cores taken with increment borers to estimate wood density. Since in most species wood density is higher in the inner wood than in the outer wood by up to 20% (Wiemann and Williamson 1988, Woodcock 2000, Parolin 2002; Nogueira et al. [2005] reported a figure of 5.3%), pith to bark tree cores should be taken. In addition, the wood sample has to be taken from a live tree or recently felled tree (in which the wood has not yet dried out) using a sharp increment borer, and immediately placed in an airtight container to prevent it from drying out.

Throughout the present work, wood density is defined as the ratio of the oven-dry mass of a wood sample divided by its green volume (basic specific gravity). For measurements of green volume, the sample should be maintained at constant humidity. Green volume can either be measured from the geometrical dimensions of the wood core (Parolin and Worbes 2000, Muller-Landau 2004), or by the water displacement method (Ilic et al. 2000). In the first method, the total length and the diameter of the wood core are measured by means of a caliper, avoiding pressure of the caliper blades on the wood. The water displacement method allows for reliable measurements of volume for both regularly and irregularly shaped samples. A container capable of holding the sample is filled with water and placed on a digital balance (precision at least 0.01 g, and preferably higher). The core is then carefully forced underwater, such that it does not contact the sides or bottom of the container. The measured mass of displaced water is equal to the green volume of the core (since water has a density of 1 g/cm^3). We carried out a direct comparison of the geometrical method and of the water displacement method on 26 samples from 17 species in French Guiana (J. Chave, *unpublished results*). The correlation coefficient between the two methods was very high ($r^2 = 0.976$), but the water displacement method yielded slightly smaller estimates than the geometrical method (ratio 0.94). Oven-dry mass is measured on the same sample by drying it in a well-ventilated oven at 100°C until it achieves constant mass (usually 48–72 h for a core; more time is required for larger samples).

Data compilation and taxonomy

Our data were compiled from diverse published and unpublished sources, including measurements made by us (see Supplement). Available information varied considerably among these sources. We included in our database angiosperm or gymnosperm tree species growing naturally in the Neotropics, from Central America to Argentina (with the Caribbean included). We excluded species occurring as exotic invaders or introduced species, though the status of some species remains unclear (e.g., some Mimosoideae). Although most of the species grow in moist lowland tropical forests, we also included species typical of montane forests (Andean species), and of dry forests or woodlands (cerrado-type vegetation in Brazil and in Mexico). Throughout, we treated separately species that never grow in lowland forests below 500 m above sea level (henceforth montane species). For palm species, basal area averaged values were obtained from the data published by Wiemann and Williamson (1989*b*). We excluded non-self-supporting plants (woody lianas) from this compilation.

To combine our data, we first matched species names listed in each source with the currently accepted name. This required correcting a tremendous number of spelling errors and resolving synonymy problems. Over the past decades, many species have changed names, or have been split or lumped with other species. Though we fully acknowledge that the status of accepted species is in constant flux, we did our best to resolve potential problems to the degree currently possible by comparing every species with its reported status in the Tropicos database of the Missouri Botanical Garden (*available online*).[9] Synonymous species were merged with the accepted species, and invalid species were discarded. We addressed some of these problems using TaxonScrubber, a freely available taxon-matching software program provided by the Salvias project running under Microsoft Access (*available online*).[10] We also matched genus names against a list maintained by Kew Botanic Gardens (*available online*)[11]. Family-level taxonomy followed the Angiosperm Phylogeny Group II (2003; *available online*).[12] Some notable departures from older classifications are as follows: Bombacaceae, Sterculiaceae, and Tiliaceae are all included in the Malvaceae; Fabaceae, including the Caesalpinioidae and the Mimosoidae, is considered a monophyletic family; most of the genera in the Flacourtiaceae are included in the Salicaceae; and Cecropiaceae are included in the Urticaceae, distinct from the Moraceae.

Conversion of wood density measures into a common standard

Foresters rarely report wood specific gravity, but instead a density value based on the mass of a sample at 12% or at 15% moisture (henceforth, 12%W and 15%W, respectively), divided by its volume at the same moisture content, or divided by green volume. In the French tropical literature, wood density D_{12} is the mass over volume at 12% moisture, or mass of a "unit volume" (specific mass). This measure is also commonly reported in the British literature in pounds per cubic foot (1 g/cm^3 = 62.427 lb/ft^3). Thus we converted these density values into wood specific gravity (WSG) using Sallenave's (1971) relationship:

[9] ⟨http://mobot.mobot.org/W3T/Search/vast.html⟩

[10] ⟨http://www.salvias.net⟩

[11] ⟨http://www.rbgkew.org.uk/data/genlist.html⟩

[12] ⟨http://www.mobot.org/MOBOT/Research/APweb/⟩

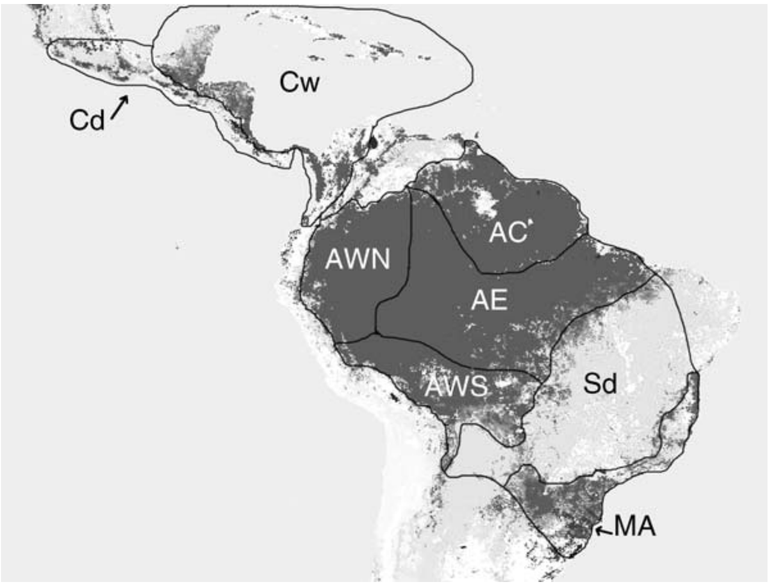

FIG. 1. A map delineating eight geographical regions in Central and South America. These regions include dry forests in Central America (Cd) and South America (Sd), wet forests in Central America (Cw), northwestern Amazon (AWN), southwestern Amazon (AWS), central Amazon (AC), eastern Amazon (AE), and the Atlantic forests of Brazil (MA).

$$\mathrm{WSG} = \frac{D_M - Md}{1 + v(S - M)}$$

where D_M is the wood density at M percentage moisture, d is a mass correction factor per 1% change in moisture content, S is the fiber saturation point, or maximal moisture content (in %), and v is the variation in volume per 1% change in moisture content. This theoretical formula can be used to convert wood density at any moisture content into wood specific gravity. The values of d, v, and S vary across species. Sallenave (1955, 1964, 1971) published values of WSG, D_{12}, d, v, and S, for a large number of wood samples originating from many tropical forests ($n = 1893$). Using these data, we found that D_M was relatively stable across moisture values, and that $\mathrm{WSG} = 0.872D_{12}$ ($n = 1893$, $r^2 = 0.983$).

Reyes et al. (1992) using a data set of 379 species (see Chudnoff 1984) reported a smaller multiplicative factor of 0.800 for WSG, instead of our 0.872. Sallenave's conversion model was based on data from individually measured trees, measured by the same laboratory and staff following a consistent methodology, and using the means of >10 assays on the same log. In contrast, the data used by Reyes et al. (1992) are species- or genus-level means and compiled from multiple studies across the tropics. We tested these two models with an independent data set reporting both wood density at 12% moisture and WSG (M. C. Wiemann, *personal communication*), and found that the model of Reyes et al systematically underestimated the WSG, while Sallenave's model provided an unbiased estimate. We therefore used Sallenave's model to convert wood density at 12% moisture into oven-dry wood specific gravity.

Biogeographic patterns in Neotropical wood density

We tested the relationship of wood density with altitude (Williamson 1984). We used the Specimen.DQ software developed by the Salvias project to extract from the Missouri Botanical Garden's database all vouchers of our species. We then computed the mean elevation of a species if at least 10 elevation data were available. Mean elevation was log-transformed prior to analyses. We then tested for a relationship between log(mean elevation) and wood density using a linear model.

We also tested the relationship of wood density to geographical location. A first natural distinction can be drawn between montane species that never occur below 500 m above sea level and lowland species that can grow below this limit. These montane species include representatives of North American (Laurasian) families (Raven and Axelrod 1974, Gentry 1982), such as Betulaceae, Clethraceae, or Cornaceae. A second natural distinction for nonmontane species is environmental and geographical. To simply capture the variety of lowland environments of the Neotropics, we defined eight geographical regions (cf. Fig. 1): dry forests in Central America (Cd), wet forests in Central America (Cw), northwestern Amazon (AWN), southwestern Amazon (AWS), central Amazon (AC), eastern Amazon (AE), dry forests in South America (Sd), and the Atlantic forests of Brazil (MA). These regions do not necessarily correspond to biogeographical regions, but are rather the finest scale at which we could analyze available data, capturing broad climatic, topographic, and biogeographic variation. We used information on species composition in permanent forest plots of Central and South America to assign species to the regions

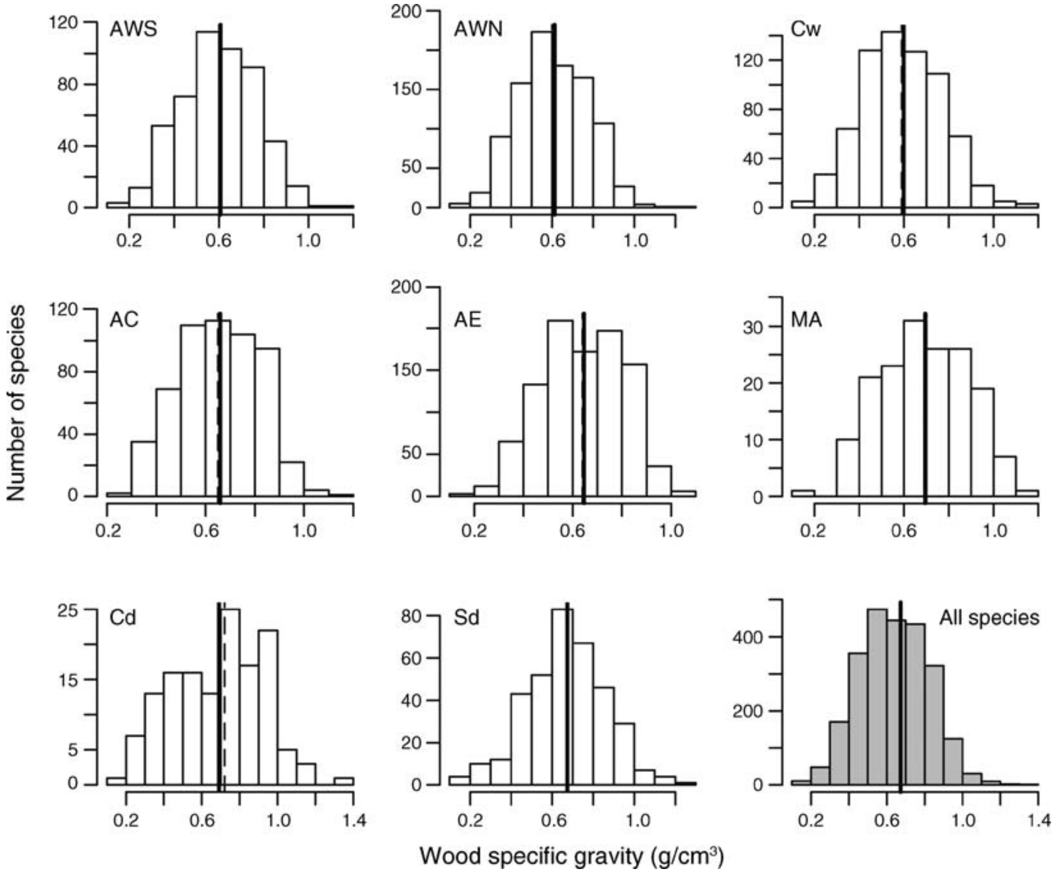

FIG. 2. Histograms of wood specific gravity in the eight geographical regions, and for the whole data set. Solid vertical lines indicate the mean; dashed vertical lines indicate the median.

AWN, AWS, AC, AE, and Cw. If species occurred in more than one region, we assumed that they had the same mean wood density across regions. Ideally, it would have been preferable to use regional-level means for species occurring in more than one region but this would have magnified methodological differences across the sources used to construct our compilation.

To detect interregional difference in mean wood density, we constructed a generalized linear model (GLM; McCullagh and Nelder 1989), including as independent variables the binary information of presence/absence of a species in each of the eight regions and as a predicted variable the wood density. Errors in the predicted variable were modeled by a Gaussian distribution. We explored how much of the variance was separately explained by these regions and by interacting effects using a stepwise selection method based on the Akaike Information Criterion (AIC; Burnham and Anderson 2002).

Phylogenetic analysis

Variation in wood density across Neotropical tree species might in part be explained by phylogenetic effects. For instance closely related species might have more similar wood densities, and therefore regional variation in wood density might be due in part to regional variation in floristic composition. To determine how total variance in the data set was partitioned among taxonomic levels, we ran a nested analysis of variance. This enabled us to determine which taxonomic levels were particularly variable or conserved in their wood densities. To explore this taxonomic variation at a finer scale, we also computed the coefficient of variation (CV) of wood density for each taxonomic group with eight or more species.

Subsequently, we examined the sequences of major changes in wood density across the phylogeny of seed plants. We constructed a phylogenetic supertree by assembling existing molecular phylogenies (see Webb and Donoghue 2005), to which we added more information. The program matched the list of extant genera against the supertree. If some genera were absent from the supertree, they were treated as polytomies (Webb and Donoghue 2005). We computed the following statistics from wood density w at tip nodes. The mean wood density for internal node i across all

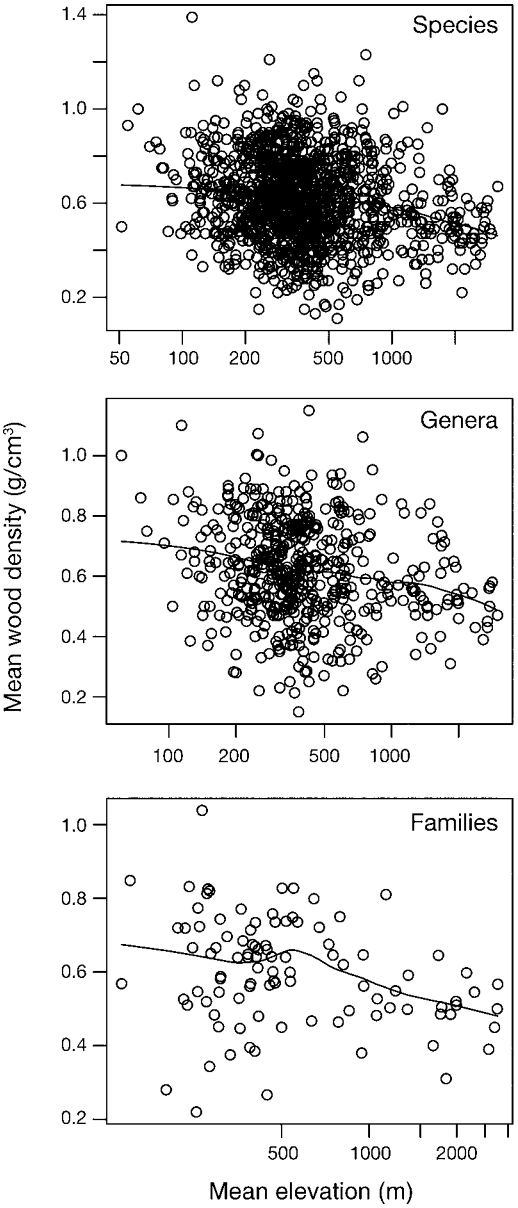

FIG. 3. Wood density as a function of mean elevation (plotted on a log-transformed scale) of species, genera, and families. The line corresponds to the lowest curve. A negative correlation between wood density and log-transformed elevation (measured in meters) is significant at all three taxonomic levels.

terminal taxa was computed as the mean character value across the tip nodes:

$$M_i = \sum_{\text{tips}\, j} w_j / N_i$$

where N_i is the number of terminal nodes descending from node *i*, and the sum runs over these terminal nodes (for terminal taxa, $M_i = w_i$). Next, we computed Σ_i, the standard deviation of node *i* across terminal nodes, and σ_i, the standard deviation across daughter nodes:

$$\Sigma_i = \left[\frac{1}{N_i - 1} \sum_{\text{tips}\, j} (M_i - w_j)^2\right]^{1/2}$$

$$\sigma_i = \left[\frac{1}{n_i - 1} \sum_{\text{daughters}\, j} (M_i - M_j)^2\right]^{1/2}$$

where n_i is the number of daughter nodes of node *i,* and the sum run over all daughter nodes.

Σ_i provides information about how much an interior node contributed to the overall variability of the trait in present-day taxa: σ_i is a measure of shifts in group means among daughter nodes, and provides information on the absolute size of divergences at node *i*. We focused on Neotropical plants including all woody species except lianas. Phylogenetic analyses of such potentially biased subsets of seed plant species raise a number of methodological issues, which we further develop in the *Discussion.*

RESULTS

Biogeographic patterns

We compiled 5406 wood density values for 2456 tree species, from 63 different primary references (see Supplement). These species belonged to 713 genera and 108 families (sensu APG II). This represents ~15% of the Neotropical tree species and 40% of the Neotropical tree genera. Of these, 251 were montane species, and 82 genera, and 22 families were restricted to the montane habitats in the Neotropics. The most represented nonmontane families were the Fabaceae (448 species) and the Lauraceae (115 species). The most represented woody genera were *Licania* (Chrysobalanaceae, 54 species), *Pouteria* (Sapotaceae, 48 species), and *Ocotea* (Lauraceae, 41 species).

The distribution of wood density across species was symmetric but nonnormal (positive kurtosis, Shapiro-Wilk test, $P < 0.0001$; Fig. 2). Mean wood density was 0.645 g/cm^3. The median was 0.64 g/cm^3, the maximum was 1.39 g/cm^3 for *Caesalpinia sclerocarpa* Standl., and the minimum was 0.11 g/cm^3 for *Erythrina ulei* Harms.

Montane species had a lower wood density than lowland species (0.599 ± 0.179 g/cm^3 [all values mean ± SD] for montane species, and 0.652 ± 0.184 g/cm^3 for nonmontane species). Across species, wood density decreased significantly with log-transformed mean elevation ($R^2 = 0.029$, $P < 0.001$, mean residual standard error [MRSE] = 0.175; see Fig. 3). This correlation remained significant both across genera ($R^2 = 0.035$, $P < 0.001$, MRSE = 0.162) and across families ($R^2 = 0.075$, $P < 0.01$, MRSE = 0.141).

Mean wood density varied significantly across regions. The lowland wet forests of Central America and of western Amazonia showed a significantly lower mean wood density than all other regions (0.502–0.612 g/cm^3 vs. 0.639–0.717 g/cm^3, $P < 0.001$; Table 1). The other significant differences were with the dry forests of South

TABLE 1. Interregional comparison of wood density across geographical zones.

		Wet forests						Dry forests	
		Southwestern Amazon	Northwestern Amazon	Central America	Central Amazon	Eastern Amazon	Atlantic forest of Brazil	Central America	South America
Regions	No. species	AWS	AWN	Cw	AC	AE	MA	Cd	Sd
AWS	535	**0.602**	468	368	221	456	31	13	0
AWN	1180	0.184	**0.614**	685	426	877	55	42	55
Cw	921	0.973	0.125	**0.602**	261	618	42	0	64
AC	678	0.001	0.001	0.001	**0.667**	502	31	0	17
AE	1290	0.001	0.001	0.001	0.001	**0.639**	56	40	59
MA	153	0.001	0.001	0.001	0.024	0.001	**0.701**	5	36
Cd	126	0.001	0.001	0.001	0.023	0.001	0.459	**0.717**	6
Sd	247	0.001	0.001	0.001	0.024	0.001	0.752	0.253	**0.695**

Notes: The diagonal term (in boldface type) indicates the mean wood density (g/m^3) of species within the zone; the upper right entries indicate the number of shared species between two zones, and the lower left entries indicate the P value of a comparison of the difference of mean wood density (t test).

and Central America and the Atlantic forest of Brazil (mean wood density between 0.695 g/cm^3 and 0.717 g/cm^3). Notably, dry forests of Central America and of South America both had a high mean wood density, and not significantly different between the two regions.

A stepwise selection of the regional effects by a GLM revealed that the best model included seven of the eight regions together with the following four interaction terms: northwestern Amazon × wet forest in Central America, northwestern Amazon × Atlantic forest of Brazil, dry forest in South America × Atlantic forest in Brazil, and southwestern Amazon × dry forest in South America. These additional terms factor in the interregional similarity in floristic composition as well as environmental similarity. Overall the best model including regional variation in wood density explained 10.3% of the variance, a low but significant figure. The regions explaining the most variance were, in decreasing order of importance: northwestern Amazon, southwestern Amazon, wet forest in Central America, and central Amazon.

Taxonomic partitioning of variance

We found that 74% of the total species-level variation was explained by intergenus variation, 34% by interfamily variation, and 20% by variation at the order level (Table 2). Among the 76 genera represented by eight species or more, the within-genus coefficients of variation ranged from 3% (*Myrcia*) to 46% (*Machaerium*), with a mean of 16%, and with a small number of highly variable genera (Appendix A). There was a significant tendency toward more variability in genera with lower mean wood density ($r^2 = 0.1$, $P = 0.011$). Fifty-three families were represented by eight species or more (Appendix B), and their mean CV was equal to 21%, with a range between 5% (Caryocaraceae) and 42% (Simaroubaceae). The most variable families were, in decreasing order, Simaroubaceae, Arecaceae, Anacardiaceae, Bignoniaceae, and Malvaceae.

We replicated the taxonomic level study in each region by asking whether genus, family, and order levels determined more or less wood density within regions than globally. An appropriate comparison of the regional subset to the entire species pool should be based on a measure of goodness-of-fit independent of sample size. To perform this comparison, we used the adjusted r^2 (Table 2). Within five regions we found slightly more phylogenetic conservatism than across the whole Neotropics, but this was not the case for the Atlantic forest or the dry forest types (Table 3). Finally, we explored the same relationship with a GLM by separately adding the taxonomic and regional effects. The interaction term between region and taxonomy was small, between 3% and 8%, depending on the taxonomic level (Table 4).

Phylogenetic effects

Overall, wood density was strongly conserved in the Neotropical species pool. The most marked divergences in wood density, as indicated by high values of σ_i (the standard deviation of the trait among daughter nodes), were observed at the node *Machaerium*, and at the node for the rhamnoids, within the Rhamnaceae (*Scutia*, *Rhamnus*, *Krugiodendron*; see Richardson et al. [2000] for insights on the phylogeny of this clade). Other nodes with high standard deviations across daughter taxa are listed in Table 5. Importantly, several of the genera that appear in this list have few species, and the observed variability may be a measurement artifact (e.g., *Attalea*, *Lithraea*, *Heliocarpus*, *Malmea*). Of the variable genera that can be analyzed with confidence three are in the Fabaceae (*Machaerium*, *Stryphnodendron*, *Chloroleu-*

TABLE 2. Fraction of variance in wood density explained by various taxonomic levels for the full wood density data set ($N = 2456$ species).

Taxonomic level	Multiple r^2	Adjusted r^2
Genus	0.737	0.631
Family	0.342	0.314
Order	0.197	0.184

Note: Explained variance is equal to the multiple r^2 values of an ANOVA.

TABLE 3. Adjusted correlation coefficient (r^2) in wood density at three taxonomic levels for the full wood density data set across geographical regions.

Taxonomic level	All regions	Wet forests: Southwestern Amazon AWS	Northwestern Amazon AWN	Central America Cw	Central Amazon AC	Eastern Amazon AE	Atlantic forest of Brazil MA	Dry forests: Central America Cd	South America Sd
Genus	0.631	0.666	0.684	0.669	0.673	0.690	0.512	0.589	0.565
Family	0.314	0.294	0.339	0.323	0.336	0.367	0.241	0.334	0.343
Order	0.184	0.206	0.238	0.206	0.215	0.226	0.161	0.132	0.272

con), one in the Bignoniaceae (*Tabebuia*), one in the Nyctaginaceae (*Neea*), and one in the Annonaceae (*Duguetia*).

The most striking interfamily changes were found in the Eurosids I (Boraginaceae, Elaeocarpaceae, Euphorbiaceae), Eurosids II (Fabaceae, Anacardiaceae, Simaroubaceae), and Euasterids I (Apocynaceae). Hence, most of the variability in our data set was observed in the rosids. Other major family or subfamily level changes were found in the *Lonchocarpus-Derris-Erythrina* clade (*Erythrina* has a very low wood density, range 0.11–0.32 g/cm^3, and *Lonchocarpus* has a medium to heavy wood, range 0.51–0.97 g/cm^3), in the Simaroubaceae (*Simarouba* and *Simaba* with a low wood density vs. the hard wood *Recchia mexicana*), the Elaeocarpaceae (*Crinodendron tucumanum* with a low wood density vs. *Sloanea* species).

DISCUSSION

Use of wood density data in biomass estimation protocols

Wood density is an important variable in biomass estimation protocols, and several projects have already endeavored to provide species-level compilations (Reyes et al. 1992, Fearnside 1997). Our results generalize and reinforce those of Baker et al. (2004), who found that 71% of the species-level variation in wood density among 229 Neotropical tree species was explained by genus affiliation and 25% by family affiliation. The present work improves our knowledge of Neotropical wood density by providing an almost 10-fold larger database, over 2400 valid tree species, including secondary forest species and species from contrasted environments. Our database is an indispensable tool for carbon accounting programs related to the implementation of the Kyoto protocol for Neotropical forests, be they old growth or regrowth after human disturbances.

We also provide guidelines for estimating wood density when species-level information is not available. We found that wood density was strongly conserved within genera, and that 74% of the variation at the species level was explained by the genus. Thus, in the absence of species-level estimates, it is usually acceptable to use genus-level means. In a few highly variable genera such as *Machaerium* and *Ceiba*, however, a genus-level mean will often fail to produce a good estimate of species wood density, and we provide a list of such genera in the Supplement. In the absence of even genus-level information on species identification and/or wood density, it is common practice to use a family-level wood density mean (e.g., Baker et al. 2004). We showed that only 34% of the species-level variation in wood density was explained by family affiliation, suggesting that use of family-level means is not generally good practice. Nonetheless, some species-rich families show surprisingly little variation (see Supplement), and in these instances family-level data will often prove adequate.

Problems in evaluating changes in wood density

Our phylogenetic analyses enabled us to analyze for the first time the evolutionary patterns underlying interspecific variation in wood density among Neotropical trees. Contrary to the belief that wood density variation is primarily driven by environmental conditions, and in agreement with a recent study on Floridian oak species (Cavender-Bares et al. 2004), we found considerable phylogenetic conservatism in this trait. This suggests that even if wood density can vary significantly over the plant's environment, this range is limited, and more importantly, that the mean wood density of a species, as reported in the present paper, is highly conserved phylogenetically. An interaction between geographic and phylogenetic affiliation is observed, but this effect is small when focusing on wood density (from 3% to 8% of the variance). The observed high wood density in dry environments is thought to be an adaptation to drought stress (Hacke et al. 2001,

TABLE 4. Fraction of variance in wood density explained by taxonomy, region, and combined effects.

Taxonomic level	Taxonomy	Region	Taxonomy + region	Taxonomy × region
Genus	0.737	0.103	0.840	0.874
Family	0.342	0.103	0.445	0.528
Order	0.206	0.103	0.309	0.356

Notes: The second column refers to the taxonomy effect alone (see also Table 2), the third column refers to the regional effect alone, and the fourth column refers to the sum of these two effects, excluding interaction terms. The last column refers to the sum of these two effects, including interaction terms. The difference between column 5 and column 4 detects the presence of interactions between regional effect and taxonomy, which we found to be significant but small.

TABLE 5. Interior nodes contributing the most to the observed variability in wood density.

Node name	Inferred age (Myr)	No. tip nodes	No. daughter nodes	$_i$	σ_i
Machaerium	39.0	11	11	0.679	0.299
Rhamnoids	24.8	3	3	0.777	0.279
Attalea	9.1	2	2	0.600	0.270
Stryphnodendron	39.0	6	6	0.623	0.268
Lithraea	25.0	2	2	0.725	0.255
Lonchocarpus–Derris–Erythrina	8.7	32	2	0.593	0.253
Simaroubaceae	38.0	9	4	0.547	0.247
Caricaceae–Brassicaceae	67.7	14	2	0.595	0.241
Chloroleucon	39.0	3	3	0.667	0.229
Cunoniaceae–Brunelliaceae	66.5	20	3	0.660	0.221
Heliocarpus	9.8	4	4	0.318	0.216
Simarouba	12.7	3	3	0.547	0.215
Tabebuia	23.0	25	25	0.771	0.214
Calyptranthes–Eugenia–Eucalyptus	56.7	24	2	0.740	0.213
Boraginaceae	80.0	35	7	0.575	0.212
Malmea	40.5	2	2	0.600	0.210
Eurosids I	101.0	1032	3	0.679	0.207
Anacardiaceae	50.0	37	15	0.659	0.204
Hernandiaceae–Lauraceae	82.5	120	2	0.568	0.203
Euphorbiaceae	69.0	106	36	0.554	0.191
Neea	9.5	8	8	0.640	0.190
Duguetia	40.5	5	5	0.688	0.188
Apocynaceae	24.6	39	3	0.705	0.186

Notes: Nodes are detected by measuring the standard deviation of the mean wood densities of the daughter nodes (σ_i). Some of these nodes may rank high in this list only because wood density could not be reliably assessed; e.g., for the two species in the genus *Attalea*. Node ages were inferred from a fossil calibration (Wikström et al. 2001) and interpolation (Webb and Donoghue 2004).

Meinzer 2003). However we also demonstrated that mean wood density was high in some wet Neotropical forests, such as in central and eastern Amazon. This may reflect alternative ways of providing defenses against insect consumers (Ehrlich and Raven 1964, Farrell et al. 1991), and would therefore also have a clear evolutionary significance.

Our inferences regarding the variation in a character across the angiosperms might be biased by our selection of one habit only (trees), and by the limited geographical range (the Neotropics). The restriction of our analyses to trees might be particularly serious because excluding lianas and nonwoody species might result in underestimation of the true variability in wood density within lineages and systematic bias in estimation of ancestral wood densities. However, several lines of evidence suggest that the ability to construct wood seems to be evolutionarily ancient and of a common origin within angiosperms. The liana habit appears to be derived from the free-standing habit (Esau 1977, Ewers and Fisher 1991), and the woody habit arises easily in herbaceous clades (Carlquist and Hoeckman 1985, Groover 2005). Thus, our selection of only woody taxa within clades with both woody and nonwoody species might be best thought of as a selection of the evolutionary events that have given rise to the effective expression of an ancestral character.

The geographical bias might also be a problem because exclusion of Paleotropical and temperate taxa may similarly result in underestimation of wood density variation within lineages and biases in reconstruction of the ancestral state. Given that South America remained connected with the rest of Gondwana until 80 Myr ago, and has many families in common with the Paleotropics, phylogenetic variation in wood density among Paleotropical taxa is likely to be broadly similar to what is found here for Neotropical taxa. Comparisons of variation in wood density between Neotropical and Paleotropical woody floras are nonetheless an interesting area for future research that should be pursued once appropriate data are available. Compared with temperate floras, tropical samples tend to over-represent the rosids and under-represent the asterids. However, this is in part because tropical floras are generally more diverse in woody species (disproportionately rosids) than in nonwoody species (disproportionately asterids; Gentry 1988), the former being better adapted to closed-canopy environments. An exploratory study of the wood density in the North American woody flora confirms that the bias in favor of rosids (oaks, hickory, maple, elm) vs. asterids (ash, dogwood) is preserved (J. Chave, *unpublished results*). This suggests that phylogenetic patterns of wood density variation are likely to remain largely unchanged if temperate taxa are included.

Causes of the regional variation in wood density

Biologists working in the Amazon have long noticed the rapid spatial turnover in plant species composition. Only after many years of field collection and museum work has it become apparent that there are nonetheless strong regional patterns in family-level composition (ter Steege et al. 2003). Recent works show that the forests of the western Amazon are surprisingly homogeneous in composition over a fairly broad scale, with particular families (Myristicaceae, Arecaceae, Moraceae) and even species dominating in both Ecuador and Peru (Pitman et al. 2001, Condit et al. 2002). It is also known that the eastern Amazonian species have broadly different patterns of family-level composition (ter Steege et al. 2003), being dominated by the Sapotaceae, Chrysobalanaceae, Fabaceae, and Lecythidaceae. Given the mean wood densities of these families (Table 3), we thus see that western Amazonian forests are dominated by tree species with low wood density, while eastern Amazonian forests are dominated by species with high wood density.

Our work confirms patterns noted by previous studies (Baker et al. 2004, Muller-Landau 2004), and provides a more detailed biogeographic breakdown. We found that the regionally averaged wood density was relatively constant not only in the western Amazon, but in wet forests from northern Argentina to Mexico. Over these regions, there was no detectable trend within this latitudinal range (see Wiemann and Willamson 2002). In comparison with the rest of the regions, this extended strip of forest shows a low region-wide mean wood density. Specifically, both central Amazonia and eastern Amazonia showed higher wood density means by ~0.05 g/cm^3, and the Atlantic forest region by as much as 0.1 g/cm^3. The dry forest regions in Central America and in Brazil (cerrado) also had a high regional mean wood density, consistent with the fact that species with higher wood density are better able to resist drought-induced embolism (Hacke et al. 2001).

Conclusions and future directions

Our study reinforces previous arguments that accounting for variation in wood density is crucial in tropical biomass estimation protocols (Fearnside 1997, Baker et al. 2004, DeWalt and Chave 2004, Muller-Landau 2004, Chave et al. 2005), and for the first time provides a readily accessible database of great relevance in carbon accounting programs of Central and South America, that encompasses about one-fourth of the tree species growing in this region. This compilation effort is also of relevance in programs aimed at quantifying functional traits of plant species worldwide (Cornelissen et al. 2003). Community-wide means for wood density around 0.6 g/cm^3, such as assumed by Brown (1997), underestimate mean wood density for most parts of the Amazon by 8–10%, and thus will result in similar underestimation of aboveground biomass, which might add up to other sources of error (Fearnside 1997, Chave et al. 2005). The present regional analysis also confirms that the structure and dynamics of western Amazonian tropical forests differ significantly from the rest of the Amazon as suggested by Malhi et al. (2004).

The significant regional and phylogenetic variation in wood density documented here raises questions about the relative influence of historical and ecological forces in shaping these patterns. The differences in community-averaged wood density between western and other Amazonian forests may be due in part to environmental filtering and lineage sorting, with the higher fertility soils of western Amazonian forests favoring species with fast growth and short maturation times (Malhi et al. 2004). Given the history of rapid geological uplifts in this area, they may also be due to largely separate histories of diversification and stochastic influences of which lineages were available where and when (Burnham and Graham 1999). New tools being developed at the intersection of phylogenetics, community ecology, and biogeography will be needed to address this question (Webb et al. 2002). The answers have important implications for our understanding of the factors influencing variation in community wood densities today, and for predicting how wood densities and thus aboveground biomass of tropical forests may change in the future (Wright 2005).

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APPENDIX A

The within-genus coefficients of variation for 76 genera represented by eight species or more (*Ecological Archives* A016-075-A1).

APPENDIX B

The mean and standard deviation of wood specific gravity within families with over eight species (*Ecological Archives* A016-075-A2).

SUPPLEMENT

Database of wood density for species naturally occurring in Central and South America (*Ecological Archives* A016-075-S1).