

Regional and phylogenetic variation of wood density across 2,456 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 analysed regional, taxonomic, and phylogenetic variation in wood density among 2,456 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/cm³. 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 Brazilian Atlantic forests, and that 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 averages give reliable approximations of species' values, 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 (Eurosids 1), and also in more recent divergences, for instance in the Rhamnoids, Simaroubaceae and Anacardiaceae. Our unprecedented wood density dataset 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, Muller-Landau 2004, Baker et al. 2004), and should therefore be included as a predictive variable in large-scale tropical biomass estimation protocols (DeWalt and Chave 2004, Baker et al. 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 solely be considered 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 it is less expensive to construct (Favrichon 1994, Suzuki 1999, Santiago et al. 2004), while high wood density provides a stronger defence 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 xylophagous insects), and lower soil fertility (Wilson and Archer 1977, Hillis and Brown 1984, Wiemann and Williamson 1989a,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 geographic – both regional and altitudinal – 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 wood core's geometrical dimensions (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 calliper, avoiding pressure of the calliper 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 weight of displaced water is equal to the core's green volume (since water has a density of 1 g/cm³). 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 weight is measured on the same sample by drying it in a well ventilated oven at 100 °C until it achieves constant weight (usually 48 to 72 hours 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 Supplementary Data 1). 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 (Caribbean included). We excluded species occurring as exotic invaders, or introduced, 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 asl (henceforth montane species). For palm species, basal area-averaged values were obtained from the data published by Wiemann and Williamson (1989b). 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 were 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 (<http://mobot.mobot.org/W3T/Search/vast.html>). 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 running under Microsoft Access (www.salvias.net). We also matched genus names against a list maintained by Kew Botanic Gardens (<http://www.rbgekew.org.uk/data/genlist.html>). Family-level taxonomy followed the Angiosperm Phylogeny Group II (APG 2003, <http://www.mobot.org/MOBOT/Research/APweb/>). Some notable departures from older classifications are as follows: Bombacaceae, Sterculiaceae, and Tiliaceae are all included in the Malvaceae; Fabaceae, including the Caesalpinioideae and the Mimosoideae 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 weight over volume at 12% moisture, or weight of a ‘unit volume’ (specific weight). This measure is also commonly reported in the British literature in lb per cubic ft ($1 \text{ g/cm}^3 = 62.427 \text{ lb./ft}^3$). Thus we converted these density values into wood specific gravity (WSG) using Sallenave’s (1971) following relationship:

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

where D_M is the wood density at M percent moisture, d is a weight 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, 1961, 1971) published values of WSG, D_{12} , d , v , and S , for a large number of wood samples originating from many tropical forests ($n = 1,893$). Using these data, we found that D_M was relatively stable across moisture values, and that

$$WSG = 0.872D_{12} \quad n=1893, r^2 = 0.983$$

Reyes et al. (1992) using a dataset of 379 species (see Chudnoff 1984) reported a smaller multiplicative factor of 0.800, 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 averages of > 10 assays on the same log. In contrast, the data used by Reyes et al. (1992) are species- or genus-level averages and compiled from multiple studies across the tropics. We tested these two models with an independent dataset reporting both wood density at 12% moisture and WSG (MC Wiemann, pers. comm.), and found that Reyes et al.’s model 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 (<http://www.salvias.net>) 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 asl 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 non-montane species is environmental and geographical. To simply capture the variety of lowland environments of the Neotropics, we defined eight geographical regions (cf. Figure 1): dry forests in Central America (Cd), wet forests in Central America (Cw), Western-North Amazon (AWN), Western-South 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 zones, 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 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 averages 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 inter-regional 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 modelled 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 in part due to regional variation in floristic composition. To determine how total variance in the dataset 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 8 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 (<http://www.phylodiversity.net>, tree version R20040402.new; see Webb and Donoghue 2005), to which we added more information (*Supplementary Data 2*). We developed a computer program in C for the purpose of the present analysis (available from the first author upon request). 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 terminal taxa was computed as the mean character value across the tip nodes $M_i = \sum_{tips\ j} w_j / N_i$, 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:

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

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 but 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 5,406 wood density values for 2,456 tree species, from 63 different primary references (electronic Appendix). These species belonged to 713 genera and 108 families

(sensu APG II). This represents ca. 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 non-montane families were the Fabaceae (448 spp) and the Lauraceae (115 spp). The most represented woody genera were *Licania* (Chrysobalanaceae, 54 spp), *Pouteria* (Sapotaceae, 48 spp), and *Ocotea* (Lauraceae, 41 spp).

The distribution of wood density across species was symmetric but non-normal (positive kurtosis, Shapiro-Wilk test, $p < 10^{-4}$, figure 2). Mean wood density was 0.645 g/cm³. The median was 0.64 g/cm³, maximum 1.39 for *Caesalpinia sclerocarpa* Standl., and minimum 0.11 for *Erythrina ulei* Harms.

Montane species had a lower wood density than lowland species (0.599±0.179 g/cm³ for montane species, and 0.652±0.184 g/cm³ for non-montane species; mean ± standard deviation in both cases). Across species, wood density decreased significantly with log-transformed mean elevation ($R^2=0.029$, $p < 10^{-3}$, mean residual standard error MRSE=0.175; see figure 3). This correlation remained significant both across genera ($R^2=0.035$, $p < 10^{-3}$, MRSE=0.162) and across families ($R^2=0.075$, $p < 10^{-2}$, mean residual SE=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 zones (0.502-0.612 vs. 0.639-0.717, $p < 10^{-3}$, Table 1). The other significant differences were with the dry forests of South and Central America and the Atlantic forest (mean wood density between 0.695 and 0.717). 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: (NW Amazon, wet forest in Central America), (NW Amazon, Atlantic forest), (dry forest in South America, Atlantic forest), and (SW Amazon, dry forest in South America). These additional terms factor in the inter-regional 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: NW Amazon, SW 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 inter-genus variation, 34% by inter-familial variation, and 20% by variation at the order level (Table 2). Among the 76 genera represented by 8 species or more, the within-genus coefficients of variation (CVs) ranged from 3% (*Myrcia*) to 46% (*Machaerium*), with a mean of 16%, and with a small number of highly variable genera (*Supplementary Data 3*). There was a significant tendency towards more variability in genera with lower mean wood density ($r^2 = 0.1$, $P = 0.011$). Fifty-three families were represented by 8 species or over (*Supplementary Data 4*), 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

artefact (eg. *Attalea*, *Lithraea*, *Heliocarpus*, *Malmea*). Of the variable genera that can be analysed with confidence three are in the Fabaceae (*Machaerium*, *Stryphnodendron*, *Chloroleucon*), one in the Bignoniaceae (*Tabebuia*), one in the Nyctaginaceae (*Neea*), and one in the Annonaceae (*Duguetia*).

The most striking inter-family 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 dataset was observed in the rosids. Other major family or sub-family level changes were found in the *Lonchocarpus*-*Derris-Erythrina* clade (*Erythrina* has a very low wood density – range 0.11-0.32, and *Lonchocarpus* a medium-heavy wood – range 0.51-0.97), in the Simaroubaceae (*Simarouba* and *Simaba* with a low wood density versus hard wooded *Recchia mexicana*), the Elaeocarpaceae (*Crinodendron tucumanum* with a low wood density versus *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 endeavoured 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 ten-fold larger database, over 2,400 valid tree species, including secondary forest species and species from contrasted environments. Our database is an indispensable tool for carbon accounting program related to the implementation of the Kyoto protocol, for neotropical forests, be they old-growth or regrowing 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 averages. In a few highly variable genera such as *Machaerium* and *Ceiba*, however, a genus-level average will often fail to produce a good estimate of species wood density, and we provide a list of such genera in

Supplementary Data 3. 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 average (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 averages is not generally good practice. Nonetheless, some species-rich families show surprisingly little variation (see Supplementary Data 4), 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 a species' mean wood density, 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 (3 to 8% of the variance). The observed high wood density in dry environment is thought to be an adaptation to drought stress (Hacke et al. 2001, 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 non-woody 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 non-woody 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, 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 non-woody 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 favour of rosids (oaks, hickory, maple, elm) versus 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 average 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 (Muller-Landau 2004, Baker et al. 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 Williamson 2002). In comparison with the rest of the zones, this extended strip of forest shows a low region-wide average wood density. Specifically, both Central Amazonian and Eastern Amazonian showed higher wood density averages by about 0.05 g/cm^3 , and the Atlantic Forest zone by as much as 0.1 g/cm^3 . The dry forest zones in Central America and in Brazil (cerrado) also had a high regional average 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 & 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 a 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 averages 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 above-ground biomass, which might add up to other sources of error (Fearnside 1997, Chave et al. 2004). 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 favouring 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 above ground biomass of tropical forests may change in the future (Wright 2005).

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663

FIGURE LEGENDS

Figure 1. Maps of the geographical zones in Central and South America.

Figure 2. Histogram of wood specific gravity in the eight geographical zones, and for the whole dataset. Solid vertical bars indicate the mean; dashed vertical bars indicate the median.

Figure 3. Wood density as a function of mean elevation of species, genera and families. The line corresponds to the lowess curve. A negative correlation between wood density and log-transformed elevation is significant at all three taxonomic levels.

TABLES

Table 1. Inter-regional comparison of wood density. The diagonal term indicates the mean wood density 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).

	<i>Number of species</i>	<i>Wet forests</i>						<i>Dry forests</i>	
		<i>West Amazon</i>		<i>Central America</i>	<i>Central Amazon</i>	<i>East Amazon</i>	<i>Atlantic forest</i>	<i>Central America</i>	<i>South America</i>
		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	$< 10^{-3}$	$< 10^{-3}$	$< 10^{-3}$	0.667	502	31	0	17
AE	1290	$< 10^{-3}$	$< 10^{-3}$	$< 10^{-3}$	$< 10^{-3}$	0.639	56	40	59
MA	153	$< 10^{-3}$	$< 10^{-3}$	$< 10^{-3}$	0.024	$< 10^{-3}$	0.701	5	36
Cd	126	$< 10^{-3}$	$< 10^{-3}$	$< 10^{-3}$	0.023	$< 10^{-3}$	0.459	0.717	6
Sd	247	$< 10^{-3}$	$< 10^{-3}$	$< 10^{-3}$	0.024	$< 10^{-3}$	0.752	0.253	0.695

681 **Table 2.** Fraction of variance in wood density explained by various taxonomic levels for the
682 full wood density dataset (N = 2456). Explained variance is equal to the multiple r^2 of an
683 Anova.

Taxonomic level	Multiple r^2	Adjusted r^2
Genera	0.737	0.631
Families	0.342	0.314
Orders	0.197	0.184

684

685 **Table 3.** Adjusted r^2 in wood density at three taxonomic levels for the full wood density
 686 dataset across regions.

		<i>All regions</i>		<i>Wet forests</i>		<i>East Amazon</i>	<i>Atlantic forest</i>	<i>Dry forests</i>	
		<i>West Amazon</i>		<i>Central America</i>	<i>Central Amazon</i>			<i>Central America</i>	<i>South America</i>
		AWS	AWN	Cw	AC	AE	MA	Cd	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

687

Table 4. Fraction of variance in wood density explained by taxonomy alone, by regions alone and by combined effects. The first column refers to the taxonomy effect alone (see also Table 2), the second column the regional effect alone, the third column the sum of these two effects, excluding interaction terms, and the fourth the sum of these two effects, including interaction terms. The difference between column 4 and column 3 detects the presence of interactions between regional effect and taxonomy, which we find to be significant but small.

	Taxonomy	Region	Taxonomy+ Region	Taxonomy x 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

694

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

These 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, for instance for the two species in genus *Attalea*. Node ages were inferred from a fossil calibration (Wikström et al. 2001) and interpolation (Webb and Donoghue 2004).

Node name	Inferred age (Myr)	Number of tip nodes	Number of daughter nodes	Σ_i	σ_i
<i>Machaerium</i>	39.0	11	11	0.679	0.299
Rhamnoids	24.8	3	3	0.777	0.279
<i>Attalea</i>	9.1	2	2	0.600	0.270
<i>Stryphnodendron</i>	39.0	6	6	0.623	0.268
<i>Lithraea</i>	25.0	2	2	0.725	0.255
<i>Lonchocarpus-Derris-Erythrina</i>	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
<i>Chloroleucon</i>	39.0	3	3	0.667	0.229
Cunoniaceae-Brunelliaceae	66.5	20	3	0.660	0.221
<i>Heliocarpus</i>	9.8	4	4	0.318	0.216
<i>Simarouba</i>	12.7	3	3	0.547	0.215
<i>Tabebuia</i>	23.0	25	25	0.771	0.214
<i>Calyptanthus-Eugenia-Eucalyptus</i>	56.7	24	2	0.740	0.213
Boraginaceae	80.0	35	7	0.575	0.212
<i>Malmea</i>	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
<i>Neea</i>	9.5	8	8	0.640	0.190
<i>Duguetia</i>	40.5	5	5	0.688	0.188
Apocynaceae	24.6	39	3	0.705	0.186

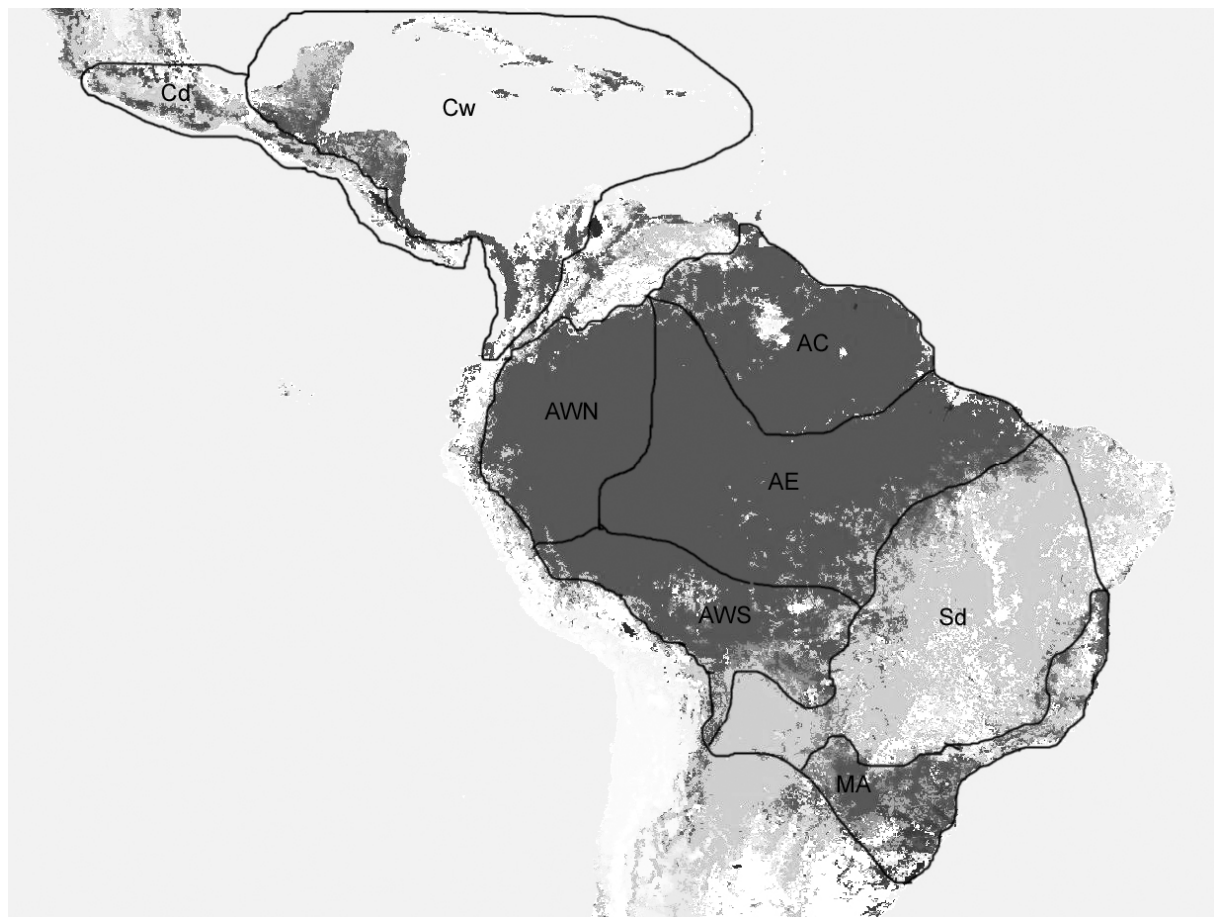


Figure 1.

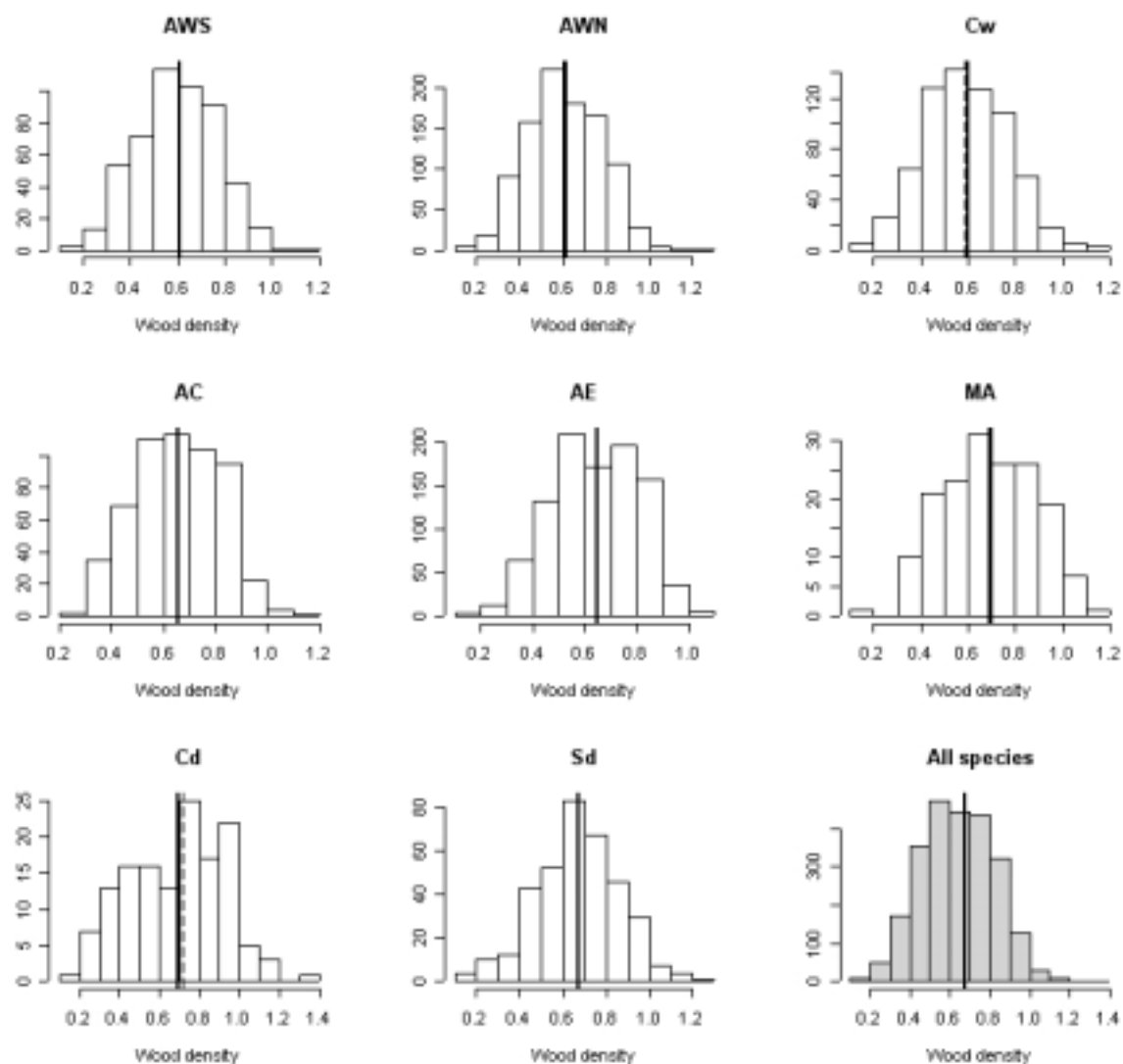


Figure 2.

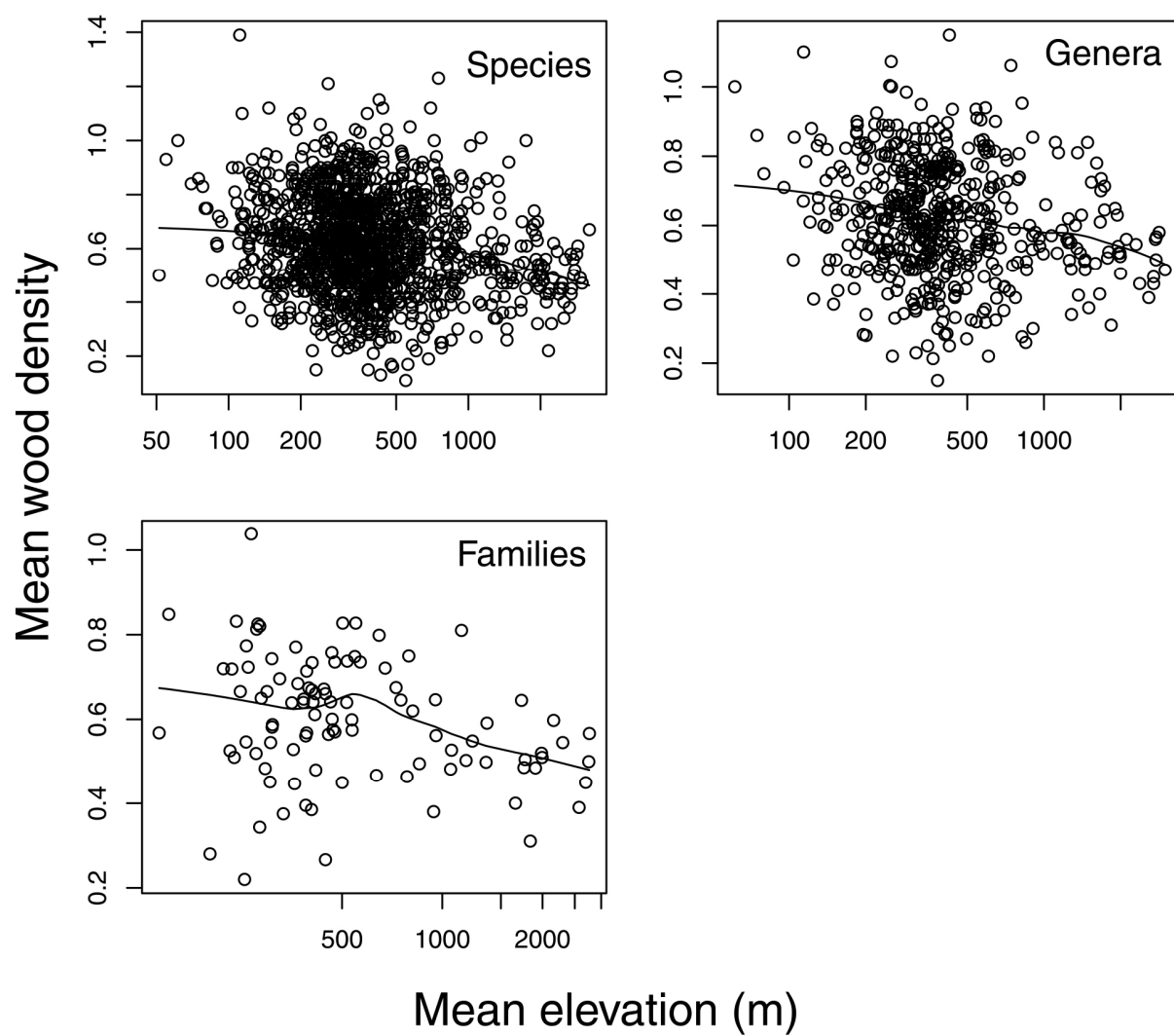


Figure 3.

Supplementary Data 1. Database of wood density for species naturally occurring in Central and in South America (Excel file).

Supplementary Data 2. Phylogenetic megatree of the angiosperms (newick file).

To megatree R20040402.new including the APG II phylogeny (APG 2003) onto which family level phylogenies were grafted (published online <http://www.phylodiversity.net>), we added more information on neotropical woody families (Lauraceae from Chanderbali et al. 2001, Moraceae from Datwyler and Weiblen 2004, Malvaceae from <http://www.malvaceae.info/index.html>, and Apocynaceae from Sennblad and Bremer 2002; Angiosperm Phylogeny Website <http://www.mobot.org/MOBOT/research/APweb/>). Because this effort was mostly carried out during 2004, we did not include more recent phylogenetic information (e.g. Davies et al. 2004, Davis et al. 2005).

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735

736 **Supplementary Data 3.** The mean (Mi) and standard deviation (Σi) of species WSG within genera, for genera with ≥ 8 species. Genera are
 737 ranked in decreasing order of the coefficient of variation CV (percent variation relative to the mean).

738

Genus	Family	Nb species	Mi	Σi	CV	Genus	Family	Nb species	Mi	Σi	CV
1 <i>Machaerium</i>	Fabaceae	11	0.679	0.299	44.04	37 <i>Vitex</i>	Verbenaceae	8	0.586	0.090	15.40
2 <i>Ceiba</i>	Malvaceae	11	0.352	0.125	35.39	38 <i>Sloanea</i>	Elaeocarpaceae	13	0.798	0.121	15.20
3 <i>Cordia</i>	Boraginaceae	28	0.529	0.160	30.23	39 <i>Astronium</i>	Anacardiaceae	8	0.879	0.129	14.71
4 <i>Neea</i>	Nyctaginaceae	8	0.640	0.190	29.68	40 <i>Xylopia</i>	Annonaceae	15	0.595	0.087	14.64
5 <i>Parkia</i>	Fabaceae	10	0.517	0.148	28.64	41 <i>Capparis</i>	Brassicaceae	8	0.661	0.096	14.59
6 <i>Tabebuia</i>	Bignoniaceae	25	0.771	0.214	27.74	42 <i>Virola</i>	Myristicaceae	18	0.496	0.072	14.54
7 <i>Ocotea</i>	Lauraceae	38	0.544	0.131	24.12	43 <i>Lonchocarpus</i>	Fabaceae	19	0.772	0.111	14.36
8 <i>Erythrina</i>	Fabaceae	11	0.276	0.066	23.77	44 <i>Ilex</i>	Aquifoliaceae	12	0.562	0.080	14.30
9 <i>Vochysia</i>	Vochysiaceae	23	0.487	0.114	23.39	45 <i>Swartzia</i>	Fabaceae	29	0.871	0.123	14.17
10 <i>Sclerolobium</i>	Fabaceae	9	0.590	0.128	21.71	46 <i>Inga</i>	Fabaceae	36	0.573	0.078	13.55
11 <i>Mimosa</i>	Fabaceae	8	0.855	0.185	21.68	47 <i>Endlicheria</i>	Lauraceae	8	0.494	0.065	13.20
12 <i>Zanthoxylum</i>	Rutaceae	16	0.625	0.135	21.59	48 <i>Licaria</i>	Lauraceae	11	0.817	0.106	12.93
13 <i>Coccoloba</i>	Polygonaceae	13	0.687	0.138	20.16	49 <i>Rinorea</i>	Violaceae	8	0.669	0.084	12.59
14 <i>Trichilia</i>	Meliaceae	17	0.656	0.131	19.91	50 <i>Erythroxylum</i>	Erythroxylaceae	8	0.758	0.094	12.38
15 <i>Guatteria</i>	Annonaceae	16	0.586	0.115	19.66	51 <i>Couratari</i>	Lecythidaceae	8	0.545	0.067	12.38
16 <i>Ficus</i>	Moraceae	18	0.418	0.081	19.50	52 <i>Licania</i>	Chrysobalanaceae	51	0.834	0.100	12.00
17 <i>Brosimum</i>	Moraceae	10	0.653	0.122	18.67	53 <i>Sterculia</i>	Malvaceae	10	0.490	0.058	11.76

18	<i>Caesalpinia</i>	Fabaceae	12	0.982	0.180	18.36	54	<i>Eugenia</i>	Myrtaceae	19	0.765	0.083	10.81
19	<i>Croton</i>	Euphorbiaceae	11	0.484	0.089	18.35	55	<i>Sapium</i>	Euphorbiaceae	9	0.408	0.044	10.71
20	<i>Diospyros</i>	Ebenaceae	12	0.666	0.122	18.27	56	<i>Chrysophyllum</i>	Sapotaceae	9	0.757	0.081	10.70
21	<i>Acacia</i>	Fabaceae	21	0.710	0.128	18.07	57	<i>Casearia</i>	Salicaceae	12	0.685	0.072	10.45
22	<i>Aniba</i>	Lauraceae	18	0.576	0.103	17.82	58	<i>Maytenus</i>	Celastraceae	13	0.728	0.074	10.11
23	<i>Protium</i>	Burseraceae	23	0.544	0.096	17.71	59	<i>Cariniana</i>	Lecythidaceae	9	0.574	0.055	9.64
24	<i>Nectandra</i>	Lauraceae	17	0.525	0.093	17.70	60	<i>Pourouma</i>	Urticaceae	8	0.373	0.036	9.56
25	<i>Alchornea</i>	Euphorbiaceae	8	0.388	0.068	17.63	61	<i>Aspidosperma</i>	Apocynaceae	28	0.762	0.072	9.47
26	<i>Terminalia</i>	Combretaceae	12	0.726	0.124	17.02	62	<i>Mouriri</i>	Melastomataceae	12	0.843	0.075	8.86
27	<i>Prosopis</i>	Fabaceae	9	0.807	0.137	17.01	63	<i>Iryanthera</i>	Myristicaceae	9	0.618	0.051	8.32
28	<i>Cecropia</i>	Urticaceae	13	0.358	0.061	16.91	64	<i>Byrsonima</i>	Malpighiaceae	14	0.652	0.054	8.22
29	<i>Pouteria</i>	Sapotaceae	48	0.774	0.130	16.80	65	<i>Lecythis</i>	Lecythidaceae	15	0.824	0.066	8.04
30	<i>Pachira</i>	Malvaceae	8	0.481	0.080	16.57	66	<i>Ormosia</i>	Fabaceae	15	0.600	0.046	7.67
31	<i>Tachigali</i>	Fabaceae	13	0.593	0.098	16.50	67	<i>Couepia</i>	Chrysobalanaceae	9	0.791	0.060	7.62
32	<i>Talisia</i>	Sapindaceae	9	0.830	0.137	16.48	68	<i>Eschweilera</i>	Lecythidaceae	22	0.862	0.065	7.56
33	<i>Miconia</i>	Melastomataceae	20	0.632	0.103	16.31	69	<i>Dalbergia</i>	Fabaceae	11	0.823	0.058	7.03
34	<i>Qualea</i>	Vochysiaceae	12	0.672	0.109	16.28	70	<i>Peltogyne</i>	Fabaceae	10	0.765	0.050	6.57
35	<i>Guarea</i>	Meliaceae	11	0.629	0.100	15.97	71	<i>Myrcia</i>	Myrtaceae	8	0.815	0.026	3.25
36	<i>Hirtella</i>	Chrysobalanaceae	10	0.795	0.123	15.47							

740 **Supplementary Data 4.** The mean (Mi) and standard deviation (Σi) of wood density within families with ≥ 8 species. Families are ranked in
 741 decreasing order of the coefficient of variation CV (percent variation relative to the mean).
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Family	Order	Nb species	Mi	Σi	CV	Family	Order	Nb species	Mi	Σi	CV
1 Arecaceae	Arecales	13	0.488	0.201	41.24	27 Verbenaceae	Lamiales	20	0.599	0.118	19.72
2 Simaroubaceae	Sapindales	9	0.547	0.219	40.13	28 Polygonaceae	Caryophyllales	26	0.639	0.122	19.07
3 Anacardiaceae	Sapindales	37	0.659	0.249	37.78	29 Clusiaceae	Malpighiales	34	0.668	0.127	19.05
4 Malvaceae	Malvales	111	0.443	0.143	32.31	30 Myristicaceae	Magnoliales	31	0.518	0.097	18.72
5 Bignoniaceae	Lamiales	45	0.670	0.216	32.21	31 Rubiaceae	Gentianales	78	0.664	0.123	18.48
6 Euphorbiaceae	Malpighiales	106	0.554	0.175	31.55	32 Ebenaceae	Ericales	12	0.666	0.122	18.27
7 Boraginaceae	Euasteridl	35	0.575	0.181	31.52	33 Humiriaceae	Malpighiales	17	0.769	0.139	18.09
8 Nyctaginaceae	Caryophyllales	15	0.611	0.172	28.08	34 Brassicaceae	Brassicales	11	0.685	0.124	18.07
9 Solanaceae	Solanales	8	0.464	0.124	26.67	35 Icacinaceae	NearGarryales	11	0.675	0.120	17.83
10 Fabaceae	Fabales	480	0.713	0.184	25.82	36 Podocarpaceae	Gymnosperma	8	0.499	0.089	17.78
11 Annonaceae	Magnoliales	82	0.572	0.142	24.89	37 Combretaceae	Myrtales	23	0.743	0.124	16.73
12 Elaeocarpaceae	Oxalidales	15	0.742	0.184	24.76	38 Sapotaceae	Ericales	86	0.772	0.126	16.31
13 Ulmaceae	Rosales	11	0.620	0.153	24.62	39 Melastomataceae	Myrtales	35	0.613	0.097	15.90
14 Rutaceae	Sapindales	32	0.748	0.184	24.56	40 Olacaceae	Santalales	16	0.713	0.106	14.87
15 Lauraceae	Laurales	118	0.572	0.140	24.46	41 Myrtaceae	Myrtales	58	0.791	0.117	14.74
16 Vochysiaceae	Myrtales	43	0.567	0.138	24.34	42 Aquifoliaceae	Aquifoliales	12	0.562	0.080	14.30
17 Rhamnaceae	Rosales	13	0.783	0.185	23.61	43 Salicaceae	Malpighiales	32	0.651	0.085	13.05
18 Asteraceae	Asterales	8	0.549	0.128	23.38	44 Chrysobalanaceae	Malpighiales	79	0.818	0.102	12.51

19	Moraceae	Rosales	67	0.560	0.131	23.33	45	Erythroxylaceae	Malpighiales	8	0.758	0.094	12.38
20	Meliaceae	Sapindales	41	0.595	0.138	23.17	46	Araliaceae	Apiales	10	0.482	0.056	11.69
21	Proteaceae	Proteales	9	0.647	0.149	22.99	47	Celastraceae	Celastrales	15	0.721	0.079	10.91
22	Burseraceae	Sapindales	46	0.517	0.114	22.12	48	Violaceae	Malpighiales	15	0.659	0.070	10.56
23	Lecythidaceae	Ericales	69	0.723	0.158	21.84	49	Ochnaceae	Malpighiales	13	0.729	0.076	10.42
24	Apocynaceae	Gentianales	65	0.649	0.140	21.56	50	Malpighiaceae	Malpighiales	20	0.669	0.066	9.90
25	Urticaceae	Rosales	30	0.385	0.083	21.50	51	Memecylaceae	Myrtales	12	0.843	0.075	8.86
26	Sapindaceae	Sapindales	45	0.732	0.157	21.40	52	Caryocaraceae	Malpighiales	10	0.696	0.034	4.90

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