

ECOLOGICAL AND EVOLUTIONARY DETERMINANTS OF A KEY PLANT FUNCTIONAL TRAIT: WOOD DENSITY AND ITS COMMUNITY- WIDE VARIATION ACROSS LATITUDE AND ELEVATION¹

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Wood density is an important trait in trees indicative of their life history and mechanical and physiological strategies. The following examines the evolutionary ecology of wood density using a large database for seed plants. In particular, we focused on the geographic and phylogenetic variation in wood density for both gymnosperms and angiosperms. A phylogenetic supertree was constructed for over 4600 taxa, allowing for comprehensive analyses of divergences across the seed plant phylogeny. Community-wide means and variances for wood densities were quantified for 171 standardized forest communities. Wood density was generally highly conserved across the entire seed plant phylogeny, yet large divergences were found within the rosid clade. Geographic and community variation in wood density, however, was significantly lower in temperate and high elevation communities, dominated by gymnosperms, than in tropical lowland communities, dominated by angiosperms, suggesting an increase in trait and, to some extent, clade filtering with latitude and elevation. Together, our results support the notion that both biotic and abiotic forces have been important in the evolution of wood density as well as in controlling the observed trait mean and variance across geographic gradients.

Key words: angiosperms; functional ecology; functional trait; gymnosperms; life-history trait; macroecology; macroevolution; phylogeny; trait conservatism.

A central goal in community ecology and macroecology is to understand the relative importance of the various forces that control local to geographic patterns of diversity (MacArthur, 1972; Brown, 1995). For example, the role of local ecological interactions (such as competition and biotic enemies), climatic filtering, drift, evolutionary/biogeographic history, and dispersal limitation can each influence the nature of local community diversity (Ricklefs, 1987; Ricklefs and Schluter, 1993; Weiher and Keddy, 1995; Hubbell et al., 1999).

Recent developments in functional ecology offer a promising approach to the problem of linking attributes of individuals to community assembly and dynamics. Specifically, one must consider not just the species in a community, but *the diversity of functional traits* those species represent (Diaz and Cabido, 1997; Weiher et al., 1999; Lavorel and Garnier, 2002). Thus, the subdiscipline of functional ecology attempts to link population, community, and ecosystem processes to the key traits that influence organismal performance (e.g., growth, metabolism, reproduction; McGill et al., 2006). These “functional traits” ultimately reflect variation in survivorship

and reproduction (i.e., fitness) across differing environments (McGill et al., 2006; Westoby and Wright, 2006).

An increasing number of botanical studies have documented prominent plant traits that appear to correlate strongly with aspects of whole-plant performance (reviewed in Westoby et al., 2002). For example, plant size (West et al., 1999; Enquist, 2002) and leaf traits (leaf mass per unit area, leaf stoichiometry, gas exchange; Reich et al., 1997; Wright et al., 2004) have been highlighted as key functional traits that are important for understanding variability in plant form, function, and diversity. Recently, Westoby et al. argued that there are likely just a few key functional trait dimensions by which most species traits could be differentiated (Westoby et al., 2002). One of the key traits that seems to encapsulate, if not link, many of these plant functional traits is tissue density. In particular, for woody plants, the density of woody tissue appears to be central in many aspects of plant form, function, and diversity.

Variation in wood density is closely tied to variation in diameter growth rate, mortality rate, timing of reproduction, hydraulic capacities of the stem, and the relative mechanical strength of a plant (Carlquist, 1975; Putz et al., 1983; Niklas, 1997; Enquist et al., 1999). Wood density, also referred to as wood specific gravity, is the ratio of dry mass to green volume. Therefore, wood density describes the proportion of a stem that is tissue and cell walls (i.e., xylem conduit walls) and the space within cell walls (i.e., xylem conduit apertures). Thus, plants with a high fiber tissue percentage per unit volume and thick fiber walls (relative to the fiber lumen diameters) have high wood densities, and plants with thin fiber walls have low wood densities.

There are two main theoretical formulations that explicitly show how wood density can influence whole-plant form and function. First, both intra- and interspecific differences in wood density are important because wood density positively correlates with greater mechanical support (Niklas, 1993,

¹ Manuscript received 18 August 2006; revision accepted 18 January 2007.

The authors thank J. Chave and his collaborators for providing a draft of their work in press; D. Ackerly for advice on calculating the contribution index used in the study; B. Boyle for invaluable assistance with standardizing the taxonomy of the wood density and forest inventory plot databases; and M. Weiser and J. Pither for assistance and/or comments concerning this work. N.G.S. was supported by the USGS Geographic Analysis and Monitoring Program. B.J.E. and N.G.S. were supported by an NSF CAREER Award to B.J.E. This work was made possible through funding and support from Conservation International and the Missouri Botanical Garden.

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1997). An increase in mechanical support with tissue density can be related to maximum plant height for a given stem diameter using the Euler–Greenhill equation:

$$H_{\max} = c \left(\frac{E}{\rho} \right)^{1/3} D^{2/3}, \quad (1)$$

where H_{\max} is the maximum height physically achievable, c is the proportionality constant, E is Young's elastic modulus, and ρ is wood density (Greenhill, 1881; McMahon and Kronauer, 1976; Niklas, 1997). Therefore, the maximum height that is possible for a given stem diameter before the plant will buckle under its own weight critically relies upon the density of wood. In light limited environments, such as forests, Eq. 1 is expected to provide a good approximation of trade-offs associated with competitive superiority (H_{\max}) and with the ability to withstand disturbances due to plant size (D) and strength (ρ). The increased whole-plant mechanical support provided by higher tissue densities also increases resistance to stem breakage, and thereby mortality, due to extrinsic forces (i.e., wind) that will ultimately influence plant community structure and dynamics (Putz et al., 1983; ter Steege and Hammond, 2001).

The second theoretical formulation shows that, on an intercellular and tissue scale, denser wood also provides increased mechanical support in the form of resistance to xylem conduit implosion or rupture (Hacke et al., 2001). The pressure required for conduit implosion (P_i) is predicted to be proportional to the ratio of conduit wall thickness to the transverse width of the conduit squared (thickness-to-span ratio; t/b). Further, the density of wood (ρ) is proportional to the thickness-to-span ratio (Hacke et al., 2001, 2005) giving the following mechanistic link between P_i and ρ :

$$P_i \propto \left(\frac{t}{b} \right)^2 \propto \rho. \quad (2)$$

Therefore, xylem conduit implosion or rupture should be proportional to wood density. As a result, denser woods should then be less vulnerable to conduit cavitation and implosion (Hacke et al., 2001).

Importantly, variation in wood density also reflects differential allocation of metabolic production. Denser wood has, by definition, more carbon and energy content per unit volume than lighter woods (Enquist et al., 1999). Therefore, along with Eqs. 1 and 2, variation in wood density is central because it ultimately reflects a larger trade-off between all of the tasks involved in allocation of metabolic production (e.g., defense, maintenance, reproduction) as well as biomechanical (Niklas, 1993) and hydraulic functioning (Sobrado, 1986; Borchert, 1994; Roderick and Berry, 2001; Santiago et al., 2004) of plants. For example, the increased resistance to the loss of hydraulic conductivity via cavitation comes with the increased cost of constructing thicker conduit walls (i.e., more carbon), thereby decreasing the amount of metabolic production allocated to vertical growth. Because differential allocation to tissue density must then sacrifice carbon and energy that could be used to grow and/or reproduce, the xylem safety vs. efficiency trade-off is fundamental to understanding the ecology and evolution of seed plants (Baas et al., 2004).

From an evolutionary perspective, in both gymnosperms and angiosperms, due to the central role of water transport in the photosynthesis-transpiration compromise, one would expect that traits linked to plant hydraulics, such as wood density, to be evolutionarily less labile or to be “phylogenetically

conserved” (i.e., wood density should be less variable within clades than expected by chance). Chave et al. (2006) have recently quantified divergences in wood density along a phylogenetic supertree containing approximately 2400 species located in the neotropics (mainly Amazonia and Central America). They found this trait to be phylogenetically conserved in general with some large divergences in the rosid clade, yet this was not tested properly using randomization techniques (Blomberg et al., 2003). Chave et al. provided an impressive first step toward quantifying the conservatism and divergences of wood density in seed plants, but as they correctly state, a more extensive geographic and taxonomic sampling of the seed plants is needed in future analyses to fully confirm their initial findings (Chave et al., 2006).

From a geographic or ecological perspective, wood anatomists and foresters have noted geographical trends in wood density (e.g., Carlquist, 1975). Numerous studies have documented significant correlations between wood density and climatic variables (i.e., temperature, precipitation, soil) and environmental gradients (i.e., elevation and latitude; Lawton, 1984; Williamson, 1984; Wiemann and Williamson, 1989, 2002; Muller-Landau, 2004; Preston et al., 2006; Chave et al., 2006). Together, these studies seem to enable one to begin to address the mechanistic and theoretical linkages between wood density and community structure. However, the generality of these geographic correlates of wood density is still unclear.

There are three potential limitations in previous studies that have linked variation in wood density with climate and whole-plant performance. First, firmly concluding mechanistic linkages between wood density and climate from correlative studies is tenuous because none of these studies listed (but see Preston et al., 2006) have accounted for shared ancestry through the use of phylogenetically independent contrasts (Felsenstein, 1985). Second, while a handful of studies have successfully analyzed variation of this trait across abiotic gradients on a regional scale (Muller-Landau, 2004; Chave et al., 2006), none have adequately addressed variation across the entire gradient—i.e., the latitudinal gradient. Lastly, the statistical inference one can glean from these studies of community-wide variation in wood density is unclear due to regional differences in species richness. To properly assess the role of the biotic and abiotic environment in influencing the observed community-wide variation in wood density, one must utilize a null modeling approach (Gotelli and Graves, 1996). A null model will enable one to assess if the observed variation in wood density is indeed a pattern, allowing one to quantify if the observed distribution of wood density in communities is greater than or less than expected given the observed value of species richness.

An additional geographic pattern is the observation that angiosperms and gymnosperms often have noticeably polarizing distributions. Interestingly, the fundamental trade-off between the probability of xylem conduit failure and the cost of constructing wood is shared between angiosperms and gymnosperms. Further, the construction cost of hydraulic safety differs greatly between angiosperms and gymnosperms (Hacke et al., 2001). Specifically, for an equivalent cost of construction (i.e., wood density), gymnosperms have a *greater* resistance to air-seeding leading to xylem conduit failure (Hacke et al., 2001, 2005). Given the fundamental difference between angiosperms and gymnosperms in the safety vs. efficiency trade-off, the question becomes, why is gymnosperm

wood, often characterized by a more cost efficient trade-off, geographically restricted to and more abundant within high elevations and latitudes? More generally, how are these trade-offs, across all woody plants, expressed across broad-scale gradients?

In this paper, we focus on the evolutionary and geographic variation in wood density, especially within and across gymnosperms and angiosperms. To account for geographic and evolutionary variation in wood density, we identify two recent hypotheses. Both hypotheses have been considered separate in the literature and each address different ends of the elevational or latitudinal gradient. However, interestingly, as we show, these hypotheses are likely not mutually exclusive because they make similar predictions for geographic and evolutionary variation in wood density.

The first hypothesis, henceforth called the canopy hypothesis, focuses on low elevations and latitudes. It states that although angiosperms have an increased metabolic cost of manufacturing denser wood for the same level of conduit safety than gymnosperms, the increased whole-plant mechanical strength allows for a greater variety of canopy morphologies (Hacke et al., 2005). Specifically, denser angiosperm wood can support canopies with greater lateral spreads thereby providing a potential competitive edge. However, lighter wood densities provide faster rates of diameter growth, that enable trees to reach the canopy faster and reproduce sooner than more dense woods (Enquist et al., 1999). Therefore, in areas where light may be limiting to plant growth (i.e., tropical lowland forests), biotic forces such as competition for limiting resources may drive the evolution of alternative wood density influenced trade-offs. In short, within warm, wet, and light-limited environments, it is expected that selection would lead to the exploration of phenotypes along the life history trade-off mediated by wood density.

The second hypothesis, which we will refer to as the stress-dominance hypothesis, focuses on how differences in environmental water stress and in xylem anatomy influence whole-plant competitive ability. This hypothesis states that tracheids allow for competitive dominance in more hydraulically stressful environments (i.e., high elevations and latitudes; Hacke et al., 2005). Applied within or across clades, the stress-dominance hypothesis states that as the environment becomes more stressful, stabilizing selection will increasingly limit ecological and evolutionary variation in plant function within a community (Weiher and Keddy, 1995).

To test the two hypotheses, we assessed the evolutionary history and role of wood density on woody plant community structure by compiling and analyzing a unique and large database comprised of wood density, community diversity, and species distribution data. We utilized both phylogenetic and null modeling approaches to assess three prominent, and yet to be adequately tested, hypotheses. Specifically, we tested the predictions that (1) in general, wood density is a highly conserved trait within clades across the seed plant phylogeny; (2) across the seed plant phylogeny, divergences in wood density are correlated with abiotic variables that affect the movement of water through plants (i.e., temperature and precipitation/water availability); and (3) the mean and variance of values for local community wood density decreases in more stressful locations along gradients (i.e., elevation and latitude) when using a null model that controls for differences in species richness.

MATERIALS AND METHODS

Global wood density database—A global wood density database for gymnosperms and angiosperms was compiled from the literature and from publicly available wood density databases. The literature and databases used to compile our global wood density database can be found in the Appendix S1 (see Supplemental Data with online version of this article). Basic wood density values, defined as oven-dry mass divided by fresh volume, were used for all calculations. For those studies that did not report basic wood density, yet did report wood density with a percentage moisture content, we converted that value to basic wood density (Sallenave, 1971). The reported range in wood densities was 100 to over 1200 kg·m⁻³, while the average wood density of the database was 666.46 kg·m⁻³ (SD 184.64 kg·m⁻³). The database spans 40 orders, 132 families, 1207 genera, and 4667 species of seed plants. The majority of the species had multiple records in the database with the total number of individual records equaling 7753. Because wood density is known to occasionally be highly variable within a species, we quantified the degree of variation in the data set attributable to intra- vs. interspecific variation. We found that 10.07% of the variation was due to intraspecific variation. Recent research using simulations has shown that this level of intraspecific variation is sufficiently low to provide robust results from comparative analyses that use phylogenetic trees (Harmon and Losos, 2005). All taxonomy was standardized by using nomenclature from The International Plant Names Index (www.ipni.org) and the program TaxonScrubber (Boyle, 2004).

Phylogenetic analyses of wood density divergences—Wood density values from the database were arrayed across a phylogenetic supertree of seed plants using software developed by Webb and colleagues (Webb and Donoghue, 2004; Webb et al., 2004). Specifically, we used the maximally resolved Phylomatic tree (tree version R20031202) as the backbone for our seed plant supertree. This backbone is based on the Angiosperm Phylogeny Group II classification of angiosperms (APG II, 2003). A proportion of the generic and species relationships within clades were uncertain due to the present lack of resolved phylogenies for many seed plant families and genera. Large clades that were unresolved by Phylomatic (i.e., Malpighiales and Pinaceae) were further resolved using recently published phylogenies (Wang et al., 2000; Davis et al., 2005; Gemant et al., 2005). The remaining unresolved clades in the phylogeny were treated as “soft” polytomies. The phylogenetic supertree generated by this procedure had 895 internal nodes. The supertree was then calibrated using the branch length-adjusting algorithm BLADJ (Webb et al., 2004), which uses published estimates for node dates (Wikstrom et al., 2001). BLADJ assigns “known” dates to nodes within the seed plant phylogeny and subsequently assigns dates to nodes between “known” nodes by dividing the branch length between the two “known” nodes evenly (Webb et al., 2004).

Following Moles et al. (2005), we calculated the divergence size and the relative contribution to tree-wide variation in wood density at each node. We also tested for tree-wide conservatism of wood density values. Divergence size was represented as the standard deviation of wood density across “daughter” clades of the focal node. The contribution of each node to tree-wide variation in wood density is simply the product of variation in the focal clade directly attributable to the focal divergence and the amount of tree-wide trait variation that is attributable to terminal taxa within the focal clade (Moles et al., 2005).

Tree-wide and nodal conservation of wood density was tested by randomizing trait values across the tips of the phylogeny 29 999 times. Next, the average magnitude of the SD between descendant trait means from each internal node across the whole supertree was quantified for each randomization. This value was then used to generate a null distribution of divergence sizes for each internal node. This technique is similar to that described by Blomberg et al. (2003), that was designed to test for “phylogenetic signal” in data, yet our analyses do not incorporate their descriptive statistic, *K*, which allows for quantitative comparisons of the absolute level of conservatism in one trait vs. another. In the present analyses, we use the term phylogenetic conservatism as a synonym for phylogenetic signal while recognizing that many other authors have differentiated between the two (Blomberg and Garland, 2002). Lastly, in order to put the amount of trait conservatism into a taxonomic context, we performed a taxonomically nested analysis of variance.

Comparative study of species composition within and across woody plant communities—Using the online database SALVIAS (www.salvias.net), we obtained unique georeferenced locations for species for which we had a wood density value. Using local plant inventories and herbarium specimens, we were able to extract 39 771 specimens for analyses from several herbaria and

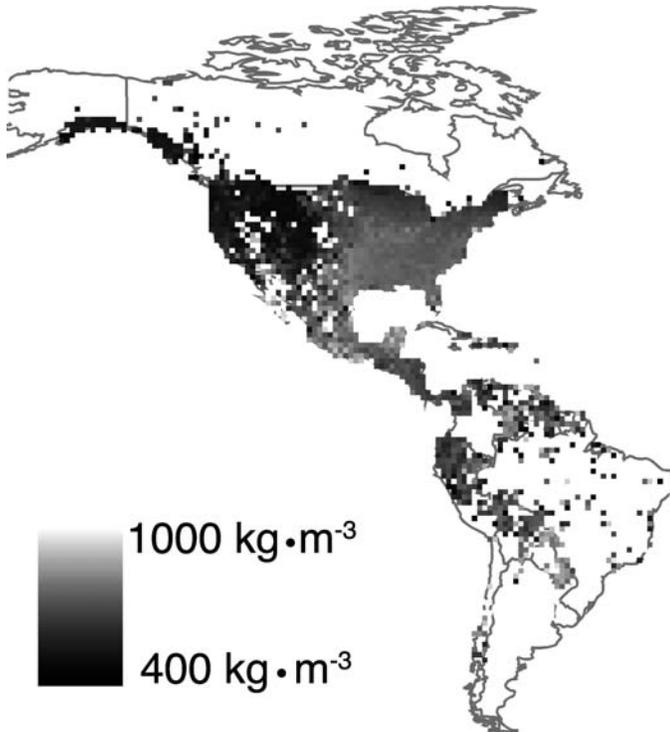


Fig. 1. The mean wood density of all the species in each 1° grid cell based upon $\sim 40,000$ specimen records stored in the SALVIAS database for which we could match a wood density value from the compiled database.

organizations associated with the SALVIAS project (Fig. 1). A geographic information system (GIS) point file was created from specimen coordinates using DIVA-GIS (Hijmans et al., 2004). Next, we extracted mean annual temperature, minimum temperature, maximum temperature, temperature seasonality, annual rainfall, minimum monthly rainfall, maximum monthly rainfall, potential evapotranspiration, and elevation values for each specimen using 10-min resolution interpolated climatic surfaces (Hijmans et al., 2005). If a species had more than one specimen with unique coordinates, a mean value for each abiotic variable was calculated and assigned to that species.

Initially, the mean abiotic values for each of the species were used to calculate a Pearson's correlation coefficient (r) with wood density. Second, in order to account for phylogenetic relatedness, we used phylogenetically independent contrasts (PIC r ; Felsenstein, 1985). Because of the multiple polytomies in the phylogeny, we used an alternative PIC method outlined by Pagel (1992). This method ranks derived taxa from a polytomous node based on the predictive trait, in this case wood density. Next, the derived taxa are split into two groups, by maximizing the difference in the predictive trait values. The mean trait values for each of the two groups is then calculated and used for a single contrast at that node. This technique therefore increases the difference between the two daughter nodes in each analysis and reduces the power of the analysis ultimately leading to a conservative test for phylogenetic signal within the daughter clades.

Comparative study of community composition—Community level diversity in wood density was quantified using 171 standardized forest inventory plots in the western hemisphere (Gentry, 1988; Online Supporting Material Fig. 1). Because wood density is highly conserved among species within a genus (see Results), genus means were used for species in the plots for which we had no wood density values. Lastly, if no con-generic wood density value was available for a species in a plot, we assigned the mean value from the species values in the plot.

After trait values were assigned to taxa within each community, the observed mean and coefficient of variation of trait values was calculated. Next, we generated 999 random communities to which our observed communities could be compared. Each random community was generated by randomly

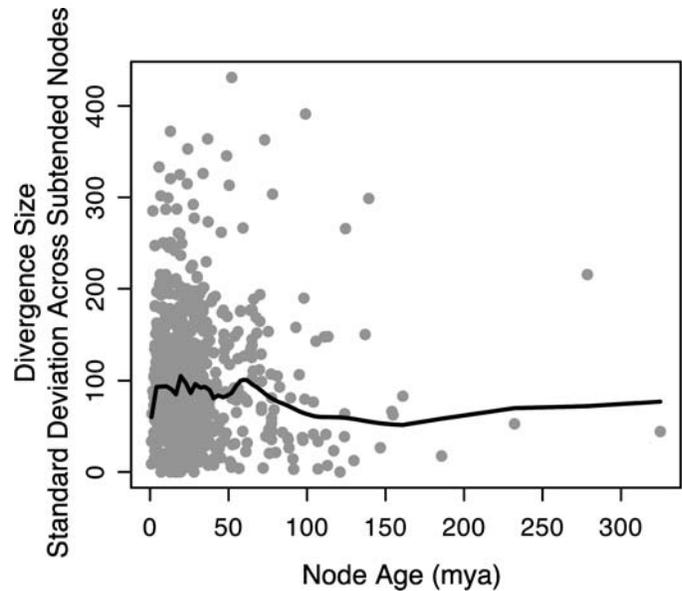


Fig. 2. Distribution of divergences in wood density through time. Each point represents one of the 895 nodes in the supertree used for this study. Black line is a lowess curve with a smoothing span of 0.05. It is important to note that the node ages represented on the x -axis are rough estimates. They are used for inferences regarding the relative timing of divergences and not the absolute timing.

drawing, without replacement, wood density values from a pool of all the taxa represented in the plots. The observed species richness of communities was conserved in the random communities. Next, the mean and coefficient of variation of wood density values in each of the random communities was calculated to generate a null distribution. Each observed community was assigned a quantile score using the null distribution in order to assess whether it had a higher mean wood density or a higher coefficient of variation of wood density values (i.e., higher quantile scores) than expected or lower values (i.e., lower quantile scores) than expected.

RESULTS

Phylogenetic analyses of wood density divergences—Wood density was highly conserved for the 4667 seed plant species used for this study. The average magnitude of trait deviation values across all nodes in the phylogeny landed in the first quantile out of 29,999 randomizations ($P < 0.0001$). Of the 895 internal nodes only 49 (5.47%) had significant divergences in wood density, whereas 221 internal nodes (24.69%) were significantly conserved. Using a taxonomically nested ANOVA, the variation in wood density was primarily attributable to genera within a family (58.2%). Family explained the next largest amount of the variance (29.9%) followed by order (11.8%) and species (0.1%).

The largest divergences in wood density have occurred relatively recently, yet caution should be taken when inferring the absolute dates of the divergences given the estimates used for node ages (Fig. 2). Many of the largest divergences in wood density were observed between clades that had few taxa in our database and thus could not be properly assessed without quantile scores from randomizations. Therefore, we chose to address only those nodes that had significant divergences in relation to the random trait distributions on the phylogeny in order to control for results potentially biased by under-sampled

TABLE 1. Significantly diverged nodes given 29 999 randomizations of trait values across tips of seed plant phylogeny. Divergence size was calculated as the standard deviation of trait values across subtended nodes (Moles et al., 2005).

Rank	Divergence size	P	Tips	Age (mya)	Clades involved
1	3.18	<0.001	23	24.0	<i>Ormosia</i> vs. <i>Erythrina</i> (Fabaceae)
2	2.01	<0.001	154	34.2	Moraceae vs. Urticaceae
3	0.79	<0.001	516	61.0	Sapindales
4	2.61	<0.001	484	45.3	Malvaceae vs. Dipterocarpaceae
5	1.93	<0.001	304	70.0	Myrtracae vs. Vochysiaceae
6	2.66	<0.001	233	59.2	Lauraceae vs. Hernandiaceae
7	1.89	<0.001	1613	98.0	Eurosid I
8	1.93	<0.001	156	31.4	<i>Erythrina</i> , <i>Lonchocarpus</i> , <i>Millettia</i> three-way polytomy (Fabaceae)
9	1.89	0.001	89	40.0	Papilionideae
10	1.29	0.002	224	70.8	Rosales
11	1.77	0.004	30	64.0	Memecylaceae vs Melastomataceae
12	1.41	0.004	53	36.1	Core Fagales
13	1.78	0.006	21	7.2	<i>Rhizophora</i> , <i>Carallia</i> , <i>Gynotroches</i> , <i>Pellacalyx</i> , <i>Bruguiera</i> , <i>Ceriops</i> , <i>Kandelia</i> seven-way polytomy (Rhizophoraceae)
14	0.71	0.006	195	71.0	Gentianales
15	0.81	0.007	601	89.5	Malpighiales and Oxalidales polytomy
16	0.99	0.007	130	18.9	Mimosoideae
17	3.13	0.007	6	50.4	Caryophyllales
18	3.03	0.007	6	78.0	Solanales
19	3.62	0.008	4	73.0	Arecaceae
20	0.92	0.008	254	53.7	Simaroubaceae, Rutaceae, Meliaceae three-way polytomy

clades. Clades within the Fabaceae contained four of the top 16 significant divergence sizes (Table 1). This suggests that this speciose family has also undergone significant radiations in wood density. Further, the observed variance of wood density within the Fabaceae is greater than expected by chance. The Fabaceae also have the fifth highest contribution to tree-wide variation in wood density values (Online Supporting Material Table 1). Along with Fabaceae, many other nodes embedded inside the Eurosid I clade showed significantly large divergence sizes. Of the top 16 significant divergences in wood density values, 10 are located within the Eurosid I clade and 14 are located within the Rosid clade (Table 1).

Comparing geographic variation in wood density in the angiosperms and gymnosperms—Across the Spermatophytes, wood density was positively correlated with mean annual temperature and maximum monthly temperature using phylogenetically informed (PIC *r*) or uninformed (Pearson’s *r*) analyses (Table 2). A negative correlation between wood density and precipitation variables was found in seed plants and angiosperms using *r*, but this correlation disappeared when using PICs. Pearson’s *r* and PIC *r* results showed significant negative correlations between wood density and elevation in seed plants (Table 2).

Comparative study of community composition—Our null model showed that the distribution of quantile scores for the community-wide coefficient of variation of wood density, across many of our plots, had less variation than expected given their richness (35%). While many of the plots did have lower observed coefficients of variation in wood density than expected, results from a multiple regression analysis using physiographic variables showed community-wide variation in wood density was negatively correlated with latitude (Estimate = -8.94, *t* = -4.50, *P* < 0.001) and elevation (Estimate = -0.16, *t* = -4.54, *P* < 0.001; Overall Model *r*² = 0.19, *P* < 0.001; Fig. 3). Latitude (Estimate = -3.82, *t* = -1.99, *P* < 0.05) and elevation (Estimate = -0.17, *t* = -5.19, *P* < 0.001) were also negatively correlated with community-wide mean wood density (Overall Model *r*² = 0.19, *P* < 0.001).

Results from separate multiple regression analyses using climatic variables showed that mean annual temperature was positively correlated with both the community-wide mean wood density quantile scores (Estimate = 16.13, *t* = 2.18, *P* < 0.05), and total annual precipitation was not correlated (Estimate = -0.002, *t* = -0.023, *P* = n.s., Overall Model *r*² = 0.10; *P* < 0.001; Fig. 4). Community-wide variation in wood density was positively correlated with mean annual temperature (Estimate = 23.09, *t* = 3.06, *P* < 0.01), while total annual precipitation (Estimate = 0.12, *t* = 0.97, *P* = n.s.) was not significantly correlated (Overall Model *r*² = 0.13; *P* < 0.001; Fig. 3).

DISCUSSION

Conservatism and divergences in wood density among seed plants—The relative importance of wood density to whole-

TABLE 2. Correlations of climatic variables and elevation with wood density using a Pearson’s correlation coefficient (*r*) and phylogenetically independent contrasts (PIC *r*). * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

Trait	All Taxa		Gymnosperms		Angiosperms	
	<i>r</i>	PIC <i>r</i>	<i>r</i>	PIC <i>r</i>	<i>r</i>	PIC <i>r</i>
Mean annual temperature	0.19***	0.23***	0.29**	0.32**	0.09*	0.18***
Maximum monthly temperature	0.24***	0.21***	0.27**	0.25**	0.19***	0.20***
Minimum monthly temperature	0.13***	0.19***	0.18	0.21**	0.03	0.11***
SD of monthly mean temperature	-0.07*	-0.08	-0.06	-0.06	-0.01	-0.08
Annual precipitation	-0.09*	0.01	0.03	0.02	-0.19***	0.01
Maximum monthly precipitation	-0.05	0.01	0.05	0.01	-0.14***	0.02
Minimum monthly precipitation	-0.10**	-0.01	0.07	-0.02	-0.17***	-0.01
SD of monthly precipitation	0.10**	0.03	0.02	0.02	0.13***	0.02
Potential evapotranspiration	0.01	0.02	0.04	0.01	0.02	0.03
Elevation	-0.12***	-0.15***	-0.02	-0.11*	-0.04	-0.14***
Latitudinal mid-point of species range	-0.25***	-0.08*	-0.18**	-0.01	-0.28**	-0.17
Latitudinal extent of species range	-0.14***	-0.09*	-0.18***	-0.26***	-0.09	-0.47*

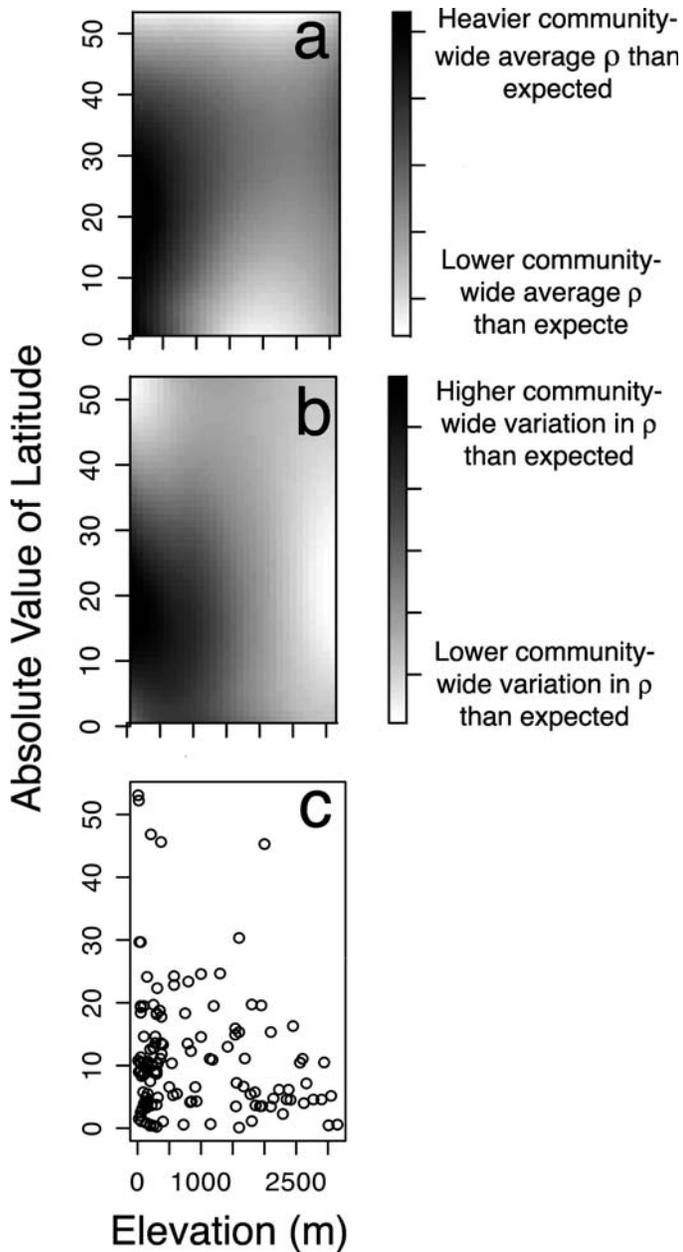


Fig. 3. An interpolation of (a) community-wide average (b) and variation in wood density in response to physiographic gradients as predicted from multiple regression analyses (see Results). The plots utilized for the interpolation are represented as points in the bottom panel (c). Because some regions of the latitude by elevation space were not sampled in the 171 plots utilized for this study, some of the interpolated areas should be interpreted with caution.

plant biomass allocation and hydraulic efficiency suggests that this trait should be phylogenetically conserved. Our results show that overall wood density is a highly conserved functional trait in seed plants. However, wood density does not appear to be strongly conserved within certain clades. Our results showed a significant degree of variation in wood density within the Fabaceae and the rosoid I clade indicating relatively recent large divergences in this trait. Interestingly, Fabaceae and many of the families in eurosoid I (Malpighiaceae, Chrysobalanaceae, Passifloriaceae, Clusiaceae, Celastraceae,

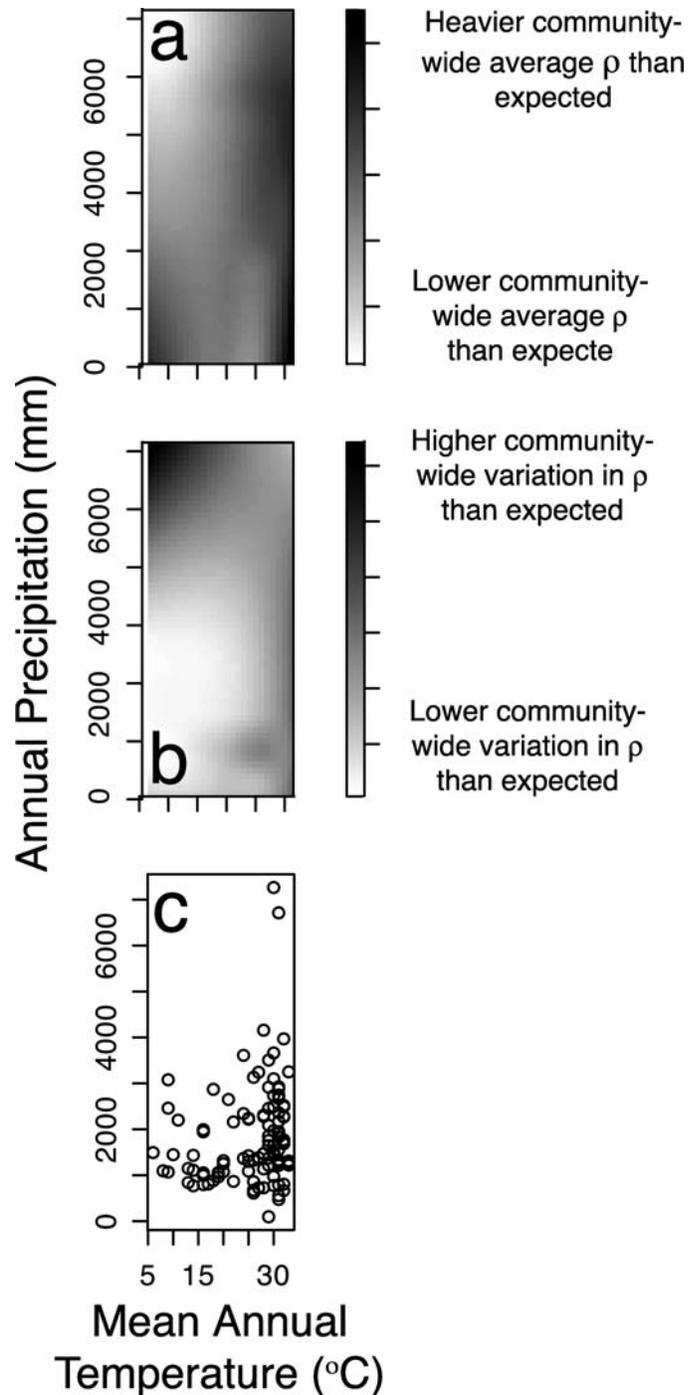


Fig. 4. An interpolation of (a) community-wide average (b) and variation in wood density in response to climatic gradients as predicted from multiple regression analyses (see Results). The plots utilized for the interpolation are represented as points in the bottom panel (c). Because some regions of the temperature by precipitation space were not sampled in the 171 plots utilized for this study, some of the interpolated areas should be interpreted with caution.

etc.) dominate lowland tropical forest. Our work verifies the recent findings by Chave et al. (2006) regarding tropical tree species. They analyzed divergences in wood density of neotropical taxa and found that these same clades were highly variable. However, they used a subset of seed plant clades that

are found in the neotropics and did not use randomization techniques to test whether the divergences they reported were larger than expected given the global distribution of wood density values (Blomberg et al., 2003). The present work utilized a global data set twice the size of the Chave et al. data set. Nevertheless, our analyses tested for significant levels of trait divergences and generally supports the findings of Chave et al. (2006).

Because wood density has been hypothesized to be indicative of a hydraulic efficiency vs. safety trade-off, we expected to find wood density to be correlated with climatic variables associated with water availability, temperature, and precipitation. Our results support previous functional ecology and physiology studies that have hypothesized that temperature has been an important selective force on plant hydraulics. However, our results do not support previous conclusions (e.g., Wiemann and Williamson, 2002) relating precipitation levels to wood density. Additional analyses using phylogenetically independent contrasts indicate that the evolution of wood density in seed plants is most strongly correlated with variation in temperature (see Table 2). Specifically, the existence of a positive relationship between wood density and temperature on a global “macroecological scale” lends support to the stress-dominance hypothesis, that predicts a mechanistic connection between vulnerability to xylem cavitation and the reduction in variation in plant function in stressful environments (Weiher and Keddy, 1995; Hacke et al., 2001).

Variation in wood density along global environmental gradients—The observed community-wide variation in wood density was typically lower than expected given species richness. This is evidence that, on a global scale, species within communities represent a winnowed subset of the global pool of wood density values. This suggests that generally there is a strong abiotic filtering of wood density values in forest communities of this scale (Weiher and Keddy, 1995). Such trait filtering supports the expectation that differences in the local environment then influences which wood density values best perform in these environments. On the other hand, although a large proportion of the study plots had little variation in wood density, some plots had remarkable variation in wood densities, which often covered a large portion of the global range of wood density values. Ecological communities with the greater ranges in trait variation were generally found in tropical lowland forests (Fig. 3). This is an intriguing empirical result, especially when thinking about the forces that structure tropical and temperate communities.

Our null model shows that many tropical plant communities have more variation in wood density than expected given their richness than do their temperate counterparts. Conversely, temperate plant communities have far *less* variation in wood density. Together, these results suggest that plant species in lowland tropical tree communities may not be as functionally constrained by their environment (Terborgh, 1973). Interestingly, the observed increased level of variation in wood density within tropical communities and reduced variation in the temperate communities supports the prediction with the canopy hypothesis and the stress-dominance hypothesis. These findings are consistent with a more general and unifying hypothesis that diversifying selection on the density of wood is primarily important in tropical communities, while simultaneously, stabilizing selection is a more important selective force in temperate communities.

Our geographic and community-level results appear to be best described by the Weiher and Keddy (1995) hypothesis. Weiher and Keddy provided a graphical representation of how a key functional trait should be dispersed along an abiotic gradient. Building upon classic work by Terborgh (1973), Weiher and Keddy’s model states that communities on the more stressful end of a given abiotic gradient (i.e., high latitudes and elevations) should generally have trait distributions that are constrained to a subset of the global pool. Within these communities, the stressful abiotic environment is the primary determinant of mean trait values and variances. However, toward the less stressful end of the gradient, one should expect to find communities with the whole spectrum of trait dispersion (i.e., clustered, random, and overdispersed subsets of the global pool). If biotic forces such as competition (i.e., competitive exclusion due to resource competition) are important, then functional traits should be more variable than expected by chance. Our results are fully compliant with Weiher and Keddy’s model.

Together, our results also support the idea that in lower latitudes and elevations, where environments are generally less hydraulically stressful, the more efficient wood construction cost to xylem safety trade-off for gymnosperms as compared to angiosperms is likely not important (Hacke et al., 2005). Thus, the ability of some angiosperms to have higher hydraulic conductivity may allow them to competitively exclude gymnosperms from lower latitudes and elevations. While there is considerable overlap in hydraulic conductivity in angiosperms and gymnosperms, angiosperms in tropical forests generally have hydraulic conductivity values higher than temperate angiosperms and gymnosperms (Tyree and Zimmerman, 2002; Sperry, 2003).

A central goal of functional ecology is to mechanistically link how traits that influence fitness then in turn ramify to influence ecological patterns of trait variation (McGill et al., 2006; Westoby and Wright, 2006). In this paper, building on a large literature, we have argued that wood density is a critical functional trait for understanding the evolution and ecology of whole-plant performance. Together, our analyses have shown that wood density is a window by which to integrate the evolutionary and ecological forces influencing the diversity of plant form and function. Specifically, observed variation in wood density, across plant clades and across differing environments, support the notion that both biotic *and* abiotic forces have likely been important in the evolution of plant form, function, and diversity on different ends of elevational and latitudinal gradients.

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