



The relationship between trunk- and twigwood density shifts with tree size and species stature



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ABSTRACT

The functional significance of wood density in tree species is widely recognized but the relationship between trunk- and twigwood density, along with any shifts due to tree size and species stature, are as yet poorly understood. We analyzed paired trunk- and twigwood samples from 674 trees, representing 71 species in a subtropical evergreen forest to fill this knowledge gap. We found that larger tree size (i.e. diameter) results in denser trunkwood but lighter twigwood, whereas species stature affects only trunkwood negatively. Trunk- and twigwood density did not vary consistently with tree size and species stature, suggesting some functional divergence between the two locations. Generally, trunk- and twigwood density scaled positively and isometrically, with trunkwood being on average 8.3% denser than twigwood. However, there was a systematic increase in the relative difference in their densities from 2% to 15% across tree size groups. The relationship between trunk- and twigwood density overall is moderately strong ($R^2 = 0.3\text{--}0.6$), but depends on both tree size and stature, becoming weaker for larger size and taller stature groups. Collectively, this study highlights the role of plant size in shaping wood density variation and coordination.

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1. Introduction

Wood density is a key functional trait for ligneous plant species because of its relevance to ecologically important characteristics such as mechanical stability, hydraulic conductance and life history (Bucci et al., 2004; Van Gelder et al., 2006; Poorter et al., 2010; McCulloh et al., 2011). It has been proposed as an integrator of a wood economics spectrum (Chave et al., 2009) and as a pivotal axis of plant functional strategies (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013).

While efforts in documenting and comparing wood density usually focus on wood structures located within tree trunks, there are only a limited number of surveys concerning wood structures of terminal twigs (De Micco et al., 2008; Patiño et al., 2009; Yao et al., 2015). Here we use the term “twigwood” in a narrow sense; it is defined *ad hoc* as small branch terminals with diameter < 2 cm but without current-year shootings (Patiño et al., 2009; Sarmiento et al., 2011). Twigwood supports foliar systems and provides hydraulic paths to maintain photosynthesis and transpiration.

Because it forms a large volume of the tree canopy, twigwood, like branchwood in a broader sense, can constitute an appreciable proportion of tree biomass (Adam et al., 1993; Hilton, 2001). More importantly, compared with trunkwood, twigwood has contrasting anatomic properties (Fegel, 1941; Manwiller, 1974; Bhat et al., 1989; Douglas and Floyd, 1994) and can deliver distinctive biomechanical and hydraulic functions (Yang and Tyree, 1993; Domec and Gartner, 2002; De Micco et al., 2008; Gurau et al., 2008; Schuldt et al., 2013). For example, twigwood has a reduced proportion of vessel lumen area, increased resistance to embolism and decreased safety margin to sustain critical buckling load. Since wood density in general is a good indicator of tree mechanics and hydraulics, twigwood density (ρ_{twig}) may also be considered an ecologically important trait (Patiño et al., 2009); but its variation and correlates are only just beginning to be explored (e.g. Patiño et al., 2009; Sarmiento et al., 2011; Schuldt et al., 2013).

One of the core questions in plant functional ecology is how wood density co-varies with other ecologically important traits (Van Gelder et al., 2006; Baraloto et al., 2010). For example, trunkwood density (ρ_{trunk}) has been shown to depend upon both tree size (McKinley et al., 2000; Githiomi and Kariuki, 2010; Deng et al., 2014) and species' stature (i.e. asymptotic height of adults, Woodcock and Shier, 2003; Falster and Westoby, 2005; Van

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Gelder et al., 2006). We sought to test whether similar relationships can be demonstrated for twigwood density (ρ_{twig}), because this would demonstrate a functional coordination or divergence at the two locations. Given the common genetic regulation and biophysical coordination within individual trees, ρ_{twig} and ρ_{trunk} should be positively related (Sarmiento et al., 2011) and they are thus expected to covary consistently with tree size and species stature. However, because twigs and trunks are subject to different ontogenetic, mechanistic and hydraulic constraints (Niklas, 1997; Domec and Gartner, 2002), ρ_{twig} and ρ_{trunk} could have contrasting relationships with tree size and/or species stature. Furthermore, the strength of $\rho_{\text{twig}}-\rho_{\text{trunk}}$ relationship could shift with tree size and species stature because organs of small-sized plants generally exhibit less within-individual variation in their physiological and structural roles (Kramer and Kozlowski, 2012). As a result we predicted that there would be larger differences and weaker correlations between ρ_{trunk} and ρ_{twig} for larger trees and taller statured species.

Here we analyzed trunk- and twigwood density for 674 paired samples from 71 subtropical forest tree species with a wide range of habitat preferences and life histories. The main objective is to evaluate the relationship between trunk- and twigwood density, along with any shifts due to tree size and species stature.

2. Materials and methods

2.1. Study site and species

Field data for this study was collected from the Heishiding Natural Reserve (N23°27', E111°52'), Guangdong province, southern China. The Reserve covers ca. 4200 ha of low, hilly terrain varying between 150 and 1000 m above sea level, supporting large areas of well-preserved forest and bushland. The average annual temperature and precipitation are 19.6 °C and 1740 mm respectively, with most of the rain occurring in summer (June–August). Evergreen broadleaf forests dominated by the families Lauraceae, Theaceae, Magnoliaceae, Fagaceae, Hamamelidaceae and Elaeocarpaceae are widespread within the Reserve. The most common canopy species are *Altingia chinensis* (Hamamelidaceae), *Castanopsis carlesii* (Fagaceae), *Artocarpus styracifolius* (Moraceae) while subcanopy layers are dominated by *Cryptocarya concinna* (Lauraceae) and *Neolitsea phanerophlebia* (Lauraceae).

In the interior of Heishiding Natural Reserve, a contiguous forest stand of about 50 ha was surveyed. The average canopy height of the surveyed area was estimated to be about 25 m. Considering only trunks with diameter at breast height (d.b.h.) >5 cm, the mean d.b.h. was 13 ± 10 cm (mean ± standard error) and the mean stand density of was 1540 stems/ha. We selected 71 widespread evergreen broadleaf species (see Appendix 1), representing 30 families and 46 genera to determine wood density. Species of Fagaceae (12 species) and Lauraceae (9 species) were the most widely represented in our dataset. The life form and maximum height for each of our species are available in Flora Republicae Popularis Sinicae (English and Chinese language versions available online at <http://foc.eflora.cn>) and Atlas of China's Higher Plants (<http://pe.ibcas.ac.cn/tujian/tjsearch.aspx>). The stature range across all 71 species is 5–35 m and averages 15 m. Based on field experience, these species occupy a diversity of habitat types including ridges and valleys, gaps and closed understories.

2.2. Wood sampling and density determination

All data were collected during September through November (after the growing season) in 2014. Wood density data were collected from a total of 674 trees, comprising samples from 5 to 20

randomly placed individuals for each species. Diameter at breast height (d.b.h.) of all trees was recorded at the time of sampling (range 5–45 cm). For each individual, trunkwood was sampled using a borer, while twigwood was sampled by harvesting suitably sized branch terminals. For each tree a trunkwood core about 3–5 cm long was extracted at a height of 1.3 m using a tree borer with 0.5 cm caliber, and a segment of twig at the canopy fringe was truncated using a tree pruner. We took care to sample twigs with diameter < 1 cm at a distance ca. 30–50 cm back from the branch tips and without the current-year shootings. All wood samples were wrapped with moist filter paper for transport to the laboratory. After removing bark material, twigwood was trimmed to approximate a cylindrical shape (mean dimensions ± 1 S.D.: 4.67 ± 0.49 cm in length, 0.48 ± 0.05 cm in diameter). Branch knots were deliberately avoided. Wood cores were also truncated at two ends so as to approximate a cylinder. The diameter at both ends and the length of well-trimmed cores and twig segments were measured using a vernier caliper to the nearest 0.01 mm. Green volume was approximated using measured dimensions under an assumption of a circular cross-sectional area. Wood dry mass was weighed to the nearest 0.0001 g after 72-h oven treatment at 80 °C. All these procedures were executed according to the protocol of Osazuwa-Peters and Zanne (2011).

We verified that ρ_{twig} and diameter of twig segments of samples were not correlated ($r = 0.027$, $P = 0.5$, $n = 674$), thereby warranting comparable ρ_{twig} estimation within a limited range of twig size and/or age. As wood cores of 3–5 cm length in small-d.b.h. trunks can include tree pith and thus underestimate wood density compared with large-d.b.h. trunks, we regressed ρ_{trunk} against the ratio of core length to trunk d.b.h. as an objective means to estimate any bias in wood cores toward including pith. While a decreasing trend in wood density toward piths was evident ($k = -0.054$, $P = 0.013$, $n = 674$), the R^2 was only 0.008. As a result we chose to use raw ρ_{trunk} values without removing the radial trend.

2.3. Statistical analyses

To test the hypothesis that twigwood and trunk wood co-vary consistently with size and stature we used a range of regression and statistical tests. Linear mixed-effects models were built to evaluate the effects of tree size and species stature on wood density:

$$\rho_{ij} = \beta_0 + \beta_1 dbh_{ij} + \beta_2 H_{\max i} + \mu_i + \varepsilon_{ij}$$

where ρ_{ij} is the wood density of the j th individual tree of the i th species; dbh_{ij} and $H_{\max i}$ are tree size (i.e. diameter) and species stature, respectively, with β_1 and β_2 being their corresponding fixed effects. β_0 is the fixed intercept, and μ_i is the random effect incorporated by species. Tree size (i.e., d.b.h.) and species stature were log-transformed before use as explanatory variables, with separate models fitted to ρ_{trunk} , ρ_{twig} and their relative differences ($R_{\Delta\rho}$), calculated as:

$$R_{\Delta\rho} = (\rho_{\text{trunk}} - \rho_{\text{twig}}) / \rho_{\text{twig}}$$

Linear mixed-effects models were estimated using restricted maximum likelihood (REML). Marginal and conditional R^2 (the variation explained by fixed and random effects, respectively) of linear mixed-effects models were calculated following the method described by Nakagawa and Schielzeth (2013).

Paired t -tests were used to test whether the difference ($\Delta\rho$) between ρ_{trunk} and ρ_{twig} exceeded zero (one-tail test). The bivariate relationship between ρ_{trunk} and ρ_{twig} was estimated as below using standard major axis regression:

$$\log(\rho_{\text{trunk}}) = \log(\alpha) + \beta \log(\rho_{\text{twig}})$$

In addition to obtaining the strength of the bivariate relationship (R^2), we also tested for any departure from a 1:1 ratio in trunk:twig density and for any systematic difference in this (i.e., the slope β and intercept α of the $\rho_{\text{trunk}}-\rho_{\text{twig}}$ relationship against one and zero, respectively). All procedures were repeated at both the individual and species levels, with species-specific values estimated as the average value of conspecific individuals.

To test the hypothesis that the relationship between trunk and twigwood density becomes weaker as tree size increases, we used categorical analysis. Tree size was divided into five classes based on d.b.h.: 5–7 cm, 7–9 cm, 9–12 cm, 12–18 cm and 18–45 cm, with bin-widths selected to give approximately the same number of individuals in each tree-size class. We tested the sensitivity of this decision by also using equal-sized d.b.h intervals of 3 and 8 cm, but this did not change qualitative results. Three stature groups were defined according to broad growth habit: understory shrubs and small arbors <10 m in height, intermediate arbors between 10 and 20 m and big canopy arbors >20 m. Standard major axis regression was used to explore the relationship between ρ_{trunk} and ρ_{twig} across size and stature classes separately. For each tree-size group, standard major axis regressions were fitted against the common slope (β_{ind}) and intercept (α_{ind}) obtained for the all-individuals dataset, while for each species–stature group, we used the common slope (β_{sp}) and intercept (α_{sp}) obtained for the all-species dataset.

To test the absolute difference between ρ_{trunk} and ρ_{twig} within each tree size and species stature group we used paired *t*-tests. To assess the difference in group-specific $R_{\Delta\rho}$ among all tree size and species stature groups we used ANOVA, incorporating species identities to avoid confounding the effect of individual tree size with species-level differences. We used Type II marginal sum of squares to account for unequal numbers of observations in each group, where the sum of squares for each factor is calculated as if it were entered last into the model. In other words, the effect of each factor is evaluated after all other factors have been accounted for. Significant effects were identified using *F* tests. We did all statistical analyses using the R programming language (R Core Team, 2015) and custom packages “smatr” (Warton et al., 2012) and “lme4” (Bates et al., 2015).

3. Results

The slope of the relationship between trunk wood density and tree size was positive, but for twigwood the opposite effect was evident with tree size having a negative slope coefficient (Fig. 1a

and b). Greater species stature was associated with decreased density of trunkwood, but not for twigwood ($P = 0.36$; Fig. 1b). The relative difference in density between locations ($R_{\Delta\rho}$) increased with increasing tree size, but had no relationship with species stature (Fig. 1c, Table 1). Size and stature explained less than 3% of the overall variation in wood density, but interspecific differences (random effects) for ρ_{trunk} and ρ_{twig} accounted for the majority of deviance ($R^2_{\text{cond}} = 74.3\%$ and 59.5% respectively, Fig. 1).

Trunkwood was denser than twigwood in individuals (paired *t*-test: $\Delta\rho = 0.034$, $df = 673$, $P < 0.001$), and species ($\Delta\rho = 0.032$, $df = 70$, $P < 0.001$). The difference between ρ_{trunk} and ρ_{twig} on average represents $8.3 \pm 0.8\%$ (mean \pm s.e.) and $6.2 \pm 1.5\%$ of twigwood density at the individual and species level, respectively. There was a positive linear relationship between ρ_{trunk} and ρ_{twig} , but the relationship was much noisier at the individual ($R^2 \approx 0.3$, Appendix 2) than at the species level ($R^2 \approx 0.6$, Fig. 2).

For the pooled dataset, standard major axis regression slopes did not differ from 1 ($\beta_{\text{sp}} = 1.13$, 95% CI 0.95–1.34; $\beta_{\text{ind}} = 1.02$, 95% CI 0.95–1.08), nor intercepts from 0 ($\alpha_{\text{sp}} = 0.04$, 95% CI –0.15 to 0.07; $\alpha_{\text{ind}} = 0.02$, 95% CI –0.01 to 0.06). For tree-size groups, standard major axis regressions showed no substantial departure from the common slope and intercept for all-individuals in the isometric relationship between ρ_{trunk} and ρ_{twig} (Table 1a). This pattern also held for each species–stature group with respect to the common slope and intercept obtained for all-species (Table 1b). Higher variability in the relationship between trunk and twigwood density in the largest size and stature classes resulted in lower explained variation, but there was no evidence of a systematic increase in variability across smaller size classes (Table 1).

Trunkwood was denser than twigwood for any tree size or species stature group except in the smallest size class (d.b.h. < 7 cm; Table 1b). The group-specific $R_{\Delta\rho}$ increased with larger tree size (Table 1a), but showed no consistent trend across species stature groups (Table 1b). Analysis of variance showed that $R_{\Delta\rho}$ differed between both species ($df = 68$, $F = 4.994$, $P < 0.001$) and tree size groups ($df = 4$, $F = 4.805$, $P < 0.001$), but not between species stature groups ($df = 2$, $F = 1.879$, $P = 0.15$).

4. Discussion

We found that the density of twigwood decreased with increasing tree size—the opposite response from that of trunkwood. Species stature was negatively associated with trunkwood density, but not significantly with twigwood density. There were positive correlations between trunk- and twigwood densities at both

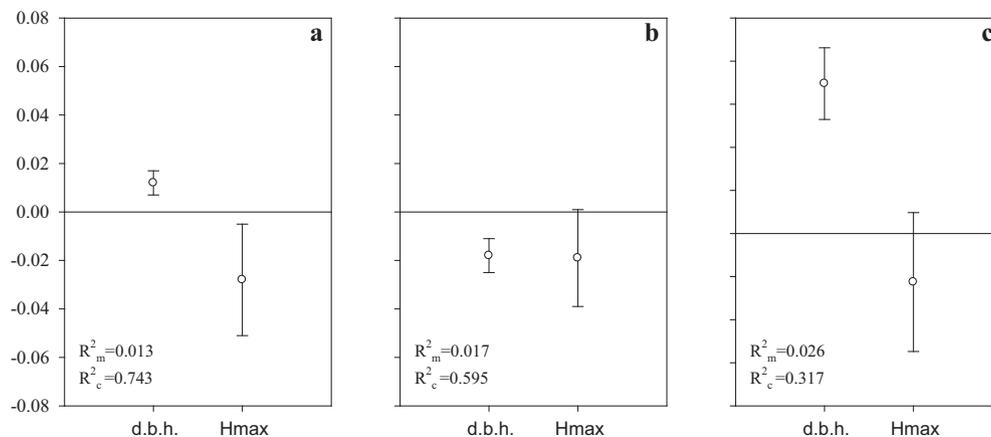


Fig. 1. Effect size (i.e. slope coefficients, mean \pm s.e.) of tree size (d.b.h.) and species stature (H_{max}) on trunkwood density (a), and twigwood density (b) and their relative differences (c) as revealed by linear mixed-effect models. Marginal R^2 is the variation explained by fixed effects (i.e. tree size and species stature), and conditional R^2 is the variation by random effects (i.e. species identity).

Table 1
Correlations and standard major axis regression coefficients for differences between trunk- and twigwood density across separate tree size and species stature groups.

	$\Delta\rho$ (g/cm ³)	$R_{\Delta\rho}$ (\pm s.e.)	α	β	R^2	n
<i>(a) Tree size groups</i>						
5–7 cm	0.004	2.1% (\pm 1.6%)	0.018	0.975	0.471 ^{***}	126
7–9 cm	0.016 [*]	4.4% (\pm 1.5%)	0.025	0.984	0.399 ^{***}	139
9–12 cm	0.030 ^{***}	8.4% (\pm 2.2%)	0.018	1.016	0.290 ^{***}	148
12–18 cm	0.053 ^{***}	11.4% (\pm 1.8%)	–0.035	1.167 ^a	0.382 ^{***}	133
>18 cm	0.066 ^{***}	15.1% (\pm 2.0%)	0.090	0.958	0.190 ^{***}	128
<i>(b) Species stature groups</i>						
<10 m	0.029 ^{**}	5.7% (\pm 1.9%)	0.059	0.939	0.650 ^{***}	30
10–20 m	0.027 [*]	4.6% (\pm 2.9%)	–0.209 ^a	1.440	0.699 ^{***}	20
>20 m	0.041 ^{**}	8.3% (\pm 3.4%)	–0.076	1.219	0.462 ^{***}	21

Notes: $\Delta\rho$ is the mean difference between trunk- and twigwood density, with superscripts denoting values larger than 0 according to paired *t*-tests; $R_{\Delta\rho}$ is the average of relative difference (i.e. the arithmetic difference in trunk- vs. twigwood density divided by the latter) within each group, with the standard error in parentheses. α and β are respectively the intercept and slope of standard major axis regressions and statistical significance of results is indicated as described below. R^2 is the coefficient of determination in the standard major axis fitting. The statistical significance of all results is indicated by superscripts.

^a $P < 0.1$.
^{*} $P < 0.05$.
^{**} $P < 0.01$.
^{***} $P < 0.001$.

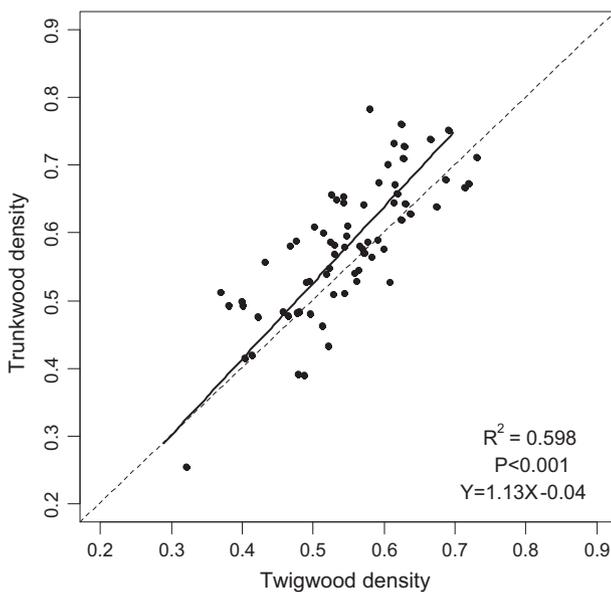


Fig. 2. The relationship between trunk- and twigwood density (unit: g/cm³) for 71 species. The dashed lines are 1:1 lines, and fitted relationships are shown by solid lines. The standard major axis regression coefficient estimates, coefficient of determination and *P*-value are presented at right lower right corner.

species and individual levels, while slope values for different size classes did not differ from the overall response. Other than in the smallest individuals, trunkwood is of higher density than twigwood and with increasing size the magnitude of these differences increases. The decline in the strength of $\rho_{\text{trunk}} - \rho_{\text{twig}}$ correlations with increasing tree size and species stature suggests a possible functional response; larger trees and taller species might more flexibly fine-tune their wood density to promote their overall fitness.

4.1. Wood density in relation to tree size and species stature

We found a positive association between trunkwood density and tree size even after accounting for species-level differences

in mean wood density, which were the major source of variability in the data. Although only explaining a small amount of total variation, this result suggests that density changes were at least partly ontogenetic in origin, as has been widely observed (Niklas, 1997; McKinley et al., 2000; Githiomi and Kariuki, 2010; Deng et al., 2014).

However, twigwood density decreased with tree size despite a positive correlation with trunkwood density. This appears surprising, but tree hydraulic efficiency offers a plausible explanation for it. Larger and older plants are more likely to face water deficit at their distal portions (Ryan and Yoder, 1997), and this might favor lower twigwood density to improve water storage potential (Bucci et al., 2004). Such a mechanism on tree anatomy would be comparable to those of hydraulic constraints on tree height (Ryan and Yoder, 1997; Koch et al., 2004), and we did observe a general decreasing trend in twigwood density with species stature (albeit with only limited statistical support). This result is consistent with a size- and stature-dependent functional divergence between twigwood and trunkwood.

Trunkwood density decreased in species of taller stature—the opposite response to that with tree size. The relationship between species stature and trunkwood density is complex, representing a trade-off between mechanical strength, hydraulic efficiency and competitive advantage. Taller stature induces a higher risk of both mechanical and hydraulic failure, which have counteracting effects on wood density (Gartner, 1995; Dahle, 2009). Disturbance-regulated environments select for mechanical stiffness and/or strength, associated with higher wood density, but elevated vertical growth and hydraulic conductance requirements in light-limiting environments produce the opposite pattern (Falster and Westoby, 2005; Van Gelder et al., 2006). If water was generally not limited in supply, an ‘arms race’ for light capture between species in closed forests could select for ever-taller stature and concomitant lower wood density (Thomas and Bazzaz, 1999; Falster and Westoby, 2005). Hence the decline of trunkwood density we observed for taller species might be associated with competition for light. It seems likely that vertical growth and hydraulic conductivity primarily regulated the wood density shift with asymptotic height, which resulted in lighter wood in taller species. Tree size itself might partly account for the overall mechanical burden, but the covariation between tree size and species stature was rather low ($R^2 = 0.048$, $P < 0.001$, $n = 674$). Nevertheless, the opposite roles of tree size and species stature in influencing wood density imply an underlying balance between hydraulics and mechanics.

4.2. The contrast and correlation between trunk- and twigwood density

Intuitively, trunkwood should be denser than twigwood because of the greater proportion of mature wood and higher secondary compound concentration in the former (Wilson and Archer, 1977; Patiño et al., 2009). Larger tissue density at older, more basipetal locations is advantageous for mechanical stability (Niklas, 1997) and is consistent with the longitudinal decline of wood density from trunk basal to terminal positions (Manwiller, 1979; Hakkila, 1998; Wielinga et al., 2008; Deng et al., 2014). However, we found a number of $\rho_{\text{trunk}}/\rho_{\text{twig}}$ ratios falling below the 1:1 line (i.e. where twigwood density was greater), indicating that mechanical stability could not solely account for the within-tree wood density variation in all individuals.

Twigwood densities either equal or higher than trunkwood have been previously observed, although these have typically been either species-specific or confined to a limited range of tree sizes or habitats (Manwiller, 1979; Phelps et al., 1982; Okai et al., 2003; Gurau et al., 2008; Dadzie et al., 2015). Domec and Gartner (2002) also found higher twigwood density in Douglas-firs

(*Pseudotsuga menziesii*) reflecting higher twigwood hydraulic safety factors (a measure of xylem vulnerability to embolism, Sperry and Tyree, 1988; Sparks and Black, 1999). Likewise, De Micco et al. (2008) found that twigwood of hygrophytes had similar hydraulic safety margins as xerophytes in Mediterranean vegetation, whereas their trunks were adapted to sustain higher hydraulic efficiency (i.e. wider vessels and larger vessel proportions). Dependent on a species hydrological niche, wood density could be lower for trunks than for twigs if mechanical strength was not the primary demand.

We found trunkwood was, in aggregate, denser than twigwood at the individual and species levels and—with the exception of the smallest size class—across separate tree-size and species-stature groups. This suggests these differences represent a common rule of allometry for this forest stand, as suggested for a broad array of tropical taxa and habitats (Sarmiento et al., 2011). Quantitatively, trunkwood was on average $8.3 \pm 0.8\%$ (mean \pm s.e.) denser than twigwood, a range which includes the value of 9% reported for tropical forest tree species by Sarmiento et al. (2011). Schuldt et al. (2013) also found wood density varied less than 10% from roots through the trunk to distal twigs for five rainforest species. We found however that the magnitude of this difference is size-dependent. For the <7 cm d.b.h. class ρ_{twig} was indistinguishable from ρ_{trunk} , suggesting that caution should be used in inferring twigwood density from that of the trunk. Larger tree-size classes had clear absolute differences ($\Delta\rho$) and increasing relative differences ($R_{\Delta\rho}$) up to a maximum of ca. 15%. This substantiates De Micco et al. (2008), who speculated that plant size can induce differences in trunk- vs. twigwood structure. The precise mechanism generating this pattern remains unclear, but it does appear to arise from individual size and ontogenetic stage rather than species stature, because the latter showed no significant associations with $R_{\Delta\rho}$.

De Micco et al. (2008) argued that the variation between juvenile and mature wood properties resembles the trends found between shrubs and trees, as well as between distal and basal portions of plants. Concerning wood density, our results are inconsistent. Denser wood was found in basal trunks than in distal twigs, and in older, larger trees than in younger smaller trees; but tall species did not have denser wood than short species. In addition, larger tree size elevated $R_{\Delta\rho}$, but taller species stature exerted no similar influences.

We found good correlations between ρ_{trunk} and ρ_{twig} at both the species and individual level ($R^2 = 0.6$ vs. 0.3 respectively). This has previously been demonstrated for a huge number of tropical tree species (Baraloto et al., 2010; Sarmiento et al., 2011) and is an example of the coordination of plant structure and function for different organs (Tjoelker et al., 2005; Reich, 2014). It is self-evident that a light-wood trunk with disproportionately dense branch wood is biophysically disabling and evolutionarily disadvantageous. Given the close correlation between trunk- and twigwood density, it seems reasonable to use this as a basis for predicting one value based on the other, as has been recommended in tropical forests (Swenson and Enquist, 2008; Sarmiento et al., 2011). However, the increase in variability of the relationship in large-size trees and species of tall stature, suggests these can be an important confounding factor in establishing allometric relationships between these functional traits.

4.3. Insights and limitations

We found that twigwood density is not associated with tree size in the same manner as trunkwood and the relative difference between twig- and trunkwood density depends on the size of the tree concerned. We identified a negative relationship between trunkwood density and species stature that is consistent with a response to light-limitation as a selective pressure. Our study

advances the understanding of within-tree wood density variation and coordination, a topic poorly explored in the past. We provide insights to the role of plant/species size in regulating wood density along with its functional significance and demonstrate a practical means for appraising the reliability of wood density prediction from less destructive sampling methods (Swenson and Enquist, 2008).

Some limitations in this work should be made explicit. We assumed no radial variation in both twig- and trunkwood, but twigwood, as sampled in this way, consists of more juvenile wood and fewer annual rings than trunkwood does. In addition, the proportion of reaction wood is probably higher in the twigs than in the trunk cores. These inner structural variations could have slightly confounding influences on our results, but we are unable to evaluate it quantitatively. There are also sources of between-tree wood density variation not included in the analysis such as microhabitats and genetic factors, leaving a large part of total variation unexplained. Future work should focus on investigating these sources, especially how they modulate twigwood density variation.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.04.015>.

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