



Community variation in wood density along a bioclimatic gradient on a hyper-diverse tropical island

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Keywords

Aridity Index; Drought; Mean annual precipitation; Mean annual temperature; New Caledonia; Phylogenetic signal

Abbreviations

MAP = mean annual precipitation; MAT = mean annual temperature; WD_{mean} = mean wood density.

Nomenclature

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Introduction

The relationship between water availability and species distribution is one of the main rules in plant ecology (Schimper 1903; Whittaker 1960) and has been widely discussed across spatial scales (Gentry 1988; Swaine 1996; Oliveira & Fontes 2000; Webb & Peart 2000; Harms et al. 2001; Engelbrecht et al. 2007; Baltzer et al. 2008).

Although forecast changes in precipitation remain uncertain, climate change is predicted to result in more frequent and intense droughts (IPCC 2014), especially during El Niño type events in the tropics, and these in turn would significantly impact the abundance of plant species. Forest dieback due to drought- or heat-induced tree mortality has

Abstract

Aims: Analyse the controversial relationship existing between wood density, precipitation, temperature and aridity, and its importance in shaping forest communities facing drought.

Location: New Caledonia (SW Pacific).

Methods: We sampled wood density in 1580 trees belonging to 175 species across nine sites (eight 1-ha plots) located in dry, mesic and humid forests. We tested whether wood density varied across species, communities and habitats, and depended on mean annual precipitation (MAP), mean annual temperature (MAT) and an aridity index (AI). We also tested whether the variations observed in community mean wood density (WD_{mean}) and in wood density standard deviation differed from those obtained by a randomized species distribution across communities. We constructed a phylogenetic supertree at genus level and tested for the non-random distribution of WD_{mean} .

Results: We found that WD_{mean} tended to increase with increasing aridity (i.e. decreasing MAP and increasing MAT) and was significantly higher than expected under randomized species distribution at the dry forest site only. However, some species with low wood density grew well at these dry sites. At genus level, wood density was not random within the phylogenetic supertree. Some lineages exhibiting higher wood density than expected by randomization were also the most represented at the dry sites.

Conclusions: Although we did not observe an environmental filter *sensu stricto*, aridity associated with a low MAP and a high MAT at the dry and mesic forest sites was likely to favour species with a high wood density. Our phylogenetic results suggested that species belonging to a few lineages exhibiting high wood density were likely to be adapted to drought, hence favoured by increasing drought.

already been observed worldwide and this phenomenon is expected to increase (Allen et al. 2010, 2015). Here we examine how wood density, a key plant functional trait, might explain plant species distribution and community assemblages along an elevation gradient. This work was conducted in New Caledonia, a global hotspot of biodiversity (Myers et al. 2000) that is under the direct influence of El Niño events (Nicet & Delcroix 2000; Barbero & Moron 2011).

Wood density, i.e. the ratio of the oven-dried mass of a wood sample divided by its fresh volume (Chave et al. 2009), has been identified as a key functional trait because it appears to depict a fundamental trade-off between growth and survival (Díaz et al. 2004, 2016; Poorter et al. 2008). For instance, fast-growing species tend to produce low-density wood, while species that produce high-density wood grow slowly but tend to be less vulnerable to physical damage, predators and pathogens, as well as drought stress (Chave et al. 2009). It has also been suggested that wood density co-varies with other leaf, seed or root traits along a drought tolerance axis (Stahl et al. 2013). On a regional scale, wood density has a strong phylogenetic signal, i.e. wood density tends to be similar among closely related tree species (Chave et al. 2006; Swenson & Enquist 2007; Zhang et al. 2011).

One of the most fundamental functions of wood is to conduct water from soil to leaves through the xylem conduits of the sapwood. During drought, the pressure of the water column decreases, and during intense drought episodes this may result in the occurrence of xylem embolisms through cavitation, triggering the death of the plant through hydraulic failure (Tyree & Sperry 1989; Sperry et al. 1996; Hacke & Sperry 2001; Hacke et al. 2001). The cavitation vulnerability of tree species is usually measured as the P_{50} , which is the xylem negative pressure at which 50% of hydraulic conductivity is lost through cavitation. It has been suggested that P_{50} is correlated with wood density (e.g. Hacke & Sperry 2001; Hacke et al. 2001; Jacobsen et al. 2005; Hao et al. 2008; Markesteijn et al. 2011), although measurement of P_{50} is difficult and prone to misinterpretation (Cochard et al. 2013). Several wood anatomy traits likely to be involved in cavitation resistance (e.g. percentage of transverse fibre cell wall area; Jacobsen et al. 2005) are often correlated to wood density (Poorter et al. 2010; Ziemska et al. 2013; Fortunel et al. 2014). However, other wood traits independent of wood density are involved in resistance to cavitation (Westoby & Wright 2006; Lens et al. 2013).

Analysing the environmental and phylogenetic variability in wood density sheds light on how climate change is likely to alter species distribution. During the extreme 1997/1998 El Niño event in South-East Asia, drought-induced mortality was shown to be negatively correlated

with wood density (Slik 2004; Van Nieuwstadt & Sheil 2005). On a regional scale, Slik et al. (2010) showed that community average wood density was positively correlated to drought intensities in Borneo, suggesting that, locally, ecological communities are shaped by past drought spells. In Amazonia, drought-induced tree mortality following the 2005 extreme drought event predominantly affected species with a low wood density (Phillips et al. 2009). However, mortality risks may also be higher for large trees compared to small trees, irrespective of wood density, hence resulting in a confounding factor in the analyses (Phillips et al. 2010). In particular, after a 7-yr experimental drought experiment in Amazonia, Lola da Costa et al. (2010) did not find any direct evidence for a relationship between wood density and drought-induced mortality, perhaps due to the small range of wood densities in the experimental plots (see also Nepstad et al. 2007).

If high wood density is an adaptive trait in drought-prone areas, then wood density should increase with increasing temperature and decreasing precipitation, i.e. with increasing aridity. Although some studies have shown that community-wide wood density increases with increasing mean annual temperature (MAT; Wiemann & Williamson 2002; Swenson & Enquist 2007; Zhang et al. 2011), the relationship with mean annual precipitation (MAP) is more controversial. Some studies have found a negative correlation between wood density and MAP (Barajas-Morales 1987; Chave et al. 2006), but others found no correlation (ter Steege & Hammond 2001; Muller-Landau 2004; Swenson & Enquist 2007), or even a weak positive correlation (Wiemann & Williamson 2002; Zhang et al. 2011).

One issue is that these previous studies explored the variability of wood density across large geographic areas, thus potentially weakening the pattern between wood density and MAP due to confounding factors such as soil fertility, temperature or geographic turnover in species assemblages. Also, these studies analysed the effects of precipitation and temperature separately, while in the tropics aridity, which is more likely to affect wood density, is a combination of low precipitation and high temperature that increase evapotranspiration demand. The main island of New Caledonia has a diverse flora with dry and humid forests exposed to relatively strong precipitation and temperature gradients in a relatively small area. Here, we explore how wood density varies from the intraspecific to the inter-community level. We test the hypothesis that tree communities located in the driest forests exhibit higher wood densities than expected under a null model, because drought should favour species with a high wood density, resulting in a higher community-wide wood density. We also analyse the distribution pattern of wood density across New Caledonian tree lineages in a phylogenetic

framework. We explore how the non-random distribution of wood density in the phylogenetic tree may shape the composition of forest communities by favouring (or excluding) phylogenetic groups with a high (or low) wood density in the driest forests.

Methods

Study sites

New Caledonia (20–23° S, 164–167° E) is an archipelago located in the southwest Pacific just above the tropic of Capricorn, about 1500 km east of Australia and 2000 km north of New Zealand. The main island of New Caledonia (Grande Terre) includes a central mountain range, peaking at 1628 m a.s.l. in the north (Mont Panié) and at 1618 m a.s.l. in the south (Mont Humboldt). MAP ranges from over 4000 mm·yr⁻¹ on mountain-tops and in some lowlands of the windward east coast to <1000 mm·yr⁻¹ in the lowlands of the leeward west coast. Relict dry forest is distributed under 300 m a.s.l. in areas receiving <1100 mm MAP. New Caledonia has a short dry season in April–May and a longer one from September to December. A 20–50% decrease in precipitation generally occurs during El Niño events (Nicet & Delcroix 2000).

New Caledonia is famous for its unparalleled plant endemism (Kier et al. 2009). In only 3800 km² of territory, humid rain forest harbours about 2100 native vascular plant species with over 80% species endemism. Even more staggering numbers are reached in dry forests, which harbour about 350 native vascular plant species with about 60% species endemism in only a few hundred km² (Jaffré et al. 2009; Morat et al. 2012).

Nine sites located in the northern province of Grande Terre were selected to investigate variation in wood density (Fig. 1). These study sites were located between 35 and 885 m a.s.l., with MAP ranging from 1085 to 2995 mm, with between 165 and 235 mm precipitation in the three driest months (Table 1). At eight sites, 1-ha (100 m × 100 m) forest plots were established. All plants with a DBH ≥ 10 cm were inventoried and identified to species level. Most species were identified in the field, but in cases where identity was in doubt, samples were collected and identified by comparison with the collection of voucher specimens in the IRD herbarium in Nouméa (NOU). These eight plots were located in rain forests without any obvious trace of recent disturbances.

The Gohapin site is located in a mesic forest, while the other sites are in humid forest. The Nekoro site is one of the last places in New Caledonia where dry forest still persists (see Gillespie et al. 2014). This site consisted of small patches of dry forest in a matrix of secondary thickets, so

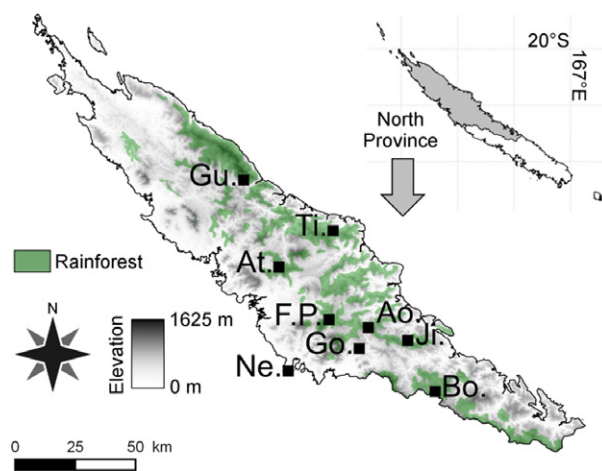


Fig. 1. Location of the study sites in the north province of New Caledonia (SW Pacific). See Table 1 for site abbreviations.

we could not apply the same sampling strategy (i.e. 1-ha plot) because of the scarcity of trees with a DBH ≥ 10 cm. We therefore chose to sample trees in forest fragments without any obvious traces of disturbance and located in a larger area (about 5 ha) in order to maximize the number of sampled species.

Wood density measurement

In the eight 1-ha plots, we sampled wood cores from tree boles at a height of 1.3 m using an increment borer (Haglöf, Västernorrland, Sweden). We sampled five wood cores for each species represented by at least five individuals and species not sampled were removed from the analysis. In Nekoro, we also sampled five wood cores for each inventoried species. Overall, we sampled a total of 1580 trees belonging to 57 families, 109 genera and 175 species (Table 2). Individuals of the sampled tree species represented from 88% to 95% of the total number of trees in the eight 1-ha plots (from 91% to 95% at genus level).

Wood density (WD in g·cm⁻³) was measured following the standardized method suggested by Perez-Harguindéguy et al. (2013). The fresh volume (V in cm³) of the wood samples was estimated using the dimensional method [$V = (0.5 \times D)^2 \times \pi \times L$]. The length (L in cm) of the wood cores was measured using an electronic calliper after removing bark and sharpening the extremities, and the core diameter was fixed by the borer diameter ($D = 0.515$ cm). The length of the wood cores varied according to the size of the sampled trees and ranged from 5 to 15 cm. The wood cores were then oven-dried at 70 °C for 72 h and weighed. Wood density (WD) was then computed as the ratio of the oven-dried mass of the wood core divided by its fresh volume.

Table 1. Characteristics of the nine study sites (MAP, Mean annual precipitation; MAT, Mean annual temperature, MAE, Mean annual evapotranspiration and AI, Aridity Index).

Site	Code	Forest Type	Long. (DD)	Lat. (DD)	Elevation (m)	MAP (mm)	MAT (°C)	MAE (mm)	AI
Aoupinié	Ao.	Humid	165.28	−21.18	882	2394	19.2	883	2.71
Atéu	At.	Humid	164.92	−20.95	756	1930	19.3	868	2.22
Bouirou	Bo.	Humid	165.55	−21.42	538	1575	20.3	942	1.67
Forêt Plate	Fo.P.	Humid	165.12	−21.15	510	1854	20.5	947	1.96
Gohapin	Go.	Mesic	165.24	−21.26	269	1562	21.5	1045	1.49
Jiève	Ji.	Humid	165.44	−21.23	376	2035	20.1	930	2.19
La Guen	Gu.	Humid	164.78	−20.63	581	2993	19.4	963	3.11
Nekoro	Ne.	Dry	164.96	−21.34	35	1084	23.0	1137	0.95
Tiwaé	Ti.	Humid	165.14	−20.82	239	2447	21.8	1049	2.33

Table 2. Characteristics of the data set. Values in bold correspond to sampling representation at each taxonomic level for wood density estimates. See Table 1 for abbreviations.

Site	Trees (All vs Sampled)									
	# Trees	# Order	# Family	# Genus	# Species	# Trees	# Order	# Family	# Genus	# Species
Ao.	1429	202	24	18	39	29	59	35	82	42
At.	672	202	20	16	39	24	58	28	81	39
Bo.	919	197	20	13	38	22	67	32	94	42
Fo. P.	885	218	19	14	38	24	66	36	96	44
Go.	805	84	15	11	25	13	35	16	38	18
Ji.	1020	203	19	13	38	29	67	35	94	44
Gu.	870	139	19	12	35	20	48	23	71	30
Ne.	74	74	7	7	16	16	18	18	20	20
Ti.	1266	261	17	12	38	27	57	35	91	50
All	7940	1580	30	25	69	57	147	109	297	175

Environmental signal

All the statistical analyses were conducted with R (R Foundation for Statistical Computing, Vienna, AT). We tested whether wood density varied across habitats, and depended on aridity. For each study site we computed an aridity index (AI) that quantified MAP deficit over atmospheric water demand as the ratio between MAP and mean annual evapotranspiration (MAE; see Zomer et al. 2008). Higher drought stress was expected at sites with a low AI. MAP values were extracted from an interpolation model with a resolution of 1 km using the mean annual rainfall compiled from 1990 to 2010 (AURELHY model, Meteo-France). MAE was computed as the sum of the monthly potential evapotranspiration (PET) using Thornthwaite's equation (Thornthwaite 1948) with temperatures from the WorldClim database and a resolution of 30 arc-s (~1 km; Hijmans et al. 2005, www.worldclim.org). AI was positively correlated with MAP (Pearson's correlation = 0.97, P -value < 0.0001) and negatively correlated with MAT (Pearson's correlation = −0.72, P -value = 0.0155).

The preferred habitat type, dry forest, humid forest or both, was compiled from the taxonomic reference of New Caledonian flora for each species sampled (Floral; Morat et al. 2012). In Floral, the authors infer the preferred habitat type based on the known species occurrences in dry or humid forests, with dry forest being defined as forest found in low precipitation areas (i.e. MAP < 1100–1200 mm and a marked dry season). We then tested whether dry forest species tended to have a higher wood density using the Mann–Whitney–Wilcoxon test. We also tested this hypothesis within a selection of genera to control for inter-genus variation.

At the community level, we analysed how the mean WD and its coefficient of variation varied with AI. If drought acts as an environmental filter that favours species with high WD, then the mean WD should increase and the coefficient of variation should decrease as drought stress increases (i.e. when AI decreases). We also tested whether the abundances of high WD species increased when drought stress increased. To test this hypothesis we compared the mean WD to community-weighted mean WD (i.e. weighted by the relative species abundance). We tested the significance of our results by comparing the observed variation in the mean and coefficient of variation for wood density to that observed with randomized ($n = 999$) species distribution across communities. In these null models species were randomly distributed across the communities but species richness was constrained. Finally, at intraspecific level, we tested whether or not trees exposed to more drought stress exhibited a higher WD.

Phylogenetic supertree construction

To analyse wood density variation in a phylogenetic framework we built a phylogenetic supertree at genus level. We used the phylogenetic hypothesis for New Caledonian angiosperms constructed by Schlessman et al. (2014) as a preliminary backbone tree. We conserved only

the genera sampled for wood density estimation, and added two genera that were not sampled (i.e. *Agathis* and *Trimenia*).

We compared the phylogenetic relationships above family level to the most recent angiosperm molecular dating study (Magallón et al. 2015), and manually adjusted family-related conflicting relationships to fit with the latter. Most families were represented by a single genus or only two genera (considered here as sisters). The phylogenetic placements of these genera matched automatically with the family topology. For the following families, comprising more than two genera, generic-level relationships were inferred from recent genus-level studies: Apocynaceae (Simoes et al. 2007), Araliaceae (Plunkett et al. 2005), Cunoniaceae (Bradford & Barnes 2001), Euphorbiaceae (Tokuoka 2007), Myrtaceae (Thornhill et al. 2015), Rubiaceae (Wikström et al. 2015), Rutaceae (Bayly et al. 2013; Appelhans et al. 2014), Sapindaceae (Buerki et al. 2012) and Sapotaceae (Swenson et al. 2014). We inferred the ages of all nodes above family level from the fossil dating in Magallón et al. (2015) and then adjusted the other super-tree node ages and branch lengths using the BLADJ (Branch Length ADJuster) algorithm from Phylocom software (Webb et al. 2008).

Taxonomic and phylogenetic signal

We performed a nested ANOVA to assess how the total variance in wood density was partitioned among localities and taxonomic levels, from species to orders (see Messier et al. 2010). We used the 'lme' function from the 'nlme' package in R to fit a hierarchical linear model, and the 'varcomp' function from the 'ape' package of R (Paradis et al. 2004) to decompose the variance. Mean values and associated confidence intervals were estimated using a bootstrap procedure with 999 random iterations. We also tested whether or not adding DBH or AI as fixed effects improved the model. This was done by comparing the likelihood of the model with and without DBH or AI as a fixed effect.

We investigated the phylogenetic signal in WD_{mean} computed at genus level. As per Muenkemueller et al. (2012), we computed Abouheif's C_{mean} (Abouheif 1999) using the 'abouheif.moran' function from the 'adephylo' R package (Jombart & Dray 2008) and Pagel's λ (Pagel 1999) using the 'phylosig' function from the 'phytools' R package (Revell 2012) to test and measure the phylogenetic signal. Abouheif's C_{mean} tests the autocorrelation between trait values and the position of taxa in phylogenetic trees; $C_{\text{mean}} = 0$ indicates independence, while $C_{\text{mean}} > 0$ indicates that closely related taxa tend to have similar trait values. Pagel's λ indicates whether the phylogeny correctly predicts the pattern of covariance among taxa for a given trait; $\lambda = 0$ indicates independence from the phylogeny,

while $\lambda = 1$ indicates complete agreement with the phylogeny. Both estimated C_{mean} and λ were compared to those obtained with 999 random permutations to test whether the estimated values differed significantly from values obtained under a null model where wood density was independent from phylogeny.

We then used Phylocom software (Webb et al. 2008) to graphically analyse and decompose the phylogenetic signal in wood density variability at genus level. We used the *analysis of trait* (or AOT) module to compute, for each node, the tip- and node-based mean and SD in wood density and to compare them to a null model computed with 9999 randomizations. We used the node-based SD to identify the main divergences in wood density observed in the phylogenetic tree, and the tip-based mean to identify clades with higher or lower wood densities than expected under a null model. We graphically analysed the phylogenetic placement of species known to grow in dry forests.

Results

The species average wood densities ranged from $0.32 \text{ g}\cdot\text{cm}^{-3}$ for *Pisonia gigantocarpa* (Nyctaginaceae) to $0.92 \text{ g}\cdot\text{cm}^{-3}$ for *Arytera chartacea* (Sapindaceae), and followed a normal distribution (Shapiro–Wilk test, $P > 0.05$) with a mean of $0.65 \text{ g}\cdot\text{cm}^{-3}$ and SD of $0.12 \text{ g}\cdot\text{cm}^{-3}$ (Fig. 2). The within-species coefficient of variation for wood density ranged from 1.5% to 31.1% ($8.1 \pm 4.4\%$ mean). At community level, the species mean wood density followed a normal distribution irrespective of site (Shapiro–Wilk test, $P > 0.05$) except in Nekoro (Shapiro–Wilk test, $P < 0.001$). The community-wide means ranged from $0.56 \pm 0.12 \text{ g}\cdot\text{cm}^{-3}$ in La Guen to $0.79 \pm 0.15 \text{ g}\cdot\text{cm}^{-3}$ in Nekoro (Fig. 2).

Both the mean wood density and community-weighted mean wood density increased with decreasing AI, i.e. increasing drought stress (Fig. 3, see also Appendix S1 for the relationships with MAP and MAT). However, only the mean wood densities of the communities located on the extreme of the gradient (i.e. Nekoro and La Guen) diverged significantly from a null model where species were randomly distributed across the communities. Note also that unlike the other sites, the community-weighted WD_{mean} in the mesic forest (Gohapin) was higher than the mean wood density. The mean wood density was significantly higher in the dry forest (Nekoro) than in all the humid forest sites, but only marginally higher than in the mesic forest (Gohapin; Table 3). These differences were associated with a high turnover in species composition. Indeed Nekoro shared few species with the other sites. Converse to the WD_{mean} , the coefficient of variation did not follow any pattern with AI and did not significantly diverge from a null model at any of the sites (not shown).

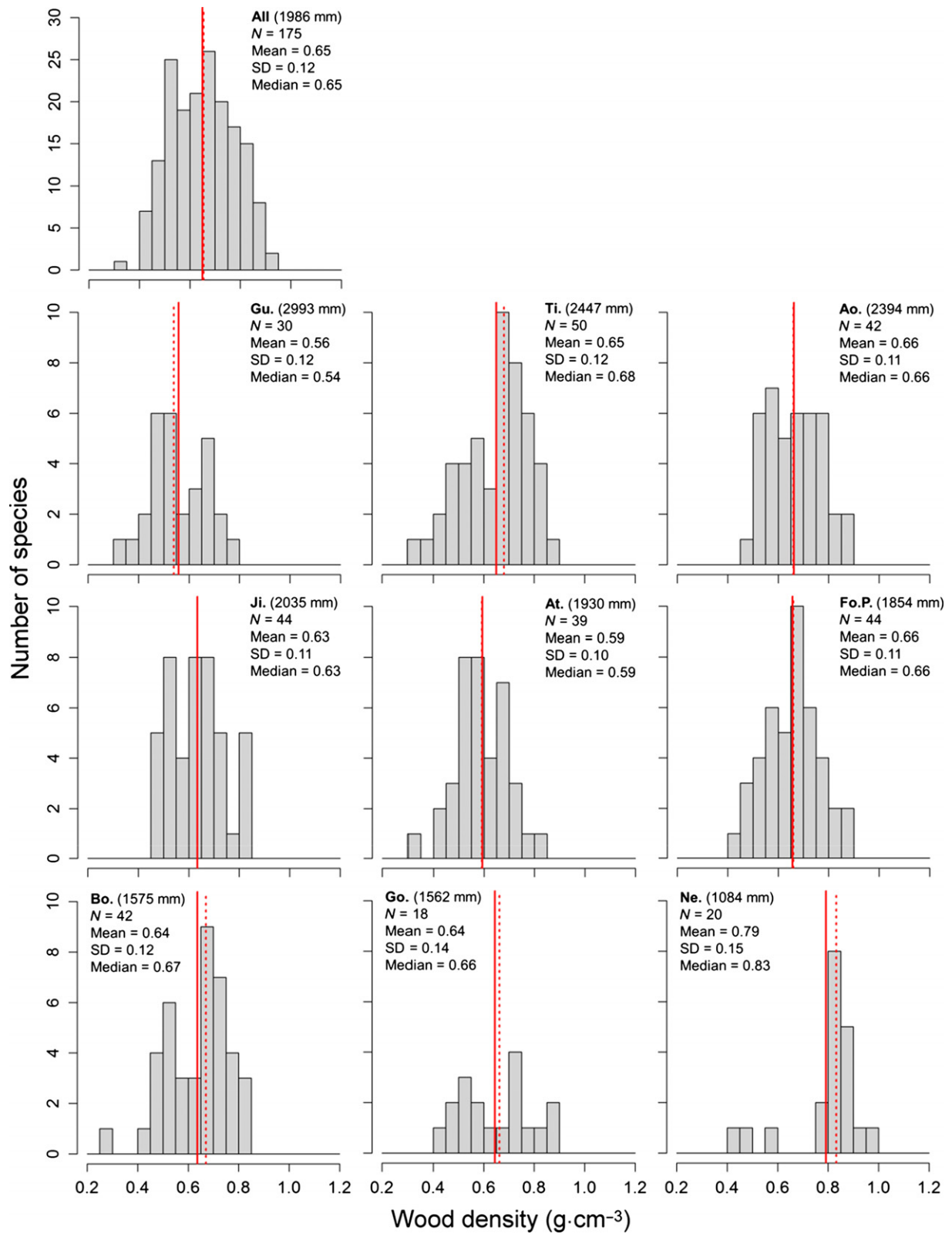


Fig. 2. Distribution of mean species wood densities in the whole data set, and for the nine study sites. The sites are arranged in decreasing order of mean annual precipitation. Solid vertical lines represent the mean, and dotted vertical lines the median values. See Table 1 for abbreviations.

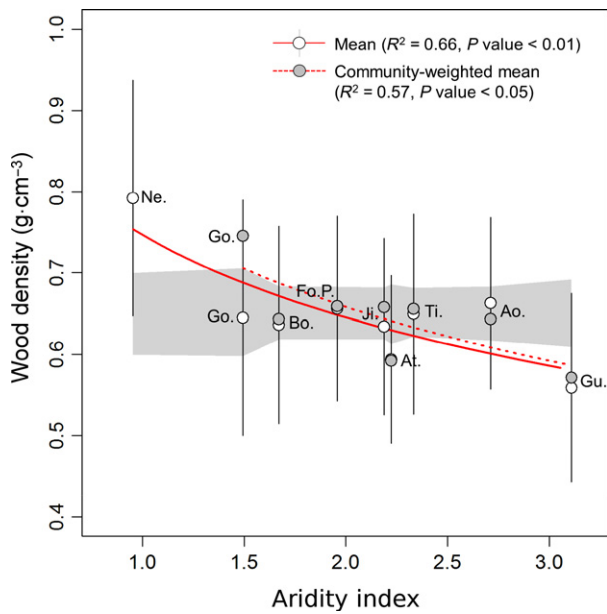


Fig. 3. Relationships between mean wood densities, community-weighted mean wood densities and aridity at the nine study sites. Lines represent log-linear relationships, the grey area represents the distribution of wood density under a null species distribution model (95% CI with 999 randomizations). See Table 1 for abbreviations. The community-weighted mean was not calculable for Nekoro (Ne.) because of the constraints imposed by the sampling design at that site.

Taxonomy explained 83.9% of the observed variance in wood density (Table 4). Adding the AI of the sites where trees were sampled significantly improved the model (likelihood ratio = 30.86, $P < 0.0001$) although the associated slope parameter was very small (-0.02). Conversely, adding the DBH of the sampled trees did not improve the model (likelihood ratio = 2.61, $P = 0.1061$). We detected a significant phylogenetic signal across the 109 sampled genera. Both Abouheif's C_{mean} and Pagel's λ were significantly higher than expected by null models, suggesting that closely related genera tended to have more similar wood densities than randomly selected genera ($C_{\text{mean}} = 0.26$ and

$\lambda = 0.76$, $P = 0.002$ and 0.004 , respectively). Moreover, when we compared observed tip-based means to those obtained with random permutations, 23 of the 108 internal nodes (i.e. 21.3%) had a mean wood density that differed significantly from random expectations (see Table 5).

Three internal nodes had higher divergences in wood density than expected from randomization (Fig. 4). The most noteworthy was the divergence between the Superrosidae and the Superasteridae (at the Pentapetalae crown node, node-based $SD = 0.08 \text{ g}\cdot\text{cm}^{-3}$, $P = 0.0013$). The Superrosidae had a higher tip-based mean wood density ($WD_{\text{mean}} = 0.70 \pm 0.13 \text{ g}\cdot\text{cm}^{-3}$) than the Superasteridae ($WD_{\text{mean}} = 0.61 \pm 0.16 \text{ g}\cdot\text{cm}^{-3}$), and both were significantly different from randomization ($P < 0.001$ and $P = 0.021$, respectively). In the Superrosidae, Myrtales and Sapindales included genera with a high wood density ($0.77 \pm 0.09 \text{ g}\cdot\text{cm}^{-3}$ and $0.72 \pm 0.13 \text{ g}\cdot\text{cm}^{-3}$ on average, respectively), while in the Superasteridae, the Campanuliidae ($WD_{\text{mean}} = 0.52 \pm 0.20 \text{ g}\cdot\text{cm}^{-3}$) and more particularly the clade grouping Apiales, Escalloniales and Paracryphiales included genera with low wood densities ($WD_{\text{mean}} = 0.48 \pm 0.21 \text{ g}\cdot\text{cm}^{-3}$; see Table 5).

Of the 109 sampled genera, only 23 included at least one sampled dry forest species (Fig. 3). Most of dry forest genera belonged to the Superrosidae (20 of the 61 sampled genera) and more particularly to the Sapindales (eight of the 17 sampled genera). In contrast, only three of the 23 genera belonged to the Superasteridae (35 sampled genera), and none to the Campanuliidae (ten sampled genera). Overall, the species preferentially growing in dry forests had a higher wood density ($N = 6$, $0.85 \pm 0.04 \text{ g}\cdot\text{cm}^{-3}$) than generalist species ($N = 30$, $0.73 \pm 0.12 \text{ g}\cdot\text{cm}^{-3}$), which in turn had higher wood densities than humid forest species ($N = 231$, $0.63 \pm 0.11 \text{ g}\cdot\text{cm}^{-3}$, pair-wise Mann–Whitney–Wilcoxon test, $P < 0.001$).

Within the same genus, dry forest species (e.g. *Planchonella cinerea* in *Planchonella* or *Diospyros pustulata* in *Diospyros*) also had a higher wood density than

Table 3. Inter-community comparison of wood density. The diagonal values in bold indicate species average wood density ($\text{g}\cdot\text{cm}^{-3}$). The upper right entries indicate the number of shared species between communities and the lower left entries indicate the P -value of the Mann–Whitney–Wilcoxon pair-wise test (*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, ! $P \leq 0.1$ and 'n.s.' $P > 0.1$).

Locality	Code	# Species	Ao.	At.	Bo.	Fo.P.	Go.	Ji.	Gu.	Ti.	Ne.
Aoupinié	Ao.	42	0.66	9	9	5	1	3	6	5	0
Atéu	At.	39	n.s.	0.59	18	10	2	10	12	11	2
Bouirou	Bo.	42	n.s.	n.s.	0.64	14	3	14	15	22	2
Forêt Plate	Fo.P.	44	n.s.	n.s.	n.s.	0.66	9	18	7	14	5
Gohapin	Go.	18	n.s.	n.s.	n.s.	n.s.	0.64	10	2	6	3
Jiève	Ji.	44	n.s.	n.s.	n.s.	n.s.	n.s.	0.63	6	18	2
La Guen	Gu.	30	*	n.s.	n.s.	.	n.s.	n.s.	0.56	13	1
Tiwaé	Ti.	50	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.	0.65	2
Nekoro	Ne.	20	**	***	***	**	.	***	***	***	0.79

Table 4. Variance partitioning in wood density among nested taxonomic levels [95% confidence interval].

Taxonomic level	Variance Explained (%)	Cumulative Variance Explained (%)
Order	7.2 [4.0–9.7]	7.2 [4.0–9.7]
Family	23.4 [18.3–28.1]	30.6 [26.2–35.2]
Genus	32.5 [26.2–37.6]	63.1 [58.2–67.3]
Species	20.8 [16.9–25.5]	83.9 [82.1–85.7]
Residuals	16.1 [14.3–17.9]	100 [100–100]

congeneric species, be they generalist or found in humid forests (Fig. 5). In contrast, generalist species did not have higher wood densities than their congeneric humid forest species. Finally, we found no clear pattern in the relationship between intraspecific wood density variability and aridity: trees sampled at low AI sites did not have a significantly higher wood density than those sampled at higher AI sites (Fig. 6). At the dry forest site (Nekoro) however, the trees tended to have higher wood densities.

Discussion

Our results support the hypothesis that community-wide wood density increases with increasing aridity (i.e. decreasing MAP and increasing MAT). One hypothesis is that high wood density is an adaptation to drought stress, although the mechanistic basis for this pattern is difficult to unravel (Sperry et al. 2002). We also stress that this negative relationship was non-linear and that it could thus only be seen if the following two observation conditions were met; (1) the studied data set covered a large range of MAP and included low MAP values (about <1500 mm), (2) low MAP values were associated with high MAT values to provide enough drought stress to act as a filter favouring species with a high wood density (Weiher et al. 1995). The study of Hacke & Sperry (2001) and Hacke et al. (2001) showed that this relationship is non-linear, i.e. investing more in wood density substantially increases drought resistance only when wood density is beyond a given threshold (angiosperm $WD_{\text{mean}} > 0.6\text{--}0.7 \text{ g}\cdot\text{cm}^{-3}$).

Table 5. Internal nodes with a tip-based average wood density that differed significantly from the 9999 randomizations (+ = higher and – = lower).

Rank	Age (Ma)	N Tips	Average ($\text{g}\cdot\text{cm}^{-3}$)	SD ($\text{g}\cdot\text{cm}^{-3}$)	Variation	P Value	Clades Involved
1	118.50	61	0.70	0.13	+	<0.001	Superrosidae
2	93.70	8	0.48	0.21	–	<0.001	Apiales, Escalloniales, Paracryphiales
3	60.20	6	0.45	0.23	–	0.001	Apiales
4	85.60	7	0.48	0.22	–	0.002	Escalloniaceae, Paracryphiaceae, Araliaceae, Myodocarpaceae
5	116.40	27	0.72	0.12	+	0.003	Malvidae
6	79.10	14	0.75	0.11	+	0.004	Sapindaceae, Meliaceae, Rutaceae, Simaroubaceae
7	102.70	10	0.52	0.20	–	0.004	Campanuliidae
8	96.60	8	0.77	0.09	+	0.015	Myrtales
9	64.40	6	0.78	0.08	+	0.016	<i>Eugenia</i> , <i>Syzygium</i> , <i>Piliocalyx</i> , <i>Cloezia</i> , <i>Carpolepis</i> , <i>Metrosideros</i>
10	32.20	3	0.82	0.03	+	0.016	<i>Cloezia</i> , <i>Carpolepis</i> , <i>Metrosideros</i>
11	30.10	2	0.32	0.45	–	0.017	Myodocarpaceae
12	63.28	7	0.77	0.11	+	0.020	Sapindaceae
13	123.70	96	0.67	0.14	+	0.020	Pentapetalae
14	119.90	35	0.61	0.16	–	0.021	Superasteridae
15	31.64	4	0.80	0.08	+	0.022	<i>Storthocalyx</i> , <i>Gongrodiscus</i> , <i>Cupaniopsis</i> , <i>Arytera</i>
16	16.70	2	0.85	0.01	+	0.028	<i>Geigeria</i> , <i>Sarcomelicope</i>
17	80.50	7	0.76	0.09	+	0.031	Myrtaceae
18	79.90	17	0.72	0.13	+	0.035	<i>Sapindales</i>
19	15.82	2	0.84	0.12	+	0.035	<i>Storthocalyx</i> , <i>Gongrodiscus</i>
20	102.60	19	0.71	0.11	+	0.036	Malpighiales
21	106.70	25	0.60	0.17	–	0.038	Campanuliidae, Garryidae
22	35.50	2	0.84	0.03	+	0.040	<i>Oleaceae</i>
23	91.20	2	0.46	0.07	–	0.049	<i>Hernandia</i> , <i>Hedycarya</i>

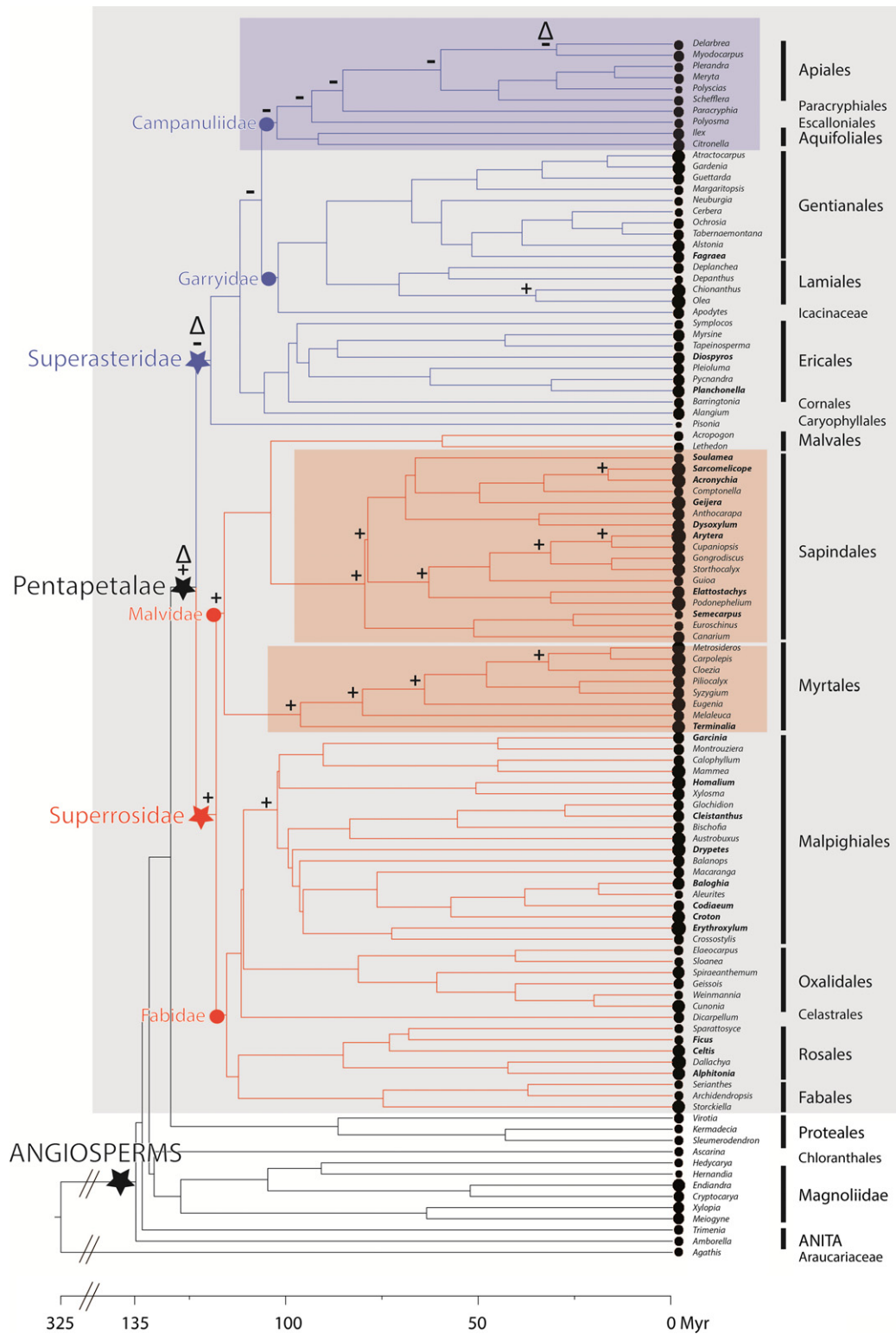


Fig. 4. Phylogenetic supertree of the sampled genera. The size of the points is proportional to the average wood density of the genus, and genera in bold represent genera that nested at least one sampled species known to grow in dry forest. At the internal nodes, – or + highlight nodes where the observed tip-based average was significantly lower or higher than expected from 9999 randomizations, and Δ highlights nodes where the observed node-based SD (i.e. divergence) was significantly higher than that expected from the randomizations.

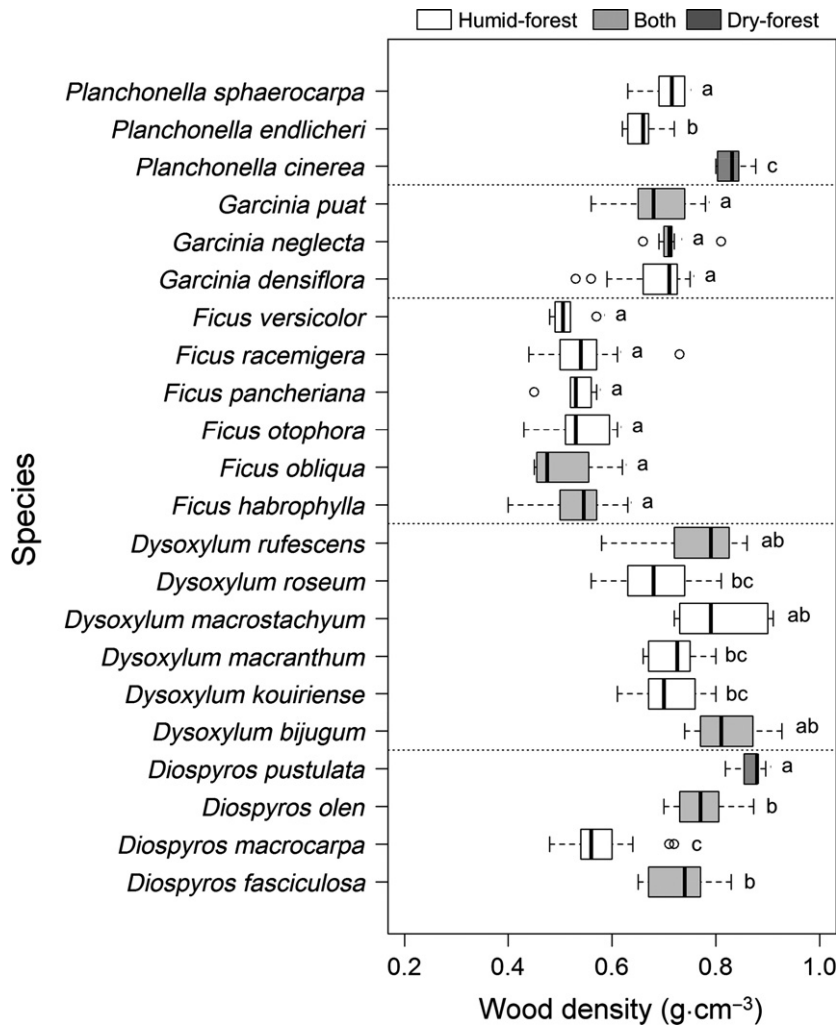


Fig. 5. Variation in species wood density according to the preferred habitat type. Letters represent non-significant differences in wood density distributions (Mann-Whitney-Wilcoxon test, $P > 0.05$). Only genera represented in two different habitat types are shown.

Consequently, we suggest that the lack of relationship between WD_{mean} and MAP both in ter Steege & Hammond (2001) in Guyana and in Muller-Landau (2004) in the Neotropics, may have been caused by a too narrow span in MAP at the study sites, excluding the dry sites (MAP > 1600 mm and >2300 mm, respectively). Other studies have found a positive relationship between wood density and MAT but a weak or no relationship with MAP, but these included non-tropical sites, where low MAP values were associated with low MAT values, which decreased the impact of drought on community assemblages (Wiemann & Williamson 2002; Swenson & Enquist 2007; Zhang et al. 2011). We also found a positive relationship between WD_{mean} and MAT, which supported this hypothesis.

We found that higher aridity appeared to favour species with a high wood density in the dry and mesic forest sites, resulting in a higher mean wood density than expected

under the null species distribution model. However, we did not find that the observed wood density SD was lower than with a null species distribution model (under-dispersion) as expected from the model of Weiher et al. (1995) under drought stress conditions. We cannot conclude that we observed a clear drought stress filter *sensu stricto* (see Kraft et al. 2015). For instance, we found species with relatively low wood densities at the two driest sites: *Polyscia sbracteata* ($WD_{\text{mean}} = 0.41 \text{ g}\cdot\text{cm}^{-3}$) and *Cerbera manghas* ($WD_{\text{mean}} = 0.46 \text{ g}\cdot\text{cm}^{-3}$) at the dry forest site, and *Ficus fraseri* ($WD_{\text{mean}} = 0.42 \text{ g}\cdot\text{cm}^{-3}$) and *Aleurites moluccana* ($WD_{\text{mean}} = 0.46 \text{ g}\cdot\text{cm}^{-3}$) in the mesic forest site. Thus, our results provided puzzling exceptions of low wood density species growing in drought-prone environments, and this suggests alternative drought tolerance mechanisms.

For instance, the species with the lowest wood density in our data set was *Pisonia gigantocarpa* (Nyctaginaceae), with a mean wood density of $0.32 \text{ g}\cdot\text{cm}^{-3}$. *Pisonia artensis*,

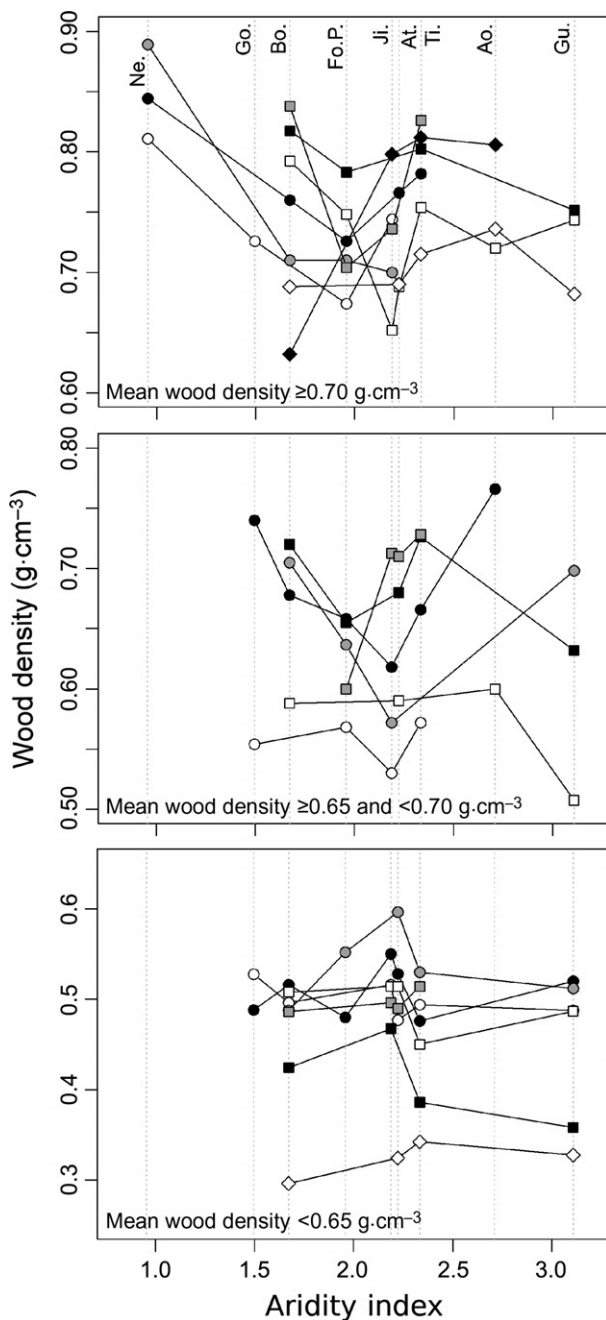


Fig. 6. Inter-site variability in species mean wood density as a function of aridity. Each point type represents one species. Only species occurring at least four sites are shown ($N = 21$ species). The species have been grouped in three different panels to improve visibility. See Table 1 for abbreviations.

which also exhibited a low wood density, was inventoried at our mesic forest site and is known to grow in dry forest (Morat et al. 2012). The low wood density of *Pisonia* probably resulted from the presence of successive cambia, which is characteristic of the Nyctaginaceae. Successive

cambia produce sequences of strands of fibro-vascular tissue embedded in low density conjunctive tissue (see Carlquist 2004). This particular stem anatomy provides a larger stem area for photosynthate and water storage (Carlquist 2007). Also, we inventoried *Polyscias bracteata* (Araliaceae) at the dry forest site. This Araliaceae exhibited low wood densities ($WD_{\text{mean}} = 0.41 \text{ g}\cdot\text{cm}^{-3}$) compared to most of the co-occurring species ($WD_{\text{mean}} > 0.75 \text{ g}\cdot\text{cm}^{-3}$). It has been proposed that vasicentric tracheids, which are observed in the wood of several Araliaceae, may be an alternative pathway for water conductance if embolism occurs in xylem vessels (Carlquist 1985). This suggests that the presence of this low-density species in a drier environment reflects alternative strategies that potentiate water storage over conductive safety.

Lastly, along the lines of previous studies, we found a substantial phylogenetic signal in wood density, with taxonomy explaining about 84% of the observed variability (Chave et al. 2006; Swenson & Enquist 2007; Zhang et al. 2011). As for Zhang et al. (2011) in China, the most striking divergence was observed in Angiosperms in the Pentapetales, between the Superrosidae and the Superasteridae. This divergence was driven by the Myrtales and Sapindales ($WD_{\text{mean}} = 0.72 \text{ g}\cdot\text{cm}^{-3}$) in the high wood density Superrosidae, and the Apiales, Escalloniales and the Paracryphiales ($WD_{\text{mean}} = 0.48 \text{ g}\cdot\text{cm}^{-3}$) in the low wood density Superasteridae. This suggests that in spite of the high endemism in the New Caledonian flora, they may have retained some shared ancestral trait features, e.g. with the Chinese flora. The higher wood density of the Superrosidae clade may explain why seven of the ten largest families of the dry forest flora of New Caledonia (Jaffré et al. 2008), as well as other Pacific locations, are nested in the Superrosidae (Gillespie et al. 2014). This suggests that the response of trees to the forecast increasing drought stress would not be homogeneous, with some phylogenetic groups displaying higher wood densities adapted to these changes and being favoured. Forests located in the driest areas might experience major phylogenetic changes in their species composition.

Conclusion

Our results support the hypothesis that aridity associated with low precipitation and high temperatures promotes species with a high wood density. However, we stress that this relationship is very likely to be non-linear and that in our study the relationship was mainly driven by the dry forest site. The shape and the robustness of the relationship between aridity and wood density need to be confirmed through an analysis of a wider aridity gradient. Our phylogenetic results also suggest that species belonging to a few lineages exhibiting a high wood density are likely to be

adapted to drought and should thus be favoured by increasing aridity.

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Supporting Information

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

Appendix S1. Relationships between mean wood densities, community-weighted mean wood densities MAP and MAT in the nine study sites.