

## RESEARCH PAPER

# Insights into intraspecific wood density variation and its relationship to growth, height and elevation in a treeline species

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**Keywords**Elevational gradient; heartwood; *Nothofagus pumilio*; Patagonia; sapwood; southern Andes; treeline.**Correspondence**Alex Fajardo, Centro de Investigación en Ecosistemas de la Patagonia (CIEP) Conicyt-Regional R10C1003, Universidad Austral de Chile, Camino Baguales s/n, Coyhaique 5951601, Chile.  
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**ABSTRACT**

- The wood economics spectrum provides a general framework for interspecific trait–trait coordination across wide environmental gradients. Whether global patterns are mirrored within species constitutes a poorly explored subject. In this study, I first determined whether wood density co-varies together with elevation, tree growth and height at the within-species level. Second, I determined the variation of wood density in different stem parts (trunk, branch and twigs).
- *In situ* trunk sapwood, trunk heartwood, branch and twig densities, in addition to stem growth rates and tree height were determined in adult trees of *Nothofagus pumilio* at four elevations in five locations spanning 18° of latitude. Mixed effects models were fitted to test relationships among variables.
- The variation in wood density reported in this study was narrow (ca. 0.4–0.6 g cm<sup>-3</sup>) relative to global density variation (ca. 0.3–1.0 g cm<sup>-3</sup>). There was no significant relationship between stem growth rates and wood density. Furthermore, the elevation gradient did not alter the wood density of any stem part. Trunk sapwood density was negatively related to tree height. Twig density was higher than branch and trunk densities. Trunk heartwood density was always significantly higher than sapwood density.
- Negative across-species trends found in the growth–wood density relationship may not emerge as the aggregate of parallel intraspecific patterns. Actually, trees with contrasting growth rates show similar wood density values. Tree height, which is tightly related to elevation, showed a negative relationship with sapwood density.

**INTRODUCTION**

Given the current need to lock carbon up in forests to reduce atmospheric CO<sub>2</sub> concentrations, accounting for the wood density of trees is highly important and timely (Bunker *et al.* 2005). Wood density is a trait under strong selective pressure; across species, it is positively associated with survival and lifespan (*e.g.* Muller-Landau 2004; Poorter & Kitajima 2007; Poorter *et al.* 2010) and mostly negatively associated with growth rate (*e.g.* Enquist *et al.* 1999; Muller-Landau 2004; King *et al.* 2005). Wood density reflects the balance between solid material (*i.e.* cell wall) and the lumen of conductive elements (*i.e.* vessels and tracheids) present in the xylem tissue (Chave *et al.* 2009; Méndez-Alonzo *et al.* 2012). Given these characteristics, wood density constitutes a carbon investment trait resulting from the trade-off involved in construction costs (Swenson & Enquist 2007; Chave *et al.* 2009).

In the last decade, trait-based approaches have rapidly gained prominence in plant ecology. Central to the trait-based approach, many studies have focused on plant functional trait relationships that constitute coordinated spectra related to variation in plant functional strategies. One example is the wood economics spectrum (WES). The WES describes trade-offs in a suite of woody traits related to plant carbon balance across species and resource availability gradients (Preston *et al.*

2006; Chave *et al.* 2009). In the WES, species with low wood density have high growth rates (resource-acquisitive), whereas species with high wood density have low growth rates (resource-conservative; *e.g.* Enquist *et al.* 1999; Chave *et al.* 2009; Poorter *et al.* 2010; Wright *et al.* 2010). Whether this global pattern is mirrored within species constitutes a poorly explored subject in ecology, despite its potential to enhance understanding of the evolutionary importance of plant functional traits as well as its potential for carbon sequestration. In principle, all of the mechanistic hypotheses proposed to explain global patterns of wood density variation across species should also apply within species; the environment should filter species from a regional pool in the same way as for phenotypes from a population.

Plant species can display high intraspecific variation in functional traits, reflecting heritable genetic variation and phenotypic plasticity associated with environmental gradients, ontogeny and/or phenology; this variation influences plant responses to abiotic filters and biotic interactions (*e.g.* Violle *et al.* 2012; Siefert *et al.* 2015). One conspicuous environmental gradient is driven *via* decreasing temperatures with increasing elevation in mountain systems; in this case, intraspecific trait variation is expected to occur (Fajardo & Piper 2011; Körner 2012a; Mayor *et al.* 2017). Previous works have proposed that arborescent life forms are more strongly affected in their

growth and survival by low temperatures at high elevations than smaller-stature plants due to tree architecture and its associated aerodynamics; by being closer to the ground smaller-stature plants are able to decouple from low atmospheric temperatures (Körner 2012b; Fajardo & Piper 2014). Thus, all of the tree species that grow at the treeline elevation have considerably reduced height and growth rates (e.g. Gamache & Payette 2004; Fajardo & McIntire 2012; Körner 2012a; Fajardo & Piper 2017), which may imply contrasting wood density values when compared to conspecifics growing at lower elevations (Coomes *et al.* 2007). Trees at treeline are more exposed to wind and need mechanically stronger wood, hence higher wood density. Alternatively, the short stature of trees at treeline elevation (typically ~3-m tall) may imply lower wood density because they have lower structural requirements, especially for the stem, when compared to taller trees at lower elevations.

Intraspecific trait variation not only occurs across environmental gradients, but also within individuals subjected to similar environmental conditions (Messier *et al.* 2010). For instance, different stem parts – trunk, branches and twigs – may be responsible for variation in wood density at the within-individual level. Relatively different mechanical requirements on trunk, branches and twigs may drive within-tree variation: trunk sapwood can serve structural, hydraulic and storage functions; heartwood does not function as a storage site, but it receives compounds (e.g. gums, phenols, resins) from other sites in the wood (Evert 2006); branches and twigs may be more devoted to hydraulic transport and storage, because they are closer to leaves (carbon source; Piper *et al.* 2016) than to mechanical support (but see Butler *et al.* 2011). Few studies have reported variation of wood density among different stem parts (e.g. De Micco *et al.* 2008; Sarmiento *et al.* 2011; He & Deane 2016). He & Deane (2016), for example, found that trunk wood density of taller trees was higher than twig wood density when several species were compared in a subtropical evergreen forest in southern China. Given that trunk heartwood density is generally higher than sapwood density (Woodcock & Shier 2002; Fajardo 2016b), the most plausible expectation is that trunk wood density, which contains both heartwood and sapwood, will be higher than branch and twig wood densities, which mostly contain only sapwood. However, these within-individual wood density relationships may be altered across environmental gradients, like the temperature-related elevational gradient (Coomes *et al.* 2007).

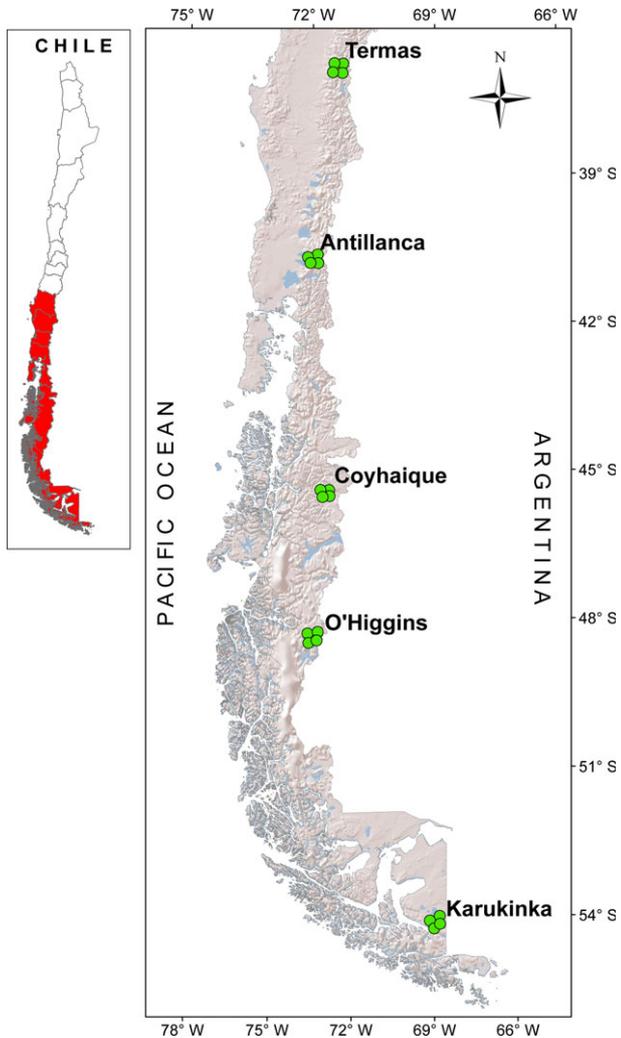
The first aim of this study was to determine if an elevational gradient affected tree growth, height and wood density, and if there was any relationship among these three at the within-species level. In a previous study, Fajardo (2016b) found no relationship between growth rates and wood density when working with similar-age conspecifics of contrasting stand social status (*i.e.* dominant and suppressed) growing in the same environmental conditions. Here, searching for generality, I used a widely distributed treeline species, *Nothofagus pumilio*, which dominates the southern Andes, covering different climates and resource availability gradients, from Mediterranean-like to cold temperate climate conditions in the southern tip of the continent. If we assume a negative growth–wood density relationship, wood density should then increase with elevation, given the reduction of growth with elevation (e.g. Fajardo & McIntire 2012; Körner

2012a; Fajardo & Piper 2017). Alternatively, because of a decrease in tree height, and hence less structure to support, wood density may not increase with elevation as initially suspected. As a second aim, I assessed the relationship between the wood density of different stem parts – trunk, branch and twig – across elevations and tree height. One expectation is that wood density increases from the trunk towards the branches as tree heights (stem length) increase, but this difference should be negligible at the treeline elevation, where short-stature trees prevail. In other words, it is more likely that wood density will tend to show less variation among its within-individual woody parts as trees decrease in height. Alternatively, trunk wood density should always be higher than branch and twig wood densities because of ontogenetic differences; trunk includes heartwood, which is known to be denser than sapwood (Woodcock & Shier 2002; Fajardo 2016b). The intraspecific variation of wood density and its relationship with tree growth and elevation should ultimately shed some light on the causes of global interspecific relationships like those contained in the wood economics spectrum (WES). Given that intraspecific variation is a pivotal assumption within the WES, it is essential to examine this level of variation.

## MATERIAL AND METHODS

### Species and research site descriptions

*Nothofagus pumilio* (Poep. et Endl.) Krasser (Nothofagaceae) is a deciduous broadleaf light-demanding tree species that extends through a wide latitudinal and altitudinal range in the southern Andes of Chile and Argentina. Its wide distribution provides a unique opportunity to study potential mechanisms responsible for trait variation under contrasting climates while controlling for phylogenetic effects (Fajardo & Piper 2011). For this study, I selected five locations, covering 18° of latitude, with different climates, from Mediterranean-like to cold temperate climate conditions (Fig. 1). The first location was in Termas de Chillán (36° 54'S, 71° 23'W), where the treeline occurs at 2080 m a.s.l. The annual precipitation here is 1520 mm (Las Trancas weather station, Dirección General de Aguas, 2005–2014, 1250 m a.s.l.). The second location was in the Antillanca area within the Puyehue National Park (40° 47'S, 72° 11'W), where the treeline occurs at 1340 m a.s.l. The annual precipitation is 3660 mm (Daniels & Veblen 2004; Aguas Calientes weather station, 1991–1997, 475 m a.s.l.). In these two locations the soils are derived from andesitic rocks of volcanic origin. The third location was in the Coyhaique National Reserve (45° 31'S, 72° 02'W), where the treeline occurs at 1215 m a.s.l. The annual precipitation here is 890 mm (Coyhaique National Reserve weather station, Dirección General de Aguas, 2004–2013, 400 m a.s.l.). The soil is derived from aeolian volcanic ash deposits. The fourth location was near Villa O'Higgins (48° 29'S, 72° 30'W), where the treeline occurs at 1120 m a.s.l., and the annual precipitation is of 1050 mm (Villa O'Higgins weather station, Dirección General de Aguas, 2000–2007, 270 m a.s.l.). The last location was in the Karukinka Private Reserve in Tierra del Fuego (54° 20'S, 68° 49'W), where the treeline occurs at 630 m a.s.l. The annual precipitation here is 565 mm (Lago Deseado weather station, Dirección General de Aguas, 2006–2013, 400 m a.s.l.) and the soil is of granitic



**Fig. 1.** Map of the five sites sampled in this study covering 18° of latitude, from central Chile (location: Termas de Chillán) to Tierra del Fuego (location: Karukinka).

origin. In all locations most precipitation falls as snow from May to September.

Although the five treeline locations occurred at different elevations, the temperature gradient with elevation was of comparable magnitude as elevational treelines occur at analogous isotherms – treelines worldwide share a similar mean growing season temperature of 6.4 °C, including the *Nothofagus pumilio* treeline (Hoch & Körner 2012; Fajardo & Piper 2014). In these treeline ecotones, trees of comparable age may differ in height up to seven-fold between the treeline (~3 m) and the lower elevations (~21 m; Fajardo 2016a). In addition, I tried to select treeline locations that have not been noticeably affected by direct human activities or disturbed by landslides or avalanches. At each location, I defined the treeline as the uppermost limit of individual trees with an upright growth form of at least 3 m (Körner 2003).

#### Sampling, tissue collection and processing

At each location, I selected trees at four elevations, covering the last ~300 m a.s.l. of the treeline ecotone. When selecting

the elevations at each site my main criterion was to cover the complete treeline ecotone; from the uppermost crooked-shape (krummholz) trees at treeline elevation down to where large (DBH ~30 cm), erect trees form a closed and relatively dense forest. In this way, I could be certain I was comparing individual trees at treeline elevation that are manifestly affected by low temperature with others located at lower elevations, that are therefore not affected (or are much less affected) by low temperature, *i.e.* with no growth constraints (high diameter and erect stem). For clarity and brevity, I hereafter refer to elevations by their short names: E1, closed tall, lowest elevation forest; E2, intermediate stand located between E1 and the timberline; E3, timberline; and E4, treeline. Sampling was conducted in late January 2013 for the Termas and Antillanca locations, early February 2014 for the Coyhaique and Karukinka locations, and late January 2017 for the O'Higgins location. At this time of year, leaf expansion and shoot growth are complete (Fajardo & Siefert 2016). At each of the four elevations, for tissue collection I selected eight to 11 individuals that were at least 30 m apart and always at the edge of a patch; *i.e.* no shade branches were collected, particularly at low elevations. I thus restricted the sampling to adult, unshaded trees without browsing or other damage. For each individual tree, I identified and cut one 2-m long terminal, fully expanded and sun-exposed branch using a 5.6 m telescoping pole (ARS Corporation, Sakai, Japan). From each of these branches, I first selected and cut a 3-year-old twig. Annual nodes were easily identifiable by bud scars (Puntieri *et al.* 1999), shoot epidermis of different colours and different shoot diameters. I then selected and cut one 2-cm diameter piece of wood from the base of the branch. This sample was intended for wood density determination. The twig and branch samples were labelled and placed in a cooler box for transportation.

For each individual, I collected at least two cores that were extracted perpendicular to the bark from cross-slope sides of the trunk to avoid sampling tension wood, which is denser because of the thicker fibre walls (Evert 2006). The first core intended for wood density determination was extracted at a height of ca. 50 cm using a 12-mm increment bore (Haglöf, Långsele, Sweden). This core covered both sapwood and heartwood; the distinction between these two types of wood is easily made in the field for *Nothofagus* species, where heartwood is distinctly darker than sapwood, thus no special chemical product (*e.g.* bromocresol green) was necessary for this purpose. Nonetheless, I marked the border between these two types of wood with a pen in the field. These thick cores were placed in plastic bags, labelled and stored in a cooler box for transportation. A second to-the-pith long core was extracted at a height of less than 30 cm using a 5.15 mm increment bore (Haglöf). This second core was intended for growth rate, tree age and sapwood width determinations. When trees were thicker than 20 cm in DBH (1.35 m height), two of these to-the-pith cores were extracted in order to get the best estimates of growth rates and sapwood extensions (see *Tree growth determination* below). Finally, for each individual I measured DBH with a diameter tape, bark length for both core heights using a bark gauge, and tree height using a clinometer (Suunto, Vantaa, Finland).

In the laboratory, I cut the thick 12-mm cores along their sapwood–heartwood borders using a chisel and a rubber mallet. In order to determine the fresh volume of each piece of wood, I submerged ca. 4-cm long thick cores, branches and

twigs in a glass beaker on a balance. The mass difference produced by the sample, which equals the volume of water displaced by the sample, was recorded and converted to volume based on the density of water, considered as  $1.0 \text{ g cm}^{-3}$  at standard temperature and pressure. In this measurement I did not include bark but included the branch and twig pith, which was nonetheless negligible (*personal observation*). The samples were then placed to dry in a forced-air oven (Memmert, Schwabach, Germany) at  $70^\circ \text{C}$  for 72 h and the dry mass was subsequently measured. Wood density was then calculated as the oven-dry mass per green volume.

### Tree growth determination

Thin 5.15-mm cores were prepared following standard dendrochronological techniques (Stokes & Smiley 1996): cores were dried, mounted and glued firmly on grooved wooden sticks, and sanded with successively finer grades of sandpaper until optimal surface resolution allowed annual rings to be distinguished under magnification ( $\times 10$ ). Following visual cross-dating, inside-bark bole radius, sapwood length and tree ring width were measured to the nearest 0.001 mm using a microscope mounted on a dendrochronometer with a Velmex sliding stage (Bloomfield, NY, USA). Only cores that either passed through the stem pith or were close to it (the arc of the innermost rings was visible) were retained. With these, I followed procedures described by Duncan (1989) to estimate the number of missing rings in cores that missed the pith of the tree. No correction was applied for the time required to grow to coring height. Approximate tree ages were estimated by counting all tree rings. Sapwood basal area ( $BA_{\text{sap}}$ ), and basal area increment of the last 10 years ( $BAI_{10}$ ) were then computed as:

$$BA_{\text{sap}} = \pi(R_1^2 - R_{\text{heartwood}}^2)$$

$$BAI_{10} = \pi(R_1^2 - R_2^2)$$

where  $R_1$  is the radius of the stem,  $R_{\text{heartwood}}$  is the radius of the stem corresponding to heartwood, and  $R_2$  is the radius of the stem without the ten outermost years. The radius of the stem,  $R_1$ , was computed by considering the diameter at coring height, bark depth and the distance between pith and the last year's ring in the core. When trees were larger than 20 cm DBH,  $R_1$ ,  $R_{\text{heartwood}}$  and  $R_2$  were averaged using the two to-the-pith cores in order to be more precise. The sapwood basal area proportion was computed as  $BA_{\text{sap}}$  divided by total BA. Considering that trees at lower elevations are generally bigger than trees growing at the treeline elevation, I computed the mean annual increment (MAI), as the quotient between individual tree basal area and tree age.

Following Fajardo (2016b), I used a standardised measure of wood density, which considers sapwood and heartwood densities and the proportion of both types of wood in the stem cross-section:

$$WD_{\text{st}} = WD_{\text{sap}} * \text{Sap}_p + WD_{\text{heart}} * \text{Heart}_p$$

where  $WD_{\text{st}}$  is the standardised stem wood density,  $WD_{\text{sap}}$  is sapwood density,  $\text{Sap}_p$  is the sapwood proportion in the cross-

section stem area,  $WD_{\text{heart}}$  is heartwood density and  $\text{Heart}_p$  is the proportion of heartwood in the cross-section stem area;  $\text{Heart}_p$  is  $1 - \text{Sap}_p$ .

### Data analysis

All statistical analyses were conducted in R version 3.3.0 (R Development Core Team 2016). In each analysis, I first normalised all of the data with  $\log_{10}$  transformations. The data was analysed using linear mixed-effect regression models (LMM) using the *nlme* package (Pinheiro *et al.* 2016) in R, with fixed effects for  $BAI_{10}$  and elevation (as a covariable with four levels: four elevations), and random effects for sites (five). First, I tested the relationship between the different variables (*e.g.* WD, tree height) and elevation fitting LMMs. In principle, I was interested in knowing whether there is a relationship between tree growth rate ( $BAI_{10}$  or MAI) and wood density (model  $WD \sim BAI_{10}$ ). Given that elevation affects wood density, I also ran another analysis that included elevation in the model (model  $WD \sim \text{elevation}$ ); whether or not this growth-wood density relationship is mediated by elevation (model  $WD \sim BAI_{10} \times \text{elevation}$ ). Second, to test whether stem parts (trunk, branch and twigs, and trunk heartwood *versus* trunk sapwood) differ in their densities, I fit another list of linear mixed-effects regression models where wood density was the dependent variable with fixed effects for stem parts (model  $WD \sim \text{stem part}$ ), elevation (model  $WD \sim \text{elevation}$ ) and tree height (model  $WD \sim \text{height}$ ), and tested for any interaction between stem parts and elevation (model  $WD \sim \text{stem part} \times \text{elevation}$ ) or between stem parts and tree height (model  $WD \sim \text{stem part} \times \text{height}$ ). For both objectives I used a null model that only contained random effects (model 0:  $WD \sim 1$ ), and Akaike's Information Criterion for small samples ( $AIC_c$ ) as a model selection approach (Burnham & Anderson 2002). The model with the lowest  $AIC_c$  was deemed as the best fitting the data. It is common practice to consider models with equivalent support when the difference between both models' AIC is lower than or equal to 2 ( $\Delta AIC \leq 2$ ). When stem parts differed in their densities, I conducted *post-hoc* multiple comparisons (Tukey's procedure) among them using the *multcomp* package (Hothorn *et al.* 2008) in R.

### RESULTS

The trunk sapwood, trunk heartwood, branch and twig densities as well as the main stem growth rates were determined in 168 adult trees of *N. pumilio* growing at four elevations (including treeline elevation) and five locations spanning  $18^\circ$  of latitude in the Southern Andes (from central Chile to Tierra del Fuego). As anticipated, most mean values of tree characteristics were affected by elevation (Table 1). Tree height ( $\chi^2 = 362.43$ ,  $P < 0.001$ ), DBH ( $\chi^2 = 202.72$ ,  $P < 0.001$ ) and age ( $\chi^2 = 6.126$ ,  $P = 0.013$ ) decreased significantly with elevation (Table 1). Mean  $BAI_{10}$  ( $\chi^2 = 8.799$ ,  $P = 0.003$ ) and MAI ( $\chi^2 = 12.071$ ,  $P < 0.001$ ) also decreased significantly with elevation. Among wood densities, only twig density increased significantly ( $\chi^2 = 12.948$ ,  $P < 0.001$ ); trunk sapwood density increased marginally ( $\chi^2 = 3.549$ ,  $P = 0.060$ ). The minimum wood density value was found in the trunk sapwood ( $0.401 \text{ g cm}^{-3}$ ), whereas the maximum value was found in the

trunk heartwood ( $0.704 \text{ g cm}^{-3}$ ). Standardised main stem wood density varied between  $0.411$  and  $0.614 \text{ g cm}^{-3}$ , giving an intraspecific variation in wood density of 1.49-fold. Tree growth showed higher variation than standardised main stem wood density;  $\text{BAI}_{10}$  had a variation of 39-fold ( $8.117$ – $326.472 \text{ cm}^2 \text{ year}^{-1}$ ), whereas MAI showed a variation of 20.5-fold ( $1.091$ – $23.564 \text{ cm}^2 \text{ year}^{-1}$ ).

Contrary to what was expected, none of the models representing the relationship between wood density (heartwood, sapwood or main stem) and tree growth ( $\text{BAI}_{10}$  and MAI) were deemed different from the null model; *i.e.* the  $\Delta\text{AIC}$  between all of the tested models and the null model was  $\leq 2$  (Table 2, Fig. 2). Only MAI was negatively related to trunk heartwood density, and only marginally so ( $\chi^2 = 2.913$ ,  $P = 0.088$ ,  $b = -0.018$ ; Table 2). When wood densities were compared across tree heights, the model representing the relationship between tree height and trunk sapwood density was deemed the best model (Table 2), differing from the null model by more than 2 units ( $\Delta\text{AIC} = 3.9$ ); tree height was negatively related to sapwood density. Similarly, standardised main stem wood density varied negatively and significantly with tree height (Table 2, Fig. 3;  $b = -0.029$ ). Thus, tree height had a significantly negative effect on wood density.

When the wood density of different stem parts was compared across elevations, the results showed that there is a significant variation among stem parts (the model representing the type of stem parts was deemed the best model, *i.e.* with the lowest AIC and very different from the null model; Table 3, Fig. 4). After conducting a *post-hoc* analysis, twigs had a significantly higher density than branches ( $z = 7.693$ ,  $P < 0.001$ ) and the trunk ( $z = 5.462$ ,  $P < 0.001$ ; Fig. 4). Branch and trunk wood densities were different, but only marginally so ( $z = 2.23$ ,  $P = 0.066$ ). As previously shown, tree height was significantly correlated with wood density; negatively related to standardised wood density and positively related to branch and twig densities, although the stem size  $\times$  height interaction was not significant (Table 3). The stem part  $\times$  elevation interaction was not significant (the interaction model's AIC did not differ from the null model's AIC; Table 3). This means that elevation did not mediate any shift in the stem part and wood density relationship (Table 3). Despite this lack of model support, it is clear that trunk and twig wood densities tended to converge in value with elevation ( $\text{WD}_{\text{st}} = 0.51$ ,  $\text{WD}_{\text{twig}} = 0.522$ );  $\text{WD}_{\text{st}}$  (*i.e.* trunk sapwood) tended to increase with elevation more than  $\text{WD}_{\text{twig}}$  changed

with elevation (Fig. 4). When trunk heartwood and sapwood were compared, trunk heartwood was significantly denser than trunk sapwood (lowest AIC =  $-635.07$ , and very different from the null model,  $P < 0.01$ ). Trunk heartwood density was 7.40% higher than trunk sapwood density. This difference was not altered by elevation; the stem part  $\times$  elevation interaction was not significant.

## DISCUSSION

### Growth is not related to wood density at the intraspecific level

In this study, even though trees showed significant differences in growth rate, particularly across the elevational gradient, wood density was not related to growth ( $\text{BAI}_{10}$  or MAI), as was expected. This lack of relationship is contrary to what has been found at the interspecific level, where, in general, growth rates relate negatively to wood density (Enquist *et al.* 1999; Muller-Landau 2004; King *et al.* 2005; van Gelder *et al.* 2006; Chave *et al.* 2009). Similarly to a previous study (Fajardo 2016b), where it was shown that wood density was not related to the contrasting competitive abilities of tree individuals of two *Nothofagus* species growing in high-density stands at lower elevations, here I found that wood density does not encompass the high variation in tree growth. Although the general variation in wood density reported in this study was relatively narrow (ca.  $0.4$ – $0.62 \text{ g cm}^{-3}$ ) when compared to global density variation (ca.  $0.3$ – $1.0 \text{ g cm}^{-3}$ ; Zanne *et al.* 2010), but not when compared to studies reporting intraspecific variation (Fajardo & Piper 2011; Siefert *et al.* 2015), and also relative to the density variation in studies linking density with growth rates (ca.  $0.2$ – $0.9 \text{ g cm}^{-3}$ ; Chave *et al.* 2009), the relative variation of growth was of higher magnitude (*e.g.*  $\text{BAI}_{10}$  varied between  $8.12$  to  $326.47 \text{ cm}^2 \text{ year}^{-1}$ ). Elevation was not involved in the lack of relationship between growth and wood density, as evidenced by the poor support for the model with the interaction term.

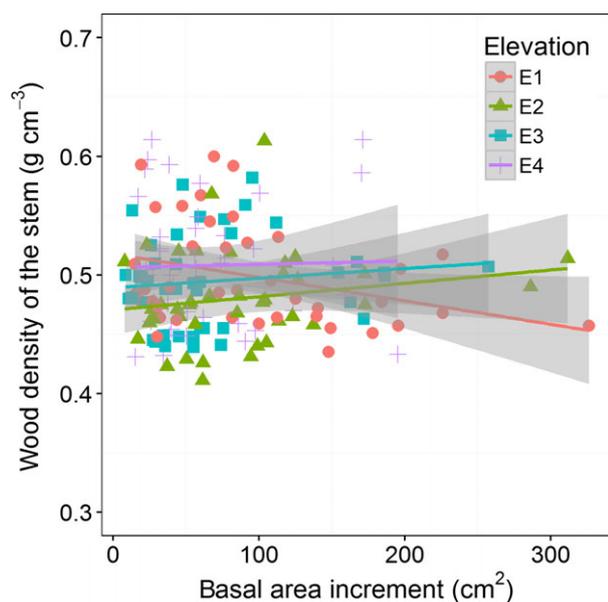
Although it has been stated that wood density mediates a trade-off between strength and economy of construction at the interspecific level, a higher wood density providing more strength at a higher cost (van Gelder *et al.* 2006), recent studies have hypothesised that high wood density, instead of increasing strength, may be associated with a reduction in metabolic costs, chiefly respiration rates, due to lower trunk surface area (Anten & Schieving 2010; Larjavaara & Muller-Landau 2010). One

	Tall forest (E1) $n = 41$	Intermediate (E2) $n = 40$	Timberline (E3) $n = 42$	Treeline (E4) $n = 45$
Height	16.64 (0.46) a	11.51 (0.33) b	7.29 (0.28) c	3.72 (0.09) d
DBH	29.43 (1.55) a	22.32 (0.95) b	16.35 (0.46) c	12.03 (0.58) d
Age	101.78 (9.90) a	88.73 (9.34) ab	89.38 (7.49) ab	64.11 (2.81) b
$\text{WD}_{\text{twig}}$	0.528 (0.006) a	0.519 (0.005) a	0.518 (0.005) a	0.517 (0.005) a
$\text{WD}_{\text{branch}}$	0.504 (0.007) a	0.494 (0.004) ab	0.481 (0.005) b	0.481 (0.005) b
$\text{WD}_{\text{sap}}$	0.491 (0.008) ab	0.475 (0.006) b	0.488 (0.006) ab	0.503 (0.007) b
$\text{WD}_{\text{heart}}$	0.513 (0.007) a	0.500 (0.009) a	0.514 (0.008) a	0.521 (0.011) a
$\text{WD}_{\text{st}}$	0.502 (0.006) a	0.485 (0.007) a	0.503 (0.007) a	0.507 (0.008) a
$\text{Sap}_{\text{prop}}$	60.85 (3.15) a	71.37 (2.83) b	67.87 (2.45) ab	76.71 (1.94) b
$\text{BAI}_{10}$	95.66 (11.07) a	88.09 (10.14) a	69.73 (8.99) a	62.45 (6.89) b
MAI	6.49 (0.79) a	5.97 (0.75) a	4.39 (0.63) b	3.87 (0.34) b

**Table 1.** Means ( $\pm 1$  SE) of tree height (m), DBH in cm (at 1.35 m), twig ( $\text{WD}_{\text{twig}}$ ), branch ( $\text{WD}_{\text{branch}}$ ), trunk sapwood ( $\text{WD}_{\text{sap}}$ ), trunk heartwood ( $\text{WD}_{\text{heart}}$ ) and standardised (trunk) wood densities ( $\text{WD}_{\text{st}}$ , in  $\text{g cm}^{-3}$ ), basal area increment of the last 10 years for the main stem ( $\text{BAI}_{10}$  in  $\text{cm}^2 \text{ year}^{-1}$ ) and mean basal area increment (MAI in  $\text{cm}^2 \text{ year}^{-1}$ ) of dominant individuals of *Nothofagus pumilio* growing in five treeline ecotones in the southern Chilean Andes. Different letters stand for significant mean differences between elevations.

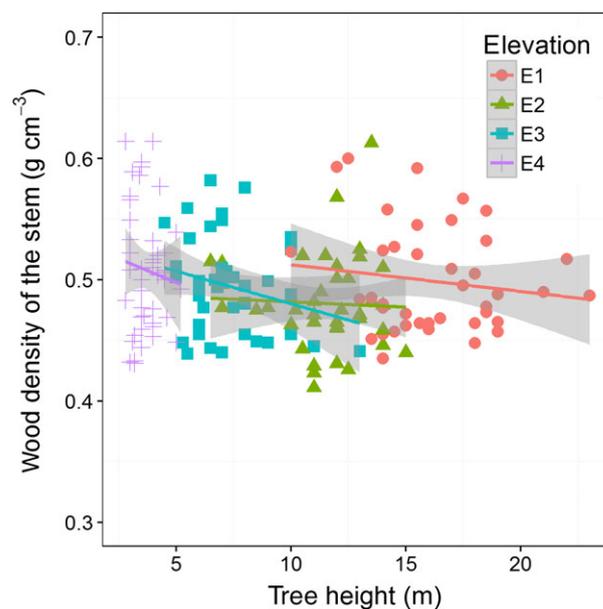
**Table 2.** Akaike Information Criterion (AIC) and probability values ( $P$ ) for the different hypothesised models relating wood density ( $\text{g cm}^{-3}$ ) to growth rate ( $\text{BAI}_{10}$  and MAI,  $\text{cm}^2$ ), elevation (low, intermediate, timberline and treeline) and tree height, and related interactions, of the treeline species *Nothofagus pumilio* in the southern Chilean Andes. Wood densities were represented by trunk sapwood ( $\text{WD}_{\text{sap}}$ ), trunk heartwood ( $\text{WD}_{\text{heart}}$ ) and trunk ( $\text{WD}_{\text{st}}$ ) densities. Probability values ( $P$ ) account for the relevance of several variables when compared with a null model ( $\sim 1$ ), or for significant interactions. Significant effects ( $\Delta\text{AIC} > 2$ ,  $P < 0.05$ ) in bold.

Models	$\log(\text{WD}_{\text{sap}})$	$P$	$\log(\text{WD}_{\text{heart}})$ AIC	$P$	$\log(\text{WD}_{\text{st}})$	$P$
$\sim 1$	-351.84		-298.25		-364.03	
$\text{BAI}_{10}$	-349.84	0.974	-297.81	0.212	-362.87	0.361
MAI	-350.50	0.415	-299.17	0.088	-364.90	0.091
elevation	-353.39	0.060	-296.94	0.406	-364.19	0.142
height	<b>-357.45</b>	<b>0.006</b>	-297.40	0.347	<b>-366.83</b>	<b>0.029</b>
$\text{BAI}_{10}$ + elevation	-351.56		-296.12		-362.55	
$\text{BAI}_{10}$ * elevation	-349.67	0.738	-294.14	0.911	-360.60	0.818
$\text{BAI}_{10}$ + height	-355.69		-296.54		-365.11	
$\text{BAI}_{10}$ * height	-353.82	0.717	-294.56	0.890	-363.30	0.667
MAI + elevation	-351.56		-297.32		-364.03	
MAI * elevation	-349.67	0.738	-295.81	0.485	-362.18	0.702
MAI + height	-354.06		-297.49		-365.50	
MAI * height	-352.18	0.392	-295.90	0.523	-363.61	0.741
Elevation + height	-360.25		-295.71		-368.15	
Elevation * height	-358.58	0.567	-293.93	0.641	-366.95	0.371



**Fig. 2.** Relationships between growth rate ( $\text{BAI}_{10}$ , basal area increment of the last 10 years in  $\text{cm}^2$ ) and wood density ( $\text{g cm}^{-3}$ ) for stems of *Nothofagus pumilio* growing across four elevations (including treeline elevation) in five elevational gradients in the southern Chilean Andes. Elevations are low (E1), intermediate (E2), timberline (E3) and treeline (E4). Confidence envelopes around the correlation line indicate a 95% confidence interval. The slope of the wood density–tree growth relationship in general (and for the elevations in particular) was not different from zero ( $P > 0.05$ ).

explanation is that wood density appears to be a very conservative trait because intraspecific wood density variation in general shows the lowest variation (typically  $< 10\%$ ) among many plant functional traits (Siefert *et al.* 2015), even when compared across abrupt environmental gradients. Additionally, when wood densities of conspecifics of comparable age, but contrasting growth rates, are compared, wood density shows little variation (Fajardo 2016b). In principle, when different species are compared, fast-growing tree species have lower wood density than slow-growing species. Although one explanation for this

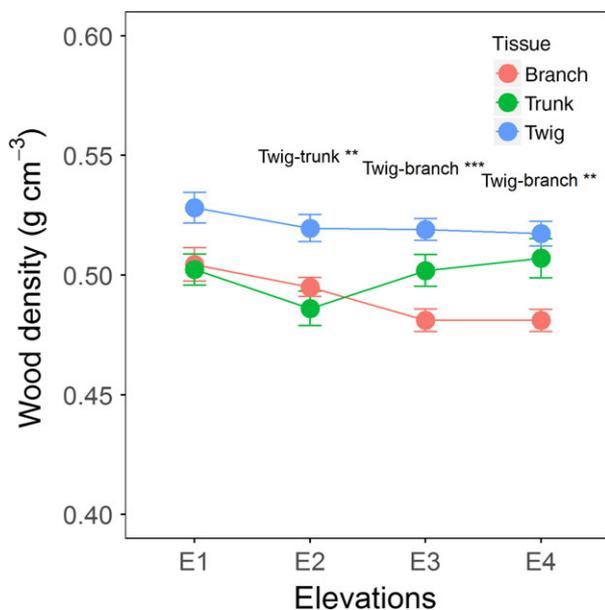


**Fig. 3.** Relationships between tree height (m) and trunk sapwood density ( $\text{g cm}^{-3}$ ) for *Nothofagus pumilio* growing across four elevations (including treeline elevation) in five elevational gradients in the southern Chilean Andes. Elevations are low (E1), intermediate (E2), timberline (E3) and treeline (E4). Confidence envelopes around the correlation line indicate a 95% confidence interval. The slope of the wood density–tree height relationship was negative and significantly different from zero ( $P = 0.006$ ).

is that fast-growing tree species have wider vessels than slow-growing species, the evidence for a negative relationship between wood density and vessel diameter is mixed. Some studies have found support for this relationship (Pratt *et al.* 2007; Pfautsch *et al.* 2016) and others have not (Preston *et al.* 2006; Zanne *et al.* 2010; Ziemińska *et al.* 2013). Logically, if everything else were constant, increasing vessel diameter would decrease wood density, because vessel lumen fraction would increase. But usually, increasing vessel diameter is balanced out by decreasing vessel number so that vessel fraction does not

**Table 3.** Akaike Information Criterion (AIC) values for the different hypothesised models relating wood density to stem parts (trunk, branch and twig), elevation (low, intermediate, timberline and treeline), tree height (m) and related interactions (including DBH), height of the treeline species *Nothofagus pumilio* in the southern Chilean Andes. Probability values (*P*) account for the relevance of several variables when compared with a null model (~1), or for significant interactions. Significant effects ( $\Delta\text{AIC} > 2$ ,  $P < 0.05$ ) in bold.

	Wood density	<i>P</i>
Models		
~1	-1130.88	
Stem part	<b>-1184.65</b>	<b>&lt;0.001</b>
Elevation	-1132.40	0.060
Height	<b>-1184.65</b>	<b>&lt;0.001</b>
DBH + elevation	-1186.58	
DBH × elevation	-1186.82	0.135
DBH + height	-1185.56	
DBH × height	-1184.45	0.346
Elevation + height	-1130.59	
Elevation × height	-1132.22	0.057



**Fig. 4.** Relationship of wood density of different stem parts ( $\text{g cm}^{-3}$ ) with elevation in adult trees of the treeline species *Nothofagus pumilio* growing across four elevations (including treeline elevation) in five elevational gradients in the southern Chilean Andes. Elevations are low (E1), intermediate (E2), timberline (E3) and treeline (E4). In the *post-hoc* comparisons between stem parts wood density,  $**P < 0.01$ ,  $***P < 0.001$ .

change much (Zanne *et al.* 2010) and wood density can be unaffected. Alternatively, other studies (Martínez-Cabrera *et al.* 2009; Zanne *et al.* 2010; Ziemińska *et al.* 2013) have found that fibres, not vessels, are most responsible for wood density.

### Tree height

Although wood density did not vary across an elevational gradient, it did vary across contrasting tree heights; the taller the

tree the lower the trunk sapwood (and standardised) wood density. This is an intriguing result; the expectation is that as trees grow in size they need more strength and, therefore, higher wood density, although trees can also adjust their stem diameter to make up for low density and low mechanical strength (see Butler *et al.* 2011). The fact that the trunk heartwood density did not vary in relation to tree height, while trunk sapwood decreased with tree height, may be explained following Sanio's laws (Mencuccini *et al.* 2007), *i.e.* xylem conduits widen predictably from the stem tip toward the base as a result of natural selection that favours the maintenance of constant hydraulic resistance as plant height increases (Coomes *et al.* 2007; Mencuccini *et al.* 2007; Olson *et al.* 2014; Carrer *et al.* 2015). As such, the taller the tree the wider its vessels will be at its base, which makes sense when twig density and stem density are compared (see below). Finally, in this study, it was clearly tree height and not elevation that drove wood density, at least trunk sapwood density.

### Wood density variation across woody parts

Sapwood is the woody tissue that primarily conducts water, but also helps to strengthen the stem and to some extent store carbon (Pallardy 2008; Bresinsky *et al.* 2013). Heartwood, in contrast, constitutes the 'non-living' woody tissue, which mostly provides mechanical support to the stem (Evert 2006); it is not involved in any physiological processes (Pallardy 2008). As such, heartwood density is expected to be less responsive to the environment, as found here. This means that secondary processes involved in heartwood formation may partly cancel out potential variation in wood density. Heartwood vessels are commonly filled with tylosis, thus heartwood density was, on average, 7.4% higher than sapwood density. Previous research has also found heartwood was denser than sapwood (Wiemann & Williamson 1989a,b; Parolin 2002; Fajardo 2016b). The explanation for this trend relates to the deposition of compounds and residues in vessel lumens that increase the weight of the wood for a given volume, therefore increasing its density. Another explanation may be a radial increase in conduit diameters (a direct consequence of the apex-to-base widening within a tree ring), which would decrease wood density: the taller or older the tree, the lower its sapwood density (Coomes *et al.* 2007; Mencuccini *et al.* 2007; Olson *et al.* 2014; Carrer *et al.* 2015).

Twig wood density proved to be the densest tissue in the trees; on average, twig wood density was 7.64%, 0.24% and 5.3% higher than sapwood, heartwood and stem wood densities, respectively. In principle, this is contrary to results of He & Deane (2016) across 71 species in a subtropical evergreen forest in southern China, *i.e.* stem wood density was, on average, 8.3% higher than twig wood density. In another comparative study, twig wood densities were 25% lower than core densities taken from trunks in tree species of a Bolivian tropical forest (Lusk *et al.* 2016). The fact that twig wood density in the current study was higher than stem wood density may be explained by wood anatomy, *i.e.* a basipetal vessel widening (Sanio's laws, see above). This effect should be more evident in tall trees, and is somewhat evident in Fig. 4, where the difference between twig and stem wood density was greatest at lower elevations where the trees sampled were the tallest (see also De Micco *et al.* 2008; He & Deane 2016).

## CONCLUSIONS

It is first important to consider that, currently, with so much political interest in reducing greenhouse effects of a high atmospheric CO<sub>2</sub> concentrations, the general belief is that faster-growing species or phenotypes (in afforestation) will store (sequester) more carbon than slower-growing species or phenotypes (Canadell & Raupach 2008). Although Körner (2017) claims that it is tree longevity and not growth rate that really matters in terms of carbon sequestration, according to the present study, trees that grow faster may be able to sequester more carbon than slow-growing trees because there was no decrease in their wood densities with growth. Thus, there may be some support for genetic programmes seeking fast-growing phenotypes for afforestation efforts that aim to increase carbon sequestration.

Negative across-species trends found in the growth–wood density relationship may not emerge as the aggregate of parallel intraspecific patterns. While my results await confirmation from other species, given the extraordinarily wide ecological and geographic range of *Nothofagus pumilio*, it would seem that if there were a within-species trend, it would appear in this species. Overall, the results of this study are consistent with the

notion that wood density *per se* may not be the most relevant trait underlying differences in tree growth rates (and probably mortality). Perhaps other more specific traits of wood (e.g. xylem anatomy; Carrer *et al.* 2015) could be more relevant to stress resistance, and these may or may not be correlated with wood density across species. Finally, tree height appears to be more related than elevation to wood density values, particularly trunk sapwood density, *i.e.* the *living* wood.

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## REFERENCES

- Anten N.P.R., Schieving F. (2010) The role of wood mass density and mechanical constraints in the economy of tree architecture. *The American Naturalist*, **175**, 250–260.
- Bresinsky A., Körner C., Kadereit J.W., Neuhaus G., Sonnwald U. (2013) *Strasburger's Plant Sciences. Including Prokaryotes and Fungi*. Springer, Berlin, Germany.
- Bunker D.E., DeClerck F., Bradford J.C., Colwell R.K., Perfecto I., Phillips O.L., Sankaran M., Naeem S. (2005) Species loss and aboveground carbon storage in a tropical forest. *Science*, **310**, 1029–1031.
- Burnham K.P., Anderson D.R. (2002) *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach*. Springer, New York, USA, pp.488.
- Butler D.W., Gleason S.M., Davidson I., Onoda Y., Westoby M. (2011) Safety and streamlining of woody shoots in wind: an empirical study across 39 species in tropical Australia. *New Phytologist*, **193**, 137–149.
- Canadell J.G., Raupach M.R. (2008) Managing forests for climate change mitigation. *Science*, **320**, 1456–1157.
- Carrer M., von Arx G., Castagneri D., Petit G. (2015) Distilling allometric and environmental information from time series of conduit size: the standardization issue and its relationship to tree hydraulic architecture. *Tree Physiology*, **35**, 27–33.
- Chave J., Coomes D., Jansen S., Lewis S.L., Swenson N.G., Zanne A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.
- Coomes D.A., Jenkins K.L., Cole L.E.S. (2007) Scaling of tree vascular transport systems along gradients of nutrient supply and altitude. *Biology Letters*, **3**, 86–89.
- Daniels L.D., Veblen T.T. (2004) Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. *Ecology*, **85**, 1284–1296.
- De Micco V., Aronne G., Baas P. (2008) Wood anatomy and hydraulic architecture of stems and twigs of some Mediterranean trees and shrubs along a mesic-xeric gradient. *Trees*, **22**, 643–655.
- Duncan R.P. (1989) An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrycarpus dacrydioides*). *New Zealand Natural Science*, **16**, 31–37.
- Enquist B.J., West G.B., Charnov E.L., Brown J.H. (1999) Allometric scaling of production and life-history variation in vascular plants. *Nature*, **401**, 907–911.
- Evert R.F. (2006) *Esau's Plant Anatomy. Meristems, Cells, and Tissues of the Plant Body – Their Structure, Function, and Development*. John Wiley & Sons, Hoboken, NJ, USA.
- Fajardo A. (2016a) Are trait-scaling relationships invariant across contrasting elevations in the widely distributed treeline species *Nothofagus pumilio*? *American Journal of Botany*, **103**, 821–829.
- Fajardo A. (2016b) Wood density is a poor predictor of competitive ability among individuals of the same species. *Forest Ecology and Management*, **372**, 217–225.
- Fajardo A., McIntire E.J.B. (2012) Reversal of multi-century tree growth improvements and loss of synchrony at mountain tree lines point to changes in key drivers. *Journal of Ecology*, **100**, 782–794.
- Fajardo A., Piper F.I. (2011) Intraspecific trait variation and covariation in a widespread tree species (*Nothofagus pumilio*) in southern Chile. *New Phytologist*, **189**, 259–271.
- Fajardo A., Piper F.I. (2014) An experimental approach to explain the southern Andes elevational treeline. *American Journal of Botany*, **101**, 788–795.
- Fajardo A., Piper F.I. (2017) An assessment of carbon and nutrient limitations in the formation of the southern Andes tree line. *Journal of Ecology*, **105**, 517–527.
- Fajardo A., Siefert A. (2016) Phenological variation of leaf functional traits within species. *Oecologia*, **180**, 951–961.
- Gamache I., Payette S. (2004) Height growth response of tree line black spruce to recent climate warming across the forest–tundra of eastern Canada. *Journal of Ecology*, **92**, 835–845.
- van Gelder H.A., Poorter L., Sterck F.J. (2006) Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytologist*, **171**, 367–378.
- He D., Deane D.C. (2016) The relationship between trunk- and twig-wood density shifts with tree size and species stature. *Forest Ecology and Management*, **372**, 137–142.
- Hoch G., Körner C. (2012) Global patterns of mobile carbon stores in trees at the high-elevation treeline. *Global Ecology and Biogeography*, **21**, 861–871.
- Hothorn T., Bretz F., Westfall P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.
- King D.A., Davies S.J., Nur Supardi M.N., Tan S. (2005) Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Functional Ecology*, **19**, 445–453.
- Körner C. (2003) *Alpine Plant Life*. Springer, Berlin, Germany.
- Körner C. (2012a) *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*. Springer, Basel, Switzerland.
- Körner C. (2012b) Treelines will be understood once the functional difference between a tree and a shrub is. *Ambio*, **41**, 197–206.
- Körner C. (2017) A matter of tree longevity. *Science*, **355**, 130–131.
- Larjavaara M., Muller-Landau H.C. (2010) Rethinking the value of high wood density. *Functional Ecology*, **24**, 701–705.
- Lusk C.H., Jimenez-Castillo M., Aragón R., Easdale T.A., Poorter L., Hinojosa L.F., Mason N.W.H. (2016) Testing for functional convergence of temperate rainforest tree assemblages in Chile and New Zealand. *New Zealand Journal of Botany*, **54**, 175–203.

- Martínez-Cabrera H.I., Jones C.S., Espino S., Schenk H.J. (2009) Wood anatomy and wood density in shrubs: responses to varying aridity along transcontinental transects. *American Journal of Botany*, **96**, 1388–1398.
- Mayor J.R., Sanders N.J., Classen A.T., Bardgett R.D., Clément J.-C., Fajardo A., Lavorel S., Sundqvist M.K., Bhan M., Chisholm C., Cieraad E., Gedalof G., Grigulis K., Kudo G., Oberski D., Wardle D.A. (2017) Elevation alters ecosystem properties across temperate treelines globally. *Nature*, **542**, 91–95.
- Mencuccini M., Hölttä T., Petit G., Magnani F. (2007) Sanio's law revisited. Size-dependent changes in the xylem architecture of trees. *Ecology Letters*, **10**, 1084–1093.
- Méndez-Alonzo R., Paz H., Cruz Zuluaga R., Rosell J.A., Olson M.E. (2012) Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology*, **93**, 2397–2406.
- Messier J., McGill B.J., Lechowicz M.J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, **13**, 838–848.
- Muller-Landau H. (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica*, **36**, 20–32.
- Olson M.E., Anfodillo T., Rosell J.A., Petit G., Crivellaro A., Isnard S., León-Gómez C., Alvarado-Cárdenas L.O., Castorena M. (2014) Universal hydraulics of the flowering plants: vessel diameter scales with stem length across angiosperm lineages, habits and climates. *Ecology Letters*, **17**, 988–997.
- Pallardy S.G. (2008) *Physiology of Woody Plants*. Academic Press, Burlington, MA, USA.
- Parolin P. (2002) Radial gradients in wood specific gravity in trees of central Amazonia floodplains. *IAWA Journal*, **23**, 449–457.
- Pfautsch S., Harbusch M., Wesolowski A., Smith R., Macfarlane C., Tjoelker M.G., Reich P.B., Adams M.A. (2016) Climate determines vascular traits in the ecologically diverse genus *Eucalyptus*. *Ecology Letters*, **19**, 240–248.
- Pinheiro J., Bates D., DebRoy S., Sarkar D.; R Core team. (2016) *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-128. Available from URL: <http://CRAN.R-project.org/package=nlme> (accessed 10 September 2017).
- Piper F.I., Viñeola B., Linares J.C., Camarero J.J., Cavieres L.A., Fajardo A. (2016) Mediterranean and temperate treelines are controlled by different environmental drivers. *Journal of Ecology*, **104**, 691–702.
- Poorter L., Kitajima K. (2007) Carbohydrate storage and light requirements of tropical moist and dry forest tree species. *Ecology*, **88**, 1000–1011.
- Poorter L., McDonald I., Alarcón A., Fichtler E., Licona J.-C., Peña-Claros M., Sterck F., Villegas Z., Sass-Klaassen U. (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytologist*, **185**, 481–492.
- Pratt R.B., Jacobsen A.L., Ewers F.W., Davis S.D. (2007) Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist*, **174**, 787–798.
- Preston K.A., Cornwell W.K., DeNoyer J.L. (2006) Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperm. *New Phytologist*, **170**, 807–818.
- Puntieri J., Raffaele E., Martínez P., Barthélémy D., Brion C. (1999) Morphological and architectural features of young *Nothofagus pumilio* (Poepp. and Endl.) Krasser (Fagaceae). *Botanical Journal of the Linnean Society*, **130**, 395–410.
- R Development Core Team. (2016) R: A language and environment for statistical computing. Version 3.3.0. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org> (accessed 10 September 2017).
- Sarmiento C., Patiño S., Paine C.E.T., Beauchêne J., Thibaut A., Baraloto C. (2011) Within-individual variation of trunk and branch xylem density in tropical trees. *American Journal of Botany*, **98**, 140–149.
- Siefert A., Violle C., Chalmandrier L., Albert C.H., Taudiere A., Fajardo A., Aarssen L.W., Baraloto C., Carlucci M.B., Cianciaruso M.V., Dantas V.L., de Bello F., Duarte L.D.S., Fonseca C.R., Freschet G.T., Gaucherand S., Gross N., Hikosaka K., Jackson B., Jung V., Kamiyama C., Katabuchi M., Kembel S.W., Kichenin E., Kraft N.J.B., Lagerström A., Bagousse-Pinguet Y.L., Li Y., Mason N., Messier J., Nakashizuka T., Overton J.M., Peltzer D., Pérez-Ramos I.M., Pillar V.D., Prentice H.C., Richardson S., Sasaki T., Schamp B.S., Schöb C., Shipley B., Sundqvist M., Sykes M.T., Vandewalle M., Wardle D.A., Wright I. (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, **18**, 1406–1419.
- Stokes M.A., Smiley T.L. (1996) *An Introduction to Tree-Ring Dating*. The University of Arizona Press, Tucson, AZ, USA.
- Swenson N.G., Enquist B.J. (2007) Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, **94**, 451–459.
- Violle C., Enquist B.J., McGill B.J., Jiang L., Albert C.H., Hulshof C., Jung V., Messier J. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, **27**, 244–252.
- Wiemann M.C., Williamson G.B. (1989a) Radial gradients in the specific gravity of wood in some tropical and temperate trees. *Forest Science*, **35**, 197–210.
- Wiemann M.C., Williamson G.B. (1989b) Wood specific gravity gradients in tropical dry and montane rain forest trees. *American Journal of Botany*, **76**, 924–928.
- Woodcock D., Shier A. (2002) Wood specific gravity and its radial variations: the many ways to make a tree. *Trees*, **16**, 437–443.
- Wright S.J., Kitajima K., Kraft N.J.B., Reich P.B., Wright I.J., Bunker D.E., Condit R., Dalling J.W., Davies S.J., Díaz S., Engelbrecht B.M.J., Harms K.E., Hubbell S.P., Marks C.O., Ruiz-Jaen M.C., Salvador C.M., Zanne A.E. (2010) Functional traits and the growth–mortality trade-off in tropical trees. *Ecology*, **91**, 3664–3674.
- Zanne A.E., Westoby M., Falster D.S., Ackerly D.D., Loarie S.R., Arnold S.E.J., Coomes D.A. (2010) Angiosperm wood structure: global patterns in vessel anatomy and their relation to wood density and potential conductivity. *American Journal of Botany*, **97**, 207–215.
- Ziemińska K., Butler D.W., Gleason S.M., Wright I.J., Westoby M. (2013) Fibre walls and lumen fractions drive wood density variation across 24 Australian angiosperms. *AoB Plants*, **5**, plt046.