

Diversity and competition influence tree allometric relationships – developing functions for mixed-species forests

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Summary

1. Promoting mixed-species forests is an important strategy for adaptation and risk reduction in the face of global change. Concurrently, a main challenge in ecology is to quantify the effects of species diversity on ecosystem functioning. In forests, the effects of individual tree species on ecosystem functions depend largely on their dimensions, which are commonly predicted using allometric equations. However, little is known about how diversity influences allometry or how to incorporate this effect into allometric equations. Ignoring the effects of interspecific interactions on allometric relationships may result in severely biased predictions.

2. This study examined the effects of tree-species diversity, competition and tree social status on crown-projection area (*cpa*), height (*h*) and live-crown length (*lcl*) of trees using a European-wide data set containing 17 target species and 12 939 trees. The *cpa*, *h* and *lcl* were predicted as functions of stem diameter at 1.3 m, tree-species diversity, tree height relative to the stand mean height (*rh*) and a competition index (*CI*) that accounted for stand density and interspecific differences in competitive ability based on species-specific wood density or shade tolerance.

3. Averaged across species, diameter had the greatest effect on *cpa* and *lcl*, followed by the competition index, while *rh* had the greatest effect on *lcl*. Tree-species diversity had the smallest effect on *cpa*, *h* and *lcl*. Interspecific variability in *cpa*, *h* or *lcl* responses to diversity, *CI*, or *rh* was sometimes related to wood density or shade tolerance.

4. Synthesis. This study shows the strong influence of stand structure and species composition on allometric relationships. These influences can be quantified using measures of competition, tree-species diversity and relative tree height so that general equations can be developed for a given species to be applied to a wide range of species compositions and stand structures. This new approach will greatly improve predictions of biomass and carbon stocks in structurally and compositionally diverse forests.

Key-words: biodiversity, biomass partitioning, complementarity, plant allometry, plant–plant interactions, stand structure, tree height

Introduction

Terrestrial ecosystems remove nearly 3 billion tonnes of anthropogenic carbon from the atmosphere every year (Canadell *et al.* 2007). This carbon sequestration function makes a valuable contribution to climate change protection (Canadell *et al.* 2007; Canadell & Raupach 2008) and economic incentives have been devised to encourage practices

that increase forest carbon sequestration (Agrawal, Nepstad & Chhatre 2011). One of the most widely advocated elements of adaptation and risk reduction strategies in the face of global change is the use of mixed-species forests (Messier, Puettmann & Coates 2013). This relates to their potential to provide higher levels of ecosystem services than monocultures in terms of productivity and for mitigating the effects of ecosystem disturbances such as droughts and pest organism outbreaks (Jactel & Brockerhoff 2007; Cardinale *et al.* 2011; Grossiord *et al.* 2014; Thompson *et al.* 2014). Quantifying the effects of species diversity and stand structure on

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ecosystem functioning proves to be one of the most important current challenges in ecology (Naeem *et al.* 2009).

Studies aiming to quantify ecosystem functions in forests often require the use of tree allometry, which describes scaling relationships between the size of a tree component and the tree as a whole. However, relatively little is known about the influence of tree-species diversity on allometric relationships in trees or how tree-species diversity might be incorporated into allometric equations. Allometric relationships are critical for many aspects of ecology and forestry for at least two broad applications. One is to predict tree and stand variables for the assessment of forest productivity, biomass and carbon stocks and related ecosystem services (Henry *et al.* 2013; Chave *et al.* 2014; Sileshi 2014; Bouriaud *et al.* 2015). To do so, variables that are easy to measure accurately, such as stem diameter, are used to predict target variables, such as crown projection area, leaf area, transpiration, height, biomass and stem volume. These predictions are required to scale up from one level, such as the tree, to another level, such as the stand and consequently to landscape and regional levels. They will also be required to calibrate and validate remotely sensed predictions of ecosystem characteristics (Jucker *et al.* in press). The second broad application of allometric relationships is to examine and model forest functioning; many forest growth and yield models contain allometric equations (Pretzsch, Forrester & Rötzer 2015), and also to examine fundamental physiological or morphological trade-offs, e.g., producing leaves as opposed to stems or roots, as growing conditions change. Tree allometry depends on the current and past environmental conditions (Poorter *et al.* 2012) but also reflects how trees have influenced those conditions themselves. At the same time, within-tree carbon partitioning, which is reflected in allometric relationships, influences the trees' ability to acquire and compete for resources. Allometric relationships indicate how trees react to, and modify their growing conditions and provide clues about the physiological, mechanical and environmental factors that drive their development.

Recognition of the critical role played by allometric relationships for quantifying and understanding forest functioning is illustrated in the recent development of several international data bases containing allometric equations (e.g., Henry *et al.* 2013; Falster *et al.* 2015). However, while it is well-known that allometry and carbon partitioning are influenced by resource availability and climatic conditions (Mokany, Raison & Prokushkin 2006; Litton, Raich & Ryan 2007; Poorter *et al.* 2012), it is also well-known that species interactions in mixed-species forests can change resource availability and micro-climatic conditions (Richards *et al.* 2010; Forrester 2014). Therefore, interspecific interactions can modify tree allometric relationships and in some cases the predicted variable can differ by more than 100%, for a given diameter (Getzin & Wiegand 2007; Laclau *et al.* 2008; Thorpe *et al.* 2010; Bayer, Seifert & Pretzsch 2013; Metz *et al.* 2013; Barbeito, Collet & Ningre 2014; Forrester & Albrecht 2014; Jucker *et al.* 2014; Pretzsch 2014). Despite this evidence, allometric functions rarely account for interspecific

interactions. Due to the prevalence of mono-specific forests and plantations during the development of traditional forest management, the allometric functions developed for monocultures have long been regarded as sufficient for practical and scientific applications. However, mixed-species forests are increasingly recognized for their potentially superior productivity (e.g., average of 24%; Paquette & Messier 2011; Zhang, Chen & Reich 2012; Forrester & Bauhus 2016), their multifunctionality benefits (Gamfeldt *et al.* 2013) and their ecological and aesthetic value (Nadrowski, Wirth & Scherer-Lorenzen 2010; Lindemann-Matthies *et al.* 2013). Allometric functions developed for monospecific stands may prove to be imprecise and biased when applied to the study and management of mixed-species forests (Forrester & Pretzsch 2015). This study aims to improve our understanding of the drivers of tree allometry and to develop allometric functions for important European tree species that account for the influence of tree-species diversity and competition.

Tree allometric relationships are often expressed as

$$Y = aX^{b_{Y,X}} \quad \text{eqn 1}$$

where a and b are constants. If variable X is tree diameter, and Y is height, then eqn 1 implies that if diameter increases by 1% then height will change by $b\%$. There has been much debate about the value of the exponent b (Sileshi 2014). The contributions to this debate relate to mechanical constraints to prevent the tree from buckling under its own weight (Greenhill 1881; McMahon 1973), hydraulic constraints (Ryan, Phillips & Bond 2006) and particularly, biophysical constraints. For example, geometric scaling (Yoda *et al.* 1963; Gorham 1979; Pretzsch, Matthew & Dieler 2012), has been used to suggest proportionality between different linear dimensions, such that all linear tree dimensions (e.g., height, diameter) are related to quadratic or area-related dimensions (e.g., basal area, leaf area, crown projection area) as linear \propto quadratic^{1/2} and to cubic variables (e.g., stem volume, biomass, crown volume) as linear \propto cubic^{1/3} or quadratic \propto cubic^{2/3}. A competing argument is largely centered on the metabolic scaling theory proposed by West, Brown & Enquist (1999) and West, Enquist & Brown (2009) that describes resource distribution through hierarchical branching networks. In contrast to geometric scaling, it predicts that, for example, $b_{\text{volume,diameter}} = 8/3$, $b_{\text{mass,diameter}} = 8/3$, $b_{\text{crown projection area, diameter}} = 4/3$, $b_{\text{volume,height}} = 4$, $b_{\text{height,diameter}} = 2/3$.

In reality, however, many studies have shown that b is not invariant for any of these relationships and that the frequency distribution of b is not necessarily centered on the value of b predicted by the geometric or metabolic scaling theories (Coomes 2006; Pretzsch 2006; Ducey 2012; Lines *et al.* 2012; Pretzsch & Dieler 2012; Pretzsch, Matthew & Dieler 2012; Pretzsch, Daubert & Biber 2013; Sileshi 2014). Differences in b between species have been related to their shade tolerance, wood density, deciduous vs. evergreen foliage and the climate of their occurrence (Dietze, Wolosin & Clark 2008; Ducey 2012; Franceschini & Schneider 2014; Hulshof, Swenson & Weiser 2015). Intraspecific variability in b has

been related to tree age, environmental characteristics, shading and competition in terms of basal area (Vanninen & Mäkelä 2005; Duursma *et al.* 2010; Genet *et al.* 2011; Lines *et al.* 2012; Barbeito, Collet & Ningre 2014; Franceschini & Schneider 2014), and the fact that resources (e.g. light) and the efficiency with which they are used, are not distributed evenly within trees (e.g. vertical gradients within crowns) or between trees within the same stand (Coomes 2006; Muller-Landau *et al.* 2006).

The potential effects of interspecific interactions are rarely taken into account when developing allometric equations. Similarly, few forest growth models account for the effect of interspecific interactions on tree allometric relationships (Thorpe *et al.* 2010; Pretzsch, Forrester & Rötzer 2015). This is despite the fact that allometric relationships can vary in the presence of interspecific competition, and different competing species have different effects, as has been shown at the tree level for heights, crown projection areas, height to the crown base, leaf biomass and stem biomass (Getzin & Wiegand 2007; Laclau *et al.* 2008; Thorpe *et al.* 2010; Bayer, Seifert & Pretzsch 2013; Metz *et al.* 2013; Forrester & Albrecht 2014; Pretzsch 2014). This is consistent with a much larger number of studies in monocultures that have shown that allometry is influenced by stand density and resource availability (Mokany, Raison & Prokushkin 2006; Litton, Raich & Ryan 2007; Lines *et al.* 2012; Poorter *et al.* 2012). Both of these can vary significantly between mixtures and monocultures (Richards *et al.* 2010). Therefore, the use of allometric relationships from monocultures to examine mixed-species forests can lead to biased predictions, which could mislead forest managers, scientists and policy makers who use these predictions (Forrester & Pretzsch 2015).

A major hurdle facing the further development of allometric equations for mixtures is that the effects of interspecific interactions will depend on the identity of competing species. For example, the relationship between crown projection area and stem diameter for *Fagus sylvatica* varies depending on whether it was growing in mixtures with *Picea abies*, *Larix decidua*, *Fraxinus excelsior* or *Quercus petraea* (Pretzsch 2014). An obvious problem is that a different equation is required for each two-species combination. Given the huge number of possible species combinations in more species diverse forests, this is impractical. It would be more practical to develop for a given species a single allometric equation that is independent of the identity of the species with which the target species is competing, and instead quantifies the competitive ability of the mixed species in terms of quantitative variables such as their wood density or a measure of shade tolerance.

In this study we hypothesized that: (i) the effect of stand species composition and stand density on tree allometric relationships can be quantified by using competition indices that take into account the effects of competing trees based on their wood density or shade tolerance rather than species identity; (ii) in addition to the competition index, allometric relationships are also influenced by stand structural variables such as Shannon's diversity index and relative tree height (to quantify

vertical canopy structure); and (iii) the allometric response of a given species to competition, diversity or relative height is related to the wood density or shade tolerance of that species. To test these hypotheses we used a European data set spanning six regions representing major European forest types, each containing a gradient in tree-species diversity, totalling 17 target tree species (and many more competing species) and 12 939 trees. We also aimed to develop a set of allometric equations for 17 European tree species that can be used in forests with a range of species compositions and stand structures and which include the identity of competing species only indirectly in terms of traits such as wood density or shade tolerance.

Materials and methods

SITE DESCRIPTION AND EXPERIMENTAL DESIGN

The study was conducted using a European-wide permanent plot network that was established in 2011 (Baeten *et al.* 2013; FunDivEU-ROPE). The plots are located in six regions that are representative of major European forest types, and include Finnish boreal forests, Polish hemiboreal forests, German mixed beech forests, Romanian montane mixed beech forests, Italian thermophilous deciduous forests, and Spanish Mediterranean-mixed forests. Within each region, 28–43 plots (30 m × 30 m) were established, resulting in 209 plots. Of 17 target species included, some occur at more than one site, but none occur at all sites (Table 1). These target species comprise conifers, deciduous broadleaves and evergreen broadleaves. The tree-species richness of the plots ranged from 1 to 3 in Finland, 1 to 4 in Romania, Germany and Spain, and 1 to 5 in Italy and Poland. In each region, each target species was represented at all richness levels, which were replicated twice for 59 of the 91 combinations. Three main criteria were used when selecting the plots, such that (i) they were in closed forest (age range from about 25–150 years, mean ages for each region of 35–85 years; Jucker *et al.* 2016) that had received minimal management during the past decade or longer, (ii) plots of a given region had comparable topography, soil and bedrock, and (iii) the relative abundance of each target species within a given plot was as similar as possible while the presence of non-target species was usually restricted to less than 5% of the total plot basal area. The site conditions at the study plots are characteristic for important landscapes within each respective region (Baeten *et al.* 2013). This study follows an earlier study using this data set to examine the relationships between canopy packing and tree-species richness or basal area focusing on crown volumes (Jucker, Bouriaud & Coomes 2015). In contrast with that study, we examine whether species traits such as wood density or shade tolerance define their contrasting responses to competition, species diversity and the effects of vertical stand structure in terms of tree social status (i.e. whether a tree is dominant, co-dominant, intermediate or suppressed in relation to the main canopy layer).

TREE-LEVEL MEASUREMENTS AND CALCULATIONS

Within each plot, the diameter at 1.3 m (d ; m), height (h ; m), height to the live-crown base (m) and crown radius (m; in two orthogonal directions) were measured for all trees with $d \geq 7.5$ cm. The height to the live-crown base was defined as the height of the lowest live branch (excluding epicormic branches). This measure and h were

Table 1. Characteristics of the species and the stands where they occurred (minimum/mean/maximum)

Species	Species code	Shade tolerance*	Wood density (g cm ⁻³)†	Diameter (m)	Relative height	Competition index (from eqn 3c)	Shannon's index	Basal area (m ² ha ⁻¹)	Trees per ha	Number of trees measured in each region					
										Finland	Germany	Italy	Poland	Romania	Spain
<i>Abies alba</i>	Aa	4-60	0.35	0.07/0.34/0.77	0.12/0.93/1.76	423/1096/1637	0.00/0.66/1.34	29/67/86	300/648/867					327	327
<i>Acer pseudoplatanus</i>	Ap	3-73	0.51	0.08/0.29/0.93	0.00/1.00/1.75	177/838/1637	0.16/0.98/1.50	15/47/86	156/777/1767		200		1	262	463
<i>Betula pendula</i>	Bp	2-03	0.53	0.08/0.25/0.84	0.19/1.15/1.76	160/450/1504	0.09/0.68/1.47	15/28/86	400/687/1900	314	4	208		2	528
<i>Betula pubescens</i>	Bu	1-85	0.53	0.07/0.13/0.24	0.44/0.98/1.41	160/216/309	0.09/0.80/1.06	15/24/31	444/1210/1900	214					214
<i>Carpinus betulus</i>	Cb	3-97	0.71	0.08/0.19/0.65	0.00/0.82/1.50	184/764/1399	0.25/0.92/1.47	16/39/72	222/581/978		79	12	892	2	985
<i>Castanea sativa</i>	Cs	3-15	0.52	0.01/0.19/0.67	0.00/0.92/1.62	189/293/519	0.00/0.71/1.54	14/23/32	211/838/1356		549				549
<i>Fagus sylvatica</i>	Fs	4-56	0.59	0.07/0.27/0.93	0.00/0.92/2.15	184/937/1637	0.00/0.81/1.50	14/48/86	156/598/1767	1	634	4	1	531	1171
<i>Fraxinus excelsior</i>	Fe	2-66	0.56	0.08/0.27/0.92	0.00/1.04/1.85	177/722/1291	0.00/0.84/1.50	14/38/76	156/673/1767		427		3	3	433
<i>Ostrya carpinifolia</i>	Oc	3-94	0.67	0.08/0.14/0.67	0.00/0.93/1.60	163/283/519	0.36/0.79/1.54	11/20/32	289/931/1356		565				565
<i>Picea abies</i>	Pa	4-45	0.37	0.07/0.24/0.82	0.00/0.97/2.22	160/513/1637	0.00/0.69/1.50	15/37/86	156/828/1900	874	276		474	299	1923
<i>Pinus nigra</i>	Pn	2-10	0.41	0.05/0.22/0.63	0.00/1.12/2.77	44/178/356	0.00/0.54/1.17	11/24/39	244/788/1289						511
<i>Pinus sylvestris</i>	Ps	1-67	0.42	0.04/0.25/0.88	0.00/1.08/2.26	44/353/1399	0.00/0.63/1.47	11/30/72	244/778/1900	672			250	1	1288
<i>Quercus cerris</i>	Qc	2-55	0.70	0.08/0.23/0.55	0.00/1.07/1.90	163/439/833	0.00/0.76/1.54	11/26/39	211/757/1189		404				404
<i>Quercus faginea</i>	Qf	3-02	0.85	0.02/0.12/0.48	0.00/0.93/1.79	20/164/277	0.00/0.45/1.17	5/20/33	244/1244/2556						1158
<i>Quercus ilex</i>	Qi	3-02	0.82	0.01/0.16/0.75	0.00/0.86/1.73	9/202/833	0.00/0.67/1.54	4/18/39	244/823/1489		107	410	8	426	836
<i>Quercus petraea</i>	Qp	2-73	0.56	0.08/0.31/0.82	0.00/1.14/1.97	189/522/1291	0.11/0.82/1.54	14/31/63	267/708/1189			302			417
<i>Quercus robur</i>	Qr	2-45	0.56	0.08/0.36/0.95	0.00/1.15/1.73	485/810/1399	0.13/1.05/1.47	27/42/72	222/603/778		1		232		233

*Shade tolerance from Ninemets & Valladares (2006), see also Appendix S1.

†Sources for wood density were found in Zanne *et al.* (2009).

used to calculate the live-crown length (*lcl*; m) of each tree. The mean squared crown radii were used to calculate the crown projection area (*cpa*; m²) of each tree. The position of each tree within the canopy (social status) was defined in terms of its relative height (*rh*) which was calculated as *h*/mean plot height. A total of 12 939 trees were measured including 12 005 trees that were target species.

STAND-LEVEL VARIABLES

Two stand variables were calculated to examine the effects of competition and tree-species diversity on allometric relationships. Tree-species diversity was quantified using Shannon's index, *S* (Shannon 1948), which was calculated based on all the target species within a plot using eqn 2.

$$S = - \sum_{j=1}^n \frac{BA_j}{BA_T} \ln \left(\frac{BA_j}{BA_T} \right) \quad \text{eqn 2}$$

where *BA_j* is the basal area of species *j* within the given plot, *BA_T* is the total basal area of the plot and *n* is the number of species in the plot.

Species identity, stand density, age and site quality were collectively considered using competition indices (*CI*) (eqn 3).

$$CI = \begin{cases} \sum_{i=1}^n ba_i & (3a) \\ \sum_{i=1}^n ba_i \times \rho_j & (3b) \\ \sum_{i=1}^n d_i^2 \times h_i \times \rho_j & (3c) \\ \sum_{i=1}^n d_i^2 \times h_i \times \text{Shade tolerance}_j & (3d) \end{cases} \quad \text{eqn 3}$$

where *ba_i* is the basal area of tree *i* (m²), *n* is the number of trees within the plot, *ρ_j* is the wood density (oven dry mass per fresh volume; g cm⁻³) of species *j*, and *Shade tolerance_j* is the shade tolerance value assigned to species *j* by Niinemets & Valladares (2006) (Table 1). The *CI*s were divided by the plot area (in ha) to express them on a per hectare basis. The sources of wood density and shade tolerance data are described in detail in Appendix S1, Supporting Information. In eqn 3a, the basal area is used to account for the combined effects of stand density, site quality and age, similar to the approach of Stout & Nyland (1986). The species-specific wood density was used to quantify the competitive ability of a given species. This is based on the fact that it is related to many structural and functional characteristics of trees and is a key variable of the hypothesized wood economics spectrum (Chave *et al.* 2009; Hoffmann *et al.* 2011). Furthermore, wood density and wood strength have been shown to correlate with interspecific differences in tree-level allometry (Dietze, Wolosin & Clark 2008; Ducey 2012) and stand-level allometry (Woodall, Miles & Vissage 2005; Ducey & Knapp 2010), although no significant effect was found in Spanish forests (Lines *et al.* 2012). We assumed that if wood density is useful for explaining differences in allometric relationships, it may also be useful for predicting the competitive ability of different species, such that for a given individual tree diameter, a species with a higher wood density is more competitive (Kunstler *et al.* 2012, 2016; Lasky *et al.* 2014).

The use of basal area in eqn 3a is assumed to reflect the 'current' competitive intensity in relation to leaf area or sapwood area and hence light absorption, transpiration and metabolic activity. The replacement of basal area with *d*²*h* (eqn 3c) is more closely related to tree biomass and is assumed to reflect its previous productivity and the 'cumulative' competitive effects it has been exposed to. Since the allometric relationships develop over time, the retrospective competition indices are assumed to be more appropriate than those that reflect only the current situation.

The use of wood density as an index of an ecophysiological process such as biomass partitioning should be done cautiously and in eqn 3d, wood density was replaced by shade tolerance. Shade tolerance is a measure of the ability of a species to withstand competition for light (Niinemets & Valladares 2006) and also depends on the response of trees to competition for soil resources (Coomes & Grubb 2000). To absorb more light, intolerant species are more likely to allocate carbon to height growth while the allocation of shade tolerant species may be more towards lateral growth (Givnish 1988; Chen, Klinka & Kayahara 1996). It was assumed that shade tolerance is also a measure of competitive ability (for a given *d*). Shade tolerance and wood density were not correlated for the species in our study (*P* = 0.95) or for 86 species in the northeastern United States (*P* = 0.88; Ducey 2012). No shade tolerance values were available for some species, including one target species (*Quercus faginea*). The shade tolerance of *Q. ilex* was used for *Q. faginea* because these species are considered to have a similar shade tolerance (Sánchez-Gómez, Valladares & Zavala 2006). The mean shade tolerance of the other 16 target species was allocated to 116 trees (out of 12 939) of species with no shade tolerance values when calculating the competition indices.

ALLOMETRIC RELATIONSHIPS

To examine how allometric relationships were modified by competition, tree-species diversity, tree size and tree dominance, the *cpa*, *h* and *lcl* of each species were described as functions of tree variables (*d*, *rh*), stand variables (*CI*, *S*) and two-way interactions (eqns 4.1 and 4.2):

$$\ln(Y) = \beta_0 + \beta_1 \ln(d) + \beta_2 rh + \beta_3 \ln(CI) + \beta_4 \ln(S) + \beta_5 \ln(S) \times \ln(CI) + \beta_6 \ln(d) \times \ln(CI) + \beta_7 \ln(d) \times \ln(rh) + \varepsilon \quad \text{eqn 4.1}$$

where *Y* is either *cpa* or *lcl*. For some species the *cpa* or *lcl* were ln-transformed to linearize relationships and to reduce heteroscedasticity. When *Y* = *h*, the *rh* was not included in the model because they are automatically correlated:

$$\ln(Y) = \beta_0 + \beta_1 \ln(d) + \beta_3 \ln(CI) + \beta_4 \ln(S) + \beta_5 \ln(S) \times \ln(CI) + \beta_6 \ln(d) \times \ln(CI) + \varepsilon \quad \text{eqn 4.2}$$

For both equation variants 4.1 and 4.2, $\varepsilon \sim N(0, \sigma)$, and $\forall k \in [1, 4]$, $\beta_k = \alpha_k + a_{k,j}$ where α_k is the fixed part of the parameter β_k , and a_k is the random component, $a_{k,j} \sim N(0, \sigma_k)$, at the level of the region *j* when the given species was common (>100 trees) in more than one region, or at the level of the plot *j* when it was only common in one region but *CI* was not significant in the model; when *CI* was significant we assumed that it accounted for the plot effects and did not include any random effects. All parameters were fixed when neither region nor plot were significant: $\forall k \in [1, 4]$, $\beta_k = \alpha_k$.

None of the 17 target species occurred in all six regions and most were common (>100 trees) only in one or two regions; only *P. abies* and *P. sylvestris* were common in three regions (Table 1). When fitting eqns 4.1 and 4.2 for a given species, data were not included for regions with less than 100 trees of that species. To obtain the final allometric equations, equations with all possible combinations of variables (Table S2), including the full model (eqns 4.1 and 4.2), were compared. The final models were obtained after removing all variables that were insignificant (*P* > 0.05) and selecting those with the lowest AIC values and highest *R*² values. All analyses were performed using R software version 3.2.1 (R Core Team, 2015).

Our approach is similar to the mixed-effects modelling approach used by Ducey (2012). An alternative approach to eqns 4.1 and 4.2 would have been to fit, for each individual plot, the variables *cpa*, *h* or *lcl* as functions of only diameter and then examine how β_1 varies with relative height, competition index and Shannon's index (e.g., Franceschini & Schneider 2014). However, assuming that this would require at least five trees per plot per species, 30% of the 696 species-plot combinations would have been excluded from the analyses. The approach of eqns 4.1 and 4.2 also allows all variables to be included simultaneously, including the two-way interactions with diameter, which would not be possible using the alternative approach.

The models fitted to eqns 4.1 and 4.2, which do not directly include the species identity of the trees that are competing with the target tree, were compared with models where the actual species composition (e.g., '*F. sylvatica*' or '*F. sylvatica*+*P. abies*' or '*F. sylvatica*+*P. abies*+

P. sylvestris' ...) is specified as a categorical variable in eqn 5, and where Region was included as a random variable. These comparisons were only made for crown projection area and height of the three most abundant species, *F. sylvatica*, *P. abies* and *P. sylvestris* to reduce the probability that the result was affected by the sample size.

$$\ln(Y) = \beta_0 + \beta_1 \ln(d) + \beta_2 \text{composition} + \beta_3 \ln(d) \times \text{composition} + \varepsilon \quad \text{eqn 5}$$

where $\forall k \in [1,3]$, β_k are fixed-effect parameters, and $\varepsilon \sim N(0, \sigma)$.

The predictions from eqns 4.1 and 4.2 and eqn 5 were compared using the relative average error (average bias, *e%*, eqn 6), the relative mean absolute error (MAE%, eqn 7) and the mean square error (MSE, eqn 8) (Janssen & Heuberg 1995; Vanclay & Skovsgaard 1997):

$$e\% = 100 \frac{\bar{P} - \bar{O}}{\bar{O}} \quad \text{eqn 6}$$

$$\text{MAE}\% = 100 \frac{((\sum_{i=1}^n |P_i - O_i|)/n)}{\bar{O}} \quad \text{eqn 7}$$

$$\text{MSE} = \frac{\sum_{i=1}^n (P_i - O_i)^2}{n} \quad \text{eqn 8}$$

where *O* are the observed crown projection areas or heights and *P* are the predicted values from eqns 4.1 and 4.2 or eqn 5, and \bar{O} and \bar{P} are the means.

SENSITIVITY COMPARISONS

Equations 4.1 and 4.2 was used to compare the relative sensitivity to the independent variables by computing the predicted crown projection area, height or live-crown length based on the estimated fixed-effect parameters. For each species, the sensitivity was estimated by computing the changes in the predicted values caused by changing one independent variable by one standard deviation while the other independent variables were kept constant and equal to the observed mean value for the given species. Changes are expressed as a percent change compared with predictions where all parameters are equal to their observed means.

Results

COMPETITION EFFECTS ON ALLOMETRY

The competition indices calculated using eqn 3 were often correlated with crown-projection area, height and live-crown

length, however, the strength of the correlations varied between species. The strength of the correlations was generally lowest for the index when based only on basal area and was marginally higher when using the product of basal area and wood density (Fig. S1). A larger improvement in the strength of correlations was achieved when basal area was replaced with d^2h . There was a minor further improvement in the correlations when wood density was replaced with shade tolerance in the d^2h -based competition indices (Fig. S1). Therefore, due to the greater difficulty in quantifying shade tolerance than wood density (Appendix S1), the wood density index of eqn 3c was used for all of the following analyses.

The allometric equations developed for the 17 target species to predict crown-projection area, height and live-crown length are shown in Table S3 (see also Figs. S2–S5). The statistics used to select these from the full list of variants of eqns 4.1 and 4.2 are provided in Table S5. The competition index was significant in most of these allometric equations (42 of 51). Overall, the influence of competition on the crown-projection area and the live-crown length was second to diameter (Fig. 1; Table S6), indicating that it is important to include it in the equations.

Increasing competition decreased the crown-projection area and increased height and live-crown length for most species, but the opposite patterns were also observed for a minority of species (Fig. 1). The interspecific variability in responses of crown projection area and live-crown length to competition was related to the wood density of the target species. This effect was quantified as the change in crown projection area and live-crown length in response to a change in the mean competition index (as measured in forests containing the given target species, Table 1) by one standard deviation, while all other variables were kept constant at their means for the given species. When competition increased, the crown projection area of species with the lowest wood density was reduced by about 15%, but this negative effect of competition declined as the wood density increased such that the species with the highest densities actually had even a minor increase in crown projection area (Fig. 2a). In response to the increase in competition, there was a negligible reduction in live-crown length for species with low wood density, but species with higher wood density increased their live-crown length by nearly 10% (Fig. 2c). In contrast, the response of height to competition was not correlated with wood density and none of the responses of crown projection area, height and live-crown length to competition were correlated with the shade tolerance of the target species ($P > 0.05$, data not shown). There were no correlations between the crown projection area, height or live-crown length responses to competition (or to relative height or Shannon's index; $P > 0.05$).

EFFECTS OF RELATIVE HEIGHT ON TREE ALLOMETRY

The relative height of a tree had a large influence on the live-crown length for all species, such that more dominant trees (higher relative height) had significantly longer crowns (Fig. 1k). Across all species the mean size of this effect

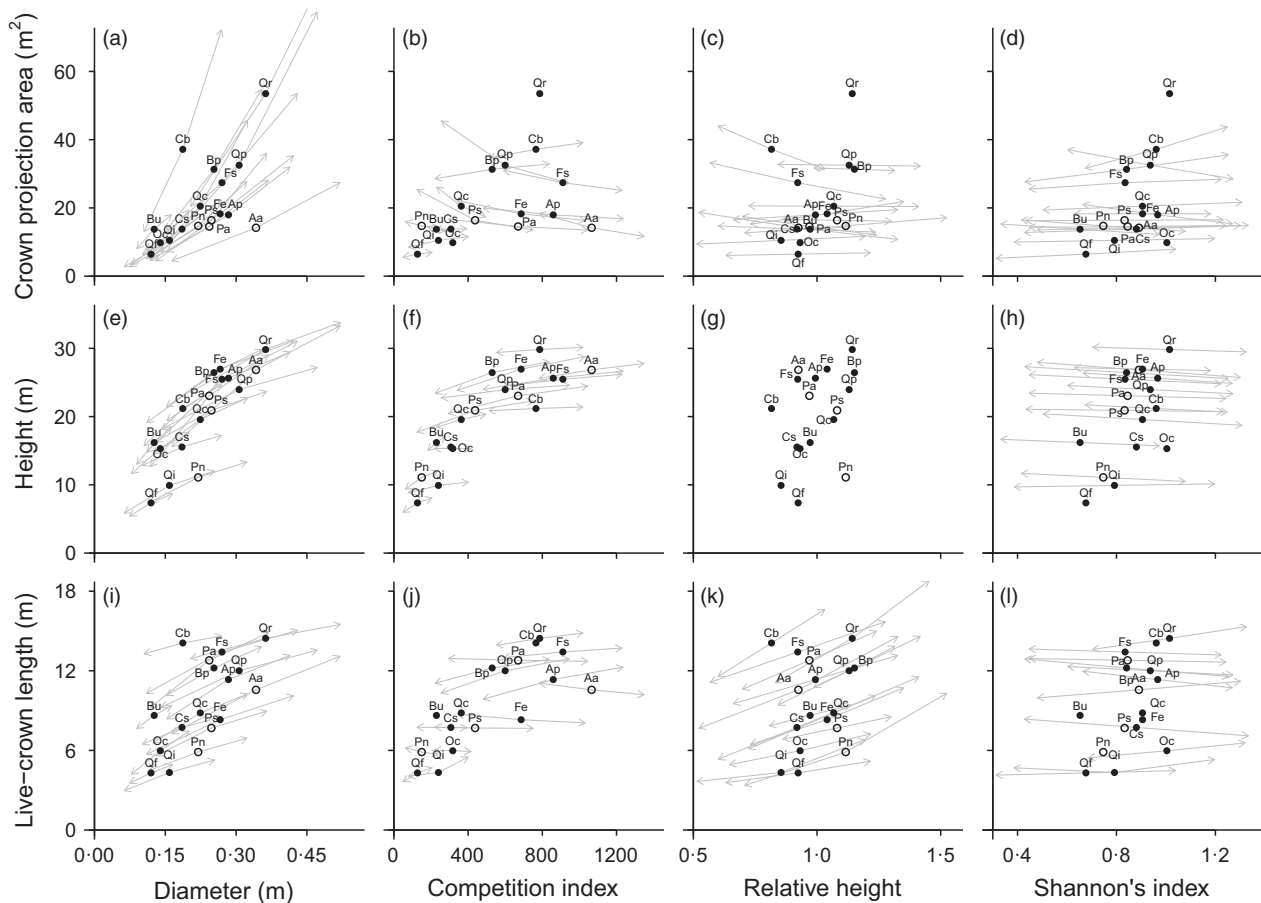


Fig. 1. Predicted changes in crown projection area (a–d), height (e–h) or live-crown length (i–l) in response to changes in diameter (a, e, i), competition index calculated using eqn 3c (b, f, j), relative height (c, g, k) and Shannon's index (d, h, l). The points represent the mean values for each species across all sites (Table 1) and the grey arrows show the predicted changes (based on models in Table S3) in these variables with a one-standard deviation increase or decrease in diameter, competition, relative height or Shannon's index when all other variables that are not on the respective *x*- or *y*-axes are kept constant at their means for the given species. The absence of grey lines indicates no effect; relative height was not included in height equations but means are shown for consistency. The letters in the graph indicate the species using the species codes in Table 1. Open circles are conifers and closed circles are broadleaved species.

(23%) was even greater than that of tree diameter (18%; Table S6) and occurred for 14 out of the 17 species. Since all species showed a similar live-crown length response to changes in relative height, there were no significant relationships between these responses and the wood density or the shade tolerance of each target species ($P > 0.05$, data not shown). In contrast, the relative height of a tree had only a minor, although significant, influence on the crown projection area of most species (Fig. 1c), but this response was correlated with the shade tolerance of the given target species (Fig. 3).

EFFECTS OF TREE-SPECIES DIVERSITY ON ALLOMETRY

Averaged across all 17 target species, tree-species diversity had the smallest effect on crown projection area, height and live-crown length of all the explanatory variables (Table S6), although it was significant in 38 of the 51 allometric equations fitted in Table S3. The interaction term between Shannon's index and the competition index was often significant but weak.

The crown projection area and live-crown length responses to tree-species diversity were variable (Fig. 1d,l) and not related to the species-specific wood density or shade tolerance ($P > 0.05$, data not shown). The response of height to diversity was more consistent, such that height generally decreased with increasing diversity (Fig. 1h), and the size of this change was correlated with the species' wood density (Fig. 2b). For species with the highest wood density there was no predicted change in height, but for the lowest wood density species, the height was predicted to decline by about 3% (Fig. 2b).

To examine whether large-diameter and small-diameter trees respond differently to changes in Shannon's index, the relative response (as a percent) of the small trees to a change in Shannon's index was subtracted from that of large trees and regressed against wood density or shade tolerance. A positive value means that changes in Shannon's index influenced large trees relatively more than small trees. Large and small trees were defined as having a diameter equal to the mean diameter (for the given species) plus or minus one standard deviation, respectively. This relationship was significant for height in relation to wood density (Fig. 4). The response to

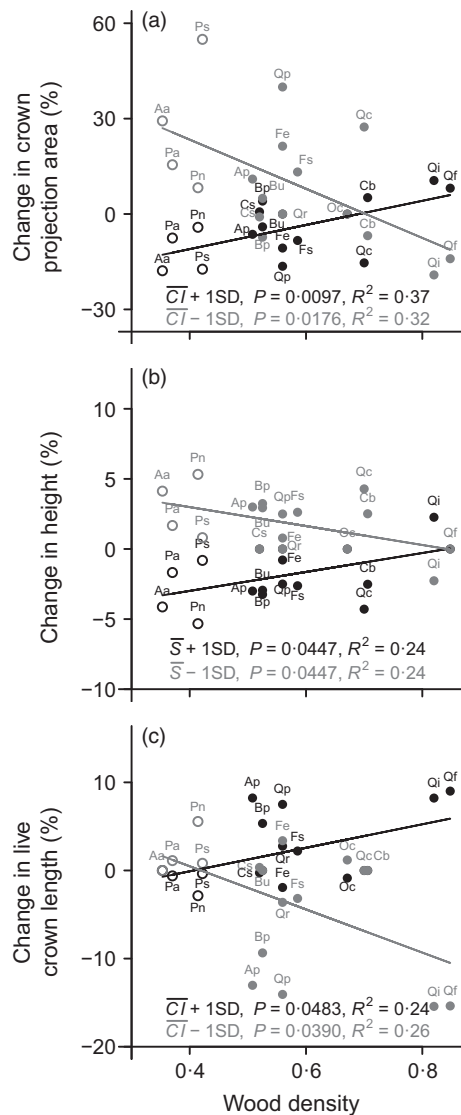


Fig. 2. Percent changes in (a) crown-projection area, (b) height, or (c) live-crown length in response to an increase (black points/text) or decrease (grey points/text) by one standard deviation ($\pm 1SD$) in competition index (CI) calculated using eqn 3c (a, c) or Shannon's index (S , b) compared with the mean values for the given species shown in Table 1. The predictions in (a), (b) and (c) are based on those in Fig. 1b, h, j, respectively. The letters in the graph indicate the species using the species codes in Table 1. Open circles are conifers and closed circles are broadleaved species.

changes in Shannon's index was about 5% greater for large trees than small trees for species with low wood density, but there was very little difference for species with high wood density. There were no other clear differences between large trees and small trees for crown projection area, height or live-crown length in response to competition, relative height or Shannon's index.

COMPARISON OF GENERAL EQUATIONS WITH COMPOSITION-SPECIFIC EQUATIONS

The equations based on eqn 4-1 and 4-2 were compared with those that contain stand species composition (as a categorical

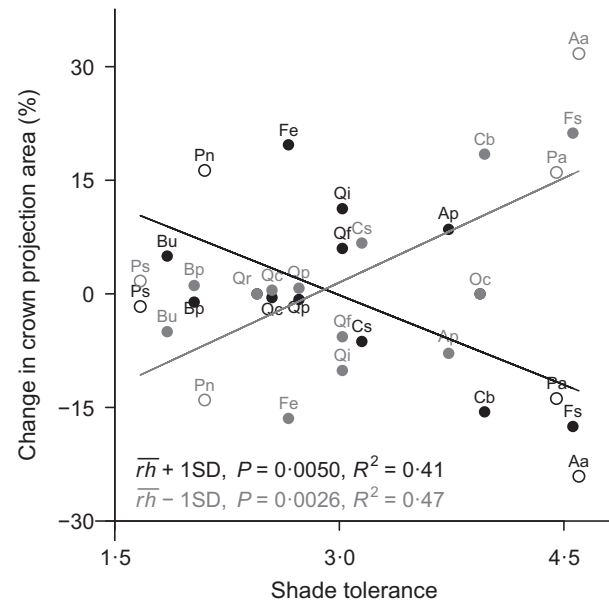


Fig. 3. Changes (%) in crown-projection area in response to an increase (black points/text) or decrease (grey points/text) in relative height (rh) by one standard deviation ($\pm 1SD$) from the mean relative height for the given species as shown in Table 1. These predictions are based on those in Fig. 1c. The letters in the graph indicate the species using the species codes in Table 1. Open circles are conifers and closed circles are broadleaved species.

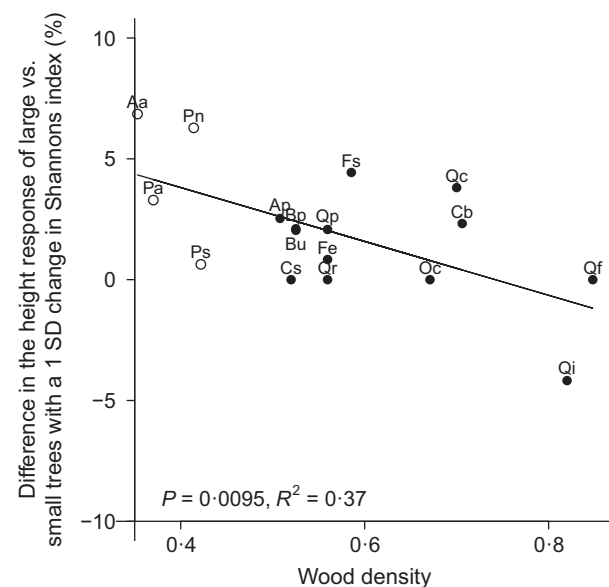


Fig. 4. The difference in the height response of large trees to a change in Shannon's index by one standard deviation compared with that of small trees, as a function of wood density. Positive values indicate that changes in Shannon's index influenced large trees relatively more than small trees. Large and small trees were defined as those with a diameter equal to the mean diameter of the given species plus or minus one standard deviation (SD), respectively. The letters in the graph indicate the species using the species codes in Table 1. Open circles are conifers and closed circles are broadleaved species.

factor, eqn 5) instead of the competition index, relative height and Shannon's index. This was done for crown projection area and height of the three most abundant species in the data

set: *P. abies*, *P. sylvestris* and *F. sylvatica*. Generally, the composition-specific equations had lower bias, although the bias was low for each type of equation (Table S7). The RMSE and R^2 were generally very similar for each equation type. Based on this data set of 17 species from six regions across Europe with a wide range of species compositions and structures, the most important variables and interactions to include in allometric equations are diameter, competition index, relative height and the interactions between diameter and the competition index and diameter and relative height. A set of equations for each species was developed using these variables (Table S4).

Discussion

The allometric functions to predict crown projection area, height and live-crown length varied greatly between species, as did the effects of relative height, competition and, to a lesser extent, tree-species diversity. This is consistent with other studies reporting interspecific variability in height and crown allometric relationships (Dietze, Wolosin & Clark 2008; Ducey 2012; Lines *et al.* 2012; Franceschini & Schneider 2014). It is also consistent with studies showing that species-specific crown projection area, height or live-crown length allometric relationships varied with competition (Medhurst *et al.* 1999; Thorpe *et al.* 2010; Lines *et al.* 2012) or interspecific interactions (Thorpe *et al.* 2010; Bayer, Seifert & Pretzsch 2013; Dieler & Pretzsch 2013; Pretzsch 2014). This emphasises the fact that allometric relationships in trees are not a static trait for any given species. Instead they represent the response of any individual tree to the growing conditions experienced in the past. Furthermore, the plasticity of these responses varies greatly between species. This study shows that the inclusion of stand structural variables such as competition indices, relative height and Shannon's index in allometric equations can help to account for this large variability in stand densities, vertical structures and species composition, consistent with our first two hypotheses.

COMPETITION EFFECTS ON ALLOMETRIC RELATIONSHIPS

Species growing in stands with higher competition generally had a greater mean height (Fig. 1f). The higher competition indices are likely to represent improvements in soil and climatic conditions. This spatial gradient in height is consistent with other large-scale studies where heights were lower in arid or cold environments, or environments with high climatic seasonality (Wang *et al.* 2006; Feldpausch *et al.* 2011; Banin *et al.* 2012; Lines *et al.* 2012; Hulshof, Swenson & Weiser 2015). It reflects a growth strategy for allocating more carbon below-ground to obtain soil resources at the cost of above-ground (e.g. height) growth (Litton, Raich & Ryan 2007; Poorter *et al.* 2012).

For many species, crown projection area declined with increasing competition, while height and live-crown length

increased, consistent with other studies of crown projection area (Thorpe *et al.* 2010; Lines *et al.* 2012; Dieler & Pretzsch 2013), height (Lines *et al.* 2012) and live-crown length (Medhurst *et al.* 1999). However, for a minority of species (*Betula pendula*, *Carpinus betula*, *Q. ilex* and *Q. faginea*) the opposite response of crown projection area to competition was observed. This variability in the relative response sizes of crown projection area and live-crown length were related to the species' wood density, consistent with our third hypothesis. As wood density increased, the crown projection area response to increasing competition went from about a 15% reduction in crown projection area to a minor increase in crown projection area. In addition, with increasing wood density, the live-crown length response went from a very small reduction to an increase in nearly 10% for the highest-wood-density species. Several studies have shown that interspecific differences in height and crown allometric relationships are related to wood density, wood strength or shade tolerance (Dietze, Wolosin & Clark 2008; Ducey 2012), and this study found that interspecific differences in responses to competition can also be related to wood density or possibly other species traits related to wood density. This pattern also indicates that wood density may indeed be a useful indicator of competitive ability because species with higher wood density responded to increased competition by developing larger crowns while lower-wood-density species developed smaller crowns. However, in addition to crown dimensions, the competitive ability would also depend on crown density (e.g. leaf area per unit of crown volume), for which we have no information.

Regardless of wood density, many of the responses to competition, particularly for crown projection area, were large, indicating that competition can be an important explanatory variable in these allometric relationships, consistent with our first hypothesis. For example, the mean effect of a change in competition by one standard deviation was a 12% change in crown projection area and the maximum was a 55% increase in crown projection area for *P. sylvestris* when competition decreased by one standard deviation. Ignoring this competition effect could result in biased predictions of the crown projection area in *P. sylvestris*. More general equations that do not include competition as an explanatory variable are useful for broader scale uses (Paul *et al.* 2013; Chave *et al.* 2014). However, these are less useful when examining the effects of stand structure or species composition on allometric relationships in trees or on forest functions that are predicted using allometric relationships (e.g., biomass production, carbon sequestration, transpiration).

RELATIVE HEIGHT EFFECTS ON ALLOMETRIC RELATIONSHIPS

The relative height of a tree had little influence on the crown projection area of most species but it had a large positive effect on live-crown length for all species. The live-crown length of target trees also increased as the height of neighbouring trees decreased (i.e. relative height) in sub-boreal

mixed-species forests in Canada (Thorpe *et al.* 2010) because taller trees have more of their crown above the minimum light level within the canopy that defines the light compensation point of the given species.

The effect of relative height on crown projection area was related to the shade tolerance of the species, such that less tolerant species increased crown projection area as relative height increased while tolerant species actually reduced crown projection area as relative height increased. This pattern is consistent with the changes in crown architecture of some shade tolerant species as they shift from overtopped to overtopping positions within canopies. For example, the most shade tolerant species in this study, *Abies alba* and *F. sylvatica* develop flatter (sometimes umbrella-shaped) crowns when growing under a forest canopy, but then develop narrower crowns as they become more dominant and allocate more to height growth (Givnish 1988). In contrast, the less shade tolerant species are not capable of surviving for prolonged periods below the canopy, let alone developing wide crowns to avoid self-shading in these positions, and may be more likely to widen their crowns only after overtopping their neighbours or growing into a gap in the canopy.

The relative height had an even larger effect (mean of 23% with one standard deviation change in relative height) on live-crown length than tree diameter (mean of 18%). Therefore, while the competition index helped to account for the stand density component of stand structure, the relative height was important for quantifying the vertical structure of the stand for individual trees. The largest effect of an increase in relative height by one standard deviation occurred for *P. nigra*, where live-crown length increased by 75% (for a given diameter). Therefore, allometric equations that are used to examine the effects of vertical stand structure and dominance (and age) on forest functions likely require a variable like relative height, at least for some species.

TREE-SPECIES DIVERSITY EFFECTS ON ALLOMETRIC RELATIONSHIPS

Tree-species diversity generally had a smaller effect on allometric relationships than competition or relative height (2–8% vs. 4–23%; Fig. 1, Table S6). Tree-species diversity was also found to have a lower effect on growth than basal area and climate in European forests (Vilà *et al.* 2013). Nevertheless, despite its smaller effect, diversity was significant in 39 out of 51 of the allometric models.

The crown projection area increased with diversity for ten of the 17 species, decreased for four species and did not change for three species. This variability is consistent with other studies where crown projection area, in response to the species mixing, increased (Thorpe *et al.* 2010; Bayer, Seifert & Pretzsch 2013; Dieler & Pretzsch 2013; Pretzsch 2014) or did not change (Forrester & Albrecht 2014; Guisasaola *et al.* 2015). An increase in crown projection area in response to mixing may result when each species can occupy a slightly different layer within the canopy so crowns can spread sideways more than they can in monocultures, where a higher proportion of trees may occupy the same layer, or when interspecific differences in crown

architecture or intraspecific crown plasticity allows each species to fit into the mixed-species canopy without competing for the same space as conspecific trees in a monospecific canopy (Bauhus, van Winden & Nicotra 2004; Forrester & Albrecht 2014; Sapijanskas *et al.* 2014; Jucker, Bouriaud & Coomes 2015). An improvement in the packing of the crowns within the canopy or an increase in canopy volume can result in increased tree- and stand-level light absorption, respectively, in the mixtures (Forrester & Albrecht 2014; Sapijanskas *et al.* 2014). For example, in *P. abies* and *A. alba* mixtures, 10% increases in crown projection area and live-crown length were predicted to increase individual tree light absorption by about 5% and 10%, respectively (Forrester & Albrecht 2014). Conversely, the reduced crown projection area with increasing diversity for some species, suggests that those species were less competitive, and may have occupied similar layers, to the species that they were mixed with.

For a given diameter, trees in more diverse forests were shorter. This does not mean that trees were generally shorter in diverse stands, but they had a higher stem taper for a given height in diverse stands. This is consistent with the increase in crown projection area for the majority of species; for a given diameter, trees with larger crowns tend to have greater stem taper (or lower height to diameter ratios) (Lindén & Ågestam 2003; Bauhus, van Winden & Nicotra 2004; Forrester, Bauhus & Khanna 2004; Erickson, Harrington & Marshall 2009). The effect on tree height of increasing diversity by one standard deviation was related to the wood density of the species, such that height was 5% lower for low-wood-density species (e.g., *A. alba*, *P. nigra*) and was not changed or slightly increased for high-wood-density species (e.g., *Q. faginea*, *Q. ilex*). It is important to note that past management might also have influenced these results. While the stands had generally not been managed for about two decades or so prior to this study, some of the crown architectural and stand structural characteristics would have developed prior to the recent period without management. The effects of tree-species diversity may therefore be confounded with previous silvicultural management which often varies with species composition and productivity. However, these influences of past management could not be quantified for this study.

USING COMPETITION INDICES TO ACCOUNT FOR STAND STRUCTURAL EFFECTS ON ALLOMETRIC RELATIONSHIPS

The responsiveness of trees to intra- and interspecific competition, as shown in this study, confirms that allometric equations developed for a specific stand density or species mixture may not be representative or applicable to other stand structures (Forrester & Pretzsch 2015). Conversely, allometric equations developed using trees from a wide range of stand structures but without variables that consider the stand structure, may be inappropriate for quantifying the effects of stand structure on forest functioning. The competition indices used as a proxy for stand structure were significant in 44 of the 51 allometric equations in Table S3 and the mean size of the

competition effect was usually second only to that of the tree diameter in the equations predicting crown projection area and height. This facilitated the development of species-specific allometric equations that could be applied to monocultures or mixtures with many other species, as well as forests within a wide range in stand density. Alternative allometric equations that directly specified the species composition (instead of using a competition index) were not necessarily better. This may be attributable to the inclusion of diameter, which was the most important variable in equations predicting crown projection area and height, in both types of equation. Even when composition-specific equations provide slightly better fits than those using a competition index (and relative height or Shannon's index), they are restricted to a given set of species compositions, whereas the equations developed in this study can be applied to a much broader range of species compositions and stand structures.

An advantage of the composition-specific equations often developed for mixed-species stands (e.g., Laclau *et al.* 2008; Dieler & Pretzsch 2013) is that they will account for the combined effect of all types of interspecific interactions; competition, competitive reduction and facilitation (for definitions see Vandermeer 1989). In contrast, the competition indices in the more general equations developed in this study should account for competition but will only account for facilitative or competitive reduction interactions if those effects are positively correlated with the competition index or Shannon's index. Therefore, these general equations may not be as useful in stands with large positive complementarity effects (e.g., symbiotic nitrogen fixation) unless an additional variable is added to account for this type of complementarity.

The replacement of basal area with d^2h in the competition indices resulted in a much greater improvement in correlations between the index and the response variables height, crown projection area or live-crown length than the addition of wood density as a proxy of competitive ability. This is probably because d^2h integrates the cumulative growth radially as well as in height.

As an alternative to wood density, shade tolerance may provide a better representation of a species' physiology and ability to withstand competition but its addition to the indices provided only marginal improvements in their correlations with height, crown projection area or live-crown length. Shade tolerance was also found to have little influence on interspecific differences in allometric height relationships in data sets containing 86 species from the northeastern United States (Ducey 2012) or 293 species across the United States (Hulshof, Swenson & Weiser 2015), while wood density was correlated with height allometry (Ducey 2012). Shade tolerance may therefore be a less useful variable. In addition, it is difficult to quantify shade tolerance without masking plant plasticity and ontogenetic variation (Hulshof, Swenson & Weiser 2015). Since many traits, including wood density and shade tolerance, are not static for a given species and vary with factors such as ontogeny (Erickson & Harrison 1974; Bouriaud *et al.* 2004; Valladares & Niinemets 2008; Deng *et al.* 2014; Niinemets 2015), improved indices might be

obtained if alternative variables are found that better describe interspecific differences in competitive ability.

Allometric relationships and biomass partitioning can also vary with soil resource availability (Litton, Raich & Ryan 2007; Poorter *et al.* 2012). In this study, there was little variability in soil properties within a given region (Baeten *et al.* 2013). While the competition index should account for some of the site effects, it would be sensible to test this approach using sites with a range in soil resource availability.

In conclusion, allometric relationships to predict crown projection area, tree height and live-crown length were significantly influenced by stand structure and composition, which were expressed by attributes such as competition, relative height and tree-species richness. The interspecific differences in the response to these stand attributes were sometimes related to the wood density or shade tolerance of tree species. This study shows that for a given species general allometric equations can be developed for mixed-species forests that do not require the species composition to be directly included in the equation. The approach presented here allows a single equation to be applied in a wide range of stand structures and species compositions. Stand structure is likely to be an important consideration for allometric relationships that are used in studies to examine how stand density, species mixing and tree social status influence ecosystem functions.

Authors' contributions

D.I.F. and A.B. conceived the ideas and designed methodology; A.B. and O.B. collected the data; D.I.F. and A.B. analysed the data; D.I.F. led the writing of the manuscript. D.I.F., A.B., O.B. and J.B. all contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.234> (Zanne *et al.* 2009) FunDivEUROPE online data portal (FunDivEurope; <http://fundiv.befdata.biow.uni-leipzig.de/>). See also Baeten *et al.* (2013).

Plot data:

Plot descriptors Finland: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/67>

Plot descriptors Germany: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/82>

Plot descriptors Italy: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/68>

Plot descriptors Poland: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/69>

Plot descriptors Romania: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/66>

Plot descriptors Spain: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/70>

Tree data:

Exploratory plot descriptors - tree data - Finland: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/59>

Exploratory plot descriptors - tree data - Germany: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/76>

Exploratory plot descriptors - tree data - Italy: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/73>

Exploratory plot descriptors - tree data - Poland: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/71>

Exploratory plot descriptors - tree data - Romania: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/65>

Exploratory plot descriptors - tree data - Spain: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/74>

Stem quality data for all exploratory plots: <http://fundiv.befdata.biow.uni-leipzig.de/data/sets/366>

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Wood density and shade tolerance.

Table S1. Average wood density values of species used in our study with sources.

Table S2. Different combinations of explanatory variables tested when fitting Equation 4.

Table S3. Statistics for the final models for *h*, *cpa* and *lcl*.

Table S4. Statistics for models for *h*, *cpa* and *lcl* that do not include Shannon's index.

Table S5. The full list of all models tested and their statistics.

Table S6. Size of stand structural effects on *h*, *cpa* and *lcl*.

Table S7. Comparison between composition-specific models and those based on Equation 4.

Fig. S1. Frequency distributions of statistics describing *CI* – *h*, *cpa* and *lcl* relationships.

Figs. S2–S5. Effects of stand variables on *d* – *h*, *cpa* and *lcl* relationships for each species.