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Tree allometry variation in response to intra- and inter-specific competitions

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Abstract

Key message **Crown, height and stem allometry vary with stand density and species composition, the plasticity in response to inter- and intra-specific competitions being related to species shade tolerances.**

Abstract Determining the way in which variability in tree allometry is modulated by intra- and inter-specific competitions in different species and stand compositions is of particular interest for forest modelling and practice. In this study, we explore this variability by developing models for tree crown diameter, total height and diameter at a height of 4 m, which include intra- and inter-specific competition terms. More than 19,000 Scots pine, silver fir, sessile oak and European beech trees from 4711 sample plots belonging to the Spanish National Forest Inventory were included in the study, covering both monospecific and two species mixed stands in Northern Spain. Trees growing under conditions of high competition displayed narrower crowns, greater heights and less taper for a given tree diameter, the plasticity in crown and height in response to intra-specific competition being related to species shade tolerance. The inter-specific competition effect on crown diameter and height was related to the difference in shade tolerance between the two species of the mixture, while stem taper did not exhibit this pattern. These results suggest that trees in mixed stands indeed show a modified allometry, which might be related to complementary resource acquisition strategies. The large variability observed in tree allometry indicates the need to consider both intra- and inter-specific competitions in allometric models.

Keywords Species interactions · Competition reduction · Crown plasticity · Height–diameter relationship · Stem tapering

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Introduction

Tree allometry, i.e. the relationship between the sizes of tree components, not only has an important influence on stand structure, dynamics and the competitive performance of trees, but it is also determined by them (Pretzsch 2014). Tree allometry is generally expressed in the form $Y = a \cdot X^b$, where X and Y are sizes of tree components, parameter a is the scaling coefficient and b is the scaling exponent. Although general scaling theories try to explain overarching scaling exponents between the different plant components (West et al. 1999; Enquist and Niklas 2002; Niklas 2004; Enquist et al. 2007), it is known that there are great inter- and intra-specific variabilities in these exponents (e.g. for tree species see Mäkelä and Valentine 2006; Duursma et al. 2010; Pretzsch and Dieler 2012; Bravo-Oviedo et al. 2014). The intra-specific variability is, in general, influenced by ontogeny, environment, and competition conditions (e.g. Lines et al. 2012; Pretzsch and Dieler 2012; Pretzsch et al. 2013; Poorter et al. 2015;

Forrester et al. 2017a). Both inter- and intra-specific variations in tree allometry have been related to structural and functional traits of species such as wood density or shade tolerance (Dietze et al. 2008; Ducey 2012; Franceschini and Schneider 2014; Forrester et al. 2017b).

Determining the way in which this variability is influenced by tree competition status in different species is particularly important for tree allometry applications in forest practice and modelling (volume and carbon stock estimations, tree growth modelling, upscaling from tree to stand level, etc.). Trees growing under conditions of high competition usually exhibit a smaller crown cross-sectional area, shorter crown depth, greater height and lower taper for a given diameter (e.g. Larson 1963; Mäkelä and Vanninen 1998; Baldwin et al. 2000; Karlsson 2000). However, the plasticity of the tree allometry response to competition varies considerably from one species to another and is also highly dependent on the species composition of the competitors (Thorpe et al. 2010; Lines et al. 2012; Pretzsch 2014; Forrester et al. 2017b). A number of studies have identified significant effects of inter-specific interactions on tree allometry in mixed stands. Most of these studies have focused on crown dimensions–diameter at breast height, and height–diameter allometric relationships (Dieler and Pretzsch 2013; Jucker et al. 2015; Pretzsch 2014; Forrester et al. 2017b), although scarce information exists as regards the effect on stem taper.

Changes in the relative importance of intra- and inter-species interactions in mixtures lead to differences in the performance of mixtures compared to monospecific stands at different scales, i.e. from individual tree to stand level (Forrester and Pretzsch 2015). Temporal and spatial niche complementarity, differential resource partitioning or changes in tree allometry of coexisting species are considered mechanisms affecting both tree and whole stand dynamics (Forrester 2014; Larocque et al. 2013). Species crown and height sizes determine canopy structure and partitioning in mixed stands, as well as light interception and growing conditions (Forrester 2017; Pretzsch 2017). Tree height–diameter ratio and stem taper are closely related to tree stability and to roundwood quality (Pretzsch and Rais 2016). Thus, there is a need for tree allometry models considering neighbour species identity to further our understanding of mixed stand dynamics and to develop forest practice applications.

In this study, we explore the effect of intra- and inter-specific competitions on tree allometry in four temperate species with different traits, *Pinus sylvestris* L., *Abies alba* Mill., *Quercus petraea* (Matts.) Liebl., and *Fagus sylvatica* L., growing in monospecific and two species mixed forest stands in northern Spain. Previous studies undertaken in these forests reported significant differences between monospecific and mixed stands in terms of tree growth and tree mortality, with both greater inter-specific competition and competitive reduction, depending on the identities of the target and competing species (del Río et al. 2014; Condés and del Río 2015). Therefore, we expect that tree allometric relationships may also be influenced by species composition. We hypothesize that tree allometry response to competition is species specific and linked to species traits, and that inter-specific interactions modify tree allometry response to competition. The specific objectives of this study are, therefore: (i) to study how tree allometry (crown diameter, total height and diameter at a height of 4 m in relation to diameter at breast height as an indicator of stem taper) responds to competition in monospecific stands of the studied tree species; (ii) to analyse whether inter-specific competition modifies species-specific tree allometry; (iii) to determine the effect of mixing on crown diameter, height and diameter at 4 m in selected mixtures.

Materials and methods

Data

Data from the second Spanish National Forest Inventory (SNFI) were used. The dataset consists of sample plots located in monospecific and mixed stands of the main temperate species in the Pyrenees and the North Iberian mountain range, in northwest Spain (from 41.57 to 43.28°N, −6.20 to 2.75W). The four studied species exhibit different traits, including shade tolerant and intolerant species (Niinemets and Valladares 2006), wood densities from 0.35 to 0.59 g/cm³ (Zanne et al. 2009) and evergreen conifers and deciduous broadleaves (Table 1). A set of 3976 sample plots were located in monospecific stands of Scots pine (*Pinus sylvestris*), silver fir (*Abies alba*), sessile oak (*Quercus petraea*), and European beech (*Fagus sylvatica*), while 735 sample plots were located in two

Table 1 Studied species traits

	Pinus sylvestris	*Abies alba*	*Quercus petraea*	*Fagus sylvatica*
Wood density (g/cm³)	0.42	0.35	0.56	0.59
Shade tolerance	1.67	4.6	2.5	4.56
Leaf phenology	Evergreen	Evergreen	Deciduous	Deciduous

Mean reference values of wood density and shade tolerance according to Zanne et al. (2009) and Niinemets and Valladares (2006), respectively

species mixtures of these species (Supplementary Table 1). For the purposes of this study, we considered a sample plot to be located in a monospecific stand when the main species represented more than 90% of total basal area, and in a mixed stand when the sum of the basal area of the two species present was greater than 90% of the sample plot basal area. Furthermore, as the distribution areas of monospecific stands are larger than those of mixed stands, monospecific sample plots were only selected if they were located within the same biogeographic region (Rivas-Martínez 2007) as their corresponding mixtures, so that monospecific and mixed sample plots are distributed in areas with similar bioclimatic conditions.

Sample plots from the second SNFI were distributed at the nodes of a one kilometre square grid and consist of four concentric sampling circles with radii of 5, 10, 15 and 25 m, in which the breast height–diameters (d) and heights all trees with d over 7.5, 12.5, 22.5 and 42.5 cm, respectively, were measured. A subsample of four to six sample trees of the main species was selected in each sample plot to measure additional tree variables such as two crown diameters and stem diameter at a height of 4 m. The main stand variables for the selected sample plots, both total and per species (Supplementary Table 1), were estimated from individual tree data weighted according to the area of the concentric subplots. All the subsampled trees from the selected plots were used to study three allometric relationships: crown diameter (cd)—diameter at breast height (d) (cd estimated as the average of the two measured crown diameters); total height (h)—d; and the diameter at a height of 4 m (d_4)—d. A description of the individual tree data for the different species and stand composition are shown in Table 2 and Supplementary Fig. 1–3.

Competition measures

In this study, the stand density index (SDI) (Reineke 1933) and the stand density index of trees larger than the target tree (SDIL) (Pretzsch and Biber 2010) were used as measures of size-symmetric competition and size-asymmetric competition, respectively. SDI is an expression of relative stand density and it characterizes the degree of crowding with reference to standard conditions. Hence, it excludes the normal change in absolute density with increasing stand development. SDIL was derived from the combination of the concepts of SDI and basal area of larger trees (BAL) (Wykoff 1990). Both SDI and SDIL indices have been used previously in individual tree models, which highlights their suitability for studying mixture effects in these stands (del Río et al. 2014; Condés and del Río 2015).

SDI and SDIL were calculated, respectively, for each species according to:

$$\text{SDI} = N\left(\frac{25}{\text{dg}}\right)^{E}, \tag{1}$$

$$\text{SDIL} = N_l\left(\frac{25}{\text{dg}_l}\right)^{E}, \tag{2}$$

where N is the number of stems per hectare; dg is the quadratic mean diameter in centimetres (in both variables including target tree); E is Reineke's maximum stand density exponent; and N_l and dg_l are the number of stems per hectare and quadratic mean diameter of trees larger than the target tree. Species-specific values of E were used instead of the general value proposed by Reineke (1933) when available in the literature. So, for Scots pine the value obtained by del Río et al. (2001) was assumed, $E_{\text{pine}} = -1.75$; for beech the value proposed by Pretzsch and Biber (2005) $E_{\text{beech}} = -1.789$; and for oak and fir the generic figure proposed by Reineke $E = -1.605$.

Intra- and inter-specific competitions were considered by splitting the two competition terms, SDI and SDIL, into species-specific components, i.e. those corresponding to the target species, which represented the intra-specific competition, and the two or three possible inter-specific competition components, one for each one of the possible companion species.

Modelling approach

To analyse the effect of competition on tree allometry, we considered that the three allometric relationships were species specific and depended on the tree size (d), the tree competition status, and the site conditions. So for each target species,

$$Y_{\text{species}} = f\,(d,\ \text{competition status},\ \text{site conditions}), \tag{3}$$

where tree competition status was described by the above-mentioned competition measures, i.e. size-symmetric (SDI) and size-asymmetric competitions (SDIL), and site conditions by available environmental variables for SNFI sample plots (annual precipitation, mean annual temperature, slope, aspect and elevation). To identify possible mixing effects on tree allometry, we tested whether the inclusion of competition terms split into intra- and inter-specific competitions (species-specific competition terms as explained in Section "Competition measures"), improved the model without considering competitors identity, i.e. total SDI and total SDIL. After a preliminary analysis (results not shown), taking into account the model parsimony and the values of the Akaike Information Criterion (AIC), the models which were found to be statistically better were those which included elevation as site variable, the SDI split by species (SDI_k) and the total SDIL.

$$Y_{\text{species}} = f(d,\ \text{SDI}_k,\ \text{SDIL},\ \text{Elevation}). \tag{4}$$

For crown diameter and diameter at a height of 4 m, the log-transformed expression of the general allometry equation ($\log(Y) = a_0 + a_1 \cdot \log(d)$) was used as basic model to be

Table 2 Tree characteristics and competition status in monospecific and mixed stands

Species composition	nº (trees)		d (cm)	cd (m)	h (m)	d_4 (cm)	SDI (intra)	SDI (inter)	SDI (total)	SDIL
Monospecific stands Pinus sylvestris	10,682	Mean	24.4	4.4	10.7	19.3	445	–	460	195
		sd	10.6	1.6	4.5	9.1	285	–	290	204
		Min	7.5	0.5	2.0	8.0	9	–	10	0
		Max	112.4	13.3	31.0	70.0	1605	–	1745	1301
Pinus sylvestris Abies alba	80	Mean	34.6	4.8	14.1	25.2	364	181	558	202
		sd	15.3	2.0	4.5	11.3	293	209	280	186
		Min	12.5	1.6	5.5	9.0	21	11	107	0
		Max	90.7	11.9	27.0	62.0	1194	863	1248	892
Pinus sylvestris Quercus petraea	412	Mean	23.6	4.4	11.1	17.9	290	92	404	149
		sd	9.1	1.5	3.7	7.7	194	105	206	149
		Min	12.3	1.2	4.0	8.0	11	11	33	0
		Max	62.6	11.4	30.0	55.0	854	638	983	724
Pinus sylvestris Fagus sylvatica	817	Mean	28.4	4.5	13.3	22.5	401	120	549	215
		sd	12.1	1.7	4.6	10.2	246	137	249	190
		Min	12.5	1.0	2.0	8.0	10	9	28	0
		Max	76.4	10.4	28.5	56.0	1119	868	1522	977
Monospecific stands Abies alba	145	Mean	37.1	4.6	17.4	31.9	604	–	616	292
		sd	18.9	1.7	6.9	14.8	353	–	356	284
		Min	11.7	1.5	4.5	8.0	43	–	43	0
		Max	130.5	10.8	34.5	99.0	1427	–	1427	1334
Abies alba Pinus sylvestris	74	Mean	30.8	5.4	15.8	26.3	326	208	556	267
		sd	17.7	2.0	5.8	16.9	227	143	193	179
		Min	12.6	1.8	6.0	8.0	11	14	107	0
		Max	111.4	10.4	28.0	99.0	863	655	1036	832
Abies alba Fagus sylvatica	151	Mean	38.2	4.7	18.0	33.3	458	167	645	287
		sd	20.5	2.0	7.3	18.2	251	181	259	232
		Min	12.6	1.2	5.0	8.0	12	10	50	0
		Max	149.6	14.1	38.5	99.0	1022	943	1251	937
Monospecific stands Quercus petraea	620	Mean	29.5	5.5	10.3	22.0	345	–	351	126
		sd	21.4	2.8	4.1	13.4	235	-	237	145
		Min	7.6	0.9	2.5	8.0	12	–	12	0
		Max	203.7	19.8	25.0	99.0	993	–	993	711
Quercus petraea Pinus sylvestris	262	Mean	21.4	4.5	9.3	15.0	185	175	378	158
		sd	11.1	1.9	2.9	7.8	161	177	192	143
		Min	7.9	1.1	2.5	8.0	11	11	33	0
		Max	82.8	11.8	21.0	57.0	638	854	983	684
Quercus petraea Fagus sylvatica	332	Mean	40.4	6.2	14.0	28.6	281	228	544	180
		sd	29.2	2.8	4.7	19.6	241	221	281	177
		Min	12.6	1.7	5.5	8.0	11	10	47	0
		Max	187.8	17.9	26.5	99.0	965	943	1568	936
Monospecific stands Fagus sylvatica	4435	Mean	33.6	7.1	16.3	26.3	469	–	479	198
		sd	17.8	3.4	5.9	12.9	220	–	234	176
		Min	7.6	0.5	2.0	8.0	12	–	12	0
		Max	122.9	23.1	37.0	99.0	1402	–	1644	1198
Fagus sylvatica Pinus sylvestris	558	Mean	27.0	6.3	13.3	20.2	248	233	512	233
		sd	16.0	2.7	4.3	11.0	186	217	224	192
		Min	7.9	1.6	3.5	8.0	9	10	28	0
		Max	118.1	21.9	29.5	65.0	868	1119	1522	993

Table 2 (continued)

Species composition	n° (trees)		d (cm)	cd (m)	h (m)	d_4 (cm)	SDI (intra)	SDI (inter)	SDI (total)	SDIL
Fagus sylvatica *Abies alba*	127	Mean	29.4	5.2	16.3	23.6	291	293	606	340
		sd	14.0	2.1	5.6	10.4	220	247	258	240
		Min	11.1	0.8	6.5	8.0	10	12	50	0
		Max	76.4	11.8	31.0	45.0	943	1022	1251	1080
Fagus sylvatica *Quercus petraea*	497	Mean	30.1	6.4	14.0	22.9	412	127	579	256
		sd	15.6	3.0	5.0	10.8	234	158	259	213
		Min	12.5	1.0	4.5	8.0	10	11	47	0
		Max	98.4	18.6	32.0	65.0	957	965	1568	1271

d breast height–diameter, *h* total height, *d4* diameter at 4 m height, *cd* crown diameter, *SDI* size-symmetric competition expressed by the stand density index, *SDIL* size-asymmetric competition as defined in Section "Competition measures", *sd* standard deviation, *Min* minimum value, *Max* maximum value

expanded by competition status and site conditions, allowing interactions with tree size. The expression of the model fitted by species is as follows:

$$\log(Y_{ij}) = (a_0 + a_{0j}) + (a_1 + a_{1j}) \cdot \log(d_{ij}) + \sum_{sp} a_{2k} \cdot \text{SDI}_{jk}$$
$$+ \sum_{sp} a_{3k} \cdot \text{SDI}_{jk} \cdot \log(d_{ij}) + a_4 \cdot \text{SDIL}_{ij}$$
$$+ a_5 \cdot \text{Elevation}_j + \varepsilon_{ij}, \quad (5)$$

where Y_{ij} is the response variable cd or d_4, for the tree i in the plot j, d_{ij} is the breast height–diameter of tree i in the sample plot j, SDI_{jk} is the SDI of the species k in the sample plot j, SDIL_{ij} is the total SDIL for the tree i in the sample plot j, and Elevation_j is the elevation of the sample plot j. Data came from a hierarchical structure with several trees measured in the same sample plot j, so we included random effects with the sample plot as the grouping structure in the parameters a_0 and a_1.

In the case of tree height, the basic model was modified ($h = a_0 + a_1 \cdot \log(d)$) to achieve an adequate distribution of residuals, resulting in the model

$$h_{ij} = (a_0 + a_{0j}) + (a_1 + a_{1j}) \cdot \log(d_{ij}) + \sum_{sp} a_{2k} \cdot \text{SDI}_{jk}$$
$$+ \sum_{sp} a_{3k} \cdot \text{SDI}_{jk} \cdot \log(d_{ij}) + a_4 \cdot \text{SDIL}_{ij}$$
$$+ a_5 \cdot \text{Elevation}_j + \varepsilon_{ij}, \quad (6)$$

where h_{ij} is the height of tree i in plot j, the rest of the variables as in Eq. 5.

All models (Eqs. 5 and 6) were fitted using the ML (maximum likelihood) method of the lme procedure (Pinheiro et al 2017). AIC was used for comparing models, together with the marginal and conditional R^2, calculated using the lmmR2 procedure (Maj 2011), as a goodness-of-fit measure.

An alpha level of 0.05 was used for significance testing of variables in the model. The bias induced by logarithmic transformation was corrected using the Beauchamp and Olson (1973) coefficient.

Species plasticity in response to competition

Taking the phenotypic plasticity concept sensu lato (Valladares et al. 2006) as a reference, species plasticity in tree allometry in response to competition can be defined as the capacity of the species to change tree allometry under different competitive environments. For each of the studied variables, i.e. cd, h and d_4, the species change according to the competition status was estimated for monospecific stands and for mixtures using the fitted models for a reference tree of 25 cm diameter, to quantify interspecific differences (Pretzsch 2014). Thus, the plasticity of a species in response to intra-specific competition was measured as the percentage change in the target variable when the stand density index SDI (size-symmetric competition) was reduced from SDI = 1000 to SDI = 500 trees/ha for a reference tree of 25 cm diameter. The plasticity of a species in response to inter-specific competition was defined (considering only one competitor species) as the percentage change in the target variable when the total size-symmetric competition of SDI = 1000 was divided 50% between intra- and interspecific competitions, i.e. the SDI of both target and competitor species was 500 trees/ha.

Results

Crown diameter

Table 3 shows the parameter estimation and fitting statistics for the four studied species as regards crown diameter, cd,

and models (residual graphs in Supplementary Fig S4). In all the models the SDI of the target species, i.e. intra-specific size-symmetric competition, was always significant, both on its own or interacting with tree diameter. However, the inter-specific size-symmetric competition terms were clearly species specific, varying among the target species modelled and with the identity of the admixed species. In some cases the inter-specific terms were not significant, which implies an increase of cd for a given total symmetric competition (SDI). The size-asymmetric competition term, SDIL, was only significant for pine and oak, resulting in smaller cd for a given tree size when SDIL was greater. The models also showed that the higher the elevation the smaller the crown diameter for all species except fir, which was not influenced by elevation.

When applying these models to monospecific stands, we found that beech and oak had larger crown diameters for a given diameter and level of competition than pine and fir (Fig. 1). If we examine the plasticity of the response to competition in monospecific stands, i.e. intra-specific competition (Table 4), European beech and silver fir cd showed higher plasticity than Scots pine or sessile oak, with an increase of 8 and 17% in cd in comparison with 3.5 and 6%, respectively. Similarly, beech and fir also showed a more general plastic response to interspecific competition (Table 4).

According to the models, the pine competition term was not significant in the oak or European beech cd models, i.e. pine did not act as a real competitor and, therefore, oak and beech had larger cd when mixed with pine than in monospecific stands for a given SDI (Fig. 2). For silver fir, competition from pine even was significant (positive effect), while the beech term was not significant. In beech mixtures, however, the wider crowns of this species interact negatively with the oak and pine, which had less-developed crowns when competing with beech than in monospecific stands. Nevertheless, oak competition does have a weak effect on pine and beech crowns.

Height

The height–diameter model results and fitting statistics are shown in Table 5 (residual graphs in Supplementary Fig S5). Intra-specific symmetric competition was significant for all species, both on its own or interacting with tree size, while the inter-specific competition effect was dependent on the species composition of the mixture. Elevation always had a negative effect on tree heights, while SDIL was only significant for pine and beech.

The effect of stand density on tree height in monospecific stands, i.e. intra-specific competition, though always significant, showed different degrees of influence depending on the species (Fig. 3). Silver fir displayed low plastic response to competition, around 6% reduction in height when competition is reduced from $SDI = 1000$ to $SDI = 500$ for a tree of $d = 25$ cm, in comparison with 16% for pine and oak (Table 4).

The height–diameter allometry was less modified by mixture than the crown diameter (Fig. 4). However, the effect was always significant and models which included SDI by species always performed better than a similar model in which the identity of competitors is not considered (results not shown). Pine and oak competitions resulted in a negative effect on beech height, i.e. the higher the inter-specific competition from these species the lower the beech trees for a given total SDI, this effect being greater in the case of larger beeches. The opposite effect was found in pine height, i.e. for a given diameter, pines grew higher in beech, oak and fir mixtures than in monospecific stands. The effect of inter-specific competition on the height of oak varied depending on the mixture (Fig. 4), while fir trees were higher in monospecific stands than in mixtures, although the plasticity of fir trees in response to inter-specific competition was lower (around −6%) in comparison with pine, oak, and beech (Table 4).

Diameter at a height of 4 m

The third allometric relationship was that of diameter at a height of 4 m and breast height–diameter, which can be interpreted as a measure of stem taper for the first saw log. Table 6 shows the results and fitting statistics of the models (residual graphs in Supplementary Fig S5). As in the previous models, the intra-specific SDI was significant for the four species. The SDIL was significant only for pine and beech, as in the height model. Land elevation had a negative effect on d_4, meaning that, as expected, stem taper was greater at higher elevations.

Figure 5 shows that in monospecific stands, in general, the higher the competition the more cylindrical the stems. This plasticity in the response to intra-specific competition was similar among species, with a reduction in d_4 of between 4 and 7% for a reduction in SDI from 1000 to 500 (Table 4).

Stem taper was also affected by the mixture, and this variation was also species specific (Fig. 6). However, the response to inter-specific competition in d_4 was lower than in cd or tree height (Table 4). The effect of pine on oak was negative, with less cylindrical stems than in monospecific stands. Pine, oak and fir had also a negative effect on beech d_4, while for pine and fir the effect depended on the admixed species.

Table 3 Parameter estimation, standard errors, Akaike's Information Criterion (AIC) and R^2 coefficient of the four species crown diameter models

Response variable log(cd)	Target species							
	Scots pine		Silver fir		Sessile oak		European beech	
AIC	−3299.0				36.1			
R^2 (Marginal)	0.6182				0.3317			
R^2 (Conditional)	0.8173				0.8613			
Parameters	Value	Std.Error	Value	Std.Error	Value	Std.Error	Value	Std.Error
Intercept	− 0.574255	0.035530	− 0.165691	0.123375	− 0.501242	0.081875	0.051082	0.067485
log(d)	0.700418	0.010885	0.499167	0.036517	0.721910	0.023811	0.645160	0.017746
SDI_{pine}	0.000189	0.000087	ns		ns		ns	
$SDI_{pine}\cdot\log(d)$	− 0.000080	0.000025	0.000191	0.000062	ns		ns	
SDI_{fir}	0.003625	0.000882	ns		ns		ns	
$SDI_{fir}\cdot\log(d)$	− 0.001194	0.000255	− 0.000052	0.000023			− 0.000195	0.000025
SDI_{oak}	ns				ns		− 0.000203	0.000080
$SDI_{oak}\cdot\log(d)$	ns				− 0.000037	0.000016		
SDI_{beech}	− 0.000434	0.000052	ns		0.001360	0.000347	− 0.000722	0.000129
$SDI_{beech}\cdot\log(d)$	ns		ns		− 0.000459	0.000098	0.000125	0.000037
SDIL	− 0.000334	0.000019	ns		− 0.000211	0.000064		
Elevation	− 0.000086	0.000010	ns		− 0.000138	0.000039	− 0.000227	0.000020
	Intercept	log(d)	Intercept	log(d)	Intercept	log(d)	Intercept	log(d)
Random effects standard dev	0.466475	0.133167	0.930696	0.253772	0.673430	0.205739	0.637315	0.157229

cd crown diameter, d breast height–diameter, SDI size-symmetric competition, SDIL size-asymmetric competition
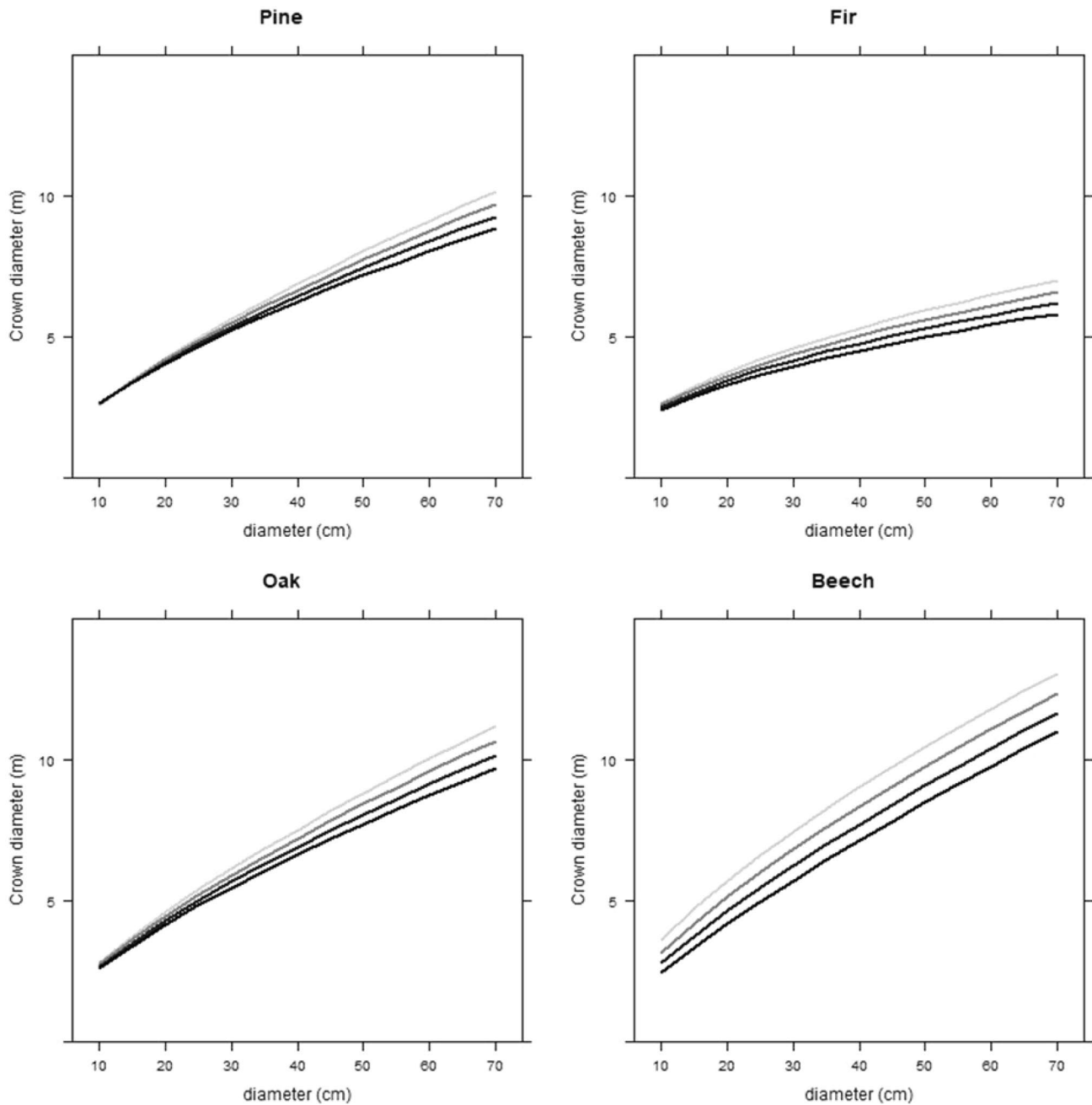
Fig. 1 Crown diameter in monospecific stands for increasing size-symmetric competition conditions from SDI = 100 (light grey) to SDI = 1000 (black) stems/ha. Elevation 1000 m and null size-asymmetric competition

Discussion

Tree allometry response to competition in monospecific stands

Trees growing in high-density stands generally displayed narrower crowns, greater heights and less taper for a given tree diameter. Although the four species are classified as species with high morphological plasticity (Pretzsch and Rais

2016), the plasticity as regards tree allometry in response to competition varied among them. Furthermore, crown diameter and tree height responded more strongly to increased crowding than diameter at a height of 4 m.

Inter-specific variation in crown and height allometry was previously found to depend on wood density (Ducey 2012; Forrester et al. 2017b), evergreenness (Ducey 2012), shade tolerance (Dietze et al. 2008; Franceschini and Schneider 2014) or light conditions (Harja et al. 2012), although

Table 4 Plasticity of the response to competition in allometric relationships expressed in monospecific stands by the percentage of change in the variable when the size-symmetric competition is reduced from SDI = 1000 to SDI = 500 trees/ha for a reference tree of 25 cm diameter; in mixed stands by the percentage of change in the variable when the 50% of the competition is due to the admixed species in comparison with monospecific stands for a total SDI = 1000 and a reference tree of 25 cm diameter

	Target species	Monospecific	Admixed species			
			+ Pine	+ Fir	+ Oak	+ Beech
Crown diameter (cd)	Scots pine	3.5		− 7.3	3.5	− 16.7
	Silver fir	8	48.3			8
	Sessile oak	6.2	6.2			0.3
	European beech	17.3	17.3	− 14.3	5.9	
Height (h)	Scots pine	− 15.3		13.6	7.2	18.2
	Silver fir	− 6.3	− 6.3			− 6.3
	Sessile oak	− 16.7	− 10			17.4
	European beech	− 14	− 11.6	0.2	− 14	
Diameter at 4 m height (d_4)	Scots pine	− 5.7		3.2	− 5.7	7.6
	Silver fir	− 4.3	7			− 4.3
	Sessile oak	− 7	− 7			0.5
	European beech	− 4.1	− 4.1	− 4.1	− 7.7	

other studies found no dependence on species traits (Hemery et al. 2005; Lines et al. 2012). Despite the fact that our results are limited to four species, they all exhibited larger crowns as species-specific wood density increased (Fig. 1), i.e crown diameters for a given diameter were larger in beech > oak > pine > fir. This finding is in accordance with the mechanical explanation of the trunk being the support system for the crown; hence, the higher the specific wood density, the greater the amount of foliage that the tree can support (Dean and Baldwin 1996; Woodall et al. 2005). This implies larger crowns and fewer individuals of species with high specific wood density to fully occupy the stand, as predicted by Ducey and Knapp (2010). This relationship between stand density and mechanical properties (i.e. wood density) is modulated by climate and shade tolerance of different forest types (Ducey et al. 2017; Bravo-Oviedo et al. 2018). This may, therefore, explain our observation of greater crown plasticity to stand density in species with higher shade tolerance (beech and fir). Based on another measure of plasticity, Pretzsch (2014) reported a similar order in crown plasticity to that of our study (beech > fir > oak > pine). The opposite order between species was found for the variation in height–diameter response to competition, with greater response exhibited by less shade-tolerant species (Table 4). Forrester et al. (2017b), in a study which included 17 tree species, found that this plasticity in crown projection area and live-crown length decreased with species wood density, but found no relationship for height allometry. The intra- and inter-specific variations in stem taper in monospecific stands were much lower than that of crown diameter and height allometry (Fig. 6). Even so, it could imply considerable changes in the volume and quality of the first timber log (Steele 1984; Zhang 2003).

With regards to the effect of shading, expressed in the models through the size-asymmetric competition term, its effect differed among species and also depended on the particular allometric relationships. In the case of crown diameter it was only significant for pine and oak (Table 4). This is in line with results reported by Forrester et al. (2017b), who found a small effect of tree relative height (related to tree level asymmetric competition) on crown projection area, but this was greater for shade-intolerant species. Asymmetric competition was found to better explain height variability than symmetric competition (Lines et al. 2012), since suppressed trees display greater slenderness. However, in the models for tree height and diameter at a height of 4 m, asymmetric competition was only significant for pine and beech, these two variables increasing with size-asymmetric competition, i.e. suppressed trees exhibit greater slenderness (Wang et al. 1998) and lower taper (Tasissa and Burkhart 1997) due to a reduction in diameter growth in the lower part of the stem while maintaining high growth in the upper part (Ikonen et al. 2006).

Trees at higher elevations had narrower crowns, lower heights and greater stem taper, these results being consistent with those of previous studies that pointed to similar changes in allometry under strong winds (Brüchert and Gardiner 2006), or lower heights where temperatures are lower (Lines et al. 2012).

Tree allometry response to interspecific competition

The identified interspecific competition effect on tree allometry was more relevant for crown projection area than for the other allometric relationships (Pretzsch 2017). Changes in crown structure due to mixing effects have previously been reported for different mixtures (Pretzsch 2014; Martin-Ducup et al. 2016; Barbeito et al. 2017). In our results, the effect of inter-specific competition on crown projection area was positive when the admixed species is less shade tolerant and negative when it is more shade tolerant, with the exception of the pine–oak mixture,
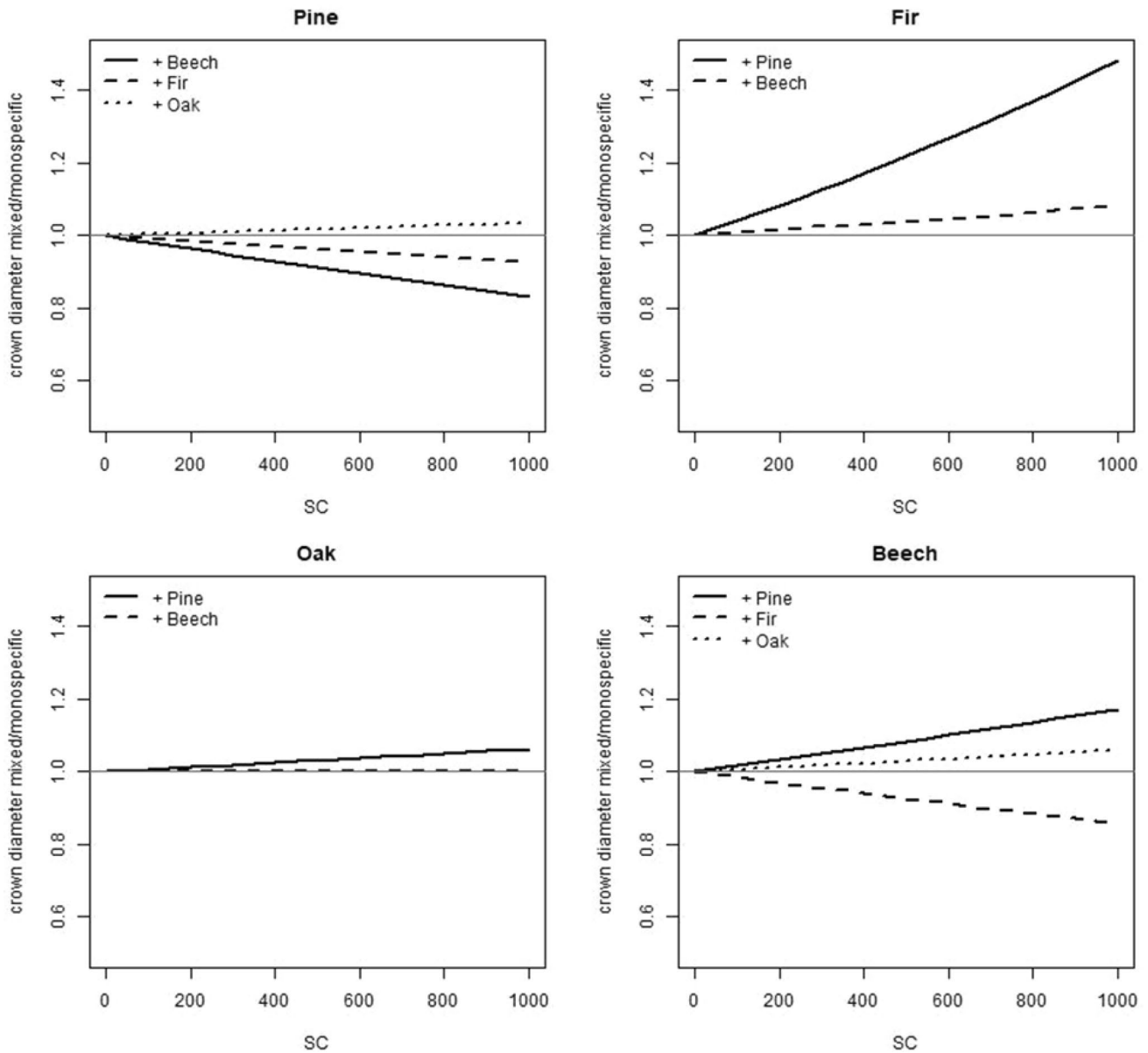
Fig. 2 Ratio between crown diameter in mixed stands (intra- and inter-specific competitions) and in monospecific stands (only intra-specific competition) for a quadratic mean diameter = 25 cm, assum-ing a proportion of 50% for target and competitor species. Elevation 1000 m and null size-asymmetric competition

where both species benefit slightly from mixing. This suggests that in these mixtures, trees adapt their crown allometry as a response to complementarity in crown architecture and light use between species (Jucker et al. 2015), such crown complementarity being greater when there are greater differences in the functional traits of the species such as growth rate or crown structure (Williams et al. 2017). Similar to crown allometry, the sign of the mean effect (positive or negative) of mixing on tree height was never the same for the two species growing together (Table 4). The less shade-tolerant species exhibited

increased height while the more shade-tolerant species had lower heights for a given diameter, suggesting some effect of species interactions on vertical structuring (Pretzsch and Forrester 2017).

Beech benefits from pine admixture in terms of crown extension, while pine benefits in terms of height, as reported in other studies (Pretzsch et al. 2016; Forrester et al. 2018). In oak and beech mixtures the effects were similar but weaker (Pretzsch 2017). Fir exhibits notable crown competition ability, achieving greater crown diameters when mixed with pine and beech, while having a negative influence on

Table 5 Parameter estimation, standard errors, Akaike's Information Criterion (AIC) and R^2 coefficient of the four species height models

Response variable h	Target species							
	Scots pine		Silver fir		Sessile oak		European beech	
AIC	52179.5		2028.7		5850.1		29575.1	
R^2(Marginal)	0.6424		0.6704		0.4496		0.4560	
R^2(Conditional)	0.9034		0.8646		0.8465		0.8611	
Parameters	Value	Std.Error	Value	Std.Error	Value	Std.Error	Value	Std.Error
Intercept	− 6.090410	0.399843	− 10.016098	2.3942535	− 3.244358	0.779048	− 3.245485	0.704823
log(d)	5.103413	0.130119	10.090142	0.4704117	4.669257	0.221997	6.251191	0.191133
SDI$_{pine}$	− 0.011240	0.000974	ns		0.017716	0.005903	0.009757	0.003657
SDI$_{pine}$·log(d)	0.004714	0.000301	ns		− 0.004922	0.002051	− 0.002773	0.001209
SDI$_{fir}$	ns		ns				ns	
SDI$_{fir}$·log(d)	0.002312	0.000408	0.000744	0.000256			0.001537	0.000363
SDI$_{oak}$	− 0.014975	0.007098			0.004677	0.000547	ns	
SDI$_{oak}$·log(d)	0.006450	0.002341			ns		ns	
SDI$_{beech}$	− 0.011957	0.004395	ns		0.025263	0.003552	ns	
SDI$_{beech}$·log(d)	0.006391	0.001349	ns		− 0.004885	0.001072	0.001513	0.000128
SDIL	0.004787	0.000206	ns		ns		0.002506	0.000398
Elevation	− 0.001385	0.000115	− 0.005861	0.001154	− 0.002499	0.000413	− 0.004390	0.000287
	Intercept	log(d)	Intercept	log(d)	Intercept	log(d)	Intercept	log(d)
Random effects standard dev	5.628176	2.142261	7.995130	2.622902	3.814522	1.838801	7.242213	2.720365

h tree height, d breast height–diameter, SDI size-symmetric competition, SDIL size-asymmetric competition
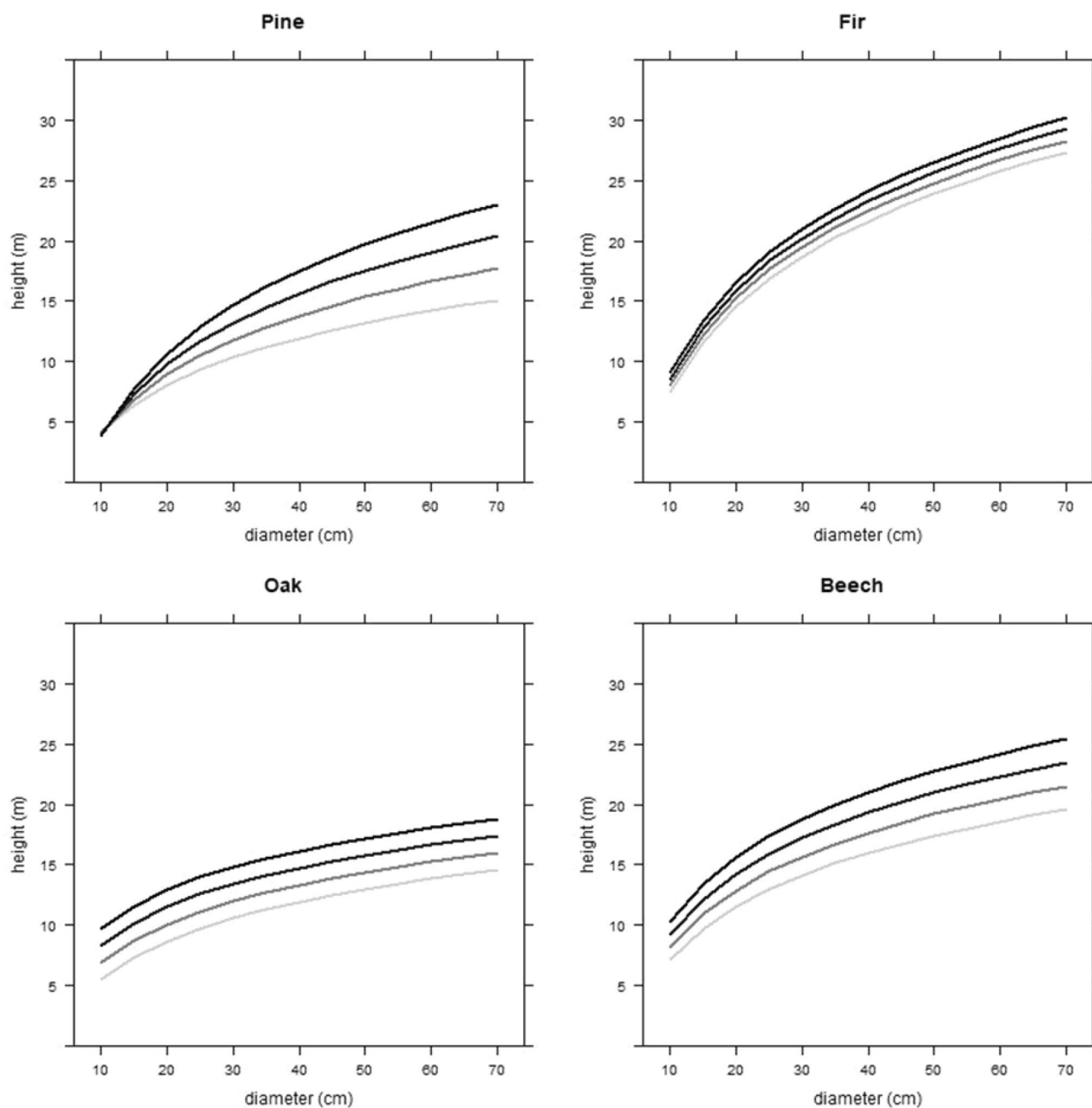
Fig. 3 Total height in monospecific stands for increasing size-symmetric competition conditions from SDI = 100 (light grey) to SDI = 1000 (black) stems/ha. Elevation 1000 m and null size-asymmetric competition

the crown diameters of these two species. Accordingly, the respective mixing effects on tree height were the opposite for fir.

Although height–diameter ratio was found to be related to stem taper (Pretzsch and Rais 2016), the change in stem taper when mixing species exhibited a different pattern to that of tree height for some mixtures (Table 4). Cameron and Watson (1999) also found differing stem taper response in Sitka spruce depending on the admixed species. As

mentioned above, although the changes in stem form caused by the mixture effect only accounted for about 5%, it could have important consequences as regards log processing and wood quality. A recent study found no influence of species diversity on wood quality (Benneter et al. 2018), although the study did not include stem taper among the analysed wood quality characteristics.
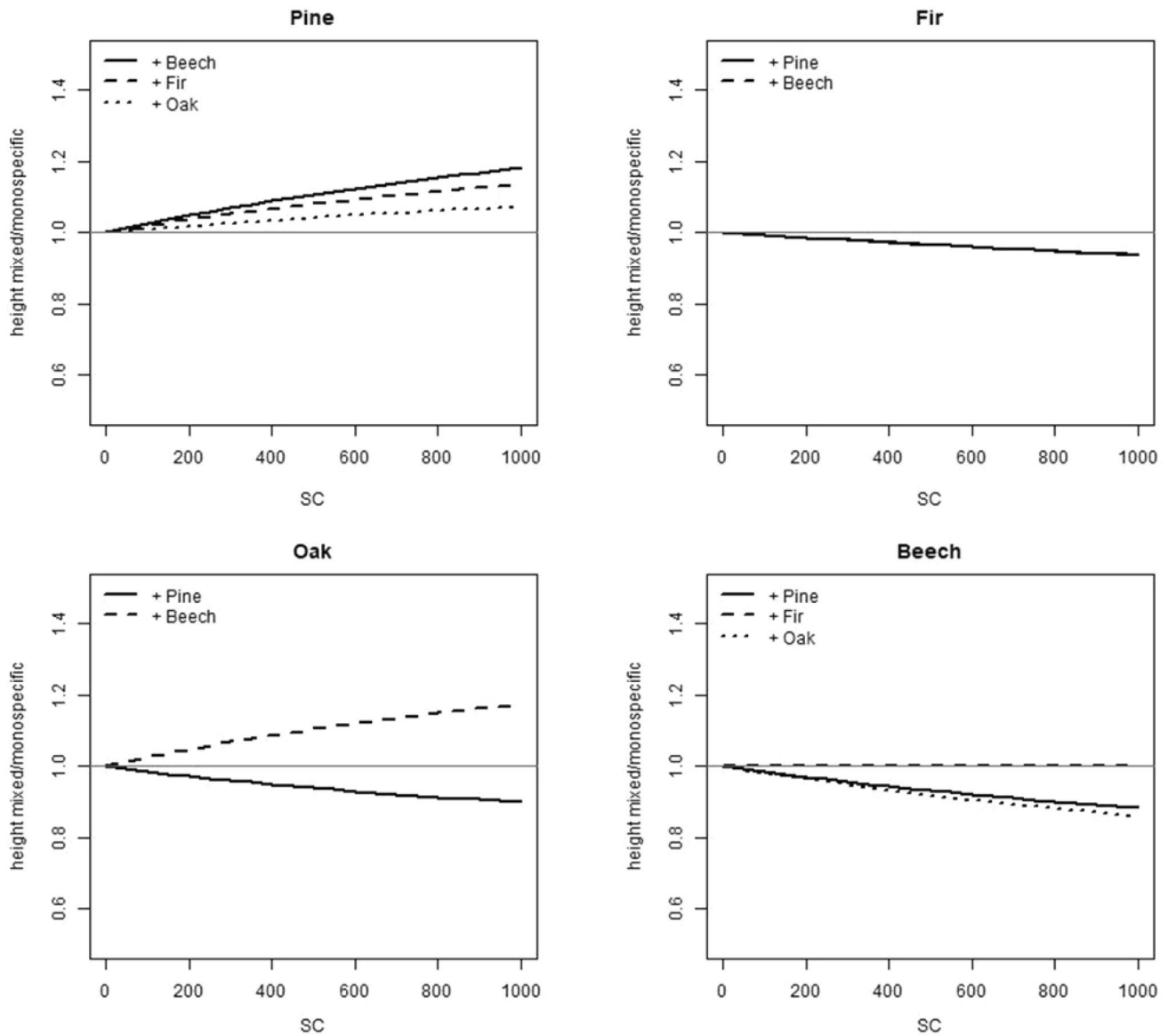
Fig. 4 Ratio between total height in mixed stands (intra- and inter-specific competitions) and in monospecific stands (only intra-specific competition) for a quadratic mean diameter = 25 cm, assuming a pro-portion of 50% for target and competitor species. Elevation 1000 m and null size-asymmetric competition

Implications

Tree competition status (e.g. expressed by crown size) has been identified as a modifier of general allometric scaling in trees (e.g. Mäkelä and Valentine 2006; Duursma et al. 2010; Pretzsch 2014). Our results corroborate the large intra-specific variability in allometry according to tree competition conditions. The differing response of trees to competition between monospecific and mixed stands highlights the need to develop allometric equations for mixed-species stands (Forrester and Pretzsch 2015; del Río et al. 2016). Building general allometric equations which include stand structure and diversity indices as predictors may provide

a useful option for general forest practice (Forrester et al. 2017b). However, the admixed species-dependent effects on tree allometry highlight the importance of considering species composition instead of species diversity, since tree allometry can be influenced by between-species interactions.

Tree allometry models which depend on intra- and inter-specific competitions are crucial when evaluating mixing effects (Forrester and Pretzsch 2015), as they allow upscaling of results from tree to stand level. For instance, using volume equations developed for monospecific stands in mixed stands might result in over- or under-estimation of volume productivity and, therefore, of overyielding, since the observed variation in stem taper is not considered.

Table 6 Parameter estimation, standard errors, Akaike's Information Criterion (AIC) and R^2 coefficient of the four species diameter at 4 m height models

Response variable $\log(d_4)$	Target species							
	Scots pine		Silver fir		Sessile oak		European beech	
AIC	−10045.6		−336.2		−503.9		−3305.1	
R^2(Marginal)	0.8840		0.9326		0.9109		0.8864	
R^2 (Conditional)	0.9479		0.9514		0.9703		0.9519	
Parameters	Value	Std.Error	Value	Std.Error	Value	Std.Error	Value	Std.Error
Intercept	−0.818450	0.021768	−0.316225	0.087883	−0.744887	0.092173	−0.405570	0.033873
$\log(d)$	1.143080	0.006805	1.057391	0.019412	1.160061	0.029150	1.043989	0.008690
SDI_{pine}	ns		ns		ns		ns	
$\text{SDI}_{\text{pine}}\cdot\log(d)$	0.000036	0.000003	0.000069	0.000024	ns		ns	
SDI_{fir}	0.000181	0.000074	ns				ns	
$\text{SDI}_{\text{fir}}\cdot\log(d)$	ns		0.000027	0.000008			ns	
SDI_{oak}	ns				0.000894	0.000213	0.000773	0.000341
$\text{SDI}_{\text{oak}}\cdot\log(d)$	ns				−0.000233	0.000067	−0.000264	0.000106
$\text{SDI}_{\text{beech}}$	ns		ns		0.001291	0.000277	0.000083	0.000016
$\text{SDI}_{\text{beech}}\cdot\log(d)$	0.000082	0.000011	ns		−0.000353	0.000082	ns	
SDIL	0.000167	0.000011	ns		ns		0.000098	0.000020
Elevation	−0.000072	0.000008	−0.000123	0.000037	−0.000119	0.000027	−0.000061	0.000012
	Intercept	$\log(d)$	Intercept	$\log(d)$	Intercept	$\log(d)$	Intercept	$\log(d)$
Random effects standard dev	0.239427	0.066581	0.324488	0.092464	0.422638	0.141563	0.328347	0.113834

d4 diameter at 4 m height, *d* breast height–diameter, *SDI* size-symmetric competition, *SDIL* size-asymmetric competition
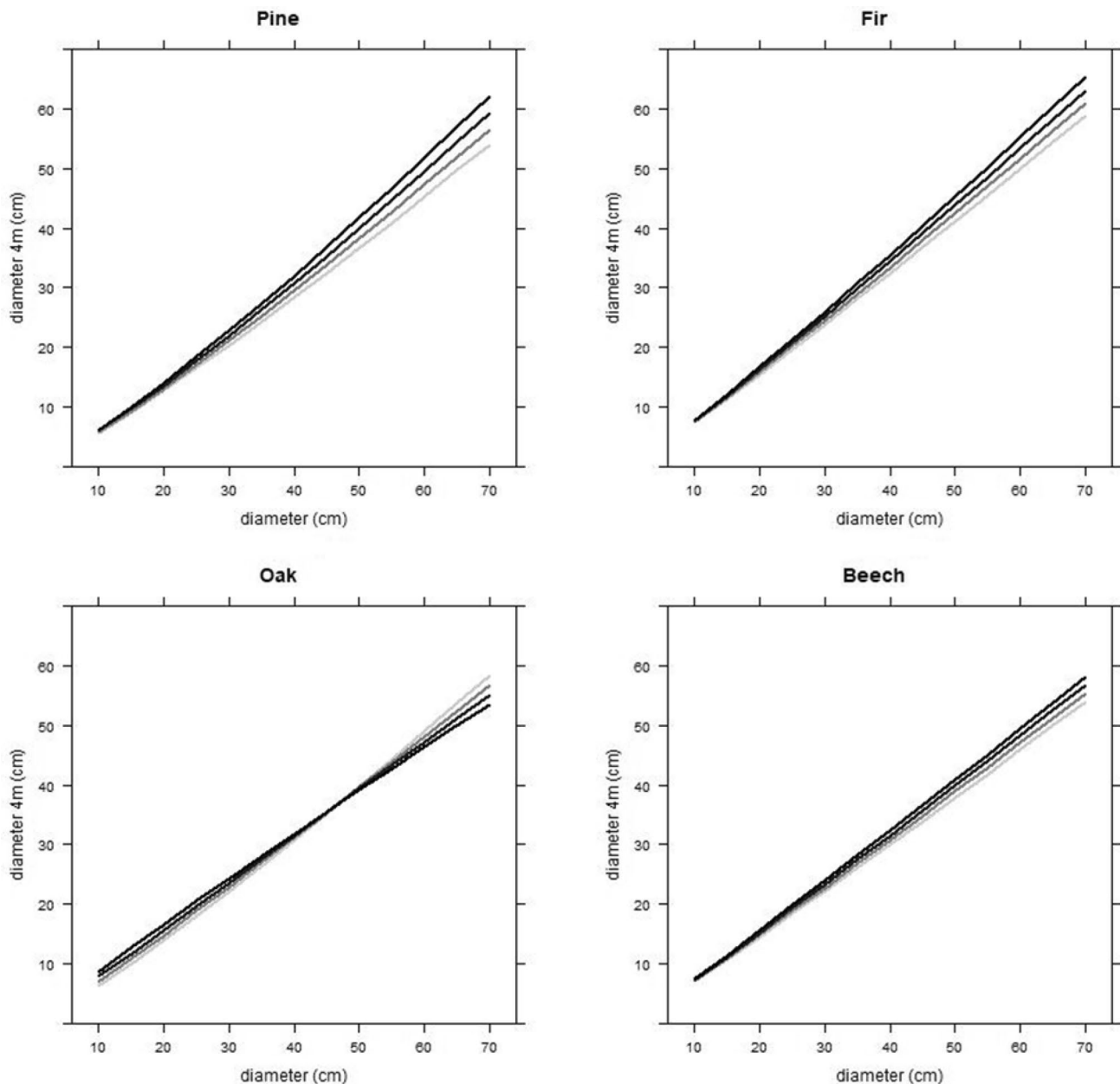
Fig. 5 Diameter at 4 m height in monospecific stands for increasing size-symmetric competition conditions from SDI = 100 (light grey) to SDI = 1000 (black) stems/ha. Elevation 1000 m and null size-asymmetric competition

Accordingly, when adapting growth models developed for monospecific stands to mixtures, tree functions such as height–diameter equations, tree crown or tree volume functions need to be sensitive to species composition so that the effect of mixing is taken into account (Pretzsch et al. 2015).

However, it is important to consider certain limitations inherent to NFI data. Tree allometry at a given time is the result of growing conditions throughout tree development. Although the response of tree crowns to changes in canopy structure or competition occurs over a shorter time period, tree height and stem taper are highly influenced by past

growing conditions of the trees, including those that are not recorded in NFI data. Long-term data would allow us to better understand the influence of competition on tree allometry, although long-term experimental plots are still scarce and only exist for some species compositions (Bielak et al. 2014; Ruiz-Peinado et al. 2018). Moreover, other tree allometry features which are not reflected in the Spanish NFI can be highly influenced by the tree competition environment, such as crown length and branch characteristics (Bayer et al. 2013; Pretzsch 2017). Nevertheless, the NFI information has allowed us a first approach to the question,
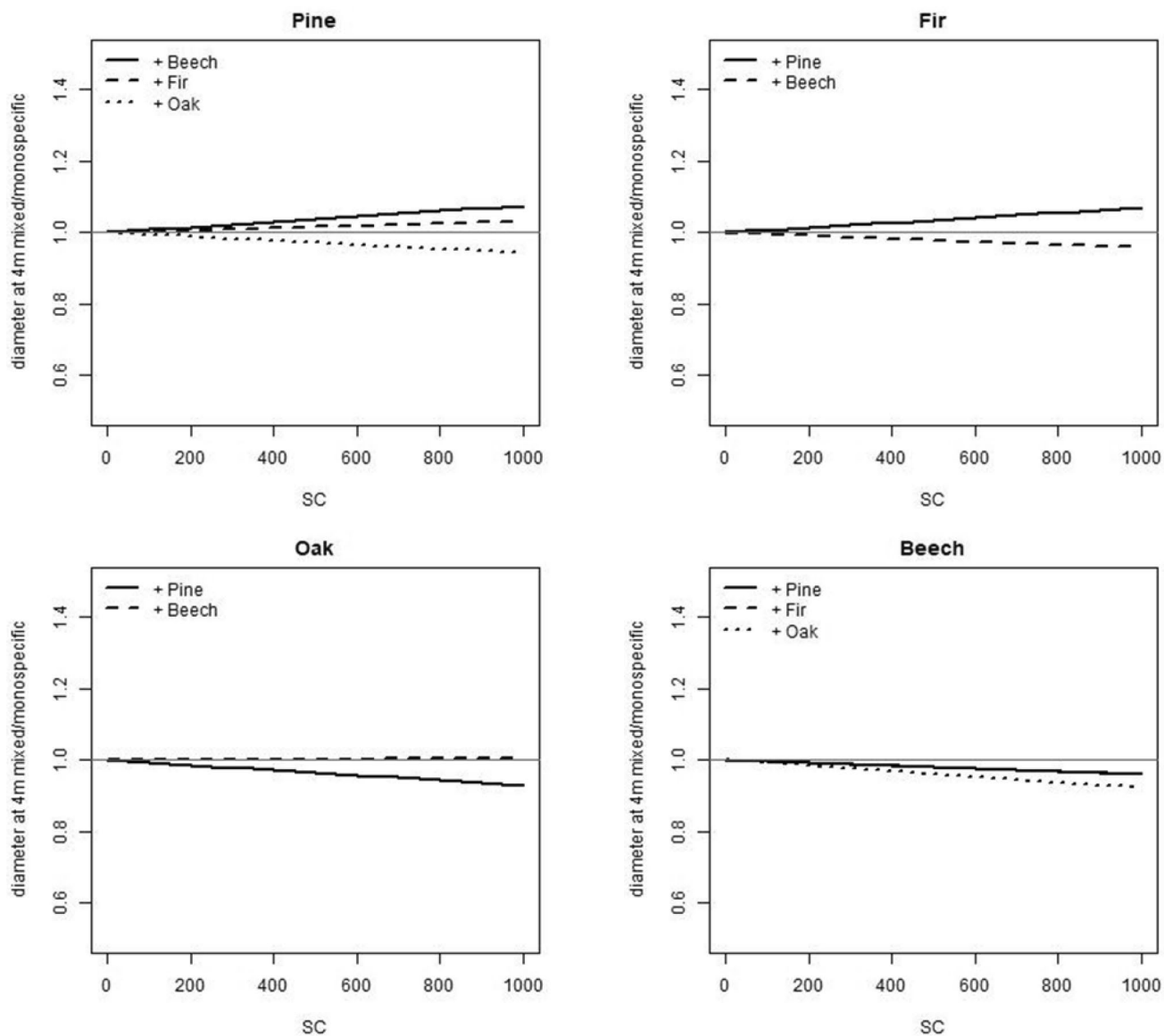
Fig. 6 Ratio between diameter at 4 m height in mixed stands (intra- and inter-specific competitions) and in monospecific stands (only intra-specific competition) for a quadratic mean diameter = 25 cm, assuming a proportion of 50% for target and competitor species. Elevation 1000 m and null size-asymmetric competition

providing valuable insights into tree allometry variability in monospecific and mixed stands.

Author contribution statement MdR and SC conceived the idea and analysed the data; all authors contributed to the result interpretation and to the manuscript writing.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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