



Species admixture can increase potential tree growth and reduce competition

Sonia Condés^{a,*}, Hans Pretzsch^b, Miren del Río^c

^a Department of Natural Systems and Resources, School of Forest Engineering and Natural Resources, Universidad Politécnica de Madrid, Madrid, Spain

^b Chair of Forest Growth and Yield Science, Department of Life Science Systems, TUM School of Life Sciences, Technical University of Munich, Freising, Germany

^c Instituto de Ciencias Forestales (ICIFOR-INIA), CSIC, Madrid, Spain

ARTICLE INFO

Keywords:

Complementarity
Competition reduction
Climate
Basal area growth
Inter-specific competition

ABSTRACT

Trees often show better growth in mixed as opposed to monospecific neighborhoods as consequence of competition reduction and facilitation between species. However, it can be challenging to discern the effect of these factors as they occur simultaneously, so often they are jointly refereed as complementarity. By using tree growth models based on potential tree growth reduced by a competition modifier and including species mixing effects on both components (potential tree growth and competition modifier), we aim to verify that tree potential growth is modified by admixture, which may provide further information on species interactions and complementarity.

We used tree data from the Spanish National Forest Inventory, selecting plots located in two different mixtures, Scots pine – European beech and Scots pine – Oak mixtures, as well as in the corresponding monospecific stands of those species. To analyse whether the species mixture increases the potential basal area growth, we developed linear mixed quantile regressions to model the potential growth, while to analyse the competition reduction we developed linear mixed models. We include the Martonne aridity index as a measure of the site conditions in the models to explore whether climate conditions modify the effects of species mixture.

Our results show a slight effect of the mixture on the potential basal area growth of pine while the potential growth of beech clearly benefited from the pine/beech mixtures. For the pine/oak mixtures the potential growth of both species was higher in mixtures than in monospecific stands. Moreover, we found a positive influence of humidity on potential growth for all the species and mixtures, although the magnitude of the effect was less important for beech and more notable in the case of the pine/oak mixtures. We also found that for the studied species, admixed species reduced competition, with lower inter-specific than intra-specific competition effects, and that these effects were mediated by climate conditions.

We concluded that the potential tree basal area growth is influenced by the species admixture, which suggest that species mixing effects can be relevant also under low stand densities. Our results highlight the importance of integrating the effect of species interactions on both the potential growth of trees and the competition modifier when the aim of the research is to further our understanding of species interactions.

1. Introduction

Interest in mixed species forests has increased significantly over the last 20 years (Bravo-Oviedo et al., 2018), in part, because promoting such forests is considered a suitable strategy for enhancing forest adaptation to climate change (Ammer, 2016). This has led to numerous studies on mixed forests (e.g. see del Río et al., 2021), addressing issues such as the influence of species interactions on tree growth, since the

trees determine forest dynamics and mixing effects at stand level (Pretzsch, 2017, pp 272-273). Competition reduction, as a consequence of niche complementarity, along with facilitation, can result in better tree growth in mixed as opposed to monospecific neighborhoods. However, trees within a stand always compete for resources, so the observed tree growth reflects the net effect of the different species interactions that can occur simultaneously (competition, competition reduction and facilitation), making it challenging to discern the

* Corresponding author at: Dept. Sistemas y Recursos Naturales, Escuela Técnica Superior de Ingenieros de Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid, José Antonio Nováis 10, 28040 Madrid, Spain.

E-mail address: sonia.condes@upm.es (S. Condés).

<https://doi.org/10.1016/j.foreco.2023.120997>

Received 15 February 2023; Received in revised form 5 April 2023; Accepted 7 April 2023

0378-1127/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

presence of facilitation from that of competition reduction (Callaway and Walker, 1997). Moreover, species interactions can vary depending on environmental conditions (Forrester, 2014; Mina et al., 2018), and therefore, their net effects (del Río et al., 2014b), making them even more difficult to be identified. As consequence, the term complementarity is often used to reflect the joint effect of facilitation and competition reduction (Loreau and Hector, 2001; Forrester and Bauhus, 2016). See Box 1 for clarification of technical terms employed with regard to species interactions.

There are several approaches to modeling tree growth in mixed stands, covering both empirical and process-based approaches (Pretzsch et al., 2015c). Many growth models at individual tree level include the use of competition indices and address species interactions by splitting competition into that exerted by the different species or groups of species, i.e. distinguishing intra- and inter-specific competition (Box 1) (e.g. Liu and Burkhardt, 1994; Canham et al., 2004). Although the underlying causes cannot be inferred, it is often suggested that when the net effect of the inter-specific competition term on growth is positive it is caused by facilitation, when it is negative it is caused by competition (Box 1), and when it is neutral or less negative than intra-specific competition term effect result from competition reduction or a combination of facilitation and competition reduction (Forrester et al., 2011; Condés and del Río, 2015; Fichtner et al., 2017).

One common tree growth model structure in empirical models is based on a potential growth component together with multiplicative modifiers that reduce the potential tree growth by several factors reflecting tree size, competition, or site conditions (Weiskittel et al., 2011), hereafter named potential modifier approach. The way potential tree growth is defined varies between models, from the maximum value of growth rate that a species can reach (e.g. Coates et al., 2009; Gómez-Aparicio et al., 2011), to size- and/or site-dependent definitions, such as the size-dependent growth of free-growing trees (without competition) (e.g. Canham et al., 2004), the growth of open-grown trees (e.g. Hasebauer et al., 2006), the growth of dominant trees (e.g. Soares and Tomé, 2003; Sanchez-Gonzalez et al., 2006), or the growth of the faster growing trees for a given size/site (e.g. Pretzsch and Biber, 2010). In the empirical models following the potential modifier approach, species interactions are only considered in the competition modifier, i.e., as mentioned above, considering species-specific competition effects. This concept assumes that mixing species does not influence potential tree growth, although facilitation by other species can enhance resource availability (e.g. by nitrogen fixation, nutrient mineralization, or hydraulic redistribution), acquisition (e.g. symbiotic associations) or

indirectly use efficiency (Forrester, 2017), which may result in changes in carbon partitioning and greater potential growth (Pretzsch and Zenner, 2017).

Although there is scarce evidence that mixing species modifies the potential tree growth, a recent study reports between 14 and 78% higher growth of the faster growing trees (reflecting potential growth) in mixed as opposed to monospecific neighborhoods for five mixtures (Pretzsch, 2022a). Beyond this positive effect on potential growth, mixing species also reduced competition for most of the species and mixtures, with a greater reduction in denser stands, explained as presence of spatio-temporal niche complementarity.

In this study we aim to identify whether species mixing modifies potential tree basal area growth, by splitting species interactions effects into those on the potential growth and those on the competition modifier. This information can provide a better picture of between species complementarity and is relevant for forest management and modelling. We estimated potential tree basal area growth as a function of tree size and site conditions using quantile regression and NFI data, defining potential tree growth as the basal area growth of the faster growing trees, i.e., the growth of trees representing the 99% percentile for given stem size and site conditions. In addition, we assume that the presence of admixed species can reduce competition and that competition effects can also vary with site conditions. Within the site conditions, we explored the effect of site climate conditions and how these effects can be modified by the inter-specific neighborhood.

To achieve our main aim we used data from two mixtures for which previous studies have reported significant species interactions at tree and stand levels (Perot et al., 2010; Condés and del Río, 2015; Pretzsch et al., 2015b; Strieder and Vospertnik, 2021): *Pinus sylvestris* L. (Scots pine) and *Fagus sylvatica*. (beech), and *P. sylvestris* and *Quercus robur* or *Q. petraea* (oak). Our specific objectives were: i) To identify whether the proportion of admixed species increases potential tree basal area growth; ii) To analyse whether competition reduction occurs in the two mixtures for both species; iii) To explore whether climate conditions modify the effects of admixed species on potential tree basal area growth and competition in the two mixtures.

Thus, our hypotheses are: H1, potential tree basal area growth is similar in mixed and monospecific stands; H2, intra- and inter-specific competition have the same reduction effect on potential tree basal area growth; H3, Climate conditions do not influence species interactions.

Box 1

To clarify the most important technical terms we have extracted the definitions from the glossary in Pretzsch et al. (2017, pp. 607–634).

Term.	Explanation.	Reference.
Competition.	Ecological interaction in which one organism or species consumes a resource that would have been available to and could have potentially been consumed by the other, and hence the fitness of one is lowered by the presence of another.	Begon et al. (1986)
Competition reduction.	Occurs when the interspecific competition for a limiting resource in mixtures is less than the intraspecific competition for this resource in the monocultures. The species in mixture therefore utilise this resource more efficiently for growth.	Kelty (1992) Vandermeer (1992)
Facilitation.	Facilitation is a form of ecological interaction between different species that benefits at least one of the participants and causes no harm to the others. Facilitations can be mutualistic, when both species benefit from the interaction, or commensalistic, when only one species benefits and the other remains unaffected.	Stachowicz (2001)
Complementarity.	The combined effects of competition reduction (or niche differentiation) and facilitation.	(Loreau and Hector, 2001)
Intraspecific, interspecific.	Occurring among members of the same species or of different species, respectively.	Helms (1998)

2. Materials and methods

2.1. Data

Data used for this study came from 893 permanent sample plots of the Spanish National Forest Inventory (SNFI). The plots were located in mono-specific and mixed stands of two different species compositions: Scots pine and beech, and Scots pine and oak. First, mixed plots were selected from SNFI data considering a plot as a mixture when the sum of the basal area of the studied species was greater than 95% of the total basal area, and that of each of them was at least the 5% of the total. The monospecific plots were then selected within a buffer of between 1.5 and 5 km around each location of the mixed plots, large enough to get a similar number of plots in mixtures and monospecific stands. The low percentage of basal area used for considering a plot in a mixture, allows us to get an almost continuous gradient from the null inter-specific competition in monospecific stands to the greatest one. The plots were re-measured at approximately ten-year intervals, in one or two periods depending on the province, i.e., during the Second and Third SNFIs, the Third and Forth SNFIs or in the three cycles. Plots where cuttings had been applied in the period between inventories were excluded from the study. This resulted in a set of 1015 plot remeasurements and 24,743 remeasured sample trees available for the study. Table 1 and Table 2 summarize the main stand and tree characteristics respectively by species and mixtures (see section 2.2. for further description of species proportion and competition variables). Note that age is not recorded in the SNFI, so no information was available on stand age or site index.

In addition, mean annual temperature (T °C) and annual precipitation (P, mm) were taken from raster maps with a 1 km resolution for the Iberian Peninsula, obtained from a functional phytoclimatic model based on raw data from meteorological stations (Gonzalo Jiménez, 2010). The ranges of T and P in the selected plots were 4.83–11.53 °C and 587–2137 mm, respectively. The Martonne aridity index (Martonne, 1926) was calculated as $M = P/(T + 10)$ and was used as a measure of site humidity conditions (Table 1), having proven its effectiveness in several studies conducted with the same mixtures (Condés et al., 2017;

Table 1

Summary of main characteristics of the species in monospecific and mixed stands at plot level. N is the number of trees per ha, G is basal area, dg the quadratic mean diameter, M is the Martonne aridity index, P_{pine} the pine proportion, P_{beech} beech proportion and P_{oak} the oak proportion (as defined in section 2.2), sd is the standard deviation, min and max are minimum and maximum values, respectively.

		N stem/ha	G m ² /ha	dg cm	N pine	G pine	dg pine	N beech	G beech	dg beech	M mm/°C	P _{pine}	P _{beech}
Pine 307 Plots	Mean	733	25.7	22.7	721	25.6	22.8	7	0.1	2.4	61.1	0.99	0.00
	Sd	541	15.8	7.7	536	15.7	7.7	34	0.3	8.1	13.9	0.01	0.01
	Min	29	1.2	8.6	29	1.2	8.6	0	0.0	0.0	29.1	0.94	0.00
	Max	3480	74.3	50.1	3480	74.3	50.1	382	2.0	54.5	101.8	1.00	0.05
Mixed 194 Plots	Mean	821	27.7	23.1	409	17.7	27.4	400	9.8	23.8	64.8	0.58	0.42
	Sd	517	13.2	8.7	422	14.9	10.0	478	9.6	16.7	15.9	0.34	0.34
	Min	10	1.8	10.9	5	0.5	8.6	5	0.4	7.6	33.1	0.01	0.01
	Max	2969	77.5	78.7	2394	73.1	56.4	2738	43.8	114.8	109.9	0.99	0.99
Beech 180 Plots	Mean	627	24.5	28.2	1	0.1	2.2	623	24.3	28.3	67.1	0.00	0.99
	Sd	527	12.5	13.9	5	0.2	8.8	526	12.4	13.9	20.7	0.01	0.01
	Min	5	0.7	9.2	0.0	0.0	0.0	5	0.7	9.2	32.1	0.00	0.96
	Max	2539	56.2	95.5	32	1.3	50.7	2539	56.2	95.5	116.4	0.04	1.00
		N stem/ha	G m ² /ha	dg cm	N pine	G pine	dg pine	N oak	G oak	dg oak	M mm/°C	P _{pine}	P _{oak}
Pine 89 Plots	Mean	706	20.3	20.0	696	20.1	20.1	5	0.1	2.0	54.2	0.99	0.00
	Sd	522	13.0	6.7	521	12.8	6.8	21	0.3	5.9	12.7	0.02	0.01
	Min	46	1.2	9.2	46	1.2	9.2	0	0.0	0.0	27.0	0.94	0.00
	Max	3275	59.3	44.6	3275	59.3	44.6	159	1.7	27.9	94.9	1.00	0.06
Mixed 73 Plots	Mean	838	19.0	19.1	457	12.8	21.6	372	6.1	18.8	54.2	0.57	0.43
	Sd	611	11.6	6.5	469	12.2	8.5	507	6.7	11.2	14.5	0.33	0.33
	Min	24	2.0	10.4	5	0.5	8.3	5	0.4	7.6	29.3	0.02	0.02
	Max	2713	53.4	44.9	2317	47.7	57.3	2624	33.3	73.2	105.5	0.98	0.98
Oak 50 Plots	Mean	518	15.8	26.9	1	0.0	0.3	508	15.7	27.1	56.9	0.00	1.00
	Sd	641	11.9	25.8	4	0.1	2.0	638	11.7	25.9	9.9	0.00	0.01
	Min	5	0.6	7.9	0	0.0	0.0	5	0.6	7.9	43.2	0.00	0.93
	Max	3392	52.3	203.7	32	0.6	15.1	3392	52.3	203.7	87.8	0.02	1.00

Condés et al., 2018; Pretzsch et al., 2020; Steckel et al., 2020).

2.2. Competition measures

The effect of competition was analyzed using the basal area, G, as well as the basal area of the trees with diameter larger than or equal to the target tree, BAL (Wykoff, 1990). Both indicators were used considering all species together or splitting them up into the different species in the mixtures, which allows us to study the different inter-specific competition effects (Hypothesis H2). To take into account the species-specific carrying capacities (del Río et al., 2016), the relative values of these indicators were calculating considering the maximum basal area of each species estimated according to the basic models (equations Eqn 1 and Eqn 2), i.e. without considering climate influence, provided by (de Prado et al., 2020). We avoided the use of climate-dependent maximum stand density index as the models by de Prado et al. (2020) include different climate variables depending on the species, which could influence the results.

$$RG_{sp} = \frac{G_{sp}}{G_{maxsp}} \quad (1)$$

$$RBAL_{sp} = \frac{BAL_{sp}}{G_{maxsp}} \quad (2)$$

Total relative basal area and total relative basal area of larger trees were then calculated as the sum of the corresponding variables by species.

$$RG = \sum_{sp} RG_{sp} \text{ and } RBAL = \sum_{sp} RBAL_{sp} \quad (3)$$

where G_{sp} is the basal area of the species sp in the plot and G_{maxsp} represents the maximum basal area for each species estimated considering the quadratic mean diameter of each species in the plot and the maximum size-density equations. Note that RG in mixed stands can be larger than 1.

Table 2

Summary of main characteristics of the trees in monospecific and mixed stands. d is breast height diameter, id annual increment of diameter, and RBAL the relative basal area of the larger trees (see section 2.2), sd is the standard deviation, min and max are minimum and maximum values, respectively.

			Monospecific Stands					Mixed Stands				
N° trees			d	id	RBAL	RBAL	RBAL	d	id	RBAL	RBAL	RBAL
			cm	cm/year		pine	beech	cm	cm/year		pine	beech
Pine pine/beech	# monosp	Mean	26.4	0.29	0.41	0.41	0.00	29.3	0.27	0.34	0.27	0.07
	9021	Sd	10.7	0.19	0.33	0.33	0.01	11.8	0.19	0.27	0.21	0.13
	# mixed	Min	7.5	-0.20	0.01	0.01	0.00	7.5	-0.24	0.01	0.01	0.00
	3318	Max	94.5	1.60	2.07	2.07	0.08	76.4	1.31	1.72	1.16	1.12
Beech pine/beech	# monosp	Mean	30.1	0.22	0.47	0.00	0.46	23.7	0.23	0.48	0.19	0.28
	4933	Sd	15.4	0.18	0.36	0.00	0.36	14.5	0.19	0.33	0.21	0.26
	# mixed	Min	7.5	-0.22	0.01	0.00	0.01	7.5	-0.16	0.01	0.00	0.01
	2478	Max	128.9	1.95	2.21	0.04	2.21	121.0	1.83	1.84	1.34	1.50
N° trees			d	id	RBAL	RBAL	RBAL	d	id	RBAL	RBAL	RBAL
			cm	cm/year		pine	oak	cm	cm/year		pine	oak
Pine pine/oak	# monosp	Mean	23.4	0.26	0.37	0.37	0.00	22.6	0.31	0.34	0.29	0.05
	2353	Sd	9.7	0.17	0.31	0.31	0.01	9.5	0.19	0.29	0.26	0.07
	# mixed	Min	7.5	-0.18	0.01	0.01	0.00	7.5	-0.19	0.01	0.01	0.00
	1063	Max	77.7	1.46	1.95	1.95	0.04	79.6	1.40	1.50	1.41	0.67
Oak pine/oak	# monosp	Mean	27.0	0.24	0.32	0.00	0.32	19.2	0.20	0.37	0.14	0.23
	904	Sd	15.9	0.20	0.25	0.00	0.25	10.7	0.17	0.28	0.19	0.24
	# mixed	Min	7.7	-0.11	0.01	0.00	0.01	7.5	-0.17	0.01	0.00	0.01
	673	Max	203.7	1.58	1.40	0.01	1.40	80.5	1.83	1.53	1.42	1.25

In addition, for testing differences between monospecific and mixed stands the proportion by area of each species was calculated as:

$$P_{sp} = \frac{RG_{sp}}{RG} \tag{4}$$

2.3. Potential growth models

Following the potential-modifier modelling approach used by several authors (Quicke et al., 1994; Canham et al., 2004; Uriarte et al., 2004), the individual growth rate can be formulated by separating the growth into two components: the potential growth rate and the modifiers that may reduce this maximum. To test hypotheses H1 and H2 we apply this approach, fitting the tree growth model in two steps or sub-models, the potential growth model (H1) and the competition reduction model (H2). The variable used to describe the tree growth was the individual basal area growth, which was formulated as the product of the potential basal area growth, igP , and the competition reduction, C :

$$ig = igP \cdot C \tag{5}$$

The potential basal area growth was considered to depend on tree size following the Hugershoff (1936) growth curve: $igP = a \cdot g^b e^{cg}$, but removing the last factor as the c parameter was non-significant. In contrast to some model structures which assume a common maximum growth rate for each species (Gómez-Aparicio et al., 2011) we considered that potential growth is species-specific and could be affected by site conditions (Pretzsch and Biber, 2010). Additionally, to test our first hypothesis (H1) we consider that the potential tree growth could be different in monospecific and mixed stands. Hence, we formulate the analytical expression of the potential growth function as a linearized model modified by including the Martonne humidity index as an indicator of site climate conditions and the species proportion by area to consider the differences between monospecific and mixed stands:

$$\log(ig_{spij}) = a_0 + a_1 \cdot \log(M_j) + a_2 \cdot \log(P_{spj}) + b \cdot \log(g_{ij}) + \varepsilon_{ij} \tag{6}$$

where ig_{spij} represents the basal area increment of the tree i of the species sp with a basal area g_{ij} growing in the plot j ; M_j was the Martonne aridity index and P_{spj} was the proportion of the species itself in the same plot j ; a_0 , a_1 , a_2 , and b were the parameters to be estimated.

For each species in each mixture, a potential growth model was fit using a linear quantile regression with a percentile of 0.99, which is not exactly the maximum but is an adequate approximation for representing

the potential growth of faster growing trees. The models were fit using the function “rq” from the “quantreg” R-package (Koenker, 2013). AIC was used for comparison between models.

2.4. Competition reduction models

The growth reduction due the competition, obtained from Eqn 5 as $C = ig/igP$, was assumed to be a consequence of both basal area, expressing stand density or growing stock, and basal area of larger trees, reflecting the one-sided competition by larger trees. The different carrying capacities per species were always taken into account, i.e. RG and $RBAL$. Thus, the competition reduction model was expressed as:

$$\frac{ig}{igP} = C = f(RG, RBAL, M) \tag{7}$$

where igP represents the potential increment estimated for every tree through the potential growth models developed according to section 2.3.

This expression can be easily linearized and therefore, the competition reduction models were formulated for each species as:

$$\log(C_{spij}) = c_0 + c_1 \cdot RG_j + c_2 \cdot RBAL_{ij} + c_3 \cdot RBAL_{ij} \cdot M_j + \varepsilon_{ij} \tag{8}$$

where C_{spij} represents the ratio between the actual basal area increment and the potential increment for the tree i of the species sp growing in the plot j , where the relative basal area was RG_j and the relative basal area of the trees larger than the tree i was $RBAL_{ij}$. M is the Martonne aridity index used in this study as a measure of climate conditions, included in the model as a modifier of the $RBAL$ term to test our third hypothesis (H3), and c_0 , c_1 , c_2 and c_3 are the parameters to be estimated. To avoid bias in the models, negative values of the ratio $C_{spij} = ig_{spij}/igP_{spij}$ were also included by correcting them, so $C_{spij}' = C_{spij} + 1 - \min(C_{spij})$.

The RG and $RBAL$ terms in Eqn 8 were also partitioned into the species components of each mixture and compared to the model without partitioning. Independent variables were incorporated into the model if they statistically significantly improved the quality of fit of the model as assessed at the $\alpha = 0.05$ significance level and Akaike’s criteria (AIC) was used to compare results and to select from among the different model structures, i.e., those in which the competition variables were not separated into species. Since the data came from a hierarchical structure, with several trees measured in the same plot j , a linear mixed model was fit using the function “lmm” from the “lme4” R-package

(Bates et al., 2015), with the plot as the grouping structure of the random effects included in the intercept. The growth predicted through the application of potential and competition reduction models was compared with the observed growth by calculating statistical errors, i.e. mean error (ME), mean absolute error (MAE) and root mean standard error (RMSE).

3. Results

3.1. Potential growth models

Potential growth models were always better in terms of AIC when including both the site humidity conditions and the proportion of species (Supplementary Table 1), although some of the variables were non-significant at 95%.

In general, for all the species and mixtures, the models showed a negative effect of the target species proportion (Table 3), meaning that trees growing in mixed stands could reach a higher potential growth than those growing in monospecific stands, so our hypothesis H1 can be rejected. The effect of humidity was always positive, trees reaching greater maximum growth in more humid sites.

The potential growth of the studied broadleaves was greater than that of the pine, especially for the larger tree sizes (Fig. 1), but this average effect was modified to varying degrees by site humidity and species proportion, depending on species and mixtures. For the pine/beech mixtures, the potential growth of pine was very similar when growing in a mixture or in monospecific stands, while the effect of humidity was more notable. In contrast, the potential growth of beech trees was more influenced by species proportion than by humidity. For the pine/oak mixtures, both pine and oak species reached higher potential growth in mixtures than in monospecific stands, although for oak the effect was not significant at 0.05 (p value = 0.0767). Moreover, the effect of humidity on the potential growth was more important for the pine/oak mixture than for the pine/beech mixture, despite the fact that the former was distributed along a shorter range of Martonne aridity values.

3.2. Competition reduction

The competition reduction models were better in terms of AIC when separating the RBAL term by species, while the separation of RG resulted in greater AICs values. Interactions between RBAL terms and Martonne aridity index also improved the goodness-of-fit of the models for all species and mixtures (Supplementary Table 2).

Except for pine in pine/oak mixtures, relative basal area always reduced potential growth. The RBALs also reduced the growth although their effect was species specific, with the RBAL of some admixed species not being significant. Moreover, the RBALs effects were modified by site humidity, although to different degrees according to species and mixtures (Table 4). These results indicate that the hypotheses H2 and H3 can

Table 3
Parameter estimates and p-values for the potential growth models.

	AIC		Intercept	log(g)	log(M)	log(P)
Pine	35,714	Value	0.6043	0.3552	0.2182	-0.0380
		Pr(> t)	0.0475	0.0000	0.0028	0.0640
Pine/ Beech	23,178	Value	-0.8085	0.6041	0.1455	-0.2275
		Pr(> t)	0.0168	0.0000	0.0515	0.0000
Pine	9910	Value	-0.1543	0.3951	0.3153	-0.2599
		Pr(> t)	0.6932	0.0000	0.0035	0.0000
Pine/ Oak	5071	Value	-3.9272	0.7307	0.7428	-0.2012
		Pr(> t)	0.0095	0.0000	0.0471	0.0767

also be rejected.

In the pine/beech mixtures, the competition with larger trees of both pine and beech species reduced the basal area growth of pines, the effect of pine competition being greater (Fig. 2). In contrast, pine competition did not reduce the potential growth of beech trees, although it was reduced by the intra-specific competition. For both species in the mixture, the influence of humidity was such that it enhanced the effect of the RBALs, i.e., greater effects at more humid sites.

In the pine/oak mixtures, only the intra-specific competition of larger trees was significant for both pine and oak, the effect of humidity being the opposite to that of the other mixture studied, i.e., humidity reduced the effect of intra-specific competition (Fig. 2).

It should be noted that Fig. 2 only shows the fixed effects of the competition reduction model related to the analysed variables, but the reduction could be much greater or slighter depending on other factors not included in the models, which were captured by the random effects (Supplementary Fig. 1).

The combined application of both potential growth and competition reduction models for dominant trees (RBAL = 0) resulted in lower basal area growth for monospecific stands in comparison to mixtures, this effect being slightly smaller for the greater RG values, except in the case of pines in pine/oak mixtures (Supplementary Fig. 3). The scarce beech admixture effect on dominant pines is worthy of note. As previously mentioned, the intra-specific RBAL competition always had a greater negative effect on species basal area growth than the inter-specific RBAL, so the pattern of admixture effect with stand density changes in the case of intermediate or suppressed trees (Fig. 3). The combined or net effect of species admixture also varies with site climate conditions, the effect being greater at more humid sites for beech and at less humid sites for pine and oak mixtures (Fig. 3).

4. Discussion

Our results based on NFI data from monospecific and mixed stands of two-species combinations demonstrate that species admixture can modify the potential growth of a given species, with positive effects on the studied species and mixtures. For a tree with a reference size of 25 cm, the increase due to species admixture (proportion = 0.5) ranges between 2.7% and 19.7%. We also identified that species admixture reduced competition in the studied species, with lower inter-specific than intra-specific competition effects, and that these effects were mediated by climate conditions. Under average humidity conditions, for a suppressed tree with a diameter of 25 cm and a RBAL of 0.2, the competition reduction effect due to admixed species (proportion = 0.5 in RG and RBAL) varies from 2.6% to 6.8%, whereas the total species admixture effect varies from 5.3% to 27.9%. Accordingly, the results indicate that the three hypotheses can be rejected. These findings reflect the complexity of between-species interactions and highlight the need to consider the possible effects of species mixing on potential growth when analyzing and modelling species interactions in terms of tree growth (Pretzsch, 2022a). The main focus of our discussion, therefore, is whether our approach provides additional information about between species complementarity, and the possible ecological causes behind our findings.

4.1. Methodological approach

In growth models using the potential modifier approach, the potential tree growth is expected to reflect the growth of free-growing trees (e.g. Canham et al., 2004). Thus, the findings that species mixing can increase species potential tree growth could suggest that admixture facilitates tree growth (Pretzsch, 2022a), as facilitation may increase the growth of all the individuals, including those trees growing under very low competition. However, this assumption depends on the definition and method used to estimate potential tree growth, which is always challenging (Weiskittel et al., 2011). Within the available alternatives,

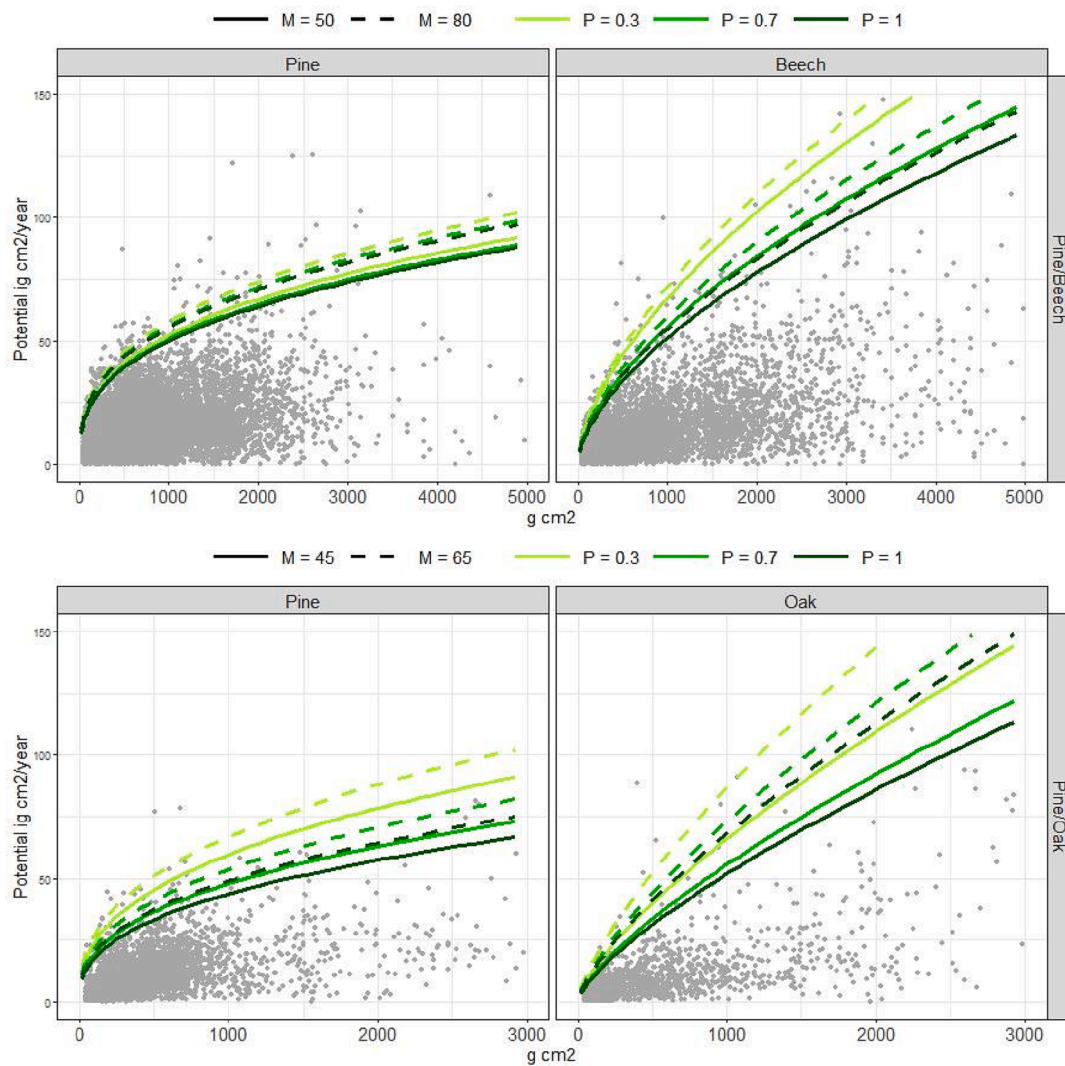


Fig. 1. Variation in potential basal area growth according to tree size ($g\ cm^2$), the species proportion by area of the target species (P) and the site humidity conditions (M $mm/^\circ C$).

Table 4

Parameter estimates and p-values (below) for the competition reduction models, c_0 is the independent coefficient, R^2_m and R^2_c represent the marginal and potential r-squared respectively and StdRnd is the standard deviation of the random effects.

Pine/Beech	R^2_m	R^2_c	StdRnd	c_0	RG	RBAL _{pine}	RBAL _{beech}	RBAL _{pine:M}	RBAL _{beech:M}
Pine	0.1246	0.4933	0.0867	0.5076	-0.0454	-0.0815	ns	-0.0010	-0.0014
Beech	0.1681	0.4900	0.0825	0.5219	-0.1435	ns	ns	ns	-0.0018
				0.0000	0.0000				0.0000
Pine/Oak	R^2_m	R^2_c	StdRnd	c_0	RG	RBAL _{pine}	RBAL _{oak}	RBAL _{pine:M}	RBAL _{oak:M}
Pine	0.0901	0.5584	0.1064	0.4805	ns	-0.3229	ns	0.0030	ns
Oak	0.1654	0.4968	0.0923	0.4481	-0.1727	ns	-0.3193	ns	0.0045
				0.0000	0.0000		0.0004		0.0068

we discarded the use of trees growing in open areas and of dominant trees, as they present some inconveniences. Trees growing in open areas usually display different allometry than trees growing in forest stands (Pretzsch et al., 2015a) and may not adequately represent the potential growth of trees growing in forest stands, not even that of trees barely exposed to competition from neighboring trees (Pretzsch, 2022a). Moreover, it would be difficult to find such trees under similar site conditions in SNFI data. Regarding dominant trees, which trees to select as dominant is not obvious in mixed stands or in uneven-aged structures

without existing standardized methods (del Río et al., 2016), there can be frequent changes in social hierarchy within the stand lifetime and can be highly influenced by previous history (Pretzsch, 2021). We chose to use quantile regression, assuming that the growth of trees with greater growth rates for given size and site conditions represent potential tree growth, as i) it is an objective method because only the choice of the tau level is arbitrary (Ducey and Knapp, 2010), and ii) it allows the use of Spanish NFI database, where the available information on individual tree competition status is limited, because not all individual trees are

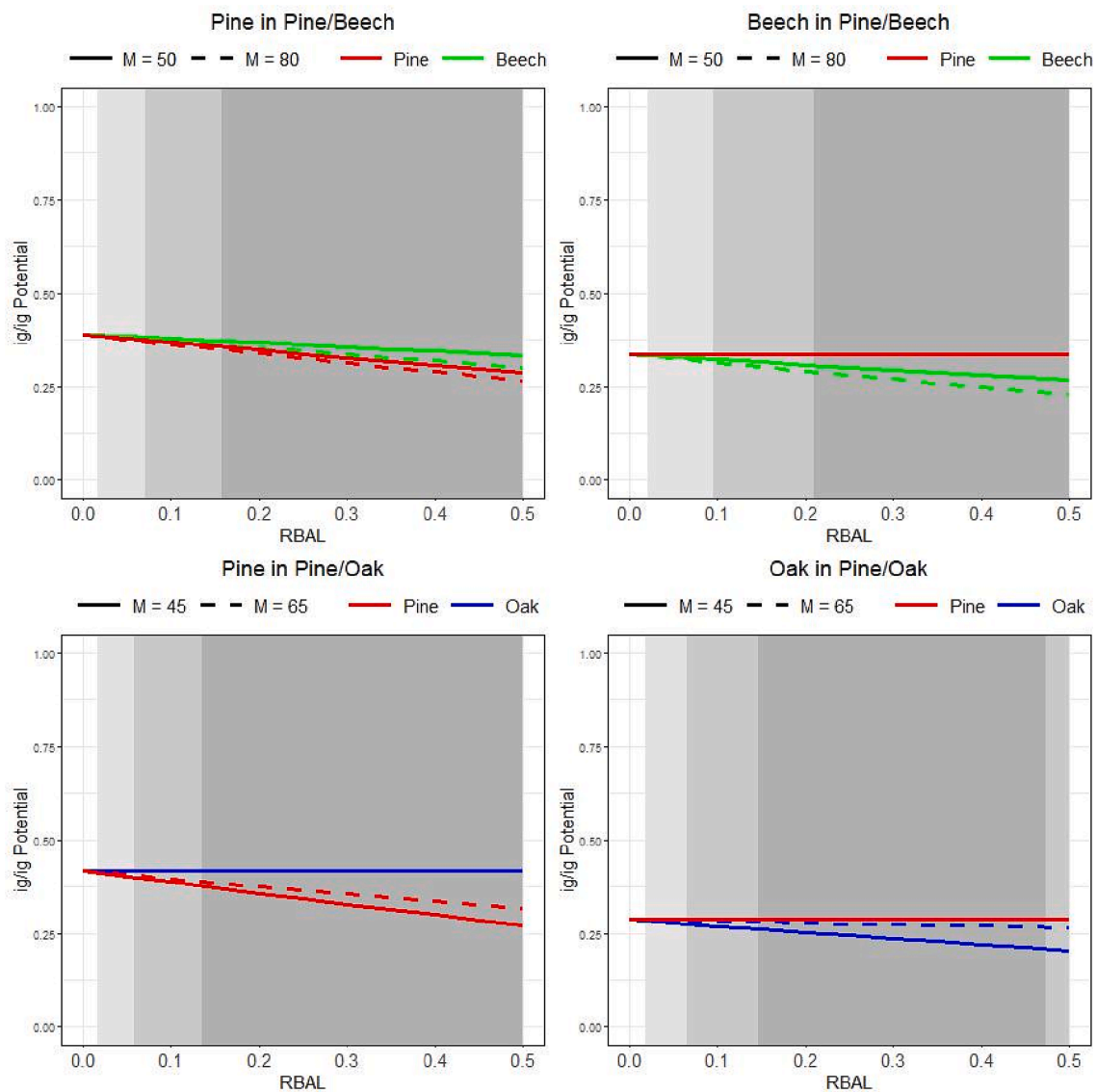


Fig. 2. Effect of the competition of larger trees (RBAL) and site humidity conditions (M) on the reduction of potential growth of trees growing in mixed stands ($P = 0.5$) with a relative basal area $RG = 0.5$. Colored lines represent the competition from larger trees being from one of the two species in the mixture. Shaded areas show the RBAL data distribution, darker shading marking the percentiles 25–75% of data values.

measured (Alberdi et al., 2016). However, the extent to which quantile regression predicts the growth of trees growing without competition is still uncertain. We selected a high τ value of 99 % (Pretzsch and Biber, 2010), so it could be expected that the model reflect the growth of trees with low level of competition, but it was not always the case (Supplementary Fig. 4). Larger trees with greater growth are not always those with lower long-term local density (Forrester 2021), so other factors different to low competition can be influencing on trees growing faster, such as possible differences in stand history, genotypes, microsites or ages (Lamonica et al., 2020), as well as the possible presence of facilitation (Binkley et al., 2003).

Once the species admixture effect on potential tree growth is considered, the lower inter- as opposed to intra-specific effect on the competition modifier may be interpreted as competition reduction caused by species niche complementarity (Pretzsch, 2022a). However, due to abovementioned limitations of potential growth definition, the effects on potential tree growth and on the competition modifier identified could also be affected by competition reduction and facilitation, respectively. Therefore, the magnitude of the facilitation and competition reduction cannot be determined by our approach, although it might

provide a more reliable approach than other model structures to identify the presence of facilitation, besides of competition reduction.

Our modelling approach presents certain limitations inherent to the database used. Potential tree growth not only depends on tree size and environmental conditions but can also vary with development stage (Genet et al., 2011). As information on tree age is not available in the Spanish NFI, we explored the use of quadratic mean diameter of the stand as a surrogate of age (Condés et al 2013), although this approach was unsuccessful. Additionally, the Spanish NFI plot structure does not allow the use local neighborhood tree competition indices, which could provide a more accurate description of inter-specific competition (Stadt et al., 2007). Despite these limitations, the evaluation statistics obtained (Supplementary Fig. 2) are good when compared with other tree basal area growth models based on NFI data (Gómez-Aparicio et al., 2011; Mina et al., 2018).

4.2. Species interactions and underlying ecological causes

For the two mixtures we found that species mixing results in positive effects on both tree potential growth and competition (lower inter- than

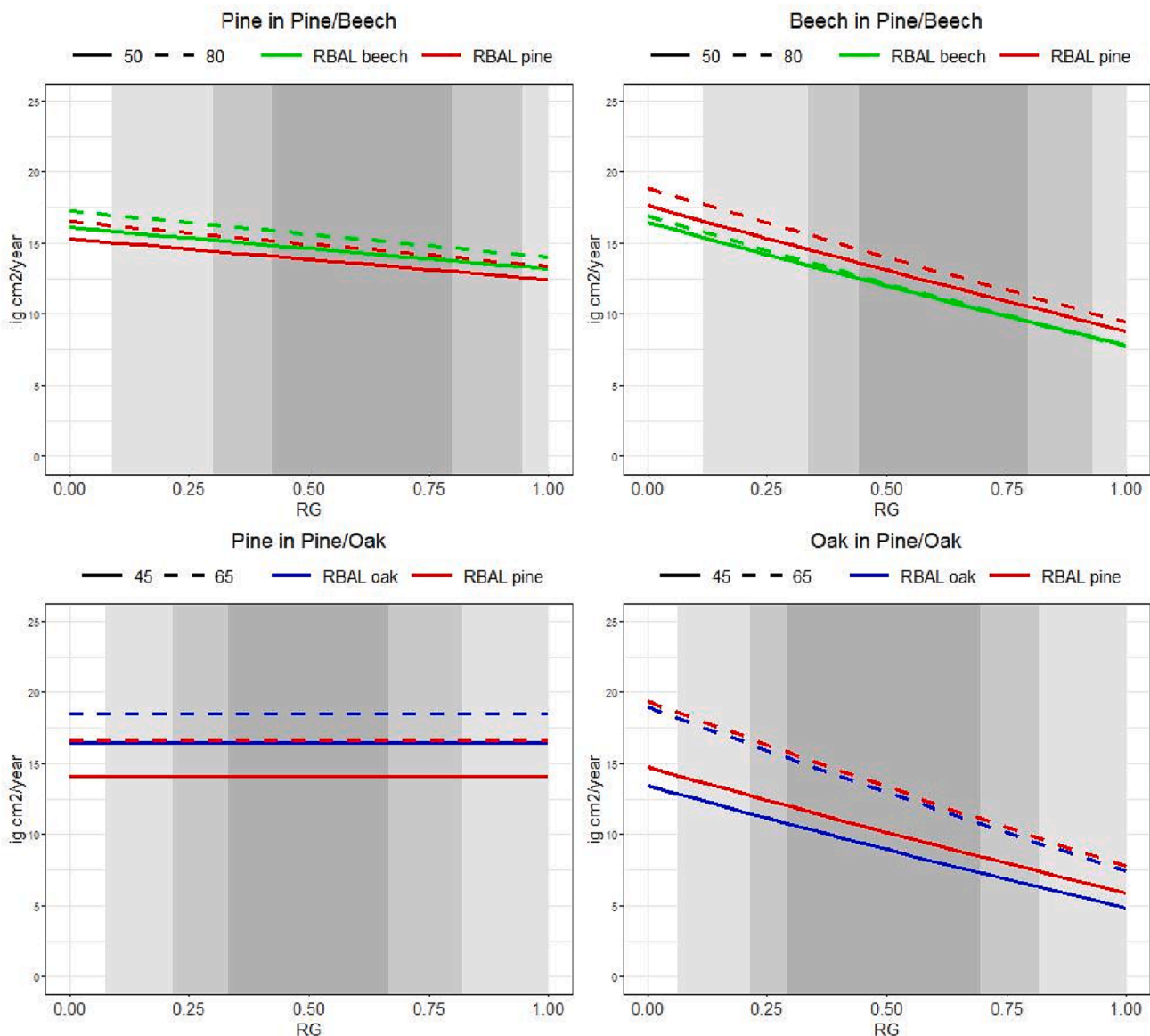


Fig. 3. Combined effect of potential growth, relative basal area (RG), and competition reduction on the basal area growth of dominated trees (RBAL = 0.2) with competition coming from inter or intra-specific trees in a stand with species proportion by area of $P = 0.5$, and two different values for site humidity conditions. Shaded areas show the RG data distribution, darker shading marking the percentiles 25–75% of data values.

intra-specific competition) for both species. The mutually positive effects on potential growth of pine and beech agrees with recent results reported by Pretzsch (2022a). For Scots pine and oak mixtures, no previous studies have addressed the effect of species admixture on potential tree growth. The general finding that species admixture increases potential tree growth suggests that there could be stand-wise facilitative effects by mixing species due to an improvement in growing conditions (soil and bioclimatic conditions) (Pretzsch, 2022b), although, as abovementioned, competition reduction may be probably influencing on potential growth.

The greater potential tree growth of pine when growing in mixtures with beech or oak could be the result of nutrient cycle enrichment related to the higher nutrient concentration of broad-leaves in comparison to pine needles, as well as to higher litterfall due to greater canopy packing, faster decomposition rates (Pretzsch et al., 2016; de Streel et al., 2021; Yeste et al., 2021). Possible mechanisms underlying pine facilitative effects on beech and oak could include protection against late frosts, improvement in the amounts of specific nutrients, or indirect effects on soil microorganisms (Conn and Dighton, 2000;

Gillespie et al., 2021).

Intra- and inter-specific competition effects on tree growth have previously been analysed for pine-beech and pine-oak mixtures, although not all studies report similar effects. Studies of pine-beech mixtures found that inter-specific competition was always lower than intra-specific competition for beech. However, in the case of pine the effects were found to be lower (as in our case) or in some cases, inter-specific competition was found to be greater than intra-specific competition (del Río et al., 2014a; Condés and del Río, 2015; González de Andres et al., 2018; de Prado et al., 2022). For pine-oak mixtures, results from previous studies also show different levels of competition reduction for both species, although in general greater intra- as opposed to inter-competition effects were identified (Perot et al., 2010; Ngo Bieng et al., 2013; Strieder and Vospernik, 2021).

Competition reduction between Scots pine and beech/oak may be linked to niche spatio-temporal complementarity as a result of differences in light requirements and use associated with each species (Bravo-Oviedo and Montero, 2008; Forrester et al., 2018); canopy space used due to differences in crown allometry and plasticity (Barbeito et al.,

2017; del Río et al., 2019; Pretzsch, 2019); root systems and water uptake/use (González de Andres et al., 2018; Bello et al., 2019); and leaf/root phenologies (Konôpka et al., 2005; Michelot et al., 2011; Strieder and Vospernik, 2021).

4.3. Climate effect on tree growth and species interactions

In some growth models that assume a constant value for potential tree growth, site conditions are only considered as modifiers of this value (Canham et al., 2004; Gómez-Aparicio et al., 2011). We preferred the alternative of including site climatic conditions directly in the potential tree growth formulation, as potential tree growth may depend on site conditions (Pretzsch and Biber, 2010). Our results corroborate this assumption, with greater potential growth in more humid sites, this effect being stronger in pine-oak than in pine-beech mixtures. Nevertheless, we also tested the effect of climate conditions on competition modifiers and found that site climatic conditions modified the intensity of intra- and inter-specific competition (Forrester et al., 2013; Condés and del Río, 2015), albeit with contrasting patterns among mixtures. As regards the data for the pine-beech mixture, competition by larger trees increased with humidity, both for the intra- and inter-specific competition terms, although due to the lower inter-specific competition it results in greater competition reduction with increasing humidity. These results suggest greater competition for light at humid sites (Weiner and Thomas, 1986; Pretzsch and Biber, 2010), which might be partially mitigated by mixing species (Forrester, 2014). The lower intra-specific competition by larger trees at more humid sites according to the pine-oak data could reflect a greater impact of competition for belowground resources than of competition for light where oak is growing, and that this belowground competition is also size-asymmetric (Bello et al., 2019). Accordingly, competition reduction also increases as humidity decreases, suggesting that complementarity might be mainly at belowground level (Forrester, 2014). This notion is supported by the enhanced performance of the two species in mixed as opposed to pure stands under extreme drought events, as reported by Steckel et al. (2020), while it contradicts the findings of Haberstroh and Werner (2022) as well as those of Pretzsch et al. (2020), who reported variations in the mixing effect across differing site conditions. However, these studies cover pine-oak mixtures across Europe, with a smaller range of Martonne aridity index values (21–63 mm °C⁻¹) than in our study (Table 1). It is important to consider the fact that we used average climate data for the second half of the last century in order to describe site climate conditions (Gonzalo Jiménez, 2010), although climate during the chosen SNFI periods could possibly influence the results.

4.4. Consequences and perspectives

Competition reduction can increase with stand density, when between-tree competition is more important and the benefit of complementarity might be greater (Forrester et al., 2013; Brunner and Forrester, 2020). However, the evidence as regards the association between species admixture and increased potential tree growth suggests that positive species-mixing effects can also occur at low stand densities (Condés et al., 2013; Pretzsch, 2022a). This has important implications for managing mixtures, as the benefits of mixing species, often linked to higher densities and greater canopy packing (Williams et al., 2017; Pretzsch, 2022b), may still be present even after heavy thinnings are applied. This implies that a broader range of silvicultural regimes could be applied in mixed as opposed to monospecific stands without suffering important losses in productivity. A number of studies have addressed the effect of stand density on species interactions (e.g. Garber and Maguire, 2004; Condés et al., 2013; Brunner and Forrester, 2020; Pretzsch, 2022b), but our findings highlight the need for further research covering a broad range of stand densities and different species mixtures. In order to confirm the positive effects of species admixture on potential tree growth, future research should involve not only thinning experiments in

mixed stands (Pretzsch and Zenner, 2017), but also other experiments aimed at testing species interactions at different densities, from open-grown trees to high densities, e.g. Nelder trials (Ruano et al., 2022). Such experiments, aimed at determining the presence of facilitation without competition, are still lacking (Forrester and Bausch, 2016), but would allow us to differentiate between facilitation and competition reduction. Beyond such experiments, undoubtedly more studies focusing on measuring directly the processes that may cause facilitation and competition reduction are also needed.

According to our results, tree-growth models should integrate the effects of species interactions in both the potential tree growth and the competition modifier. If other structures that do not include potential tree growth are used in empirical models, our findings indicate that beyond the effect of species admixture on competition, a direct effect on tree growth should be included, for instance, in the intercept or interacting with other model covariables. In process based models, mixing effects should principally be inherently integrated, as they generally focus on carbon acquisition and include all major resource limitations on tree growth (Pretzsch et al., 2015c). However, data from mixed-species stands in order to perform systematic parameterization and evaluation is still scarce (Blanco et al., 2015).

5. Conclusions

We found that the admixture resulted in positive effects on the potential tree growth for the two studied mixtures, although the magnitude of the effects differed, being notably lower in the case of pine in pine/beach mixtures. This result contradicts the H1 hypothesis that potential tree growth will be similar in mixed and monospecific stands. Moreover, we found that intra- and inter-specific competition effects were species specific and mixture dependent. Consequently, the H2 hypothesis that intra- and inter-specific competition will have the same reduction effect on potential tree growth should be also rejected. Finally, in contradiction to the H3 hypothesis, we found that the humidity conditions modified not only the potential growth but also modulated the effects of the inter- and intra-specific interactions on the reduction of potential growth.

Our results highlight the importance of integrating the effect of species interactions in both the potential tree growth and the competition modifier when the aim of the research is to further our understanding of species interactions and complementarity effects.

CRedit authorship contribution statement

Sonia Condés: Conceptualization, Data curation, Methodology, Validation, Formal analysis. **Hans Pretzsch:** Formal analysis. **Miren del Río:** Conceptualization, Data curation, Methodology, Validation, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

Acknowledgements

This study was supported by the Spanish Ministerio de Ciencia e Innovación, project PID2021- 821 1262750B-C21/C22.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.120997>.

References

- Alberdi, I., Sandoval, V., Condés, S., Cañellas, I., Vallejo, R., 2016. El Inventario Forestal Nacional español, una herramienta para el conocimiento, la gestión y la conservación de los ecosistemas forestales arbolados. *Revista Ecosistemas* 25, 88–97.
- Ammer, C., 2016. Unraveling the importance of inter- and intraspecific competition for the adaptation of forests to climate change. In: *In, Progress in Botany*, Vol. 78. Springer, pp. 345–367.
- Barbeito, I., Dassot, M., Bayer, D., Collet, C., Drössler, L., Löf, M., del Río, M., Ruiz-Peinado, R., Forrester, D.I., Bravo-Oviedo, A., 2017. Terrestrial laser scanning reveals differences in crown structure of *Fagus sylvatica* in mixed vs. pure European forests. *For. Ecol. Manage.* 405, 381–390. <https://doi.org/10.1016/j.foreco.2017.09.043>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* 67, 1–48.
- Begon, M., Harper, J.L., Townsend, C.R., 1986. *Ecology. Individuals, populations and communities*. Blackwell scientific publications.
- Bello, J., Hasselquist, N.J., Vallet, P., Kahmen, A., Perot, T., Koroboulesky, N., 2019. Complementary water uptake depth of *Quercus petraea* and *Pinus sylvestris* in mixed stands during an extreme drought. *Plant Soil* 437, 93–115. <https://doi.org/10.1007/s11104-019-03951-z>.
- Binkley, D., Senock, R., Bird, S., Cole, T.G., 2003. Twenty years of stand development in pure and mixed stands of *Eucalyptus saligna* and nitrogen-fixing *Facaltaria moluccana*. *For. Ecol. Manage.* 182, 93–102.
- Blanco, J.A., González de Andrés, E., San Emeterio, L., Lo, Y.H., 2015. Modelling mixed forest stands: Methodological challenges and approaches. *Dev Environ Model* 27, 189–215. <https://doi.org/10.1016/B978-0-444-63536-5.00009-0>.
- Bravo-Oviedo, A., Montero, G., 2008. Descripción de los caracteres culturales de las principales especies forestales de España. In: *Compendio de selvicultura aplicada en España*. INIA-Ministerio de Educación y Ciencia, Madrid.
- Bravo-Oviedo, A., Pretzsch, H., Río, M.d., 2018. Mixed forests' future. In: *Dynamics, Silviculture and Management of Mixed Forests*. Springer, pp. 397–412.
- Brunner, A., Forrester, D.I., 2020. Tree species mixture effects on stem growth vary with stand density - An analysis based on individual tree responses. *For. Ecol. Manage.* 473 <https://doi.org/10.1016/j.foreco.2020.118334>.
- Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78, 1958–1965.
- Canham, C.D., LePage, P.T., Coates, K.D., 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Can. J. For. Res.* 34, 778–787.
- Coates, K.D., Canham, C.D., LePage, P.T., 2009. Above-versus below-ground competitive effects and responses of a guild of temperate tree species. *J. Ecol.* 97, 118–130.
- Condés, S., del Río, M., 2015. Climate modifies tree interactions in terms of basal area growth and mortality in monospecific and mixed *Fagus sylvatica* and *Pinus sylvestris* forests. *Eur J Forest Res* 134, 1095–1108. <https://doi.org/10.1007/s10342-015-0912-0>.
- Condés, S., Del Río, M., Sterba, H., 2013. Mixing effect on volume growth of *Fagus sylvatica* and *Pinus sylvestris* is modulated by stand density. *For. Ecol. Manage.* 292, 86–95. <https://doi.org/10.1016/j.foreco.2012.12.013>.
- Condés, S., Vallet, P., Bielak, K., Bravo-Oviedo, A., Coll, L., Ducey, M.J., Pach, M., Pretzsch, H., Sterba, H., Vayreda, J., del Río, M., 2017. Climate influences on the maximum size-density relationship in Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) stands. *For. Ecol. Manage.* 385, 295–307. <https://doi.org/10.1016/j.foreco.2016.10.059>.
- Condés, S., Sterba, H., Aguirre, A., Bielak, K., Bravo-Oviedo, A., Coll, L., Pach, M., Pretzsch, H., Vallet, P., del Río, M., 2018. Estimation and Uncertainty of the Mixing Effects on Scots Pine-European Beech Productivity from National Forest Inventories Data. *Forests* 9.
- Conn, C., Dighton, J., 2000. Litter quality influences on decomposition, ectomycorrhizal community structure and mycorrhizal root surface acid phosphatase activity. *Soil Biol. Biochem.* 32, 489–496. [https://doi.org/10.1016/S0038-0717\(99\)00178-9](https://doi.org/10.1016/S0038-0717(99)00178-9).
- de Prado, D.R., San Martín, R., Bravo, F., de Aza, C.H., 2020. Potential climatic influence on maximum stand carrying capacity for 15 Mediterranean coniferous and broadleaf species. *For. Ecol. Manage.* 460, 12. <https://doi.org/10.1016/j.foreco.2019.117824>.
- de Prado, D.R., Riofrío, J., Aldea, J., Bravo, F., de Aza, C.H., 2022. Competition and climate influence in the basal area increment models for Mediterranean mixed forests. *For. Ecol. Manage.* 506 <https://doi.org/10.1016/j.foreco.2021.119955>.
- de Strel, G., Ammer, C., Annighöfer, P., Barbeito, I., Bielak, K., Bravo-Oviedo, A., Brazaitis, G., Buraczyn, W., Collet, C., Hurt, V., Kurylyak, V., den Ouden, J., Pach, M., Pretzsch, H., Skrzyszewski, J., Sramek, V., Stankeviciute, J., Strelcova, K., Svoboda, M., Verheyen, K., Zlatanov, T., Ponette, Q., 2021. Mixing has limited impacts on the foliar nutrition of European beech and Scots pine trees across Europe. *For. Ecol. Manage.* 479 <https://doi.org/10.1016/j.foreco.2020.118551>.
- del Río, M., Condés, S., Pretzsch, H., 2014a. Analyzing size-symmetric vs. size-asymmetric and intra- vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. *For. Ecol. Manage.* 325, 90–98.
- del Río, M., Schütze, G., Pretzsch, H., 2014b. Temporal variation of competition and facilitation in mixed species forests in Central Europe. *Plant Biol.* 16, 166–176. <https://doi.org/10.1111/plb.12029>.
- del Río, M., Pretzsch, H., Alberdi, I., Bielak, K., Bravo, F., Brunner, A., Condés, S., Ducey, M.J., Fonseca, T., von Lupke, N., Pach, M., Peric, S., Perot, T., Souidi, Z., Spathelf, P., Sterba, H., Tijardovic, M., Tomé, M., Vallet, P., Bravo-Oviedo, A., 2016. Characterization of the structure, dynamics, and productivity of mixed-species stands: review and perspectives. *Eur J Forest Res* 135, 23–49. <https://doi.org/10.1007/s10342-015-0927-6>.
- del Río, M., Bravo-Oviedo, A., Ruiz-Peinado, R., Condés, S., 2019. Tree allometry variation in response to intra- and inter-specific competitions. *Trees-Struct. Funct.* 33, 121–138. <https://doi.org/10.1007/s00468-018-1763-3>.
- del Río, M., Lof, M., Bravo-Oviedo, A., Jactel, H., 2021. Understanding the complexity of mixed forest functioning and management: Advances and perspectives. *For. Ecol. Manage.* 489 <https://doi.org/10.1016/j.foreco.2021.119138>.
- Ducey, M.J., Knapp, R.A., 2010. A stand density index for complex mixed species forests in the northeastern United States. *For. Ecol. Manage.* 260, 1613–1622. <https://doi.org/10.1016/j.foreco.2010.08.014>.
- Fichtner, A., Hårdtle, W., Li, Y., Bruelheide, H., Kunz, M., von Oheimb, G., 2017. From competition to facilitation: how tree species respond to neighbourhood diversity. *Ecol. Lett.* 20, 892–900. <https://doi.org/10.1111/ele.12786>.
- Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *For. Ecol. Manage.* 312, 282–292. <https://doi.org/10.1016/j.foreco.2013.10.003>.
- Forrester, D.I., Vanclay, J.K., Forrester, R.I., 2011. The balance between facilitation and competition in mixtures of *Eucalyptus* and *Acacia* changes as stands develop. *Oecologia* 166, 265–272. <https://doi.org/10.1007/s00442-011-1937-9>.
- Forrester, D.I., Ammer, C., Annighöfer, P.J., Barbeito, I., Bielak, K., Bravo-Oviedo, A., Coll, L., del Río, M., Drössler, L., Heym, M., Hurt, V., Lof, M., den Ouden, J., Pach, M., Pereira, M.G., Plaga, B.N.E., Ponette, Q., Skrzyszewski, J., Sterba, H., Svoboda, M., Zlatanov, T.M., Pretzsch, H., 2018. Effects of crown architecture and stand structure on light absorption in mixed and monospecific *Fagus sylvatica* and *Pinus sylvestris* forests along a productivity and climate gradient through Europe. *J. Ecol.* 106, 746–760. <https://doi.org/10.1111/1365-2745.12803>.
- Forrester, D.I., Bauhus, J., 2016. A Review of Processes Behind Diversity-Productivity Relationships in Forests. *Curr Rep* 2, 45–61. <https://doi.org/10.1007/s40725-016-0031-2>.
- Forrester, D.I., Kohnle, U., Albrecht, A.T., Bauhus, J., 2013. Complementarity in mixed-species stands of *Abies alba* and *Picea abies* varies with climate, site quality and stand density. *For. Ecol. Manage.* 304, 233–242. <https://doi.org/10.1016/j.foreco.2013.04.038>.
- Forrester, D.I., 2017. Ecological and physiological processes in mixed versus monospecific stands. In: *Mixed-species forests*. Springer, pp. 73–115.
- Garber, S.M., Maguire, D.A., 2004. Stand productivity and development in two mixed-species spacing trials in the central Oregon Cascades. *For. Sci.* 50, 92–105.
- Genet, A., Wernsdörfer, H., Jonard, N., Pretzsch, H., Rauch, M., Ponette, Q., Nys, C., Legout, A., Ranger, J., Vallet, P., 2011. Ontogeny partly explains the apparent heterogeneity of published biomass equations for *Fagus sylvatica* in central Europe. *For. Ecol. Manage.* 261, 1188–1202.
- Gillespie, L.M., Hättenschwiler, S., Milcu, A., Wambsgans, J., Shihan, A., Fromin, N., 2021. Tree species mixing affects soil microbial functioning indirectly via root and litter traits and soil parameters in European forests. *Funct. Ecol.* 35, 2190–2204. <https://doi.org/10.1111/1365-2435.13877>.
- Gómez-Aparicio, L., García-Valdés, R., Ruiz-Benito, P., Zavala, M.A., 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. *Global Change Biol.* 17, 2400–2414. <https://doi.org/10.1111/j.1365-2486.2011.02421.x>.
- González de Andrés, E., Camarero, J.J., Blanco, J.A., Imbert, J.B., Lo, Y.H., Sanguesa-Barreda, G., Castillo, F.J., 2018. Tree-to-tree competition in mixed European beech-Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions. *J. Ecol.* 106, 59–75. <https://doi.org/10.1111/1365-2745.12813>.
- Gonzalo Jiménez, J., 2010. Diagnóstico fitoclimática de la España Peninsular: hacia un modelo de clasificación funcional de la vegetación y de los ecosistemas peninsulares españoles. Organismo Autónomo de Parques Nacionales.
- Haberstroh, S., Werner, C., 2022. The role of species interactions for forest resilience to drought. *Plant Biol.* 24, 1098–1107. <https://doi.org/10.1111/plb.13415>.
- Hasenauer, H., Kindermann, G., Steinmetz, P., 2006. *The Tree Growth Model MOSES 3.0*. In: Hasenauer, H. (Ed.), *Sustainable Forest Management: Growth Models for Europe*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 64–70.
- Helms, J., 1998. *The dictionary of forestry*. Society of American Foresters. Bethesda, MD 210.
- Hugershoff, R., 1936. *Die mathematischen Hilfsmittel der Kulturingenieurs und Biologen*.
- Kelty, M.J., 1992. Comparative productivity of monocultures and mixed-species stands. In: Kelty M.J., L.B.C., Oliver, C.D. (Eds.), *The Ecology and silviculture of mixed-species forests*. Kluwer Academic Publishers, Dordrecht (The Netherlands), pp. 125–141.
- Koenker, R., 2013. *Quantreg: quantile regression*. R package version 5.
- Konópka, B., Yuste, J.C., Janssens, I.A., Ceulemans, R., 2005. Comparison of fine root dynamics in scots pine and pedunculate oak in sandy soil. *Plant Soil* 276, 33–45. <https://doi.org/10.1007/s11104-004-2976-3>.
- Lamonic, D., Pagel, J., Valdés-Correcher, E., Bert, D., Hampe, A., Schurr, F.M., 2020. Tree potential growth varies more than competition among spontaneously established forest stands of pedunculate oak (*Quercus robur*). *Ann Forest Sci* 77, 1–18.
- Liu, J., Burkhart, H.E., 1994. Modelling inter- and intra-specific competition in loblolly pine (*Pinus taeda* L.) plantations on cutover, site-prepared lands. *Ann. Bot.* 73, 429–435.

- Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412, 72–76.
- Martonne, E., 1926. Une Nouvelle Fonction Climatologique: L'Indice d'Aridité (A New climatological function: The Aridity Index). *La Météorologie* 2, 449–458.
- Michelot, A., Eglin, T., Dufrene, E., Lelarge-Trouverie, C., Damesin, C., 2011. Comparison of seasonal variations in water-use efficiency calculated from the carbon isotope composition of tree rings and flux data in a temperate forest. *Plant Cell Environ* 34, 230–244. <https://doi.org/10.1111/j.1365-3040.2010.02238.x>.
- Mina, M., Huber, M.O., Forrester, D.I., Thüring, E., Rohner, B., 2018. Multiple factors modulate tree growth complementarity in Central European mixed forests. *J. Ecol.* 106, 1106–1119. <https://doi.org/10.1111/1365-2745.12846>.
- Ngo Bieng, M.A., Perot, T., de Coligny, F., Goreaud, F., 2013. Spatial pattern of trees influences species productivity in a mature oak-pine mixed forest. *Eur J Forest Res* 132, 841–850. <https://doi.org/10.1007/s10342-013-0716-z>.
- Perot, T., Goreaud, F., Ginisty, C., Dhôte, J.F., 2010. A model bridging distance-dependent and distance-independent tree models to simulate the growth of mixed forests. *Ann Forest Sci* 67. <https://doi.org/10.1051/forest/2010004>.
- Pretzsch, H., 2019. The Effect of Tree Crown Allometry on Community Dynamics in Mixed-Species Stands versus Monocultures A Review and Perspectives for Modeling and Silvicultural Regulation. *Forests* 10, 810.
- Pretzsch, H., 2021. The social drift of trees. Consequence for growth trend detection, stand dynamics, and silviculture. *Eur J Forest Res* 140, 703–719. <https://doi.org/10.1007/s10342-020-01351-y>.
- Pretzsch, H., 2022a. Facilitation and competition reduction in tree species mixtures in Central Europe: Consequences for growth modeling and forest management. *Ecol. Model.* 464 <https://doi.org/10.1016/j.ecolmodel.2021.109812>.
- Pretzsch, H., 2022b. Mixing degree, stand density, and water supply can increase the overyielding of mixed versus monospecific stands in Central Europe. *For. Ecol. Manage.* 503 <https://doi.org/10.1016/j.foreco.2021.119741>.
- Pretzsch, H., Biber, P., 2010. Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. *Can. J. For. Res.* 40, 370–384.
- Pretzsch, H., Biber, P., Uhl, E., Dahlhausen, J., Rötzer, T., Caldentey, J., Koike, T., van Con, T., Chavanne, A., Seifert, T., du Toit, B., Farnden, C., Pauleit, S., 2015a. Crown size and growing space requirement of common tree species in urban centres, parks, and forests. *Urban for Urban Gree* 14, 466–479. <https://doi.org/10.1016/j.ufug.2015.04.006>.
- Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Schweig, J., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Vanhellefont, M., Verheyen, K., Wellhausen, K., Zlatanov, T., Bravo-Oviedo, A., 2015b. Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *Eur J Forest Res* 134, 927–947. <https://doi.org/10.1007/s10342-015-0900-4>.
- Pretzsch, H., del Río, M., Schütze, G., Ammer, C., Annighöfer, P., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., 2016. Mixing of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) enhances structural heterogeneity, and the effect increases with water availability. *For. Ecol. Manage.* 373, 149–166.
- Pretzsch, H., Forrester, D.I., Bauhus, J., 2017. *Mixed-Species Forests*. Springer.
- Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, C., Ehbrecht, M., Bielak, K., Bravo, F., Ordóñez, C., Collet, C., Vast, F., Drössler, L., Brazaitis, G., Godvod, K., Jansons, A., de-Dios-Garcia, J., Löf, M., Aldea, J., Korboulewsky, N., Reventlow, D.O.J., Nothdurft, A., Engel, M., Pach, M., Skrzyszewski, J., Pardos, M., Ponette, Q., Sitko, R., Fabrika, M., Svoboda, M., Černý, J., Wolff, B., Ruiz-Peinado, R., del Río, M., 2020. Stand growth and structure of mixed-species and monospecific stands of Scots pine (*Pinus sylvestris* L.) and oak (*Q. robur* L., *Quercus petraea* (Matt.) Liebl.) analysed along a productivity gradient through Europe. *Eur J Forest Res* 139, 349–367. <https://doi.org/10.1007/s10342-019-01233-y>.
- Pretzsch, H., Forrester, D.I., Rötzer, T., 2015c. Representation of species mixing in forest growth models A review and perspective. *Ecol. Model.* 313, 276–292.
- Pretzsch, H., Zenner, E.K., 2017. Toward managing mixed-species stands: from parametrization to prescription. *For Ecosyst* 4, 1–17. <https://doi.org/10.1186/s40663-017-0105-z>.
- Pretzsch, H., 2017. Individual tree structure and growth in mixed compared with monospecific stands. In: *Mixed-species forests*. Springer, pp. 271–336.
- Quicke, H.E., Meldahl, R.S., Kush, J.S., 1994. Basal area growth of individual trees - a model derived from a regional longleaf pine growth study. *For. Sci.* 40, 528–542.
- Ruano, I., de Aza, C.H., Bravo, F., 2022. Effect of density on Mediterranean pine seedlings using the Nelder wheel design: analysis of biomass production. *Forestry* 95, 711–726. <https://doi.org/10.1093/forestry/cpac024>.
- Sanchez-Gonzalez, M., del Río, M., Canellas, I., Montero, G., 2006. Distance independent tree diameter growth model for cork oak stands. *For. Ecol. Manage.* 225, 262–270. <https://doi.org/10.1016/j.foreco.2006.01.002>.
- Soares, P., Tomé, M., 2003. GLOBTREE: an individual tree growth model for Eucalyptus globulus in Portugal. In: *Modelling forest systems. Workshop on the interface between reality, modelling and the parameter estimation processes, Sesimbra, Portugal, 2-5 June 2002* (pp. 97–110). Wallingford UK: CABI Publishing.
- Stachowicz, J.J., 2001. Mutualism, facilitation, and the structure of ecological communities. *Bioscience* 51, 235–246. [https://doi.org/10.1641/0006-3568\(2001\)051\[0235:Mfatso\]2.0.Co;2](https://doi.org/10.1641/0006-3568(2001)051[0235:Mfatso]2.0.Co;2).
- Stadt, K.J., Huston, C., Coates, K.D., Feng, Z.L., Dale, M.R.T., Lieffers, V.J., 2007. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. *Ann Forest Sci* 64, 477–490. <https://doi.org/10.1051/forest:2007025>.
- Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G., Černý, J., Coll, L., Collet, C., Ehbrecht, M., Jansons, A., Nothdurft, A., Pach, M., Pardos, M., Ponette, Q., Reventlow, D.O.J., Sitko, R., Svoboda, M., Vallet, P., Wolff, B., Pretzsch, H., 2020. Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) - Site water supply and fertility modify the mixing effect. *For. Ecol. Manage.* 461. <https://doi.org/10.1016/j.foreco.2020.117908>.
- Strieder, E., Vospemnik, S., 2021. Intra-annual diameter growth variation of six common European tree species in pure and mixed stands. *Silva Fenn.* 55.
- Uriarte, M., Condit, R., Canham, C.D., Hubbell, S.P., 2004. A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *J. Ecol.* 92, 348–360. <https://doi.org/10.1111/j.0022-0477.2004.00867.x>.
- Vandermeer, J.H., 1992. *The ecology of intercropping*. Cambridge University Press.
- Weiner, J., Thomas, S.C., 1986. Size variability and competition in plant monocultures. *Oikos* 47, 211–222. <https://doi.org/10.2307/3566048>.
- Weiskittel, A.R., Hann, D.W., Kershaw Jr, J.A., Vanclay, J.K., 2011. *Forest growth and yield modeling*. John Wiley & Sons.
- Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C., Reich, P.B., 2017. Spatial complementarity in tree crowns explains overyielding in species mixtures. *Nat Ecol Evol* 1, 63. <https://doi.org/10.1038/s41559-016-0063>.
- Wykoff, W.R., 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. *For. Sci.* 36, 1077–1104.
- Yeste, A., Blanco, J.A., Imbert, J.B., Zozaya-Vela, H., Elizalde-Arbilla, M., 2021. Pinus sylvestris L. and Fagus sylvatica L. effects on soil and root properties and their interactions in a mixed forest on the Southwestern Pyrenees. *For. Ecol. Manage.* 481 <https://doi.org/10.1016/j.foreco.2020.118726>.