



Competitive effect, but not competitive response, varies along a climatic gradient depending on tree species identity



Teresa Valor^{a,b,*}, Lluís Coll^{a,b}, David I. Forrester^{c,d}, Hans Pretzsch^e, Miren del Río^{f,g}, Kamil Bielak^h, Bogdan Brzezicki^h, Franz Binderⁱ, Torben Hilmers^e, Zuzana Sitková^j, Roberto Tognetti^k, Aitor Ameztegui^{a,b}

^a Department of Agricultural and Forest Sciences and Engineering (DCEFA), University of Lleida, Av. Alcalde Rovira Roure 191, E25198 Lleida, Spain

^b Joint Research Unit CTFC – AGROTECNIO – CERCA, Ctra. Sant Llorenç Km. 2, 25280, Solsona, Spain

^c Swiss Federal Institute of Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903, Birmensdorf, Switzerland

^d CSIRO Land and Water, GPO Box 1700, Canberra, ACT, 2601, Australia

^e Chair of Forest Growth and Yield Science, School of Life Sciences Weihenstephan, Technical University of Munich, Hans-Carl-Von-Carlowitz-Platz 2, 85354, Freising, Germany

^f Forest Research Center, INIA-CSIC, Ctra. A Coruña Km 7.5, 28040, Madrid, Spain

^g IuFOR, Sustainable Forest Management Research Institute, University of Valladolid & INIA, Spain

^h Department of Silviculture, Institute of Forest Sciences, Warsaw University of Life Sciences, Nowoursynowska 159/34, 02776, Warsaw, Poland

ⁱ Bavarian State Institute of Forestry (LWF), Hans-Carl-von-Carlowitz-Platz 1, D-85354, Freising, Germany

^j National Forest Centre, Forest Research Institute, T.G. Masaryka 22, 960 01, Zvolen, Slovakia

^k Faculty of Agricultural, Environmental and Food Sciences, Free University of Bozen-Bolzano Piazza Università, 1 I-39100, Bolzano

ARTICLE INFO

Keywords:

Competition coefficient
Competition reduction
Interspecific competition
Intraspecific competition
Mixing effects
Mixed species forest
Neighbourhood models
Plant-plant interactions

ABSTRACT

Background: Understanding the role of species identity in interactions among individuals is crucial for assessing the productivity and stability of mixed forests over time. However, there is limited knowledge concerning the variation in competitive effect and response of different species along climatic gradients. In this study, we investigated the importance of climate, tree size, and competition on the growth of three tree species: spruce (*Picea abies*), fir (*Abies alba*), and beech (*Fagus sylvatica*), and examined their competitive response and effect along a climatic gradient.

Methods: We selected 39 plots distributed across the European mountains with records of the position and growth of 5,759 individuals. For each target species, models relating tree growth to tree size, climate and competition were proposed. Competition was modelled using a neighbourhood competition index that considered the effects of inter- and intraspecific competition on target trees. Competitive responses and effects were related to climate. Likelihood methods and information theory were used to select the best model.

Results: Our findings revealed that competition had a greater impact on target species growth than tree size or climate. Climate did influence the competitive effects of neighbouring species, but it did not affect the target species' response to competition. The strength of competitive effects varied along the gradient, contingent on the identity of the interacting species. When the target species exhibited an intermediate competitive effect relative to neighbouring species, both higher inter- than intraspecific competitive effects and competition reduction occurred along the gradient. Notably, species competitive effects were most pronounced when the target species' growth was at its peak and weakest when growing conditions were far from their maximum.

Conclusions: Climate modulates the effects of competition from neighbouring trees on the target tree and not the susceptibility of the target tree to competition. The modelling approach should be useful in future research to expand our knowledge of how competition modulates forest communities across environmental gradients.

* Corresponding author. Department of Agricultural and Forest Sciences and Engineering (DCEFA), University of Lleida, Av. Alcalde Rovira Roure 191, E25198 Lleida, Spain.

E-mail address: teresa.valor@ctfc.cat (T. Valor).

<https://doi.org/10.1016/j.fecs.2024.100176>

Received 15 November 2023; Received in revised form 8 February 2024; Accepted 9 February 2024

2197-5620/© 2024 The Authors. Publishing services by Elsevier B.V. on behalf of KeAi Communications Co. Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

On average, mixed forests provide more ecological and social functions than monospecific ones (Bravo-Oviedo et al., 2018; Coll et al., 2018). Among these functions, several studies have reported a positive relationship between forest productivity and tree species diversity (Zhang et al., 2012; Pretzsch et al., 2015), although with important differences among biomes (Ammer, 2019; Paquette and Messier, 2011; Vilà et al., 2013). The net effect of diversity on productivity is determined by a complex interplay between competition (when one tree species in a mixture exerts a negative effect on another), facilitation (when the effect is positive), and competition reduction (when interspecific competition is lower than intraspecific competition) (Vandermeer, 1989). At the individual level, tree size, climate, tree–tree interactions and soil resources are the most influential factors determining tree growth and have been the focus of numerous studies (e.g., Lebourgeois et al., 2005; Das, 2012; Begović et al., 2020). Similarly, the effect of tree size on the sensitivity of many species to changes in climate has also been widely addressed (de Luis et al., 2009; Mérian and Lebourgeois, 2011). However, much less is known about how tree size and climate (in particular) interact with the competitive ability of a given tree species. The competitive ability of a species can be studied in terms of both its competitive response (the ability of a species to tolerate the suppression of its growth by neighbours) and its competitive effect (the ability of a species to suppress the growth of other individuals by depleting resources) (Goldberg, 1990). Although it has been demonstrated that the competitive response of a number of species can vary along a climatic and size gradient (Gómez-Aparicio et al., 2011; Carnwath and Nelson, 2016), to our knowledge, few studies have analysed how the competitive effect of interacting species varies along a climatic gradient. Besides, the limited research conducted on this subject has focused on herbaceous plants (Goldberg et al., 1999) or juveniles (Fichtner et al., 2017) and only Coates et al. (2013) have studied adult trees along a soil gradient.

Understanding how the competitive ability of a species interacts with climate requires complex modelling approaches. These models need to consider key factors that directly affect tree growth (i.e., competition, climate and tree size), the potential indirect effects of climate and tree size on the competitive response (e.g., Gómez-Aparicio et al., 2011; Carnwath and Nelson, 2016) and the effect of interacting species. To the best of our knowledge, our study is the first to investigate adult trees considering variations in both forms of competition – competitive response and the competitive effect – along a climatic gradient.

Competition reduction and facilitation are collectively referred to as complementarity effects (Forrester and Bauhus, 2016), which are typically studied by comparing the growth of a given species in a mixed stand with that in a pure stand (e.g., Pretzsch and Schütze, 2008; Vallet and Pérot, 2011) or of individual trees in stands with different proportions of other species (e.g., Bottero et al., 2021; Gillerot et al., 2021). Complementarity effects in adult trees vary along spatial and temporal gradients of climatic conditions and resource availability and depend strongly on the pool of species involved (e.g., Forrester and Bauhus, 2016; Mina et al., 2018a; Toïgo et al., 2015) and on the level of study (stand or individual trees) (Condés et al., 2022). However, relative importance of complementarity effects for forest productivity is rarely identified or quantified (Barry et al., 2019; but see Pretzsch, 2022). In this study, we address this problem partially by fitting spatially explicit neighbourhood models of individual tree growth using tree data from 39 permanent monitoring plots covering a large proportion of mountainous regions in Central and Eastern Europe. Neighbourhood models allow parameters to vary non-linearly and can also account for interspecific competitive effects (Canham et al., 2004), i.e., the per capita effect of one species on another (Freckleton and Watkinson, 2001), allowing us to identify and quantify competition reduction (one side of the complementarity effect) along a climatic gradient. We focus on Norway spruce (*Picea abies* (L.) Karst., hereafter spruce), silver fir (*Abies alba* Mill., hereafter fir) and European beech (*Fagus sylvatica* L., hereafter beech), which coexist at the

interface between lowland beech forests and spruce-dominated alpine forest, covering a wide range of site conditions, elevations and climates (Hilmers et al., 2020). Previous research on mixtures of these species has shown that complementarity effects vary by stand, climate, site conditions and stress effects (Brunner and Forrester, 2020; Forrester et al., 2013; Houpert et al., 2018; Mina et al., 2018a; Uhl et al., 2021; Condés et al., 2022).

We aim to answer the following questions: (1) What is the strength of evidence for an effect of climate, tree size and competition on target species growth? (2) Does the response and/or competitive effect of interacting species vary with climate and tree size? By answering these questions, we aim to assess the role of species identity and climatic conditions on the competitive response and effect ability. In the case of the competitive effects, the goal is to determine the strength of plant–plant interactions and whether interspecific competitive effects are lower than intraspecific ones (i.e., competition reduction) or not.

2. Materials and methods

2.1. Study area

This study is based on the tree stem diameter data of 39 long-term experimental plots covering most of the mountainous regions of Europe (i.e., Poland, Germany, Slovakia and Switzerland) where spruce, fir and beech mixed forests occur (Fig. 1). To analyse the growth of our target species, we selected two or at most three consecutive censuses of each plot. These plots were surveyed on average 6 times (minimum 3 and maximum 15 times), every 8 years (minimum 3 and maximum 15 years) and between 1925 and 2016. The basal area ($\text{m}^2 \cdot \text{ha}^{-1}$) of these plots did not change by more than 10% between censuses (Supplementary Material Table S1). The altitude of the plots ranged from 425 to 1,463 m a.s.l., the average annual temperature ranged from 4.4 to 7.0 °C, and the annual precipitation ranged from 706 to 2,021 mm (Table S1).

2.2. Data set

All trees in the selected plots were georeferenced and their diameters at breast height (DBH) were measured at each repeated full survey. To avoid edge effects, we limited our growth analyses to target species (i.e., spruce, fir and beech) that were more than 10 m from the edge of a plot. The area of the plots ranged from 1,560 to 19,960 m^2 . All target species were well represented in 27 of the 39 plots. In the remaining plots, some of the target species comprised less than 20% of the total basal area of the stand (Supplementary Material Table S1). For each target tree, we calculated the diameter growth (in centimetres per year) between two surveys by dividing the total increase in the DBH (in centimetres) by the number of years between the two survey dates. The number of target trees selected per target species and the mean diameter growth of each target species are shown in Table 1. One of the strengths of this dataset is that while the average structural characteristics of each species are similar (Table 1), there is a wide range of neighbourhood densities, tree sizes/heights and species diversity within a single plot.

All trees within a plot with a DBH of ≥ 7.5 cm and that were ≤ 10 m from a target tree were considered neighbours regardless of the species' identity. We assumed that trees with a DBH < 7.5 cm are not effective competitors. This threshold is typically considered in many forest inventories (Ministerio de Agricultura Alimentación y Medio Ambiente, 2019). Furthermore, as part of a conservative strategy, trees that died in the period between two surveys were also considered competing neighbours during this period. For all target tree species, both the average number of neighbours per target tree and the average DBH of the neighbours were similar (Table 1).

Monthly mean temperature and total precipitation data for the study plots for the period 1901–2016 were obtained from the nearest meteorological stations. When local station data were not available, the CRU TS3.10 grid dataset was used (Harris et al., 2014). Thus, we were able to

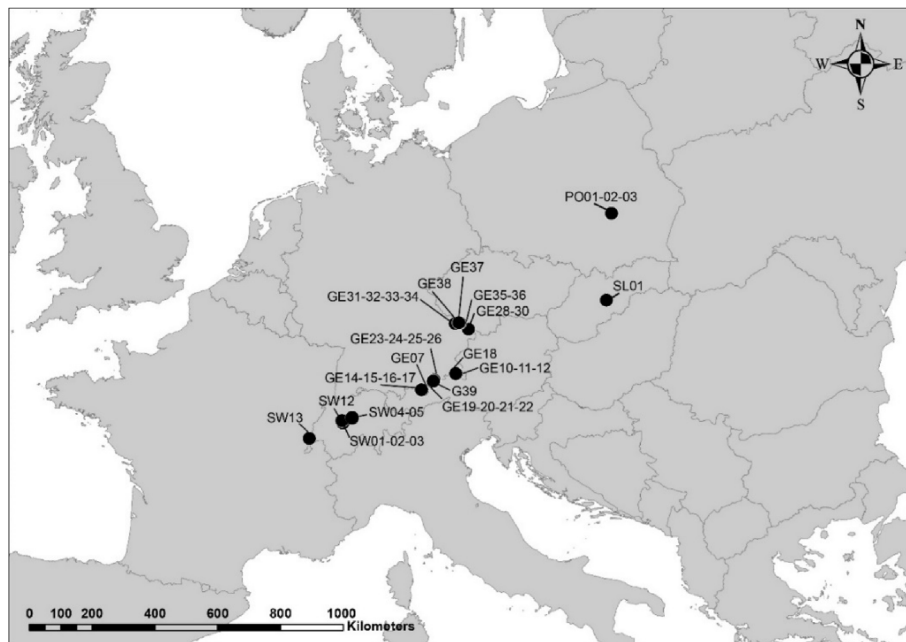


Fig. 1. Location of 39 monitoring plots (black dots) in mixed mountain forests of spruce, fir and beech. The study covered mountain forests in Poland, Germany, Slovakia and Switzerland. See Supplementary Material [Table S1](#) for descriptions of plot data.

account for the elevation correction within similar geographic plot locations (latitude and longitude) at different elevations (Supplementary Material [Table S1](#)). Climate was characterised using the standardised precipitation evaporation index (SPEI) (Vicente-Serrano et al., 2010), which takes into account precipitation and potential evapotranspiration (Vicente-Serrano et al., 2010). We used SPEI because it integrates precipitation and temperature, reducing the number of parameters to be estimated in our modelling approach (see 2.3. Maximum likelihood analysis of tree growth). SPEI was first calculated on a monthly scale by calculating the differences between precipitation and potential evapotranspiration (PET) for each month using the Thornthwaite method (Thornthwaite, 1948). Monthly SPEI values were then aggregated to determine the SPEI for three different time scales: 3, 6 and 12 months. In total, we calculated eight SPEI indices to reflect seasonal (i.e., winter, spring, summer and autumn), growing seasons (i.e., January to June, February to July, and March to August) and interannual variations in drought in our data. As the SPEI variables were highly correlated to be included in a regression model for variable selection, we applied a principal component analysis (PCA) to these eight variables to select the

SPEI index that contained the most variance (Supplementary Material [Fig. S1](#)). The first axis of PCA explained most of the variance, 54.96%, and the second axis explained 17.73% (Supplementary Material [Fig. S1](#)). SPEI from February to July ($\text{SPEI}_{\text{Feb-Jul}}$) was the most representative variable of the first axis and, therefore, was selected for modelling tree growth (Supplementary Material [Fig. S1](#)). The selected time scale and time window have been observed to influence the growth of our target species in regions with climatic conditions similar to those in our study (Gillerot et al., 2021; Vanoni et al., 2016). The mean $\text{SPEI}_{\text{Feb-Jul}}$ value was calculated for each plot and survey interval ([Table 1](#)). Negative values of mean SPEI represent periods of net negative water balance, whereas positive values indicate wet periods. Most census intervals with negative mean $\text{SPEI}_{\text{Feb-Jul}}$ values included years with SPEI values below -1 , representing dry conditions (Supplementary Material [Fig. S2](#)). Mean $\text{SPEI}_{\text{Feb-Jul}}$ was normalised, resulting in an index ranging from 0 to 1, with 0 and 1 representing the minimum and maximum mean $\text{SPEI}_{\text{Feb-Jul}}$ ($\text{nSPEI}_{\text{Feb-Jul}}$), respectively ([Table 1](#)). Normalisation was performed to facilitate comparison between species and to avoid negative values that cause mathematical problems when modelling tree growth.

Table 1

Characteristics of target trees, neighbouring trees and plots at the beginning of the growth period (first survey) of target species. Mean \pm standard deviation (minimum–maximum). DBH, diameter at breast height. $\text{SPEI}_{\text{Feb-Jul}}$, standardised precipitation evapotranspiration index from February to July. $\text{nSPEI}_{\text{Feb-Jul}}$, $\text{SPEI}_{\text{Feb-Jul}}$ normalised.

Characteristics	Spruce	Fir	Beech
No. target trees	2,897	1,145	1,717
DBH (cm)	24.6 \pm 18.0 (3.2–113.7)	27.4 \pm 18.4 (4.5–116.2)	18.6 \pm 14.6 (2.9–89.9)
Diameter growth ($\text{cm}\cdot\text{year}^{-1}$)	0.31 \pm 0.23 (–0.62–1.68)	0.34 \pm 0.30 (–0.05–2.07)	0.22 \pm 0.19 (–0.198–1.67)
Mean No. neighbours per target	30 \pm 15 (3–74)	30 \pm 16 (6–86)	34 \pm 14 (3–91)
DBH (cm)	22.0 \pm 14.3 (7.5–116.1)	23.0 \pm 7.7 (7.5–116.5)	21.8 \pm 17.3 (7.5–116.5)
No. plots	38	34	31
Basal area ($\text{m}^2\cdot\text{ha}^{-1}$)	36.0 \pm 11.5 (19.5–69.0)	36.4 \pm 11.3 (20.0–69.0)	35.8 \pm 12.6 (19.5–69.0)
Tree density ($\text{tree}\cdot\text{ha}^{-1}$)	517 \pm 202 (205–986)	562 \pm 221 (226–1,128)	560 \pm 208 (205–1,128)
No. survey intervals ^a	72	61	57
$\text{SPEI}_{\text{Feb-Jul}}$	0.06 \pm 0.40 (–0.43–1.03)	0.07 \pm 0.28 (–0.43–1.03)	0.02 \pm 0.28 (–0.43–1.03)
$\text{nSPEI}_{\text{Feb-Jul}}$	0.34 \pm 0.28 (0.00–1.00)	0.34 \pm 0.19 (0.00–1.00)	0.31 \pm 0.19 (0.00–1.00)

^a Sample size for SPEI.

2.3. Maximum likelihood analysis of tree growth

To assess our research questions, we built a set of candidate growth models (see 2.3.2. Baseline models and 2.3.3. Alternative models). To investigate question (1) *What is the strength of evidence for an effect of climate, tree size and competition on target species growth?* and question (2) *Does the response and/or competitive effect of interacting species vary with climate and tree size?* We used likelihood methods and the corrected Akaike information criterion (AICc) to select the best fitting model for each target species (see 2.3.1. Modelling strategy) and to estimate the model parameters that would maximise the likelihood of observing the growth data measured in the field (see 2.3.4. Parameter estimation).

See Fig. 2 for a schematic representation of the models constructed to answer our research questions.

2.3.1. Modelling strategy

The AICc was used for model comparison and to guide the choice of the best fitting model for each target species. Models were considered to have similar empirical support when differences in the AICc were less than two units (Burnham and Anderson, 2002). If differences exceeded two units, the model with the lower AICc was considered better, leading to dismissal of the other model. For each target species, the AICc of the full baseline model was compared to baseline models that ignored the influence of either climate, competition, or size, as well as all three factors combined (i.e., the null model). The model with the lowest AICc value was then selected because this indicated stronger empirical support (Burnham and Anderson, 2002).

For each target species, we compared the best baseline model with the full alternative model and alternative models that ignored one or two of the factors introduced into the competitive equation (i.e., the influence of climate and/or tree size on the competitive response and/or the influence of climate on species competitive effects). The AICc values of the best baseline and the best alternative model were compared for each target species, and the model with the lowest AICc value was the best model.

2.3.2. Baseline models

To answer the first research question (i.e., *What is the strength of evidence for an effect of climate, tree size and competition on target tree species growth?*)

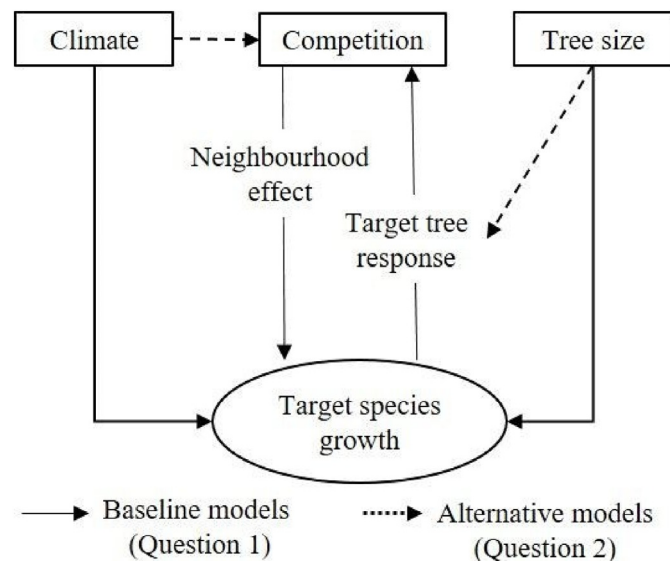


Fig. 2. Schematic representation of the factors whose effects on target tree growth were tested in the baseline (solid lines) and alternative models (dashed line) to answer the following research questions: (1) What is the strength of evidence for an effect of climate, tree size and competition on target tree species growth? (2) Does the response and/or competitive effect of interacting species vary with climate and tree size?

growth?), we modelled growth for each target tree species as a function of several multiplicative components: (1) potential diameter growth (PDG), i.e., maximum PDG; (2) size effect, i.e., the effect of the target tree size on tree growth; (3) climate effect; and (4) competition effect, which takes into account the species identity of neighbours, the number and size of neighbours, and their distance from the target tree:

$$\text{Growth} = \text{PDG} \times \text{Size effect} \times \text{Climate effect} \times \text{Neighbourhood effect} \quad (1)$$

The PDG is estimated as a parameter of the model and represents the maximum diameter growth in cm, that a target tree could achieve under optimal growth conditions. Size, climate and competition effects are scalars that range from 0 to 1 and, thus, reduce the estimated maximum PDG. That is, if target tree size, competition and climate are at levels that maximise tree growth (if their effects are equal to 1), then the observed growth is equal to the estimated potential growth.

Following classic studies that used this approach (Canham et al., 2006; Coates et al., 2009; Gómez-Aparicio et al., 2011; Uriarte et al., 2004), the size effect was modelled with a lognormal function:

$$\text{Size effect} = \exp \left[-\frac{1}{2} \left(\frac{\ln(\text{DBH}/X1_0)}{X1_b} \right)^2 \right] \quad (2)$$

where $X1_0$ represents the target tree size at which maximum growth occurs and $X1_b$ controls the breadth of the function. Depending on the value of $X1_0$, this functional form can be hump-shaped or monotonically increasing/decreasing.

The climate effect was modelled with a univariate Gaussian function:

$$\text{Climate effect} = \exp \left[-\frac{1}{2} \left(\frac{\text{nSPEI}_{\text{Feb-Jul}} - X2_0}{X2_b} \right)^2 \right] \quad (3)$$

where $X2_0$ represents the mean $\text{nSPEI}_{\text{Feb-Jul}}$ at which the maximum PDG occurs, and $X2_b$ is an estimated parameter that controls the breadth of the function.

The competition effect was modelled as a function of a neighbourhood competition index (NCI) using a Weibull function following other studies (Canham et al., 2006; Gómez-Aparicio et al., 2011). The Weibull function assumes that the competition effect on the growth of the target tree decreases monotonically as a function of the NCI:

$$\text{Competition effect} = \exp \left[-a(\text{NCI})^b \right] \quad (4)$$

Here, a and b represent species-specific estimated parameters. a is the exponential decay term, reflecting the target tree sensitivity to competition (i.e., competitive response) and b defines the rate of decrease. When $b = 1$, it is a traditional negative exponential function, and when $b > 1$, the function is sigmoidal, with an initial slow decline as the NCI increases, followed by a steeper decline. The NCI quantifies the net effect of $j = 1, \dots, n$ neighbouring trees within a radius of 10 m of $i = 1, \dots, s$ species on the growth of a target tree z . Following the long tradition of distance-dependent analysis of competition (e.g., Daniels, 1976), the NCI was assumed to vary as a direct function of size and as an inverse function of distance to neighbours. In addition, we assumed that the effects of neighbours on the target tree z vary across species. Accordingly, the net effect of a single neighbour was multiplied by a species-specific competition index (λ) (i.e., the per capita effect of one species on another) (Freckleton and Watkinson, 2001), which ranges from 0 to 1, and accounts for differences among species in their competitive effects on the target tree, so that it can be determined when the interspecific competitive effects are lower than the intraspecific ones (competition reduction) or when they are higher (competition). Species-specific competition coefficients (λ) were estimated only for neighbouring species comprising at least 100 individuals. All other neighbouring species of a target species were grouped into an 'Other species' group. The NCI is given in the following form:

$$NCI = \sum_{i=1}^s \sum_{j=1}^n \lambda_{iz} \frac{DBH_{ij}^{\alpha}}{distance_{ij}^{\beta}} \tag{5}$$

where α and β are parameters estimated by the analyses and determine the shape of the effect that size and distance to a neighbour have on the NCI. To facilitate comparison of the NCI among species, we scaled the NCI for each target species by dividing the NCI calculated for each target tree by the maximum value of the NCI for that species (Canham et al., 2006; Gómez-Aparicio et al., 2011). This produced an index where 0 and 1 represent the minimum and maximum observed NCI, respectively.

2.3.3. Alternative models

To answer the second research question (i.e., *Does the response and/or competitive effect of interacting species vary with climate and tree size?*), we introduced variations into the competition effect equation (Eq. 4) to examine the influence of climate and tree size on the competitive response of species and the influence of climate on the competitive effect of species (second question). First, to test whether the competitive response (i.e., sensitivity to competition) varies as a function of climatic conditions and target tree size, and following Gómez-Aparicio et al. (2011), we allowed the exponential decay term in Eq. 4 (i.e., a , which represents competitive response or sensitivity to competition) to vary as a function of nSPEI_{Feb-Jul} and tree size:

$$a = a' \times nSPEI_{Feb-Jul}^{\sigma} \times DBH^{\gamma} \tag{6}$$

If either σ or γ is 0, then the competitive response (i.e., a) does not vary as a function of climatic conditions (i.e., nSPEI_{Feb-Jul}) and DBH, respectively. If either σ or γ is <0, then the competitive response decreases with nSPEI_{Feb-Jul} and/or DBH, respectively. Finally, if σ or γ is >0, then the competitive response increases with nSPEI_{Feb-Jul} and DBH, respectively. As stated in Gómez-Aparicio et al. (2011), these effects are assumed to be independent of the underlying effect of climate or tree size

Table 2

Comparison of the corrected Akaike information criterion (AICc) of baseline and best alternative models for understanding target species growth. AICc values shown in bold are the best models. The equations used to model the size, competition and climate effects are presented at section 2.3.2 and the variations of the competition equation at section 2.3.3.

Baseline model	Effects	<i>Picea abies</i>	<i>Abies alba</i>	<i>Fagus sylvatica</i>
Species-specific competition with climate	Size Competition Climate	-712.2	-28.5	-1,736.9
Species-specific competition	Size Competition	-516.7	-61.8	-1,851.0
No climate – No competition	Size	-142.5	390.6	-1,035.7
Null	None	-72.5	488.4	-724.8
Best alternative model	Competitive variations			
Species-specific competition with climate	Response varies with tree size Effect varies with climate	-1078.5		
Species-specific competition	Effect varies with climate		-75.8	
Species-specific competition Best model (AICc in bold)	Effect varies with climate			-1,836
Number of parameters		14	11	8
Slope		1.00	0.99	1.00
R ²		0.30	0.40	0.48

Likelihood methods and information theoretic procedures (AICc) were used to select the best growth model. Model selection was performed in two phases. First, for each target species, the full baseline model was compared with baseline models that ignored the effects of climate, competition, or size, or of all three factors (i.e., the null model), and then the model with the lowest AICc value (in italics) was selected. Second, for selected baseline models, we tested alternative models that included variations in the competition equation. These alternative models included terms that allowed the competitive response of target trees to vary with target tree size and/or climate (Eq. 6) and/or the interspecific competitive effect, i.e., the per capita competition coefficient (λ), varied with climate (Eq. 7). The best alternative model is shown for each target species. Finally, we selected the best-fitting growth models from all the models tested (AICc in bold) and reported the total number of parameters, the slope and the R² for the relationship between predicted and observed growth.

on the potential growth of a target species (i.e., climate effect or size effect, in the absence of a competition effect).

Second, to test whether species competitive effects vary as a function of climatic conditions, in Eq. 5, λ was allowed to vary as a function of nSPEI_{Feb-Jul} with a univariate Gaussian function:

$$\lambda_{iz} = \lambda_{iz}' \times \exp \left[-\frac{1}{2} \left(\frac{nSPEI_{Feb-Jul} - X3_0}{X3_b} \right)^2 \right] \tag{7}$$

where X3₀ is the mean nSPEI_{Feb-Jul} at which the maximum species competitive effects occur, and X3_b is an estimated parameter that controls the breadth of the function.

2.3.4. Parameter estimation

Growth values were modelled with a normal distribution. To simulate annealing, a global optimisation procedure was used to determine (i) the most likely parameters (i.e., the parameters that maximise the log-likelihood) given our observed data (Goffe et al., 1994) and (ii) support intervals of two units to assess the strength of evidence for individual maximum likelihood parameter estimates (Edwards, 1992). A support interval is defined as the range of a parameter value that results in a less than two-unit difference in AIC. It is roughly equivalent to a 95% support limit defined using a likelihood ratio test (Hilborn and Mangel, 1997). All analyses were performed using R 4.0.3 and the function “anneal” from the Likelihood package (Murphy, 2012) and several functions from the neighbourhood package (Ameztegui, 2020).

3. Results

3.1. Model comparison and evaluation

For all species, the best models were unbiased, i.e., the slopes of the predicted versus observed values were not significantly different from 1

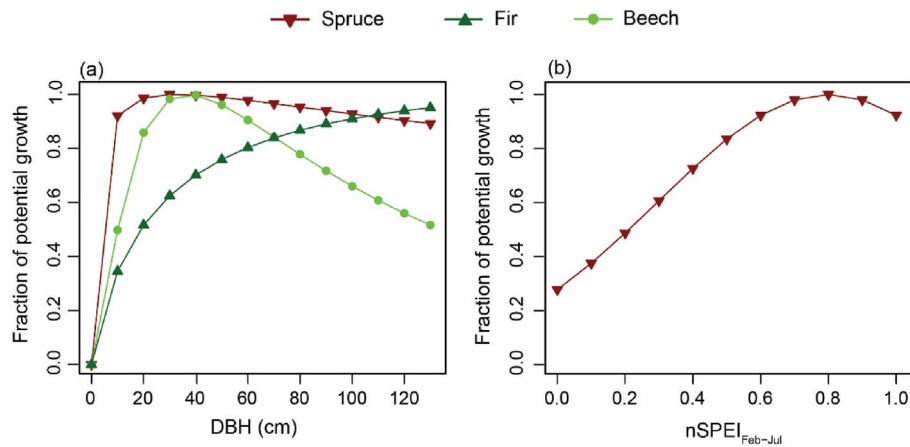


Fig. 3. Predicted effect of (a) target tree size (DBH) on the growth of target species and (b) the normalised standardised precipitation evapotranspiration index from February to July ($nSPEI_{Feb-Jul}$) on spruce growth based on the best growth model (Table 2). The effects of size and climate were calculated without considering competition (i.e., $NCI = 0$).

and explained between 30% and 48% of the variance depending on the target tree species (Table 2, AICc values are shown in bold). Models that best explained target species growth always included the effect of competition and tree size, whereas the effect of climate was only incorporated in the growth model for spruce (Table 2, AICc value shown in bold).

Our first question aimed to assess the strength of evidence for the effect of competition, tree size and climate on the growth of the target species studied. The negative effect of competition had a greater impact on target species growth than other factors given that AICc values decreased more drastically when this factor was included (Table 2, AICc values shown in italics). The best models indicated that the response of a target species to competition was not dependent on climate; however, in the case of spruce, it was influenced by tree size (Table 2, AICc value shown in bold). In addition, the competitive effect of neighbouring species (i.e., λ) on spruce and fir was also modified by climate (Table 2, AICc value shown in bold). In the case of beech, none of the variations proposed in the equation for modelling competition effects improved the model by omitting these variations.

3.2. Effect of tree size and climate on tree growth

Variation in the growth of target species as a function of DBH revealed three different patterns depending on the target species (Fig. 3a). For

spruce and beech, the maximum growth rate was achieved at a similar DBH (i.e., 32.5 and 36.6 cm, respectively). After the maximum growth rate was achieved, growth slowed in both species, but the rate of decline with tree size was much faster for beech than for spruce, whose growth declined more slowly (Fig. 3a). By contrast, the rate of growth of fir increased monotonically with tree size (Fig. 3a).

The climate effect was important for explaining spruce growth, but not the growth of the other target species (Table 2, AIC value shown in bold). For spruce, the effect of $nSPEI_{Feb-Jul}$ on growth was positive, with growth increasing with $nSPEI_{Feb-Jul}$ and reaching a maximum towards the wettest end of the gradient (Fig. 3b).

3.3. Effect of competition

The growth of the three target species decreased steeply with increasing competition (Fig. 4a). All target species showed a negative exponential rather than a sigmoidal decline in growth (i.e., $b \approx 1$) (Supplementary Material Table S2). Fir was less sensitive to competition than beech (Fig. 4a). Spruce was the only species for which the competitive response depended on tree size, with smaller trees being much more sensitive to competition than larger trees (Fig. 4b). By contrast, for all three species, the best models did not include any effect of climatic conditions on the competitive response (i.e., a parameter), that remained constant along the climatic gradient (Table 2). The

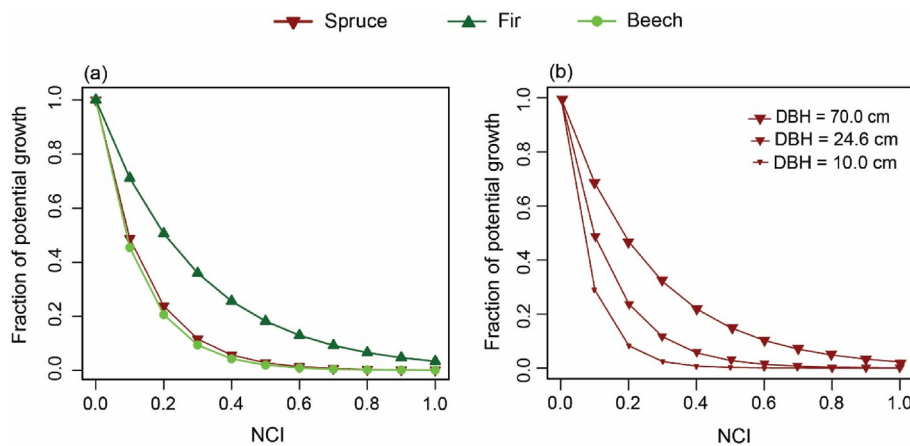


Fig. 4. Predicted effect of the neighbourhood competition index (NCI) on (a) target species growth and (b) spruce of different sizes, showing that the competitive response of spruce is dependent on tree size based on the best growth model (Table 2). In (a) the effect of competition was calculated for an average-sized tree.

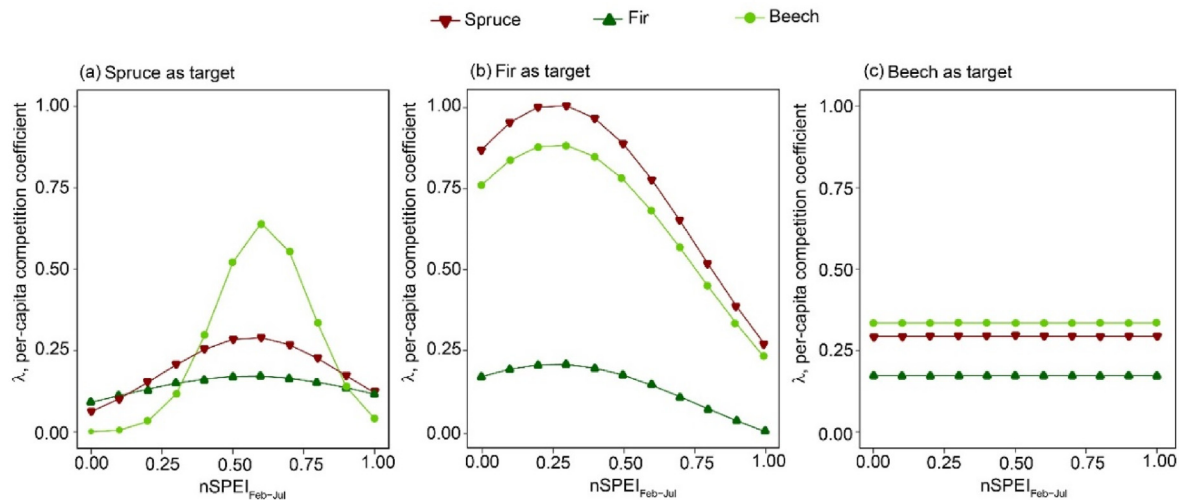


Fig. 5. Predicted variation of the per capita coefficient of competition (λ) of neighbouring species on a target tree of (a) spruce, (b) fir or (c) beech along the $nSPEI_{Feb-Jul}$ gradient. $nSPEI_{Feb-Jul}$, normalised standardised precipitation evapotranspiration index from February to July.

estimated a parameter describing the competitive response was 50.7 for spruce, 3.4 for fir and 7.9 for beech (Supplementary Material Table S2).

3.4. Variations in the interspecific competitive effects along a climatic gradient

The intensity of the competitive effect of spruce and beech, and to a lesser extent of fir, changed along the climatic gradient when they were competing with spruce or fir, but not when spruce and fir interacted with beech (Fig. 5). On average, beech and spruce were much stronger competitors than fir (Fig. 5, $\lambda_{beech} \approx \lambda_{spruce} > \lambda_{fir}$).

The competitive effect of neighbouring species on spruce growth (i.e., λ) was greater under temperate conditions than at either end of the gradient, especially for beech (Fig. 5a). Competition reduction (i.e., lower inter- than intraspecific competitive effects) was observed along the gradient. Under temperate conditions, beech was a stronger competitor than spruce, but fir was a weaker competitor than spruce (Fig. 5a, $\lambda_{beech} > \lambda_{spruce} > \lambda_{fir}$). However, at both ends of the gradient, the competitive hierarchy reversed: beech became a weaker competitor than spruce, whereas the competitive effect of fir on spruce was similar to or slightly greater than that of spruce itself (Fig. 5a, $\lambda_{fir} \geq \lambda_{spruce} > \lambda_{beech}$).

In contrast to spruce, competition reduction was not observed for fir, as the interspecific competitive effects among fir trees were always greater than intraspecific competitive effects, with both increasing in strength as climatic conditions became harsher (Fig. 5b). Moreover, the ranking of species in terms of competitive effects did not change along the climatic gradient (Fig. 5b, $\lambda_{spruce} > \lambda_{beech} > \lambda_{fir}$).

The competitive effect of neighbouring species towards beech was constant along the climatic gradient (Fig. 5c). In the case of beech competition reduction was the rule, as it always had a stronger competitive effect on its conspecifics, closely followed by spruce, while fir was the weakest competitor (Fig. 5c, $\lambda_{beech} > \lambda_{spruce} > \lambda_{fir}$).

4. Discussion

In this study, we used a spatial competition analysis to assess the extent of competitive effects of neighbour trees on the growth of target trees across a climatic gradient. Competitive effects considered the identity of neighbour species, size and distance to target trees. Our investigation also allowed an analysis of the role of climate and tree size, and of their interaction with the competitive response or sensibility to competition of the target tree species. Our main findings were: (i) that competition had the largest effect on the growth of the three main Central European tree species and (ii) that the competitive effect, rather

than the competitive response, varied along a climatic gradient according to species identity. Our competition model effectively detected variation in the strength of species competitive effects on a target tree along the present climatic gradient. This allowed us to identify competition reduction and its importance in relation to the growth-SPEI relationship of the target tree species.

4.1. Competition: competitive responses and effects along the climatic gradient

Growth models including competition from trees with a DBH of ≥ 7.5 cm fit the data better than models with tree size and SPEI (our first research question). SPEI was only included in the growth model for spruce, not in those for beech and fir. This suggests that SPEI is not a crucial factor for the growth of these species along the analysed gradient. Our results for beech are consistent with other studies that have found a low climate signal in beech growth using other climatic variables (Bosela et al., 2016; Castagneri et al., 2014; Hilmers et al., 2020; Tognetti et al., 2014). However, they contrast with several studies that have identified a temperature-induced increase in fir growth since 1980 (Bosela et al., 2018; Hilmers et al., 2020). For fir, it is plausible that the plots used in this study, despite covering a broad range of elevations, may not be subjected to water limitations. Therefore, other climate variables may better explain the data for this species.

Species competitive responses and effects varied depending on the identity of the target and neighbouring species. However, while the sensitivity of target species to competition was constant along the climatic gradient (represented by the parameter a in Eq. 4), competitive effects from neighbouring species differed along the gradient (represented by the per capita competitive coefficients λ in Eq. 5) (our second research question). This suggests that the ability of neighbouring species to suppress the growth of a target tree is related to climatic conditions. Instead, the ability of a target tree to tolerate suppression of its growth by neighbouring species is uniform along the climatic gradient and depends strongly on the identity of the target tree species ($a_{spruce} = 50.7$; $a_{fir} = 3.4$ and $a_{beech} = 7.9$). For example, we found that the intensity of interspecific competitive effects (i.e., λ) in fir trees increases with aridity, regardless of the identity of the neighbouring species. However, the high competitive response (low a parameter compared to fir and beech) of fir along the entire gradient may enable this species to dampen the negative effects on their overall competition effect under dry conditions, or even to reverse them under milder conditions. Our results contrast with those obtained for wetland plants, where competitive response, rather than effect, depended on environmental conditions (Keddy et al., 1994). They

also contrast with the results of Gómez-Aparicio et al. (2011), who showed that the competitive response of mature Mediterranean trees varied with climate. However, the study by Gómez-Aparicio et al. (2011) did not consider the possibility that the competitive effect might also vary. Further studies with adult trees that consider the possibility that both response and effect may vary along a climatic gradient, or that analyse other climatic variables or soil types, are needed to draw more comprehensive conclusions about the role of competitive ability in structuring forest communities in different environments.

On average, the hierarchy of species competitive effects ($\lambda_{\text{beech}} > \lambda_{\text{spruce}} > \lambda_{\text{fir}}$) was little affected by the identity of the target species and contrary to the hierarchy found for species competitive responses ($a_{\text{spruce}} > a_{\text{beech}} > a_{\text{fir}}$), where a lower a indicates a high competitive response. This suggests that different traits are involved in the competitive effect and response of the species studied (Goldberg and Landa, 1991). However, under dry conditions and when neighbouring species competed with spruce, the same traits could play a role in the two components of the species' competitive ability, as a rank reversal in the species' competitive effect was observed ($\lambda_{\text{fir}} > \lambda_{\text{spruce}} > \lambda_{\text{beech}}$) (e.g., fir had a highly competitive effect and response). Overall, these results indicate that changes in the hierarchy of competitive effect and response ability of the species can occur depending on the climatic conditions and the target species considered (Goldberg, 1996; Wang et al., 2010).

4.2. Competition reduction along the climatic gradient

The complementarity-competition framework proposed by Forrester and Bauhus (2016) predicts that complementarity increases as the availability of a given resource decreases when interspecific interactions improve the availability, uptake or use efficiency of that resource. The framework assumes a linear relationship between competition reduction and resource availability because the studies on which it is based do not quantify the shape of the relationship. However, we found a non-linear relationship between competition reduction (one side of complementarity) and climatic conditions. Notably, the decrease in competition (i.e., interspecific competitive effects lower than intraspecific ones) appears to be less pronounced at both ends of the wet-dry gradient (Fig. 5). This suggests that competition reduction was probably mediated by thresholds of resource availability, as recently reported for water by de Stree et al. (2019). This finding has practical implications for forest management, indicating that competition dynamics may change abruptly as resource availability shifts, requiring adaptive management strategies that account for varying resource availability along the gradient or through time.

Our study confirms that the outcome of competitive interactions between species pairs can change along a climatic gradient and largely depends on the identity of the interacting species (Mina et al., 2018b; Condés et al., 2022), highlighting the importance of considering species-specific interactions to optimize forest productivity (Fig. 5). In addition, we found that climatic conditions have a large influence on the hierarchy of species' competitive effects when the competitive effect of the target species is on average intermediate relative to that of neighbouring species. For example, we found that spruce at the drier end of the gradient benefits from the presence of beech (see also Pretzsch et al., 2010; del Río et al., 2014) but not from the presence of fir (Forrester et al., 2013; Vitali et al., 2018; Bottero et al., 2021) (Fig. 5a). By contrast, under milder conditions, spruce benefits from the presence of fir (Huber et al., 2014) but not from the presence of beech (Pretzsch et al., 2010; del Río et al., 2014) (Fig. 5a). Interestingly, our results show that when neighbouring species competed against the strongest and the weakest competitive species, the hierarchy of competitive effects of the species remained the same along the gradient. For beech, which had the strongest competitive effects, the intraspecific competitive effects were always stronger than the interspecific ones (see also Toigo et al., 2015), whereas for fir, which showed the weakest competitive effect, competition was

the rule regardless of neighbour identity.

Differences in the length of the analysed stress gradient might lead to changes in the outcome of competitive interactions between species pairs (Le Roux and McGeoch, 2010). In the case of fir, for example, our results contradict Lebourgeois et al. (2013) at dry sites (where beech had a positive effect on fir) but agree with those reported in the same study for mesic and wet sites (where beech had a negative effect, as $\lambda_{\text{beech}} > \lambda_{\text{fir}}$). There are two possible explanations for these conflicting results. First, the differences in the nature of the inventory data: we calculated the average SPEI between two surveys (so that there are temporal changes in climatic conditions within a period) whereas Lebourgeois et al. (2013) used tree rings and focused on drought periods. Second, our inventory data may be missing the driest sites for fir (and perhaps also beech), whose niche extends to lower elevations with warmer temperatures (Kölling, 2007) than those recorded at the 39 monitoring plots used in our study.

4.3. Intensity of competitive interactions along the SPEI gradient

We found a hump-shaped relationship between the per capita competitive coefficients (i.e., λ) and SPEI for spruce and fir (Fig. 5a and b). Interestingly, the competitive coefficients on spruce growth peaked at the point along the gradient (i.e., $\text{nSPEI}_{\text{Feb-Jul}} = 0.6$) where spruce growth started to increase (Figs. 3b and 5a). This is consistent with Grime's hypothesis (Grime, 1973) regarding the increase in the intensity of competition along a productivity gradient. Moreover, our results show that the relationship between the intensity of competitive interactions and the climatic conditions is not linear, and suggest that the intensity of competitive interactions may decline when favourable conditions exceed a certain threshold.

Our results suggest that either competition or competition reduction plays an important role in tree growth when climatic conditions are optimal for the growth of the target species, as the differences between the competition indices of the species are greatest (λ). However, under climatic conditions that are far from optimal, these differences may not be large enough to alter the low growth rate. Thus, although competition reductions were found at the dry end of the gradient (e.g., the effect of beech on spruce), the differences between intra- and interspecific competitive coefficients were small, suggesting that competition reductions are not as relevant under harsh conditions. Instead, under optimal growth conditions for the target species, the differences between the inter- and intraspecific coefficients for competitive effects were largest (regardless of whether they resulted in competition or competition reduction), making their effects on tree growth more meaningful. These results build on previous observations of significant differences between intra- and interspecific competition along environmental gradients. Our results are consistent, for example, with Maestre et al. (2009), who suggested that positive effects may be more pronounced under moderate environmental conditions, and with several studies that have found little evidence for a positive effect of species diversity on the resilience of different species in dry years (Gillerot et al., 2021; Versace et al., 2020, 2021; Vitali et al., 2018). To test this observation in fir, we used parameter estimates that included the climate effect ("species-specific competition with climate") and found that fir growth was also higher in situations where the intensity of competition was greater (Fig. 4b and Supplementary Material Fig. S3). Furthermore, the growth of fir peaked under our drier conditions, which further supports the idea that the width of the gradient used in this study was likely insufficient to study the sign of the species competitive effects on fir at its warm-dry limit. Similarly, in beech, we may have captured only the upper part of the hump-shaped relationship between competitive effects and SPEI, which could explain why the competitive effects of species did not vary (Fig. 5c). Overall, these results highlight the importance of considering the specific growth conditions of the target species when assessing competitive interactions.

5. Conclusions

This study shows that SPEI mediates the species competitive effects on a target tree, rather than the sensitivity of the target species to competition. Our modelling approach should prove useful in future studies to expand our understanding of how competition shapes forest communities along environmental gradients.

Our study confirms that competition reduction in mixtures and its strength depends on species identity and can vary along climatic gradients, as shifts in the species hierarchy of competitive effects were observed. We found that competition reduction (i.e., interspecific < intraspecific competition) can occur along the entire gradient, and we provided additional evidence of a non-linear relationship between competition reduction and SPEI. Furthermore, we showed that the strength of the outcome of competitive interactions between species pairs, becomes less important under more arid conditions, where growth of target species is low, so that neither competition nor competition reduction can significantly affect growth. Instead, stronger competing or competing reduction effects appear to occur at the point of the gradient where target species growth begins to increase. This suggests that plant interactions might be more relevant in stands with optimal conditions for the target species. Consequently, we propose that forest management strategies should be particularly adjusted to competition dynamics when the optimal conditions for the target species are met. Overall, the findings of this study have shed light on the complex relationship between climatic conditions and competition dynamics, offering valuable insights for developing sustainable forest management practices for maintaining the stability and productivity of mixed forests in a dynamic environment.

Data availability

The raw/processed data required to reproduce the above findings cannot be shared at this time as the data also forms part of an ongoing study.

CRedit authorship contribution statement

Teresa Valor: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **Lluís Coll:** Writing – review & editing, Methodology, Conceptualization. **David I. Forrester:** Writing – review & editing. **Hans Pretzsch:** W. **Miren del Río:** Writing – review & editing. **Kamil Bielak:** Writing – review & editing. **Bogdan Brzeziecki:** Writing – review & editing. **Franz Binder:** Writing – review & editing. **Torben Hilmers:** Writing – review & editing. **Zuzana Sitková:** Writing – review & editing. **Roberto Tognetti:** Writing – review & editing, Funding acquisition. **Aitor Ameztegui:** Writing – review & editing, Methodology, Formal analysis, Conceptualization.

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.

Acknowledgements

This publication is based upon work from COST Action CLIMO (CA15226) supported by COST (European Cooperation in Science and Technology) and the UMBRACLIM project (PID2019-111781RB-I00) funded by the Spanish Ministry for Science and Innovation. Teresa Valor was contracted with a grant “Juan de la Cierva-Formación” (FJC2018-036673-I). Z.S. received funds from the grant no. APVV-20-0365 and from project TreeAdapt supported by the MPRV SR. Aitor Ameztegui is supported by a Serra-Hünter fellowship by the Generalitat de Catalunya.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2024.100176>.

References

- Ameztegui, A., 2020. neighborhood: an R package to compute several functions within the neighborhood theory of forest dynamics. GitHub repository. <https://github.com/ameztegui/neighborhood> (accessed 1 November 2023).
- Ammer, C., 2019. Diversity and forest productivity in a changing climate. *New Phytol.* 221, 50–66.
- Barry, K.E., Mommer, L., van Ruijven, J., Wirth, C., Wright, A.J., Bai, Y., Connolly, J., De Deyn, G.B., de Kroon, H., Isbell, F., Milcu, A., Roscher, C., Scherer-Lorenzen, M., Schmid, B., Weigelt, A., 2019. The future of complementarity: disentangling causes from consequences. *Trends Ecol. Evol.* 34, 167–180. <https://doi.org/10.1016/j.tree.2018.10.013>.
- Begović, K., Rydval, M., Mikac, S., Čupić, S., Svoboda, K., Mikoláš, M., Kozák, D., Kameniar, O., Frankovič, M., Pavlin, J., Langbehn, T., Svoboda, M., 2020. Climate-growth relationships of Norway Spruce and silver fir in primary forests of the Croatian Dinaric mountains. *Agric. For. Meteorol.* 288 (289), 108000. <https://doi.org/10.1016/J.AGRFORMET.2020.108000>.
- Bosela, M., Stefančík, I., Petrás, R., Vacek, S., 2016. The effects of climate warming on the growth of European beech forests depend critically on thinning strategy and site productivity. *Agric. For. Meteorol.* 222, 21–31. <https://doi.org/10.1016/j.agrformet.2016.03.005>.
- Bosela, M., Lukac, M., Castagneri, D., Sedmák, R., Biber, P., Carrer, M., Konópka, B., Nola, P., Nagel, T.A., Popa, I., Roibu, C.C., Svoboda, M., Trotsiuk, V., Büntgen, U., 2018. Contrasting effects of environmental change on the radial growth of co-occurring beech and fir trees across Europe. *Sci. Total Environ.* 615, 1460–1469. <https://doi.org/10.1016/J.SCITOTENV.2017.09.092>.
- Bottero, A., Forrester, D.I., Cailleret, M., Kohnle, U., Gessler, A., Michel, D., Bose, A.K., Bauhus, J., Bugmann, H., Cuntz, M., Gillerot, L., Hanewinkel, M., Lévesque, M., Ryder, J., Sainte-Marie, J., Schwarz, J., Yousefpour, R., Zamora-Pereira, J.C., Rigling, A., 2021. Growth resistance and resilience of mixed silver fir and Norway spruce forests in central Europe: Contrasting responses to mild and severe droughts. *Glob. Chang. Biol.* 27 (18), 4403–4419. <https://doi.org/10.1111/GCB.15737>.
- Bravo-Oviedo, A., Pretzsch, H., del Río, M., 2018. Dynamics, Silviculture and Management of Mixed Forests. Springer, Cham, Switzerland.
- 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. Manag.* 473, 118334. <https://doi.org/10.1016/J.FORECO.2020.118334>.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Springer, New York.
- 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 (4). <https://doi.org/10.1139/X03-232>.
- Canham, C.D., Papaik, M.J., María, M., Uriarte, M., McWilliams, W.H., Jenkins, J.C., Twery, M.J., 2006. Neighborhood analyses of canopy tree competition along environmental gradients in new england forests. *Ecol. Appl.* 16, 540–554. [https://doi.org/10.1890/1051-0761\(2006\)016\[0540:NAOCTC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[0540:NAOCTC]2.0.CO;2).
- Carnwath, G.C., Nelson, C.R., 2016. The effect of competition on responses to drought and interannual climate variability of a dominant conifer tree of western North America. *J. Ecol.* 104, 1421–1431. <https://doi.org/10.1111/1365-2745.12604>.
- Castagneri, D., Nola, P., Motta, R., Carrer, M., 2014. Summer climate variability over the last 250 years differently affected tree species radial growth in a mesic *Fagus-Abies-Picea* old-growth forest. *For. Ecol. Manag.* 320, 21–29. <https://doi.org/10.1016/j.foreco.2014.02.023>.
- 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. <https://doi.org/10.1111/J.1365-2745.2008.01458.X>.
- Coates, K.D., Lilles, E.B., Astrup, R., 2013. Competitive interactions across a soil fertility gradient in a multispecies forest. *J. Ecol.* 101, 806–818. <https://doi.org/10.1111/1365-2745.12072>.
- Coll, L., Ameztegui, A., Collet, C., Löf, M., Mason, B., Pach, M., Verheyen, K., Abrudan, I., Barbat, A., Barreiro, S., 2018. Knowledge gaps about mixed forests: what do European forest managers want to know and what answers can science provide? *For. Ecol. Manag.* 407, 106–115.
- Condés, S., del Río, M., Forrester, D.I., Avdagić, A., Bielak, K., Bončina, A., Bosela, M., Hilmers, T., Ibrahimspahić, A., Drozdowski, S., Jaworski, A., Nagel, T.A., Sitková, Z., Skrzyszewski, J., Tognetti, R., Tonon, G., Zlatanov, T., Pretzsch, H., 2022. Temperature effect on size distributions in spruce-fir-beech mixed stands across Europe. *For. Ecol. Manag.* 504, 119819. <https://doi.org/10.1016/J.FORECO.2021.119819>.
- Daniels, R.F., 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. *For. Sci.* 22, 454–456. <https://doi.org/10.1093/FORESTSCIENCE/22.4.454>.
- Das, A., 2012. The effect of size and competition on tree growth rate in old-growth coniferous forests. *Can. J. For. Res.* 42, 1983–1995. <https://doi.org/10.1139/x2012-142>.
- de Luis, M., Novak, K., Čufar, K., Raventós, J., 2009. Size mediated climate-growth relationships in *Pinus halepensis* and *Pinus pinea*. *Trees Struct. Funct.* 23, 1065–1073. <https://doi.org/10.1007/s00468-009-0349-5>.

- de Streef, G., Collet, C., Barbeito, I., Bielak, K., Bravo-Oviedo, A., Brazaitis, G., Coll, L., Drössler, L., Forrester, D., Heym, M., Löf, M., Pach, M., Pretzsch, H., Ruiz-Peinado, R., Skrzyszewski, J., Stankevičiūtė, J., Svoboda, M., Verheyen, K., Zlatanov, T., Bonal, D., Ponette, Q., 2019. Contrasting patterns of tree species mixture effects on wood $\delta^{13}\text{C}$ along an environmental gradient. *Eur. J. For. Res.* 139, 229–245. <https://doi.org/10.1007/s10342-019-01224-z>.
- del Río, M., Schütze, G., Pretzsch, H., 2014. Temporal variation of competition and facilitation in mixed species forests in Central Europe. *Plant Biol* 16 (1), 166–176. <https://doi.org/10.1111/plb.12029>.
- Edwards, M., 1992. Likelihood. Johns Hopkins University Press, Baltimore.
- Fichtner, A., Härdtle, W., Li, Y., Bruehlheide, 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., Bauhus, J., 2016. A review of processes behind diversity—productivity relationships in forests. *Curr. For. 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. Manag.* 304, 233–242. <https://doi.org/10.1016/j.foreco.2013.04.038>.
- Freckleton, R.P., Watkinson, A.R., 2001. Asymmetric competition between plant species. *Funct. Ecol.* 15, 615–623. <https://doi.org/10.1046/J.0269-8463.2001.00558.X>.
- Gillerot, L., Forrester, D.I., Bottero, A., Rigling, A., Lévesque, M., 2021. Tree neighbourhood diversity has negligible effects on drought resilience of European beech, silver fir and Norway spruce. *Ecosystems* 24, 20–36. <https://doi.org/10.1007/s10021-020-00501-y>.
- Goffe, W.L., Ferrier, G.D., Rogers, J., 1994. Global optimization of statistical functions with simulated annealing. *J. Econom.* 60, 65–99. [https://doi.org/10.1016/0304-4076\(94\)90038-8](https://doi.org/10.1016/0304-4076(94)90038-8).
- Goldberg, D.E., 1990. Components of resource competition in plant communities. In: Grace, J.B., Tilman, D. (Eds.), *Perspectives of Plant Competition*. Academic Press, Cambridge, pp. 27–49.
- Goldberg, D.E., 1996. Competitive ability: definitions, contingency and correlated traits. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 351, 1377–1385. <https://doi.org/10.1098/RSTB.1996.0121>.
- Goldberg, D.E., Landa, K., 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *J. Ecol.* 79, 1013. <https://doi.org/10.2307/2261095>.
- Goldberg, D.E., Rajaniemi, T., Gurevitch, J., Stewart-Oaten, A., 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology* 80, 1118–1131.
- Gómez-Aparicio, I., 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. *Glob. Chang. Biol.* 17, 2400–2414. <https://doi.org/10.1111/J.1365-2486.2011.02421.X>.
- Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242, 344–347.
- Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H., 2014. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *Int. J. Climatol.* 34, 623–642. <https://doi.org/10.1002/joc.3711>.
- Hilborn, R., Mangel, M., 1997. *The Ecological Detective: Press, Confronting Models with Data*. Princeton University Press, Princeton, New Jersey, USA.
- Hilmers, T., Avdagi, A., Bartkowiak, L., Bielak, K., Binder, F., Bonina, A., Dobor, L., Forrester, D.I., Hobi, M.L., Ibrahimspahi, A., Jaworski, A., Klopi, M., Matovi, B., Nagel, T.A., Petr, R., Del Río, M., Staji, B., Uhl, E., Zlatanov, T., Tognetti, R., Pretzsch, H., 2020. The productivity of mixed mountain forests comprised of *Fagus sylvatica*, *Picea abies*, and *Abies alba* across Europe. *Forestry* 92, 512–522. <https://doi.org/10.1093/forestry/cpz035>.
- Houpert, L., Rohner, B., Forrester, D.I., Mina, M., Huber, M.O., 2018. Mixing effects in Norway spruce—European beech stands are modulated by site quality, stand age and moisture availability. *Forests* 9, 83. <https://doi.org/10.3390/F9020083>.
- Huber, M.O., Sterba, H., Bernhard, L., 2014. Site conditions and definition of compositional proportion modify mixture effects in *Picea abies* – *Abies alba* stands. *Can. J. For. Res.* 44, 1281–1291. <https://doi.org/10.1139/cjfr-2014-0188>.
- Keddy, P.A., Twolan-Strutt, L., Wisheu, I.C., 1994. Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments? *J. Ecol.* 82, 635–643.
- Kölling, C., 2007. Klimahüllen für 27 waldbaumarten. *AFZ/Der Wald* 23, 1242–1245.
- Le Roux, P.C., McGeoch, M.A., 2010. Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162, 733–745.
- Lebourgeois, F., Bréda, N., Ulrich, E., Granier, A., Bréda, N., Ulrich, E., 2005. Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French permanent plot Network (RENECOFOR). *Trees (Berl.)* 19, 385–401. <https://doi.org/10.1007/s00468-004-0397-9>.
- Lebourgeois, F., Gomez, N., Pinto, P., Mérian, P., 2013. Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *For. Ecol. Manag.* 303, 61–71. <https://doi.org/10.1016/J.FORECO.2013.04.003>.
- Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, C.J., 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J. Ecol.* 97, 199–205. <https://doi.org/10.1111/j.1365-2745.2008.01476.x>.
- Mérian, P., Lebourgeois, F., 2011. Size-mediated climate–growth relationships in temperate forests: a multi-species analysis. *For. Ecol. Manag.* 261, 1382–1391. <https://doi.org/10.1016/J.FORECO.2011.01.019>.
- Mina, M., Huber, M.O., Forrester, D.I., Thürig, E., Rohner, B., 2018a. Multiple factors modulate tree growth complementarity in Central European mixed forests. *J. Ecol.* 106, 1106–1119. <https://doi.org/10.1111/1365-2745.12846>.
- Mina, M., Del Río, M., Huber, M.O., Thürig, E., Rohner, B., 2018b. The symmetry of competitive interactions in mixed Norway spruce, silver fir and European beech forests. *J. Veg. Sci.* 29, 775–787. <https://doi.org/10.1111/jvs.12664>.
- Ministerio de Agricultura Alimentación y Medio Ambiente, 2019. *Cuarto Inventario 695 Forestal Nacional (IFN4)*. España, Madrid.
- Murphy, L., 2012. Likelihood: methods for maximum likelihood estimation. R package version 1.5. <http://CRAN.R-project.org/package=likelihood>. Nov 01, 2023.
- Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Glob. Ecol. Biogeogr.* 20, 170–180. <https://doi.org/10.1111/j.1466-8238.2010.00592.x>.
- Pretzsch, H., 2022. Facilitation and competition reduction in tree species mixtures in Central Europe: consequences for growth modeling and forest management. *Ecol. Model.* 464, 109812. <https://doi.org/10.1016/j.ecolmodel.2021.109812>.
- Pretzsch, H., Schütze, G., 2008. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level. *Eur. J. For. Res.* 128, 183–204. <https://doi.org/10.1007/S10342-008-0215-9>.
- Pretzsch, H., Block, J., Dieler, J., Dong, P.H., Kohnle, U., Nagel, J., Spellmann, H., Zingg, A., 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Ann. For. Sci.* 67, 712. <https://doi.org/10.1051/forest/2010037>.
- Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dimberger, G., Drössler, L., 2015. 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. For. Res.* 134, 927–947.
- Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. *Geogr. Rev.* 38, 55. <https://doi.org/10.2307/210739>.
- Tognetti, R., Lombardi, F., Lasserre, B., Cherubini, P., Marchetti, M., 2014. Tree-ring stable isotopes reveal twentieth-century increases in water-use efficiency of *Fagus sylvatica* and *Nothofagus* spp. in Italian and Chilean Mountains. *PLoS One* 9, e113136. <https://doi.org/10.1371/JOURNAL.PONE.0113136>.
- Toigo, M., Vallet, P., Perot, T., Bontemps, J.-D., Piedallu, C., Courbaud, B., 2015. Overyielding in mixed forests decreases with site productivity. *J. Ecol.* 103, 502–512. <https://doi.org/10.1111/1365-2745.12353>.
- Uhl, E., Hilmers, T., Pretzsch, H., 2021. From acid rain to low precipitation: the role reversal of Norway spruce, silver fir, and European beech in a selection mountain forest and its implications for forest management. *Forests* 12, 1–24. <https://doi.org/10.3390/f12070894>.
- Uriarte, M., Canham, C.D., Thompson, J., Zimmerman, J.K., 2004. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecol. Monogr.* 74, 591–614. <https://doi.org/10.1890/03-4031>.
- Vallet, P., Perot, T., 2011. Silver fir stand productivity is enhanced when mixed with Norway spruce: evidence based on large-scale inventory data and a generic modelling approach. *J. Veg. Sci.* 22, 932–942. <https://doi.org/10.1111/j.1654-1103.2011.01288.x>.
- Vandermeer, J.H., 1989. *The ecology of intercropping*. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CB09780511623523>.
- Vanoni, M., Bugmann, H., Nötzli, M., Bigler, C., 2016. Quantifying the effects of drought on abrupt growth decreases of major tree species in Switzerland. *Ecol. Evol.* 6, 3555–3570. <https://doi.org/10.1002/ECE3.2146>.
- Versace, S., Gianelle, D., Garfi, V., Battipaglia, G., Lombardi, F., Marchetti, M., Tognetti, R., 2020. Interannual radial growth sensitivity to climatic variations and extreme events in mixed-species and pure forest stands of silver fir and European beech in the Italian Peninsula. *Eur. J. For. Res.* 139, 627–645.
- Versace, S., Garfi, V., Dalponte, M., Febbraro Mirko, D., Frizzera, L., Gianelle, D., Tognetti, R., 2021. Species interactions in pure and mixed-species stands of silver fir and European beech in Mediterranean mountains. *iForest-Biogeosci. For.* 14 (1), 1–11.
- Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscale drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J. Clim.* 23, 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>.
- Vilà, M., Carrillo-Gavilán, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W., Haase, J., Kunstler, G., Schelhaas, M., Trasobares, A., 2013. Disentangling biodiversity and climatic determinants of wood production. *PLoS One* 8, e53530.
- Vitali, V., Forrester, D.I., Bauhus, J., 2018. Know your neighbours: drought response of Norway spruce, silver fir and Douglas fir in mixed forests depends on species identity and diversity of tree neighbourhoods. *Ecosystems* 21, 1215–1229. <https://doi.org/10.1007/s10021-017-0214-0>.
- Wang, P., Stieglitz, T., Zhou, D.W., Cahill Jr, J.F., 2010. Are competitive effect and response two sides of the same coin, or fundamentally different? *Funct. Ecol.* 24, 196–207. <https://doi.org/10.1111/J.1365-2435.2009.01612.X>.
- Zhang, Y., Chen, H.Y.H., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *J. Ecol.* 100, 742–749.