Temperature effect on size distributions in spruce-fir-beech mixed stands across Europe

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ABSTRACT

Forest composed of *Picea abies* L., *Abies alba* Mill. and *Fagus sylvatica* L. cover a large area in the European mountain regions and have a high ecological and socio-economic importance as they supply many ecosystems services. Because of climate change, these forests are exposed to warming, and this effect increases with elevation, which may impact their delivery of goods and services. Previous studies did not find significant changes in the overall productivity of these species over the last 30 years, but they observed changes in species competitiveness at the species and tree levels.

In this study, we aimed to link previous results on tree, species and stand level growth in spruce-fir-beech mixed mountain forests by analysing species size distribution dynamics under different climate conditions and their effect on stand growth. We developed a matrix model based on data from 76 long-term experimental plots distributed throughout Europe. We used the change in stand basal area to explore whether temperature modifies species size dominances and proportions, whether the temperature effects on changes in species basal area depend on species size dominance, and whether the effect of species size dominance on changes in the stand basal area varies with temperature.

Our results showed that annual mean temperature is an important climatic driver of species dynamics in spruce-fir-beech mixed mountain forests, such that stand basal area growth was favored by higher temperatures, particularly due to positive responses of silver fir which were greater than negative effects of temperature on European beech. The high temperatures also favored the size-dominance of silver fir, while European beech tended to have smaller diameters, independent of the temperature. We also found that the identity of the size-dominant species also influenced changes in stand basal area, with the highest or the lowest changes when Norway spruce and European beech were the size-dominant species, respectively. Silver fir was less influenced by the identity of the size-dominant species than by temperature.

Therefore, although mixed mountain forests of spruce-fir-beech were found to be resilient systems in terms of stand productivity, we conclude that increasing temperatures may modify species dynamics and consequently silvicultural interventions will be needed to control species proportions and dominances.

1. Introduction

In European mountain regions, a large forest area is covered by mixed mountain forests composed by Norway spruce (*Picea abies* L.), silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) (hereinafter spruce, fir and beech, respectively) (Hilmers et al., 2019). Their high ecological and socio-economic importance is evidenced by the large number of ecosystem services (ESs) they supply (e.g. Pretzsch et al., 2015a). As with other forest ecosystems, they are exposed to climate change, which may strongly impact their capacity to deliver ESs (Mina et al., 2018). Although the potential impacts of climate change on European mountain forests and their goods and services are considered to vary depending on the local context (Lindner et al., 2010), a generally higher exposure to warming with increasing elevation is observed worldwide (Pepin et al., 2015), while the changes in precipitation are still highly uncertain and will depend on the local geomorphological heterogeneity of mountainous landscapes (Maroschek et al., 2009). However, at high elevations dominate forest productivity is driven by temperature, whereas precipitation would not be such an important factor (Babst et al., 2013). Accordingly, elevation-dependent changes in forest dynamics have been recently reported for spruce-fir-beech mixed forests (del Río et al., 2021).

Productivity is a key forest feature related directly and indirectly to important goods and services such as wood yield, carbon sequestration, nutrient cycling, or water regulation (Biber et al., 2015; Dieler et al., 2017; Calama et al., 2021). Although forest productivity has always been an important issue in forest science, more attention is now being given to climate change and stand structural effects on stand growth (e. g. Zhang et al., 2012; Pretzsch et al., 2014; Dănescu et al., 2016; Forrester, 2019). Stand volume increment of spruce-fir-beech mixed stands was found to be influenced by elevation-dependent temperature, but despite a significant increase in annual mean temperature, the overall productivity has not changed significantly over the last 30 years (Hilmers et al., 2019). However, changes in species competitiveness were observed at the species and tree levels. At the species level, a positive trend was observed in the mixed stands during the last 30 years only for fir, whereas beech maintained constant productivity and spruce productivity decreased (Hilmers et al., 2019). At the tree level, growth trend analyses of dominant trees for the last few centuries showed positive trends for all three species, which were especially prominent for fir and beech at higher elevations, where their competitiveness increases at the expense of spruce (Bošeľa et al., 2014; Pretzsch et al., 2020b). Other studies comparing beech growth in monospecific and mixed mountain forests found that dominant beeches were promoted by mixture, especially at high elevations (Bosela et al., 2015; Pretzsch et al., 2021b).

It is well recognised that tree species diversity can significantly increase stand productivity (e.g. Liang et al., 2016; Pretzsch and Forrester, 2017). But there is increasing evidence that other stand structural characteristics are also important. The most relevant characteristics include vertical stratification and canopy packing (Riofrío et al., 2017; Williams et al., 2017), variation in tree sizes (Zeller et al., 2018), the partitioning of growth between different sized trees (asymmetry of competition (Forrester, 2019)), the shapes of size distributions (Dănescu et al., 2016; Forrester, 2019), and species dominance (Cheng et al., 2018). For spruce-fir-beech mixtures, it was found that stand volume increment did not depend on species proportions or species dominance in basal area (Hilmers et al., 2019), but species size distributions (skewness and species size dominance) had an important effect (Torresan et al., 2020). According to Torresan et al., (2020), the most

productive stands were spruce-fir-beech mixed stands with lower evenness, higher skewness, and where spruce occupy the size dominant stratum and beech the suppressed stratum. However, to what extent species size dominance is influenced by climate conditions in these mixed mountain forests has not been examined.

Diameter distributions have long been used in forest biometry to summarise stand structure due their easy estimation from forest inventories. They are often employed as structure indicators for density and species composition control (O'Hara and Gersonde, 2004; del Río et al., 2016). Their direct effect on stand growth depends on the relationship between tree size and tree growth, which depends on environmental and competitive conditions (Forrester, 2019). Size distributions therefore help to link tree, species and stand level growth patterns. In this study, we aim to link above mentioned results on tree, species and stand level growth in spruce-fir-beech mixed mountain forests by analysing species size distribution dynamics under different climate conditions and their effect on stand growth. When summarising the effects of important stand structural characteristics and environmental conditions on growth, it is pertinent to use forest growth models. Matrix models can be particularly useful for examining the influence of size distributions (Drozdowski, 2006). When classifying forest dynamics models depending on their level of description of the forest, Matrix models, dealing with size classes, can be placed between stand models, which predict the temporal changes of population level attributes, and individual tree models (Liang and Picard, 2013). Therefore, we selected this modelling approach and developed a matrix model using data from 76 long-term experimental plots distributed throughout Europe. We used the change in basal area (i.e., differences between the stand basal area of alive trees at two inventories, ΔG) to explore species and stand dynamics, since basal area is directly derived from diameter distributions obtained from the matrix model and is closely related to species and stand productivity.

We asked the following specific questions:

Q1. Does temperature modify species size dominances and proportions?

Q2. Do the temperature effects on changes in spruce, fir, beech basal areas depend on species size dominance?

Q3. Does the effect of species size dominance on stand changes in basal area vary with temperature?

Our main hypotheses were: H1: Temperature, mediated by site elevation and climate warming, is an important climatic driver of species dynamics in spruce-fir-beech mixed mountain forests; H2: Warming temperatures reduce spruce productivity and increase fir productivity, while the effect on beech productivity depends on size distribution; H3: Stand productivity increases with spruce size dominance.

2. Materials and methods

2.1. Data

Data from 76 permanent experimental sample plots located in mountain areas of seven countries were used (Table 1). Plots were located in mixed stands dominated by *Abies alba* Mill. (fir), *Fagus sylvatica* L. (beech) and *Picea abies* (L.) Karst (spruce), with only small percentages of other species. The mean area of the sample plots was around 0.5 ha, although there was a large variability, ranging from 0.04 to 2.63 ha. Inside the plots, all trees with diameter at 1.3 m larger than or equal to 7.5 cm were measured and classified as survivors, dead, ingrowth, cut or removed, this last group consisting of trees that disappeared between two consecutive surveys without registering whether

Table 1

Number of permanent sample plots and number of surveys at the beginning of the 10-year growth periods used for the study. For each survey, the data corresponding to the end of the growth period was also used.

Country	Number of plots	Number of plots at the initial surveys	Surveys per plot	Years
Bosnia_Herzegovina	5	5	2	2006 to 2016
Bulgaria	1	1	2	1995 to 2005
Germany	38	78	2 to 5	1953 to 2016
Poland	10	32	3 to 5	1976 to 2016
Slovakia	6	10	2 to 4	1967 to 2016
Slovenia	6	15	2 to 4	1973 to 2012
Switzerland	10	66	2 to 14	1912 to 2014
TOTAL	**76**	**207**		**1912 to 2016**

they were cut or dead. Plots were located mainly in unmanaged or lightly managed stands. To avoid possible distinct effects of heavy harvestings or high mortality events on the size distribution dynamics, surveys in which the basal area percentages of cut/removed or dead trees were larger than 20% were removed. This resulted in a set of 67,309 sample trees of 207 surveys from the 76 long term experimental plots, which were measured at approximately 10-year intervals. Table 2 shows the main stand variables of the initial surveys, for a more detailed data overview, see Supplementary tables 1–3.

Monthly data for mean temperature and precipitation were collected from the closest available meteorological stations. If the weather station was located at a different elevation to the plot, an elevation correction was used based on a lapse rate of $-0.38\,°C$ per 100 m for temperature and a scaling factor $0f + 61$ mm per 100 m for precipitation. Missing values were completed using gridded data from the Climatic Research Unit (CRU) Time-Series (TS) Version 3.10 database (Harris et al., 2020). The four closest to the plot pixels were selected from CRU and their climate values were averaged with a weighting by distance. Then, the common period of the two series (observed and CRU series) were used to adjust the CRU series to local conditions.

2.2. Matrix model structure

The matrix growth model was formulated as follows:

$$y_{spt+\Delta t} = Tr_{spt} \cdot y_{spt} + I_{spt}$$

where, for each species, y_{spt} is a column vector representing the number of alive trees of this species per diameter classes at time t. Tr_{spt} is the state-dependent transition matrix, which describes changes, between time t and t + Δt, in the number of trees per unit area in diameter classes according to their growth and mortality. I_{spt} is a state-dependent column vector representing the recruitment of this species in the smallest

diameter class between t and t + Δt.

Transition matrix for the species sp at time t was defined as:

$$Tr_{spt} = \begin{pmatrix} a_{sp1,t} & 0 & \cdots & & 0 \\ b_{sp1,t} & a_{sp2,t} & & & \vdots \\ & b_{sp2,t} & & & \\ \vdots & & a_{spn-1,t} & \\ 0 & & b_{spn-1,t} & a_{spn,t} \end{pmatrix}$$

where, for the species sp, $a_{spk,t}$ is the probability that a tree in diameter class k remains alive in the same class between times t and t + Δt, $b_{spk,t}$ is the probability that the tree remains alive and grows into the next diameter class, k + 1; n represents the number of diameter classes.

Ingrowth matrix for the species sp at time t, I_{spt}, was defined as:

$$I_{spt} = \begin{pmatrix} i_{spt} \\ 0 \\ \vdots \\ 0 \end{pmatrix}$$

The i_{spt} is the ingrowth of the species sp, i.e., the number of trees recruited in the smallest diameter class, while for the greater classes the ingrowth was assumed to be null.

The elements of the transition matrix were calculated as $b_{spk,t} = id_{spk,t}/\Delta$ and $a_{spk,t} = 1 - b_{spk,t} - m_{spk,t}$, where $id_{spk,t}$ is the annual diameter growth of a tree of species sp in the class k, Δ is the width of the diameter class, and $m_{spk,t}$ is the probability that a tree of same species and diameter class k dies in the time interval t to t + Δt. Both $id_{spk,t}$ and $m_{spk,t}$ were estimated for each year and diameter class using the diameter growth and probability of mortality models respectively (see Section 2.3), where the independent variables required for the estimation were calculated at each year t from the vector containing the number of trees per diameter class y_{spt}.

The ingrowth rate i_t was obtained as the product of the probability of positive ingrowth (recruitment occurrence) and of the expected ingrowth amount, conditional on positive recruitment, being both state and species dependent. The probability of ingrowth and the number of ingrowth trees were obtained for each year t from the two respective models described in Section 2.3.

2.3. Growth, mortality, and ingrowth models

Diameter growth $id_{k,t}$ and probability of mortality $m_{k,t}$ were obtained from individual tree models, while the probability of positive ingrowth and the expected ingrowth amount were obtained from stand level models. The same competition indicators were used in all the models, including the basal area, G, and the basal area of trees with diameter larger than or equal to the target tree, BAL (Wykoff, 1990), which are frequently used in growth models (Weiskittel et al., 2011).

For testing the presence of between-species interactions, the competition status was expressed as the sum of the species' competition, i.e., sum of per species G and BAL. In addition, the possible effect of spatio-temporal variation of temperature was analysed by including mean annual temperature T as a single independent variable or as interactions with G terms, which was decided after a preliminary exploration and in order to maintain the model as parsimonious as possible.

Table 2

Summary of main characteristics of the initial surveys, at the plot level and by species. N is the number of trees per ha, G is basal area, dg the quadratic mean diameter, T annual mean temperature, sd is the standard deviation, min and max are minimum and maximum values, respectively.

	N	G	dg	T		*Abies alba* N	G	dg	*Fagus sylvatica* N	G	dg	*Picea abies* N	G	dg
	stems/ha	m²/ha	cm	°C		stems/ha	m²/ha	cm	stems/ha	m²/ha	cm	stems/ha	m²/ha	cm
Mean	524	38.7	32.6	6.3		157	13.5	36.9	158	7.8	25.0	185	16.3	36.5
Sd	230	11.9	9.0	1.0		151	11.5	14.9	165	8.6	10.7	141	12.8	13.1
Min	152	15.6	17.7	3.0		2	0.0	9.8	1	0.0	8.5	1	0.0	7.6
Max	1341	79.8	63.2	8.5		565	56.0	90.7	754	41.8	63.2	572	68.1	84.9

Tree-level diameter growth models were formulated for each species including a size effect according to the model of Hugershoff (1936), together with competition measures and T, as well as interaction terms:

$$\log(id_{ijt}) = (a_0 + a_{0j}) + (a_1 + a_{1j}) \cdot d_{ijt} + a_2 \cdot \log(d_{ijt}) + a_3 \cdot T_{jt} + \sum_{sp} b_{sp} \cdot G_{spjt} + \sum_{sp} c_{sp} \cdot G_{spjt} \cdot T_{jt} + \sum_{sp} e_{sp} \cdot BAL_{spijt} + \varepsilon_{ijt}$$

where id_{ijt} represents the annual diameter increment of the tree i in the plot j at the survey t. d_{ijt} is the diameter at 1.3 m of that tree. G_{spjt} is the basal area of the species sp in the plot j, survey t. BAL_{spijt} the basal area of trees of the species sp larger or equal than the tree i, and T the mean annual temperature, in the same plot and survey. Finally, sp is each one of the species studied, ie. fir, beech, spruce, and other minor species grouped together. Since the data came from a hierarchical structure, with several trees measured in the same plot j, mixed models were fit including random effects in both intercept and diameter terms with the plot as the grouping structure.

Similarly, tree-level mortality models for each species were developed. As tree mortality is a discrete event and, considering the possible correlation between trees measured in the same plot, a generalized linear mixed model approach following a binomial family, i.e., logistic regression, was used. Tree size was described by d and the second power of this variable, transformation frequently included in mortality models to get the characteristic U-shape (Monserud and Sterba, 1999; Jutras et al., 2003; Zhao et al., 2004). The general expression of the *logit* function was:

$$\text{logit}(m_{ijt}) = (a_0 + a_{0j}) + a_1 \cdot d_{ijt} + a_2 \cdot d_{ijt}^2 + a_3 \cdot T_{jt} + \sum_{sp} b_{sp} \cdot BAL_{spijt} + \sum_{sp} c_{sp} \cdot BAL_{spijt} \cdot T_{jt} + \varepsilon_{ijt}$$

where m_{ijt} is the probability that the tree i with d_{ijt} dies in the plot j, survey t, and BAL_{spijt} are the basal area of larger trees of each studies species in the same plot and survey, respectively. T_{jt} is the mean annual temperature. Mortality models were fit as mixed models, including random effects in the intercept, and using the plot as the grouping structure.

Two different ingrowth plot-level models were developed for each species, first one for the probability of ingrowth in each survey, r_{jt}, and therefore formulated as a generalized linear mixed model approach following a binomial family, and a second one for the expected number of ingrowth stems, Ni_{jt}, in the plots with positive recruitment formulated as a mixed model, both of them with plot as grouping structure. After a preliminary test of models' structure, the general expression for the models was:

$$\text{logit}(r_{jt}) = (a_0 + a_{0j}) + a_1 \cdot T_{jt} + \sum_{sp} b_{sp} \cdot G_{spjt} + \sum_{sp} c_{sp} \cdot G_{spjt} \cdot T_{jt} + \varepsilon_{jt}$$

$$\log(Ni_{jt}) = (a_0 + a_{0j}) + b_1 \cdot G_{jt} + b_2 \cdot G_{jt} \cdot T_{jt} + \varepsilon_{jt}$$

The G_{spjt} was the basal areas of each species in the plot j at survey t and G_{jt} the total basal area for same plot and survey. Note that due to the reduced number of plots with positive recruitment, total basal area was used instead of separating it by species.

The diameter growth and the expected number of ingrowth models were fitted using the "lme" function while probability of mortality and

ingrowth occurrence models were fitted using the function "glmer" of the "lme4" library (Bates et al., 2015). Conditional and marginal R^2 were used as goodness-of-fit measures, and were obtained using the "r.

squaredGLMM" function in the "MuMIn" library (Barton, 2020). For all the models a level of $p = 0.05$ was used for significance testing of the variables, and Akaike's information criterion (AIC) was used to compare results and to select among different model's structures, for instance those where the competition variables were not split up by species.

2.4. Projection of diameter distributions

To answer the specific questions stated in the introduction, different species diameter distributions were set up to further simulate their dynamics. Three initial diameter distributions with similar basal area but different quadratic mean diameters were used (Fig. 1).

To analyse whether temperature modifies the species size dominances and proportions (Q1), three different mixed stands of the studied species were considered, representing different stages of stand development (quadratic mean diameter, dg, around 22.4, 27.4 and 32.5 respectively). These figures were defined according to the values in the dataset (Supplementary table 4), ensuring that after projecting the initial distributions the resulting values were inside the data range. Within each stand the three species, fir, beech and spruce, had the same diameter distribution (Fig. 1A–C). Therefore, each species contributed a third of the total stand basal area and they had the same degree of size dominance.

To analyse the interactive effects of temperature and size dominance on species and stand growth (Q2 and Q3), three mixed stands composed of the three species were considered. However, in these cases, each species contributed a third of the total stand basal area, although they had a different degree of size dominance, meaning a different dg. So, for these stands there was one size dominant species (Fig. 1C) while the other two had smaller but similar sizes (Fig. 1A).

For each one of the 3 + 3 scenarios, 1000 initial diameter distributions were randomly simulated. The distributions were truncated at the lower limit of the diameters of the study plots, i.e. 7.5 cm, and the width of the diameter classes was always 10 cm because the ingrowth trees in the study plots had diameters between 7.5 and 17.5 cm. Moreover, variability in the initial distributions was allowed, so the total stand basal area average was around 33 m^2/ha but ranged between approximately 20 and 45 m^2/ha. For the dominance in size, the dg was set so that the dominant species dg ranged from 29 to 36 cm, while the other two dg ranged from 20 to 25 cm.

From each initial distribution both the state-dependent transition matrix and the state-dependent ingrowth matrix were obtained, and then projected 10 years into the future. The obtained distributions were projected two more times to obtain the final distribution of alive trees per diameter classes 30 years later. The time interval was set to 10 years because it was approximately the time elapsed between surveys in the studied data. The projections considered three different temperature
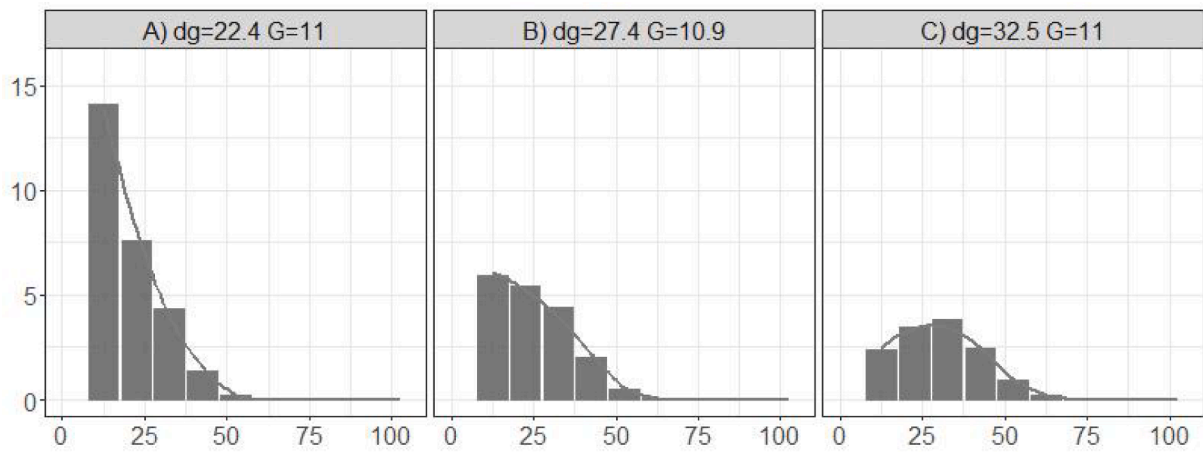
Fig. 1. Histogram and empirical distribution functions of the averaged initial diameter distributions used as starting point simulations; dg is quadratic mean diameter in cm and G is basal area in m^2/ha.

Table 3

Parameter estimates and standard errors (StdE) for the diameter growth models. StdRnd represents the standard deviation of the random effects associated with the intercept, the initial diameter, or the residual, R2m and R2c are respectively the marginal and conditional R^2.

log(id)	Fir		Beech		Spruce	
	Value	StdE	Value	StdE	Value	StdE
Intercept	−8.3983	0.1877	−4.0845	0.3733	−5.8706	0.3364
d	−0.0345	0.0023	−0.0295	0.0041	−0.0397	0.0028
log(d)	1.5923	0.0342	1.1717	0.0558	1.5706	0.0368
T	0.7405	0.0289	0.2004	0.0558	0.4453	0.0492
G.Fir						
G.Fir*T	−0.0060	0.0005	−0.0061	0.0006	−0.0082	0.0008
G.Beech			0.0742	0.0191	−0.0473	0.0087
G.Beech*T	−0.0091	0.0009	−0.0138	0.0026		
G.Spruce			−0.0837	0.0128	0.0325	0.0107
G.Spruce*T	−0.0081	0.0005	0.0045	0.0018	−0.0117	0.0019
G.Other						
BAL.Fir	−0.0163	0.0028				
BAL.Beech			−0.0404	0.0048	−0.0780	0.0075
BAL.Spruce			0.0220	0.0074	−0.0105	0.0026
BAL.Other	−0.0834	0.0244	−0.1304	0.0197		
StdRnd. Intercept	0.7419		0.6560		1.0836	
StdRnd d	0.0126		0.0177		0.0137	
StdRnd Residual	0.7659		0.7040		0.7617	
AIC	42,552		23,690		49,390	
R2m	0.3304		0.3417		0.3078	
R2c	0.6664		0.5560		0.7124	

Table 4

Parameter estimates and standard errors (StdE) for the mortality models. StdRnd represents the standard deviation of the random effects associated to the intercept, R2m and R2c are respectively the marginal and conditional R^2.

logit(m)	Fir		Beech		Spruce	
	Value	StdE	Value	StdE	Value	StdE
Intercept	−3.6930	0.3381	2.6239	1.1092	0.1282	0.7179
d	−0.0278	0.0048	−0.0846	0.0094	−0.0782	0.0065
d^2	0.0003	0.0000	0.0012	0.0001	0.0010	0.0001
T			−0.9671	0.1793	−0.5376	0.1033
BAL.Fir	−0.4662	0.0513	−0.4622	0.0868	−0.7334	0.0690
BAL.Fir*T	0.0782	0.0077	0.0763	0.0131	0.1165	0.0104
BAL.Beech	0.2614	0.0673	0.0713	0.0120	0.3801	0.0941
BAL.Beech*T	−0.0331	0.0089			−0.0447	0.0139
BAL.Spruce	0.2591	0.0410				
BAL. Spruce*T	−0.0390	0.0065			0.0067	0.0013
BAL.Other			0.2952	0.0616		
BAL.Other*T						
StdRnd. Intercept	1.1770		1.0600		1.6420	
AIC	9828		5304		9567	
R2m	0.1426		0.1859		0.1369	
R2c	0.3966		0.3931		0.5257	

scenarios, with constant temperatures of 5.3, 6.3 and 7.3 °C maintained throughout the 30 years. The diameter distributions obtained after the 30-year projections were analysed by looking for differences in species size distributions and basal area change (ΔG, the basal area at the end of 30 years of projection minus the initial basal area divided by the time interval) under different temperatures.

3. Results

3.1. Growth, mortality, and ingrowth models

There was a positive effect of mean annual temperature, T, on tree growth for all species (Table 3). In general, both inter- and intra-specific basal area had a negative effect on diameter growth; however, the effects of competition were species specific, and consequently the parameter values differed from each other (Table 3). Furthermore, these negative effects of competition were generally magnified at higher temperatures. Similarly, the competition from larger trees was in general negative. The exception was the effect of spruce on beech diameter growth, with the largest trees having a positive effect and the competition effect being less negative when the temperature increased. Interestingly, there was a positive effect of intra-specific competition in beech, and of inter-specific competition of fir in spruce, which only occurred at lower temperatures.

Temperature did not directly affect the probability of mortality although it modified the effects of competition (Table 4). As for diameter growth, the effects of intra- and inter-specific competition terms on the mortality varied among species. Generally, the greater the competition, the greater the probability of mortality (Table 4). Temperature increased the intraspecific competition effect of fir and spruce. It also modified the interspecific effect of spruce on fir, and of fir on spruce, but with opposing effects, resulting in a reduction in mortality for high temperatures in fir and for low temperatures in spruce. For fir and spruce, high temperature also influenced mortality by reducing the effect of competition with beech. The mortality of beech was affected by interspecific competition with fir so that the higher the temperature the higher the effect of competition.

The results of species ingrowth probability models show that temperature had a positive effect on the probability of ingrowth except for

Table 5

Parameter estimates and standard errors (StdE) for the ingrowth probability models. StdRnd represents the standard deviation of the random effects associated with the intercept, R2m and R2c are the marginal and conditional R^2, respectively.

logit(r)	Fir Value	StdE	Beech Value	StdE	Spruce Value	StdE
Intercept	−14.0103	4.2830	18.6932	6.4795	−18.8724	6.0440
T	2.5072	0.6839	−2.3336	0.9534	3.2974	0.9776
G.Fir			−0.7104	0.3085		
G.Fir*T			0.1023	0.0464		
G.Beech	−0.1134	0.0492				
G.Beech*T					−0.0371	0.0097
G.Spruce			−0.6687	0.2331	0.6043	0.2285
G.Spruce*T	−0.0197	0.0072	0.0862	0.0351	−0.1024	0.0372
G.Other						
G.Other*T						
StdRnd intercept	2.5780		1.9930		2.5820	
AIC	170		201		186	
R2m	0.4800		0.3719		0.4140	
R2c	0.8278		0.7154		0.8063	

Table 6

Parameter estimates and standard errors (StdE) of the number of ingrowth trees for ingrowth models. StdRnd represents the standard deviation of the random effects associated to the intercept and residuals, R2m and R2c are respectively the marginal and conditional R^2.

log(Ni)	Fir Value	StdE	Beech Value	StdE	Spruce Value	StdE
Intercept	3.8893	0.6024	3.8663	0.2787	5.2913	0.7168
T						
G.Fir	0.1970	0.0830				
G.Fir*T	−0.0323	0.0120			−0.0082	0.0032
G.Beech	−0.4574	0.1186				
G.Beech*T	0.0554	0.0156			−0.0183	0.0050
G.Spruce	−0.0698	0.0236			−0.0702	0.0215
G.Spruce*T			−0.0074	0.0025		
G.Other			−0.2235	0.0837		
G.Other*T						
StdRnd Intercept	0.9145		0.9515		1.0075	
StdRnd Residual	0.6513		0.9140		0.9788	
AIC	275		451		362	
R2m	0.2186		0.1564		0.1936	
R2c	0.7370		0.5952		0.6084	

beech (Table 5). Competition, on the other hand, had a negative effect, which was generally stronger at high temperatures. However, temperature did not affect the interspecific effect of beech on fir. Also, the higher the competition the lower the number of ingrowth trees, but this number was not directly affected by temperature (Table 6).

In summary, T directly affected the three studied species, such that the higher the T the greater the diameter growth. It also directly affected beech and spruce so that the greater the temperature the lower the probability of mortality, and for fir and spruce T also increased the probability of ingrowth. In addition, T modulated the competition effects. Intraspecific competition reduced the diameter growth and increased the probability of mortality, this last effect was enhanced with temperature except for beech. Interspecific competition reduced the diameter growth and increased the mortality, except for the interaction between fir and spruce, which at high temperatures reduced the mortality of fir and at low temperatures reduced the mortality of spruce. Interspecific competition also reduced the probability of recruitment although this effect could be more important or milder depending on the species and temperatures.

Parameter estimates for the other minor species models have been included as supplementary Table 5.

3.2. Influence of temperature on the species size dominances and proportions

Fig. 2 shows the diameter distribution obtained for each stage of stand development after 30 years of projecting initial diameter distributions (Fig. 1) using the three mean annual temperatures as possible scenarios. The species size distribution development was affected by the temperature (Fig. 2). In general, beech had a greater number of stems in the lowest diameter classes. The diameter distributions of fir and spruce were more similar to each other, although fir had more trees in the lowest diameter classes, and the differences increased with temperature, especially for the distribution A at the highest temperature scenario (7.3 °C), where fir tended to have a larger number of stems in all the size classes.
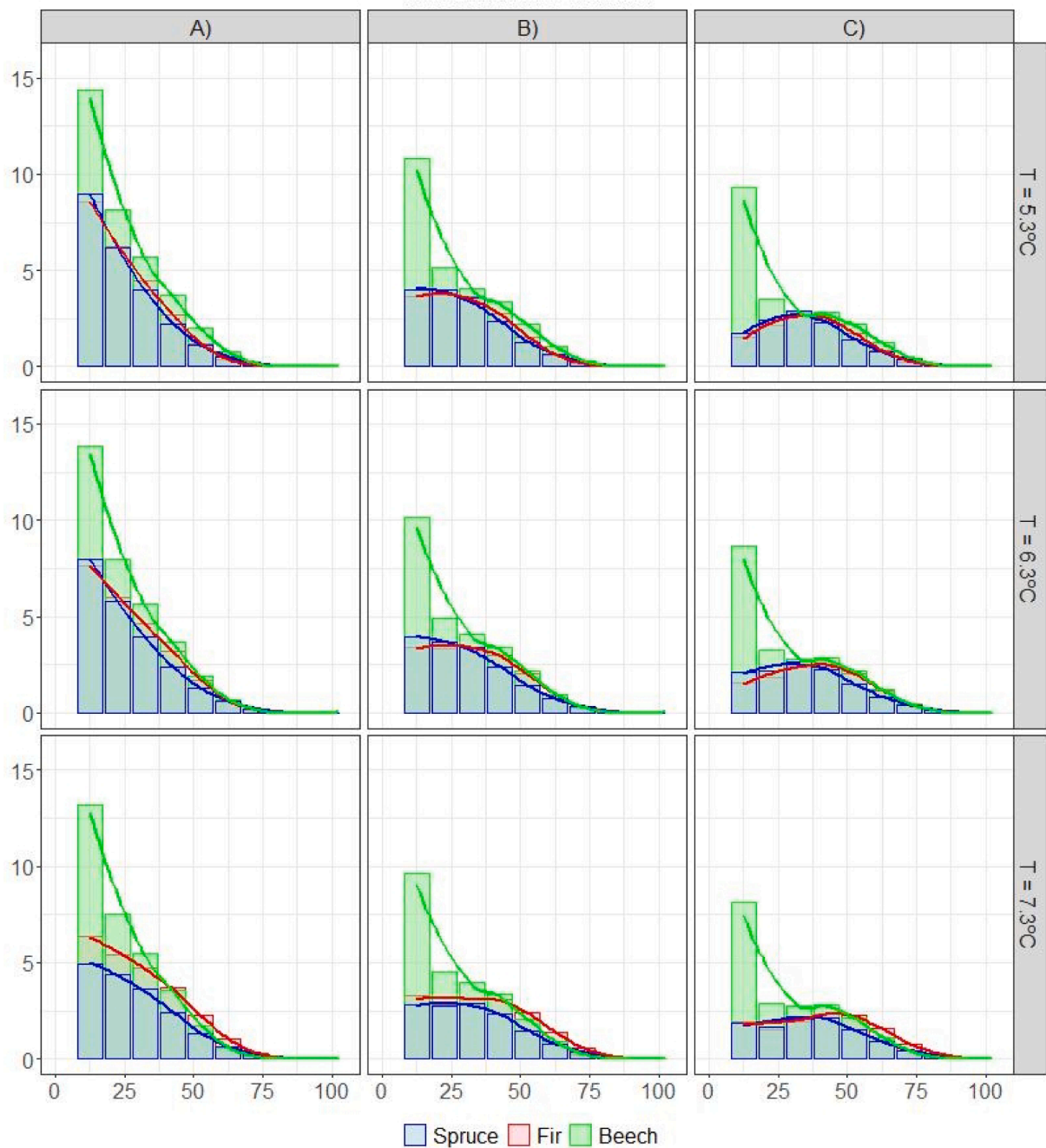
After the projection the stand structure generally tended to be organized so that beech was the smaller species in terms of dg, while the dominance of fir and spruce was similar at the coldest scenario (T = 5.3 °C) but at the warmest scenario (T = 7.3 °C) fir became the dominant species (Fig. 3). The stage of stand development also influenced the size distribution, enhancing the effect T. That is, for the youngest stands, differences among dg were not so clear, especially at the coldest scenarios, increasing the differences for mature stands (initial distribution C). Moreover, the dg of the resulting diameter distributions had more variability for fir than for beech or spruce, especially at the highest temperature scenario (Fig. 3).

In addition, high temperatures clearly favored fir and hindered beech and spruce basal area development, with a much greater negative effect on spruce. That is, independently of the stage of stand development, at the coldest scenarios the proportion of fir was reduced, and the proportion of beech was increased, while for the temperature of 7.3 °C it was the proportion of spruce which was clearly reduced (Fig. 4).

3.3. Influence of the temperature and species size dominance in species basal area changes

Fig. 5 shows the diameter distribution obtained for each case of size dominance after 30 years of projecting distributions using the three mean annual temperatures as possible scenarios. The species size dominance determined the final diameter distributions. When spruce or fir were dominant, in general they maintain their dominance, with the other species, especially beech, developing larger number of trees in the lower diameter classes. In contrast, when beech was the size dominant species the three diameter distributions tended to equalize.

The species basal area derived from the diameter distributions showed that the change in basal area of fir was much less influenced by the identity of the size dominant species (Fig. 6b) than by temperature, which strongly increased fir basal area. Beech was also affected by

Fig. 2. Diameter distributions obtained after 30 years of development for different mean annual temperatures T (°C) and different initial diameter distributions (A, B and C according to Fig. 1).

temperature, although in the opposite way, whereas the effect of T on spruce basal area was slight. Beech was the species reaching the highest basal area after 30 years (i.e., greater basal area change) at the coldest temperature (Fig. 6c), however for the mild and warmest scenarios fir showed a similar increment in basal area. Furthermore, independently of the temperature, the basal area growth of beech was lower when it was the size dominant species. The opposite occurred for spruce, which for a given temperature showed the highest basal area change when it was the dominant species (Fig. 6a) although the differences were not as evident as for beech.

3.4. Influence of temperature and species size dominance on the stand basal area change

Total stand basal area changes derived from the analysed diameter distributions (Fig. 5) can be seen in Fig. 7. In general, there were significant differences in stand basal area changes among temperatures for a given size dominance, with a positive effect of temperature, but they were less evident when fir was the dominant species (Fig. 5b). For a given temperature scenario, the highest changes in the stand basal area were obtained when the size dominant species was spruce, while when beech was the size dominant species the change in basal area was the lowest. Temperature was also important, such that the higher the temperature the greater the variability among simulations for the same size dominance case.
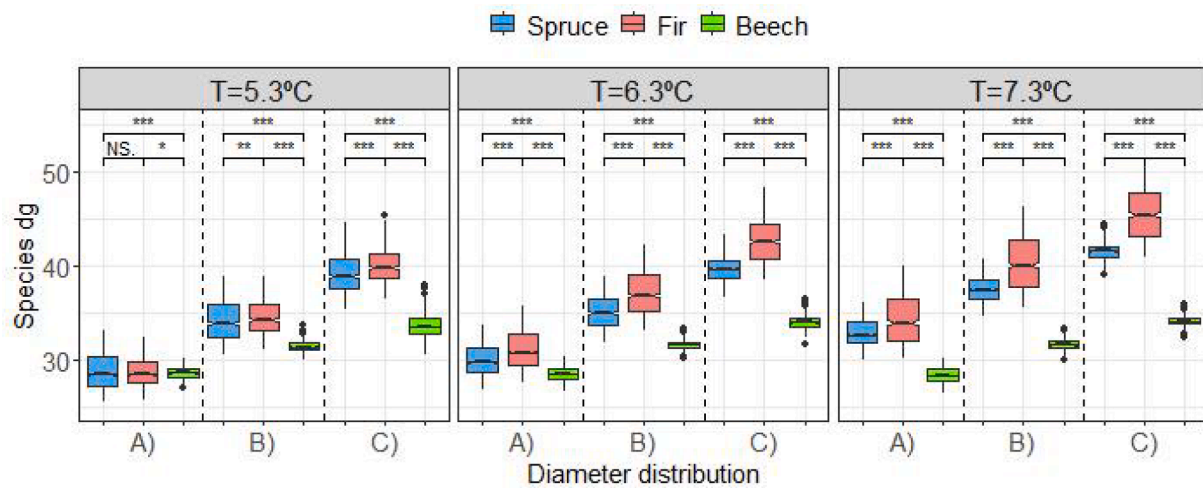
Fig. 3. Quadratic mean diameter by species (dg cm) obtained for different mean annual temperatures T (°C) and different initial diameter distributions (A, B and C according to Fig. 1). P value for significant differences "NS"=non–significant, "***"=0.001, "**"=0.01, "*"=0.05.
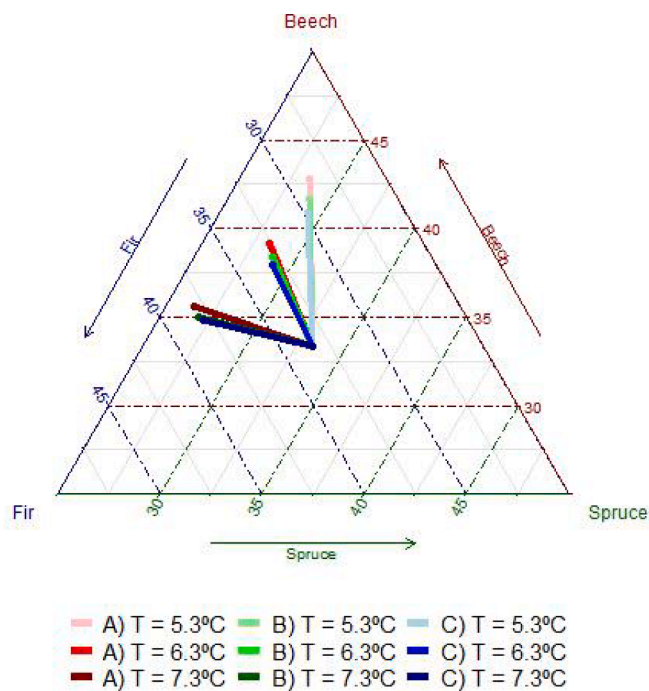

Fig. 4. Changes in the stand species proportion in basal area for different cases of mean annual temperature (T) and diameter distributions (A, B and C initial diameter distributions, with dg 22.4, 27.4 and 32.5 cm respectively, according to Fig. 1,).

4. Discussion

We developed a matrix model that allowed us to identify the combined effects of interspecific competition and temperature on the species size dynamics in mountain spruce-fir-beech forests. Our results showed that temperature influenced species specific dynamics modifying species size dominances and proportions. High temperatures favored stand basal area growth, especially increasing the basal area of fir, while reducing that of beech. However, the temperature effect on changes in stand basal area was weaker than the identity of the size-dominant species, such that the highest or the lowest changes occurred when spruce and beech were the size-dominant species, respectively (Torresan et al., 2020).
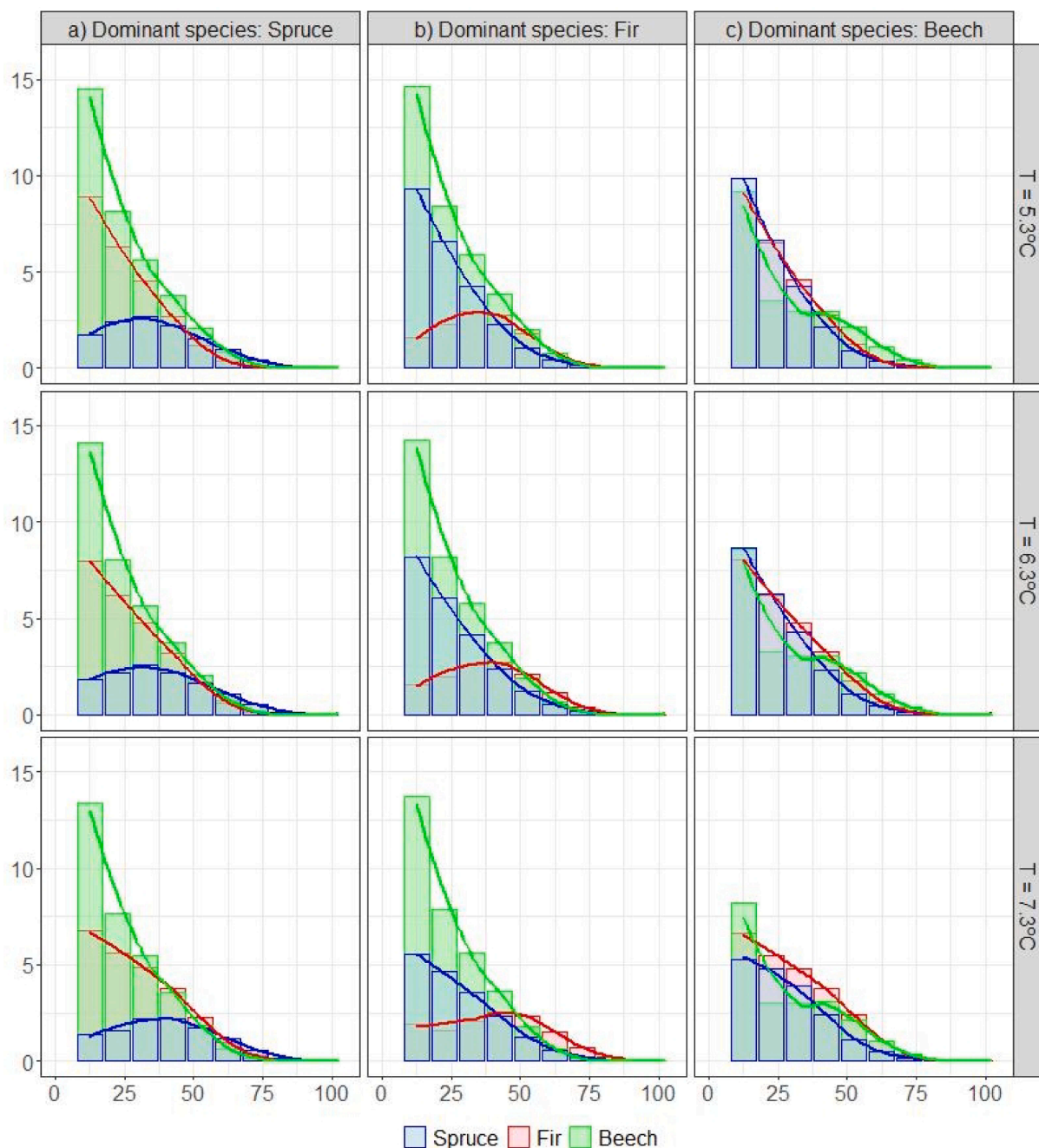
4.1. Methodological approach

Matrix models have been used for decades (Usher, 1966; Usher, 1969) to study the dynamics of uneven-aged or all-aged stands or mixed stands (Liang et al., 2005; Liang and Picard, 2013; Ficko et al., 2016), and have been developed to examine climate effects using climate variables for transition matrix calculation (Liang and Picard, 2013; Du et al., 2021), as in this study. The design of matrix models requires careful consideration of two important characteristics: the time step and the width of size classes. It is recommended that the timestep for empirical matrix models is consistent with the measurement interval between surveys (Liang and Picard, 2013), and therefore we used 10 years. The width of size classes should be selected accordingly to the time step, such that the trees do not move up more than one class (Usher, 1966). Based on Usher's assumption we selected a class interval of 10 cm, which was also consistent with the diameter range observed for the ingrowth trees, although the wider the class interval the higher the variation inside classes, which could increase the prediction bias (Liang and Picard, 2013; Pyy et al., 2020).

The model developed is based on a state-dependent transition matrix, which assumes that trees compete for resources so that growth, mortality and ingrowth is determined by inter-tree competition (e.g., Buongiorno and Michie, 1980; Picard and Franc, 2001; Zhao et al., 2004), and potentially even considers inter- and intra-specific competition, i.e., species specific requirements (e.g. Namaalwa et al., 2005; Martin Bollandsås et al., 2008). This allows the modelling of mixed forests and the scaling up of inter-specific interactions, observed at tree level in both growth and mortality (Pretzsch et al., 2015b), to the size distribution level and, therefore, of the relationship between stand structure and stand production, in a similarly detailed way as the individual-tree models but simpler and often more efficiently (Martin Bollandsås et al., 2008; Liang and Picard, 2013).

We used stand basal area as a measure of density and as a proxy for competition for resources. However, different species can have very different growing area requirements and basal area maxima per hectare. This means that their species-specific basal area values have different density effects, e.g. 40 m^2/ha is dense for beech but not for spruce. It would be preferable to use relative stand density indices, which consider species specific site occupancy (Sterba et al., 2014), however there is a lack of specific maximum size density lines at large scales suitable for the study area.

Size-asymmetric competition among trees influences the spatial arrangement of diameters and this results in interactions at the individual level that can shape the size distribution (Picard, 2019). Although

Fig. 5. Diameter distributions obtained after 30 years of development for different mean annual temperatures T (°C) and different species size dominances (dominant species with initial distribution C, and the other species with an initial distribution according to Fig. 1).

we used BAL as a measure of size-asymmetric competition (Wykoff, 1990; Weiskittel et al., 2011; Cordonnier and Kunstler, 2015; Mina et al., 2018a), many studies have shown that this assumption is often unrealistic. For example, competition from larger trees can be size-symmetric, and competition from smaller trees can be size-asymmetric, regardless of whether the competition is for light or belowground resources (e.g. see review by Forrester, (2019)). Therefore, linking BAL with asymmetric competition could be considered an oversimplification and there may be alternative variables that more directly quantify a specific type of interaction and could therefore aid interpretation of future studies.

A weakness of matrix models in general, and of our model in particular, is that it does not consider the variation within classes, for instance by adding the height variation of the trees (Pyy et al., 2020). Thus, the model could be improved by including competition indices

that take into account vertical structure, for instance through crown variables (Pretzsch et al., 2015b). In our results we implicitly consider a positive relationship between tree diameter and tree height and therefore we extrapolate the interpretation of results in terms of basal area to productivities.

One of the major challenges in forest dynamics models in general, and in matrix models in particular, is the difficulty of estimating mortality and recruitment (e.g., Buongiorno and Michie, 1980; Liang et al., 2005; Picard et al., 2008). In our study the models for probability of mortality and for the number of ingrowth trees showed low r-squared values. Mortality models also address the added difficulty of differentiating between dead and thinned trees, being in some cases indistinguishable and therefore grouped as removed and excluded from models. In general, the data source heterogeneity, arising from permanent plots
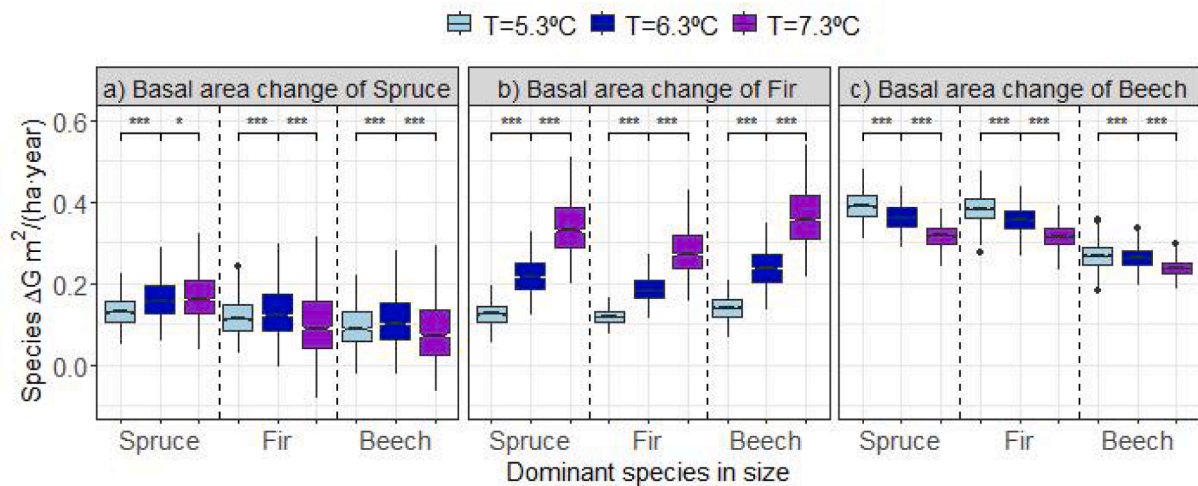
Fig. 6. species basal area change (ΔG m^2/(ha·year)) obtained for different size dominance cases and mean annual temperatures T (°C). P value for significant differences "NS"=non– significant, "***"=0.001, "**"=0.01, "*"=0.05.
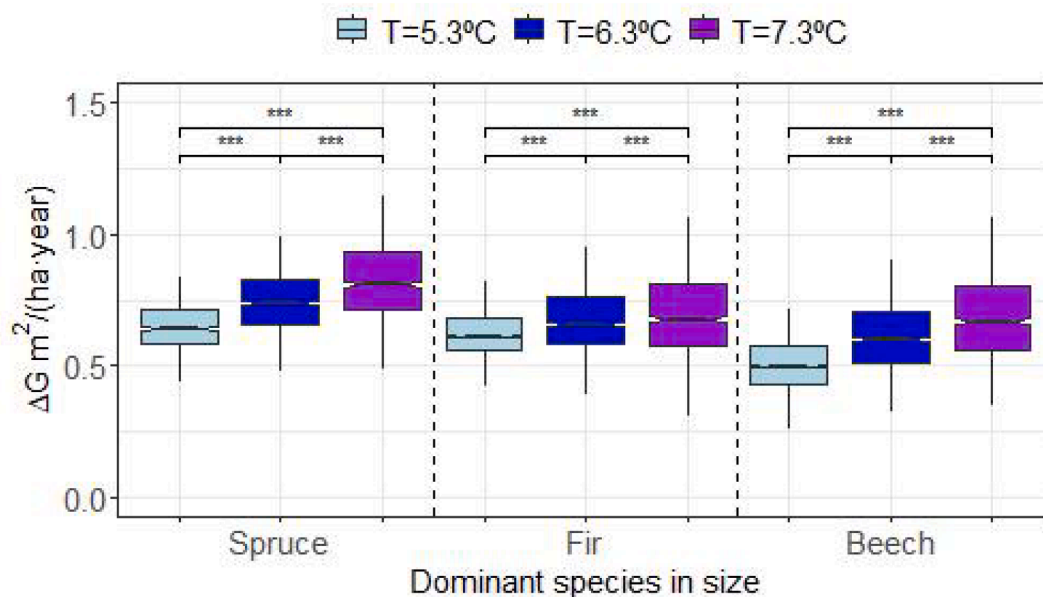

Fig. 7. Total stand basal area change (ΔG m^2/(ha·year)) obtained for different dominance cases and mean annual temperatures T (°C). P value for significant differences "NS"=non– significant, "***"=0.001, "**"=0.01, "*"=0.05.

in different countries established for different purposes, different measurement protocols, etc., made it difficult to improve estimations. Therefore, much higher variability was explained when random effects were included in the models, resulting in important differences between marginal and conditional R^2. Despite this, there was a clear advantage of using a database consisting mostly of long-term permanent sample plots that are distributed widely through Europe, and therefore established along productivity and ecological gradients, capable of providing information of forest stand dynamics which cannot be derived from forest inventories or small temporary plots (Pretzsch et al., 2019).

4.2. Temperature and competition effects on species dynamics

Temperature is often the main limiting factor of forest growth in mountain regions (Ettinger et al., 2011; Babst et al., 2013). Our results showed that higher temperatures are linked to greater tree growth rates, lower probabilities of mortality and greater probabilities of ingrowth. Positive effects of temperature on tree growth rates have been

previously reported for these species in central Europe (Čavlović et al., 2015; Mina et al., 2018b), although climate warming is recently inducing growth decline in some areas of their distribution range (Gazol et al., 2015; Knutzen et al., 2017; Bosela et al. 2021). Temperature effects on mortality seem to be more dependent on site water conditions (Etzold et al., 2019; Pretzsch et al., 2020a). Temperature also influenced competition, increasing the effect of intra-specific competition on tree growth for the three species, and on mortality for fir and spruce, which suggests less self-tolerance at warmer sites (Zeide, 1985). Interestingly, temperature had an important effect on species interactions, changing species specific competitiveness in mixed stands. Interspecific competition generally reduced competition pressure on tree growth in this mixture (Mina et al., 2018a), and this effect mainly increased with temperature. A similar temperature effect was reported for spruce (Forrester et al., 2013) and for several mixtures in Central Europe by Mina *et al.* (2017), although they did not find a significant effect on species complementarity for spruce-fir-beech mixed stands. Temperature also modified the inter-specific competition effect on tree mortality

and stand ingrowth, but with distinct effects for the three species, as found for climate effects on mortality in other mixtures (Condés and del Río, 2015; Hülsmann et al., 2018).

The different *inter-specific competition × temperature* effects on tree growth, mortality and ingrowth reveal the complexity of species interactions, whose net effects cannot be easily up-scaled from the tree to the stand level (Forrester and Pretzsch, 2015; Uhl et al., 2021). Our modelling approach allowed us to illustrate the temperature effects on species size distributions dynamics, which clearly enhances fir size dominance and proportion and hinders spruce proportion (Uhl et al., 2021). Beech was less affected by temperature than by the dominating species in terms of species proportion, which probably resulted from its greater presence in lower size classes. Climate warming and increasing drought events modify within and between species growth partitioning, having stronger effects on large than small trees in these stands (Pretzsch et al., 2018) and on more vulnerable species (spruce and beech more vulnerable than fir) (Vitasse et al., 2019; Gillerot et al., 2021). Nevertheless, other environmental factors could influence species size dominances. Many of these mixed mountain forests were strongly affected by acidic rain in the 1960–1990, which may have co-determined the growth and especially the growth partitioning within and among species. As for drought, mainly the dominant trees were affected by the SO_2-emissions, but in this case, fir was much more vulnerable than spruce and beech (Vitasse et al., 2019). However, our data show greater representativeness in the post acidic rain period (1990–2016). In summary, fir may benefit from warming due to an extension of the growing season (Leuschner and Ellenberg, 2017) and from the reduction of SO_2 emissions (Uhl et al., 2013); beech may benefit from warming due to an extension of the growing season (Leuschner et al., 2006), but can suffer from late frost (Zohner et al., 2020); and spruce, on the other hand, is more vulnerable to extreme droughts (Vitasse et al., 2019; Bottero et al., 2021) and other risks linked to climate change such as bark beetle attacks (Marini et al., 2017). Moreover, spruce often shows decreases in regeneration due to closed canopies (Pretzsch et al., 2015a), which may explain predicted changes in species size distributions.

4.3. Influence of temperature and species size dominance on stand productivity

Our results confirmed the importance of tree species size dominances on stand productivity, with greater productivity when spruce is the size dominant species and lower when it is beech (Torresan et al., 2020). The species size distribution simulations indicate that this effect is mediated by temperature, which always had a positive effect on productivity, but greater when spruce was the dominant species. These results fit the conceptual framework proposed by Forrester (2019), which highlights the influence of environmental conditions on growth partitioning among trees, and the relevance of size distributions and growth partitioning on stand growth.

The weak effect of temperature on stand level productivity is consistent with the results reported by Hilmers et al. (2019) for this mixture, who did not find any temporal changes in stand productivity despite the climate warming. However, Hilmers et al. (2019) found a significant elevation and temperature joint effect, with greater productivity at lower elevations, in accordance with our positive effect of temperature and with the findings of Torresan et al. (2020). At the species level, our results agree with the positive growth trends linked to climate warming found for fir (Hilmers et al., 2019), but not for beech and spruce which showed neutral and negative trends. As for the stand productivity, the results are not directly comparable, as Hilmers et al. (2019) analysed temporal trends after removing the elevation and temperature site effects. Moreover, in this study we used species and stand basal area change as an indicator of species and stand productivities, which presents some drawbacks as species height growth is not considered.

4.4. Implications for forest management

The stand structure is the key element for silvicultural planning in mixed, multiaged stands (O'Hara, 2014). The use of different types of diameter distributions determining target size structure for complex forest stands has been used in forest management for a long time. Changing stand structure through tree removals is the main tool in forest management, thereby interfering in the loop of stand structure-growth-tree size-stand structure (Pretzsch, 2009). The effects of stand structure on stand growth are difficult to determine using single stand structural variables (e.g., tree size inequality, stems per ha, basal area, size distributions…) because none are strongly correlated with growth unless all the others are relatively constant. In contrast, many of the effects of stand structure on stand growth can be explained by considering two or three of the more influential stand structural variables, such as the shape of size distributions, size-growth relationships, and stand density (Forrester, 2019). These were directly quantified in this study to tease apart the causes of species composition and temperature on stand structure and hence stand growth.

Matrix models have been widely applied since their appearance (Usher, 1969) to understand and predict the effects of forest management, for instance looking for sustainable harvest rates (Drozdowski, 2006; López et al., 2007), optimizing economic outcomes (Rämö and Tahvonen, 2014) or anticipating changes in stand structure and composition (Favrichon, 1998). In our model, the inclusion of the climate variable provides an additional tool that could allow analyses of management strategies under different climate scenarios. Our results suggest that increasing temperatures may modify species dynamics and interactions, resulting in different species proportions and dominances, which are crucial for silvicultural planning and should be considered in forest management and silvicultural prescriptions (Pretzsch et al., 2021a). The reviving vitality of fir following a reduction in the acid rain may be on expense of the mixing proportion and growth of spruce and beech. The essential contribution of fir to the stand productivity may reduce the species diversity and risk distribution (Jactel et al., 2017), so that silvicultural management might balance the proportions of the three species. The presently high productivity is an insufficient indicator for sustainable productivity and system stability (Bowditch et al., 2020; Uhl et al., 2021). Although mixed mountain forests of spruce-fir-beech were found to be resilient systems in terms of stand productivity (Hilmers et al., 2019; Uhl et al., 2021), specific silvicultural interventions in favour of Norway spruce and European beech are needed to control species compositions to keep the demographic stability of mixed complex mountain forest stands, especially under climate warming (Pretzsch et al., 2015a).

5. Conclusions

The international project community and cross-regional compilation of growth, structure and climate data of long-term experiments in mixed mountain forests enabled new insights into the growth trends and functioning of uneven-aged and multi-species stands of Norway spruce, silver fir and European beech. Here we used a newly developed matrix model mainly for describing and analysing the relationship between species size distribution and growth, and how it is modulated by temperature.

Our results indicate that temperature is not only related to the growth rate of trees, the probability of mortality and the probability of ingrowth, but influences the effect of intra-and inter-specific competition, changing species-specific competitiveness in mixed stands. Temperature shapes the species size distributions, such that warming enhances fir size dominance and proportion and hinders spruce proportion, whereas beech is less affected. All these patterns are in agreement with our first hypothesis H1.

In addition, tree species size dominance influences species and stand productivity, with greater stand productivity when spruce is the size

dominant species (in accordance with our hypothesis H3). This effect of species size dominance is, however, modulated by temperature. That is, warming temperatures increased the productivity of fir more than the identity of the size dominant species. On the other hand, the effect of warming on beech, which is the opposite to the effect of fir, was less important than the effect of the species dominance. Spruce was only slightly affected by warming and the positive or negative effect depends on which species was dominant, and therefore only partially confirms our hypothesis H2.

The species-specific growth trends show that silvicultural prescriptions and interventions are essential for keeping mountain forests of spruce-fir-beech in a steady state even under external disturbances such as climate change. Scenario analyses may reveal the appropriate regulation of stand density and species proportion for keeping the triad of spruce-fir-beech and maintaining their essential provisioning and regulating services.

CRediT authorship contribution statement

Sonia Condés: Conceptualization, Methodology, Validation, Writing - original draft, Writing - review & editing. **Miren del Río:** Conceptualization, Methodology, Validation, Writing - original draft, Writing - review & editing. **David I. Forrester:** Writing - review & editing. **Admir Avdagić:** Writing - review & editing. **Kamil Bielak:** Writing - review & editing. **Andrej Bončina:** Writing - review & editing. **Michal Bosela:** Writing - review & editing. **Torben Hilmers:** Data curation, Writing - review & editing. **Aida Ibrahimspahić:** Writing - review & editing. **Stanisław Drozdowski:** Writing - review & editing. **Andrzej Jaworski:** Writing - review & editing. **Thomas A. Nagel:** Writing - review & editing. **Zuzana Sitková:** Writing - review & editing. **Jerzy Skrzyszewski:** Writing - review & editing. **Roberto Tognetti:** Funding acquisition, Writing - review & editing. **Giustino Tonon:** Writing - review & editing. **Tzvetan Zlatanov:** Writing - review & editing. **Hans Pretzsch:** Conceptualization, Supervision, Writing - review & editing.

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.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119819.

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