

RESEARCH ARTICLE

The symmetry of competitive interactions in mixed Norway spruce, silver fir and European beech forests

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Abstract

Questions: We aim for a better understanding of the different modes of intra- and inter-specific competition in two- and three-species mixed-forests. How can the effect of different modes of competitive interactions be detected and integrated into individual tree growth models? Are species interactions in spruce–fir–beech forests more associated with size-symmetric or size-asymmetric competition? Do competitive interactions between two of these species change from two- to three-species mixtures?

Location: Temperate mixed-species forests in Central Europe (Switzerland).

Methods: We used data from the Swiss National Forest Inventory to fit basal area increment models at the individual tree level, including the effect of ecological site conditions and indices of size-symmetric and size-asymmetric competition. Interaction terms between species-specific competition indices were used to disentangle significant differences in species interactions from two- to three-species mixtures.

Results: The growth of spruce and fir was positively affected by increasing proportions of the other species in spruce–fir mixtures, but negative effects were detected with increasing presence of beech. We found that competitive interactions for spruce and fir were more related to size-symmetric competition, indicating that species interactions might be more associated with competition for below-ground resources. Under constant amounts of stand basal area, the growth of beech clearly benefited from the increasing admixture of spruce and fir. For this species, patterns of size-symmetric and size-asymmetric competitive interactions were similar, indicating that beech is a strong self-competitor for both above-ground and below-ground resources. Only for silver fir and beech, we found significant changes in species interactions from two- to three-species mixtures, but these were not as prominent as the effects due to differences between intra- and inter-specific competition.

Conclusions: Species interactions in spruce–fir–beech, or other mixed forests, can be characterized depending on the mode of competition, allowing interpretations of whether they occur mainly above or below ground level. Our outcomes illustrate that species-specific competition indices can be integrated in individual tree growth functions to express the different modes of competition between species, and highlight

the importance of considering the symmetry of competition alongside competitive interactions in models aimed at depicting growth in mixed-species forests.

KEYWORDS

Above- and below-ground competition, basal area increment, intra- and inter-specific interactions, mixed-species forests, mixing effects, national forest inventory, nonlinear mixed-effect models, size-symmetric and size-asymmetric competition, species interactions

1 | INTRODUCTION

The interest in mixed-species forests has risen in recent years. There is a broad consensus that forests with higher species diversity are likely to be more resistant and resilient to climate change stressors and ecological disturbances (Fares, Mugnozza, Corona, & Palahi, 2015; Seidl, Spies, Peterson, Stephens, & Hicke, 2016). In addition, mixed-species forests have potential to deliver higher levels of ecosystem services (Gamfeldt et al., 2013; Knoke, Ammer, Stimm, & Mosandl, 2008) and, under certain conditions, can also be more productive than single-species stands (Mina, Huber, Forrester, Thürig, & Rohner, 2018; Pretzsch et al., 2013a; Toigo et al., 2015). Enhancing our knowledge of how tree species interact with each other in mixed stands is fundamental in the perspective of implementing adaptation measures to climate change, such as increasing species richness and replacing monospecific, high-risk forest stands (Ammer, 2017; Bauhus et al., 2017).

Species interactions in mixed forests are often explored by comparing effects of intra- and inter-specific competition on individual tree growth (Manso, Morneau, Ningre, & Fortin, 2015). For a given tree species growing in a mixed stand, inter-specific competition might sometimes be lower than intra-specific competition due to facilitation or differentiation in niche complementarity (Cavard et al., 2011). In this case, it is typically said that there are positive complementary effects of the presence of one species on the growth of another species (Forrester & Bauhus, 2016). There are several mechanisms that can lead to positive complementary effects, from reductions in crown interference due to spatial stratification (Pretzsch, 2014), to improved nutrient conditions thanks to more efficient exploitation of soil volumes or litter deposition (Rothe & Binkley, 2001). As these processes can occur simultaneously, it is very difficult to disentangle the specific mechanism, i.e. that responsible for facilitative or competitive effects.

One possible way to better understand how species interact with each other is to study the process of competition based on symmetry. According to Weiner (1990), resource uptake among competitors can be proportional to their own size, i.e. competition is size-symmetric. If resource uptake is not relative to size, e.g. when larger plants obtain all the resources to the detriment of smaller individuals, competition is defined as size-asymmetric. In the literature, there is a general consensus that plants compete asymmetrically for light and symmetrically for below-ground resources such as water and soil nutrients (Casper & Jackson, 1997; Larocque et al., 2013; Weiner,

1990). Since the detection of mechanisms responsible for competition with direct measurements is difficult due to the complexity of processes involved in resource uptake, indirect methods based on growth models and competition indices have been increasingly proposed as an alternative (Weiskittel, Hann, Kershaw, & Vanclay, 2011). However, to date, functions in statistical tree growth models rarely consider these different modes of competition (Larocque et al., 2013; Pretzsch & Biber, 2010). In addition, modelling methods which include size-symmetric and size-asymmetric components have mainly been applied in single-species stands (Bourdier et al., 2016; Cordonnier & Kunstler, 2015). Only a few investigations have been extended to explore size-symmetry of competition in two- or multi-species forests (Coates, Canham, & LePage, 2009; Riofrio, del Rio, & Bravo, 2017).

We focus on three major species in Europe: Norway spruce (*Picea abies* L., hereafter spruce), silver fir (*Abies alba* Mill., hereafter fir) and European beech (*Fagus sylvatica* L., hereafter beech). These species have high ecological and economic value in Central and Eastern Europe (Ellenberg, 1988). More importantly, spruce–fir–beech mixtures connect beech and broad-leaf-dominated forests in the lowlands with spruce and conifer-dominated sub-alpine tree communities, and they represent a key source of ecosystems goods and services in montane and sub-montane regions (Pretzsch, Biber, Uhl, & Dauber, 2015). Previous results on mixing effects for these species were quite heterogeneous, with complementary effects varying strongly with climate, stand and site conditions (Forrester, 2014; Mina et al., 2018). Past investigations carried out mostly on mixtures of two of these three species showed that beech generally performs better when growing in mixtures with conifers thanks to a reduced intra-specific competition (Bosela, Tobin, Seben, Petras, & Larocque, 2015; Pretzsch et al., 2010), and under certain conditions spruce and fir were found to benefit from growing in two-species mixtures rather than in pure stands (Forrester, Kohnle, Albrecht, & Bauhus, 2013).

In this study, we aim for a better understanding of the different modes of intra- and inter-specific competition in mixed spruce–fir–beech forests. For this purpose, we introduce the terms “size-symmetric mixing effects” (SSME) and “size-asymmetric mixing effects” (SAME) to indicate whether there are positive or negative complementary effects between tree species and if these are more associated with below-ground (size-symmetric) or to above-ground resources (size-asymmetric). We used individual tree models fitted to data from the Swiss National Forest Inventory to explore the

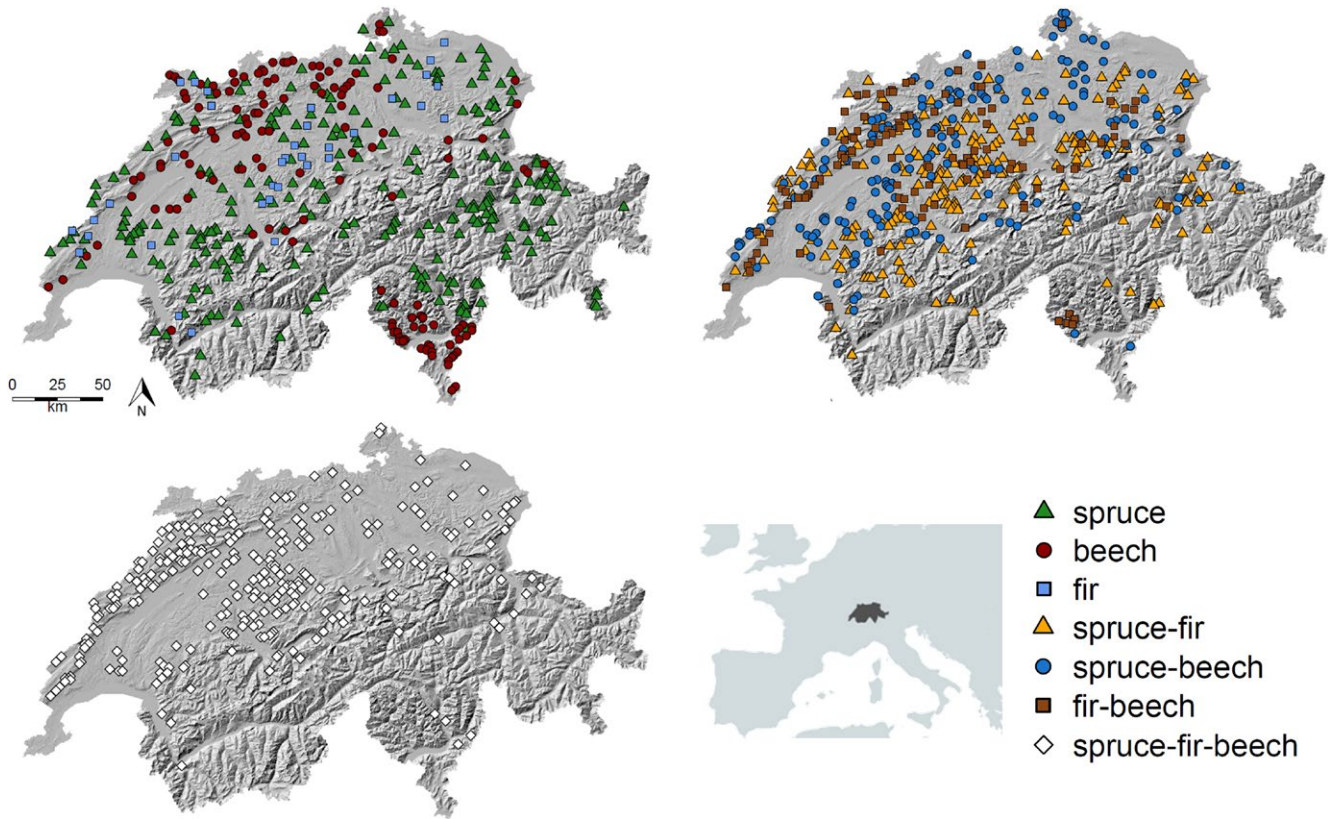


FIGURE 1 Distribution of the NFI sample plots in Switzerland based on their species composition at the time of the NFI1 (upper-left panel: monospecific plots; upper-right: two-species mixtures; lower-left: three-species mixture) and geographic location of the study region. Source digital height model: Federal Office of Topography swisstopo

following research questions: (a) how can size-symmetric and size-asymmetric competition be accounted for in functions of individual tree growth models; (b) are species interactions in spruce–fir–beech forests more associated with size-symmetric or size-asymmetric competition; (c) do competitive interactions between two of these species change from two- to three-species mixtures?

2 | METHODS

2.1 | Data

To explore size-symmetric and size-asymmetric mixing effects we selected forest stands measured in the Swiss National Forest Inventory (NFI). Spruce, fir and beech are the species with the largest number of observations in the NFI and represent the most common mixture types in Switzerland. To study size-symmetric and size-asymmetric mixing effects, we retained sampling plots with these three species (Figure 1): monospecific (basal area of one of the three species >95%; absence of the two other investigated species), two-species mixture (basal area of two of the three species >95%; absence of the third species), three-species mixture (basal area of the three investigated species together >95%). Additional description of the Swiss NFI and plot selection can be found in Supporting

information Appendix S2. The main characteristics of our data set by species and stand composition are given in Table 1.

Individual tree- and plot-level variables, such as DBH, basal area increment (BAI, $\text{cm}^2 \text{ha}^{-1} \text{year}^{-1}$), arithmetic mean value of the 100 largest DBH per ha (DDOM, cm) and stand structure type (TYP, categorical; 0 for even- and 1 for uneven-aged forest) were derived from the NFI database (Traub, Meile, Speich, & Rösler, 2017). Following the approach described in Mina et al. (2018), we obtained variables expressing climate (temperature, moisture index, solar radiation), site topography (slope, profile curvature, northness and eastness index), soil acidity (pH), available soil water-holding capacity, release effects due to management (RE) and atmospheric N deposition from multiple sources (for details see Supporting information Appendix S2; Rohner, Weber, & Thürig, 2016; Rohner, Waldner, Lischke, Ferretti, & Thürig, 2018).

2.2 | Indices for size-symmetric/size-asymmetric competition and mixing effects

As a proxy for size-symmetric competition (competition for below-ground resources), we used a simple distance-independent index, i.e. the total basal area of all trees within the sampling plot of the target tree (BA, m^2/ha) while for size-asymmetric (competition for light), we used the sum of the basal area of trees with larger diameters than the

TABLE 1 Tree- and plot-level characteristics of the data set used in this study

	Monospecific				Spruce-Fir				Spruce-Beech				Fir-Beech				Spruce-Fir-Beech			
	Spruce	Fir	Beech		Spruce	Fir	Beech		Spruce	Fir	Beech		Fir	Beech			Spruce	Fir	Beech	Total
N. BAI obs.	6352	667	3000		3426	2473	2500		2500	2473	2025		667	1408			3112	2878	2385	30893
BAI (cm ² /year)	21.2 ± 18.3	37.5 ± 30.7	16.5 ± 17.3		23.7 ± 19.4	30.4 ± 27.0	23.7 ± 20.2		23.7 ± 20.2	30.4 ± 27.0	17.6 ± 17.2		29.6 ± 28.3	19.1 ± 16.4			24.0 ± 21.1	26.9 ± 26.6	16.6 ± 16.5	22.6 ± 21.4
N. plots	358	79	215		303		244		244				174				371			1492
Stand basal area (m ² /ha)	40.0 ± 17.7	34.1 ± 13.3	31.4 ± 12.6		42.7 ± 15.4		39.9 ± 15.6		39.9 ± 15.6				33.2 ± 13.3				41.4 ± 13.2			39.3 ± 15.3
Elevation (m a.s.l.)	1071 ± 333	827 ± 231	857 ± 289		969 ± 263		836 ± 261		836 ± 261				876 ± 220				908 ± 225			933 ± 280
Annual mean temperature (°C)	6.6 ± 1.7	7.9 ± 1.2	8.0 ± 1.2		7.1 ± 1.4		7.8 ± 1.3		7.8 ± 1.3				7.6 ± 1.2				7.4 ± 1.2			7.3 ± 1.4
Annual precipitation (mm)	1394 ± 303	1371 ± 204	1409 ± 339		1481 ± 286		1372 ± 292		1372 ± 292				1442 ± 255				1441 ± 245			1423 ± 285

Note. Values following the symbol "±" indicate SD. Our data set includes measurements from multiple NFI surveys; those plots that changed mixing category between two successive surveys (252 plots) were included in more than one stand type. Ranges of species-specific basal area and basal area of trees larger than the target tree are shown in Supporting information Figure S2 and S3.

target tree in the plot (BAL, m²/ha). These formulations have been used in several studies to investigate the different modes of competition at the individual tree level (Cordonnier & Kunstler, 2015; Weiskittel et al., 2011). Both indices, however, treat each species as an equal competitor or considering that all species compete similarly for light or below-ground resources. To explore the influence of species mixture on tree growth, and thus to analyse SSME and SAME, we split these two indices into species-specific components. Size-symmetric mixing effects were expressed as the basal area of trees of a given species within the sampling plot of the target stem (BA_{SS}, m²/ha), while size-asymmetric mixing effects as the basal area of trees of a given species larger than the target tree (BAL_{SS}, m²/ha). Taking spruce as an example, the index BA_{SS-spruce} therefore indicates the intra-specific size-symmetric competition component, while BA_{SS-fir} and BA_{SS-beech} denote the two inter-specific size-symmetric competition components. Ranges of BA_{SS} and BAL_{SS} for each species are shown in Supporting information Appendix S1: Figure S2. See Supporting information Appendix S2 for the choice of distance-independent indices.

2.3 | Modelling methods

2.3.1 | Model structure

We used the NFI data set complemented with the climatic and site variables described above to fit nonlinear mixed-effect models (Pinheiro & Bates, 2000) with the package *nlme* in R 3.4.0 (R Foundation for Statistical Computing, Vienna, AT) for spruce, fir and beech. The models included BAI of individual trees as the dependent variable and were based on the growth functions initially developed for the empirical forest scenario model Massimo (Kaufmann, 2001; Thürig, Kaufmann, Frisullo, & Bugmann, 2005). Our initial models were built from the climate-sensitive "full models" described in Rohner et al. (2018), where a wide range of explanatory variables were evaluated to model possible effects on BAI. As a measure of competition, they selected Reineke's stand density index. However, unlike Rohner et al. (2018), we decided for the present study to exclude a priori the stand density index calculated according to Reineke (1933), as this index would require species-specific coefficients for the self-thinning rule in the case of stands with different species compositions. To avoid this issue, we preferred to use basal area to characterize competition (see above). The functions followed the form:

$$BAI = e^{b_1 \times \left(1 - e^{b_2 \times DBH}\right)} \times e^{f(V_1, \dots, V_i)} + \varepsilon \quad (1)$$

where b_1 and b_2 are model coefficients, ε is the residual error, and $f(V_1, \dots, V_i)$ is a function of i explanatory variables (V_1, \dots, V_i), including a random intercept with NFI plots as a grouping factor (b_{plot}):

$$f(V_1, \dots, V_i) = \beta_0 + \beta_1 V_1 + \dots + \beta_i V_i + b_{plot} \quad (2)$$

where β_0 is the estimated fixed intercept and β_1, \dots, β_i are model coefficients for each explanatory variable (Mina et al., 2018).



2.4 | Size-symmetric and size-asymmetric mixing effects

To test whether species interactions in spruce–fir–beech forests are more associated with symmetric or asymmetric competition, we included the indices BA, BAL, BA_{SS} and BAL_{SS} in the function described in Equation 2. As a first step, we tested whether models with intra- and inter-specific size-symmetric and size-asymmetric competition indices (BA_{SS} and BAL_{SS}) were more explanatory than their total components (BA and BAL). For this, we followed a similar approach as presented in del Río, Condes, and Pretzsch (2014) and compared the performance of different competition structures using combinations of the four competition indices reported above. At the same time, we included interaction terms between the species-specific competition indices (BA_{SS}, BAL_{SS}). The integration of interaction terms was needed to understand whether there were significant differences in species interactions from two- to three-species mixtures (i.e. when the third investigated species is also present), and thus to identify whether the proportion between the two other species influences the growth of the target species (e.g. fir and beech on spruce). To test this, we allowed interactions between the two competition variables expressing inter-specific competition (e.g. for spruce between BA_{SS-fir} and BA_{SS-beech} and/or BAL_{SS-fir} and BAL_{SS-beech}). We decided to focus on ecologically meaningful interaction terms and to avoid triple interactions that are often problematic to interpret.

We fitted the full models for spruce, fir and beech developed by Rohner et al. (2018) but expanding competition with different combinations of competition structures and interaction terms, for a total of nine combinations: (1) $V_1 + \dots + V_i + BA + BAL$; (2) $V_1 + \dots + V_i + BA + BAL_{SS}$; (3) $V_1 + \dots + V_i + BA_{SS} + BAL$; (4) $V_1 + \dots + V_i + BA_{SS} + BAL_{SS}$; (5) $V_1 + \dots + V_i + BA_{SS} + BAL + BA_{SS-inter1} : BA_{SS-inter2}$; (6) $V_1 + \dots + V_i + BA + BAL_{SS} + BAL_{SS-inter1} : BAL_{SS-inter2}$; (7) $V_1 + \dots + V_i + BA_{SS} + BAL_{SS} + BA_{SS-inter1} : BA_{SS-inter2}$; (8) $V_1 + \dots + V_i + BA_{SS} + BAL_{SS} + BAL_{SS-inter1} : BAL_{SS-inter2}$; (9) $V_1 + \dots + V_i + BA_{SS} + BAL_{SS} + BA_{SS-inter1} : BA_{SS-inter2} + BAL_{SS-inter1} : BAL_{SS-inter2}$. If a model including the total competition components (BA, BAL) outperforms a model with intra- and inter-specific indices, this indicates similar intra- and inter-specific competition and that there are no SSME and SAME to be investigated. If the inclusion of intra- and inter-specific indices results in a better fit, this means that there are mixing effects which can be more related to below-ground resources (size-symmetric) or above-ground competition (size-asymmetric).

Models with the different competition structures (see combinations above) were ranked by their AICc values (Burnham & Anderson, 2003). The model with lowest AICc was used for the subsequent variable selection process where a step-wise backward approach was applied to remove variables with low explanatory power. This was accomplished step-by-step by comparing the AICc value excluding one variable at a time from each model. The variable selection process included all variables incorporated in the function $f(V_1, \dots, V_i)$ (i.e. climatic, site-specific variables and competition indices; Supporting information Appendix S2). The final models were designated if excluding

further variables no longer reduced the AICc. The final models were then used to estimate BAI under different *stand/species composition scenarios* with varying BA_{SS} and BAL_{SS} and with climatic and site variables fixed at their mean (Supporting information Appendix S3). Goodness of fit of the models was evaluated using the relative root mean square error (RMSE), the percentage bias and the R² between observed and predicted values of BAI. Graphical comparison of observations and model predictions are presented in Supporting information Appendix S1: Figure S4.

3 | RESULTS

3.1 | Integration of size-symmetric and size-asymmetric mixing effects

For both spruce and fir, the competition structure that led to the best model was that in which size-symmetric competition was split into intra- and inter-specific components (Table 2). This was particularly clear for spruce as the two models including BA_{SS} had a much lower AICc than the third best model with the total BA index (Supporting information Appendix S1: Table S2). The consideration of the species-specific indices of size-asymmetric competition (BAL_{SS}) did not result in better models than those with the total BAL index (absence of SAME) for these two species. The best model for spruce did not include any interaction term between inter-specific BA_{SS} or BAL_{SS}, while in the case of fir the interaction term between inter-specific BA_{SS} indices was included in the best model. From inspection of the Akaike weights (Wagenmakers & Farrell, 2004), the best model for fir – including the interaction term – was only 1.4 times more likely to be the best model than the next-best model (no interaction), and the delta AICc between these two models was relatively low (0.73). This suggests that the effect of the proportion between the basal area of spruce and beech in a three-species mixture may not have a strong influence on fir's BAI (see further below).

In the case of beech, the best model included both size-symmetric and size-asymmetric competition divided into species-specific components. The importance of the indices split into species-specific components is evident from the ranking of the models with different competition structures: the first four best models all included BA_{SS} and BAL_{SS} and there was a large delta AICc (134.91) between the best model and that with total BA and total BAL (Supporting information Appendix S1: Table S2). Moreover, the best model for beech included the interaction term between BAL_{SS} of spruce and fir. The importance of considering interaction terms for beech was confirmed by the fact that the second-best model, also including interaction terms, was 5.1 times more likely to be a better model than the third best model that did not include any interactions.

3.2 | Basal area increment models and patterns of SSME and SAME

In the process of variable selection, two to five explanatory variables by species were removed from the “full models”, including competition

TABLE 2 Estimated coefficients with SD and *p*-values for the three final models for spruce, fir and beech

Variable	Spruce		Fir		Beech	
	Coefficient	<i>p</i>	Coefficient	<i>p</i>	Coefficient	<i>p</i>
b1	3.218 ± 0.086	<0.001	4.081 ± 0.147	<0.001	3.844 ± 0.137	<0.001
b2 (DBH)	−0.048 ± 0.002	<0.001	−0.051 ± 0.003	<0.001	−0.054 ± 0.003	<0.001
β_0	−0.876 ± 0.426	0.040	0.279 ± 0.240	0.245	−2.199 ± 0.512	<0.001
SD b_{plot} [residuals]	0.328 [12.71]	–	0.370 [16.37]	–	0.310 [10.21]	–
DDOM	−0.005 ± 0.001	<0.001	−0.003 ± 0.002	0.065	−0.006 ± 0.001	<0.001
RE	0.197 ± 0.099	0.047				
TYP					−0.044 ± 0.023	0.059
SLP	−0.002 ± 0.001	<0.001	−0.005 ± 0.001	<0.001	−0.033 ± 0.001	<0.001
NORTH	0.050 ± 0.016	0.002				
CURV	0.087 ± 0.052	0.090			0.082 ± 0.052	0.114
AWC	0.002 ± 0.000	<0.001	0.002 ± 0.001	<0.001		
TEMP	0.102 ± 0.009	<0.001	0.090 ± 0.012	<0.001	0.115 ± 0.012	<0.001
MI	1.125 ± 0.313	<0.001			1.399 ± 0.361	<0.001
SR	0.0004 ± 0.000	<0.001			0.0004 ± 0.000	0.001
NDEP	−0.007 ± 0.001	<0.001	−0.008 ± 0.001	<0.001	0.008 ± 0.002	<0.001
PH	−0.059 ± 0.009	<0.001	−0.051 ± 0.013	<0.001	−0.025 ± 0.010	0.011
BAL	−0.014 ± 0.001	<0.001	−0.010 ± 0.001	<0.001		
BA _{SS-spruce}	−0.008 ± 0.001	<0.001	−0.005 ± 0.001	<0.001	−0.009 ± 0.002	<0.001
BA _{SS-fir}	−0.003 ± 0.001	0.027	−0.007 ± 0.001	<0.001	−0.006 ± 0.002	0.017
BA _{SS-beech}	−0.017 ± 0.002	<0.001	−0.015 ± 0.003	<0.001	−0.014 ± 0.001	<0.001
BA _{SS-spruce} : BA _{SS-beech}			−0.0004 ± 0.000	0.083		
BAL _{SS-spruce}					−0.002 ± 0.002	0.382
BAL _{SS-fir}					−0.003 ± 0.003	0.337
BAL _{SS-beech}					−0.017 ± 0.001	<0.001
BAL _{SS-spruce} : BAL _{SS-fir}					−0.0005 ± 0.001	0.009
RMSE	12.35		15.7		9.8	
P-BIAS	1.7		2.2		2.0	
R ² _{all effects}	0.59		0.67		0.66	
R ² _{fixed effects}	0.40		0.45		0.48	

Notes. Last rows report fit statistics (root mean square error RMSE in cm² ha^{−1} year^{−1}, percentage bias P-BIAS and R² between observations and model predictions with and without random effects). Empty cells denote variables not included in the models because previously excluded by Rohner et al. (2018) or during model selection in the current study.

DDOM: mean of 100 largest diameters per ha; RE: release effect due to management; SLP: slope of the plot; NORTH: northness index; CURV: profile curvature; AWC: available soil water-holding capacity; TEMP: temperature; MI: moisture index (ETa/ETp); SR: global solar radiation; NDEP: N deposition; PH: soil pH; BAL: basal area of trees larger than target tree; BA_{SS} basal area of trees of a given species within the sampling plot of the target tree; BAL_{SS} basal area of trees of a given species larger than target tree. See Supporting information Appendix S2 for further information.

components (spruce: TYP, EAST; fir: CURV, EAST, NORTH, RE, TYP, MI; beech: EAST, AWC, RE, NORTH). Details are given in Supporting information Appendix S2. None of the competition indices (BA, BAL, BA_{SS} and BAL_{SS}) were removed during this process, confirming the highly explanatory power of the indices and the robustness of the competition structure in each final model.

The estimated coefficients of the final models are shown in Table 2. Estimates of the climatic, stand and site variables on individual tree growth were plausible for all three species. For instance, DDOM, SLP and PH had a negative effect on tree growth of each species, while increasing TEMP, AWC, MI, SR and CURV positively affected basal area increment for two or all three species. Other

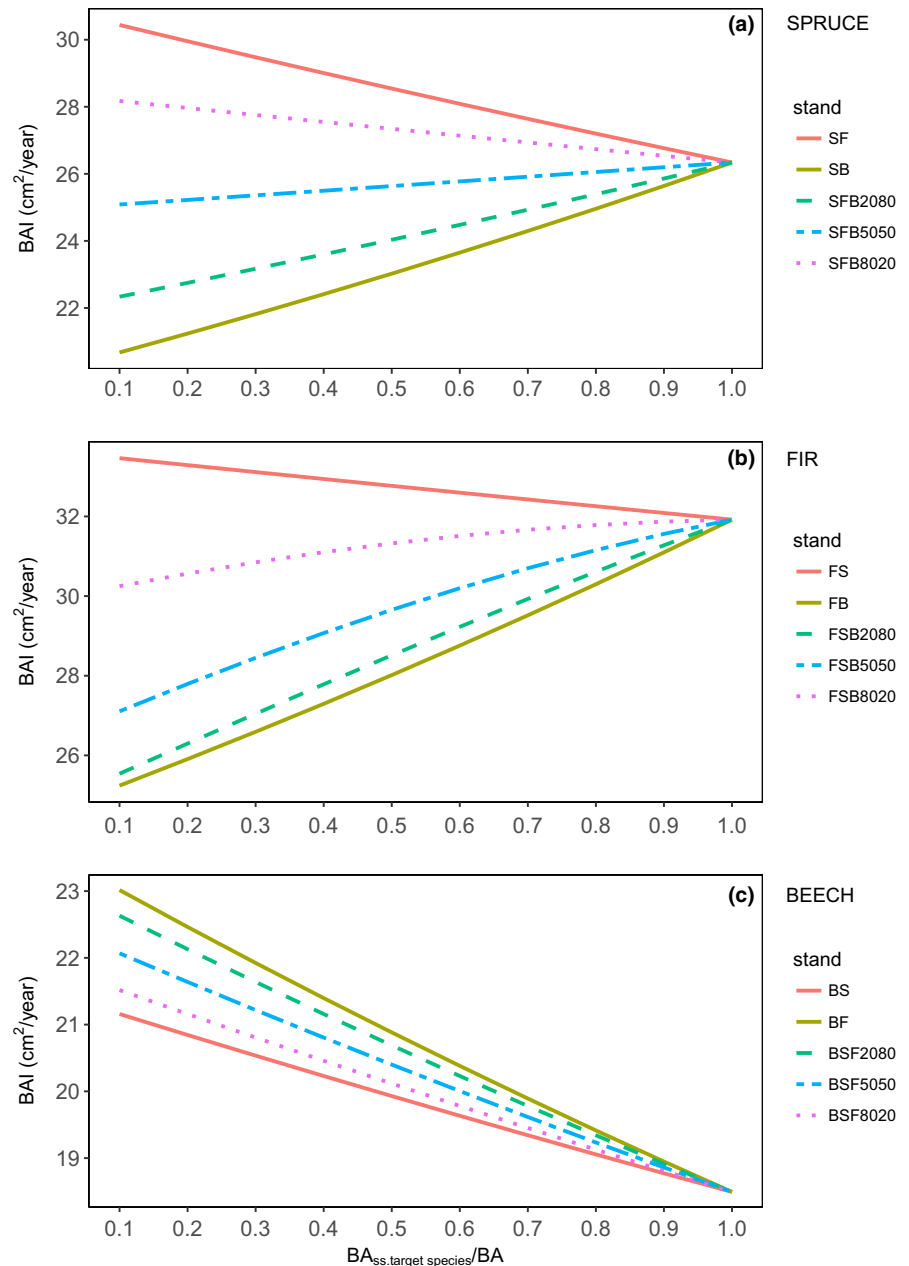


FIGURE 2 Effect of decreasing mixture in the size-symmetric component. Results are displayed for a dominant tree ($BA_L = 0$) with DBH 30 cm and for total stand basal of 30 m²/ha. Species: S = spruce; F = fir; B = beech. BAI calculated for increasing proportions of the target species ($BA_{SS,target\ species}/BA = 1$ indicates a pure stand) in different stand types: SF = spruce-fir (no beech); SB = spruce-beech (no fir); SFB2080: spruce-fir-beech in which fir and beech maintain proportions of 20% and 80%, respectively, of the remaining basal area; SFB5050: spruce-fir-beech in which fir and beech maintain proportions of 50% and 50%, respectively; SFB8020: spruce-fir-beech in which fir and beech maintain proportions of 80% and 20%, respectively. Same concept for the other stand types. All other climatic and site variables were fixed at their mean (data in Supporting information Appendix S3)

factors had a positive effect on tree growth of spruce (RE, NORTH) and only the effect of NDEP varied depending on the species (negative for spruce and fir, positive for beech). Since the focus of this study is on SSME and SAME, we refer to the studies of Rohner et al. (2018) and Mina et al. (2018) for a full description and interpretation of the effects of the single drivers on tree growth.

Coefficients of the competition indices for size-symmetric competition (BA_{SS}) indicated strong differences between intra- and inter-specific competition, as well as differences between the two species representing inter-specific competition (Table 2). In the case of spruce, size-symmetric competition of fir was found to be lower than intra-specific competition, denoting positive SSME of fir on spruce. Thus, at increasing proportions of basal area of fir in a spruce-fir stand, spruce BAI was found to increase (stand type SF

in Figure 2a). However, the effect of size-symmetric competition of beech was more than twice that of spruce, indicating strong negative SSME of beech on spruce, and resulting in a strong decrease in spruce BAI at increasing proportions of beech in a spruce-beech stand (stand type SB in Figure 2a). In the three-species mixture, positive SSME due to the presence of fir contributed to a slight increase in spruce BAI when the proportions of beech remained under a certain threshold (e.g. 20%; stand type SFB8020 in Figure 2a). At increasing proportions of beech in a spruce-fir-beech stand, spruce BAI was negatively affected (stand types SFB5050, SFB2080 in Figure 2a). For fir, the coefficient for spruce ($BA_{SS-spruce}$) was slightly lower than that expressing intra-specific competition ($BA_{SS-spruce}$). Similarly for spruce, fir's BAI was thus positively affected at increasing proportions of spruce in mixed fir-spruce stands (FS in Figure 2b)

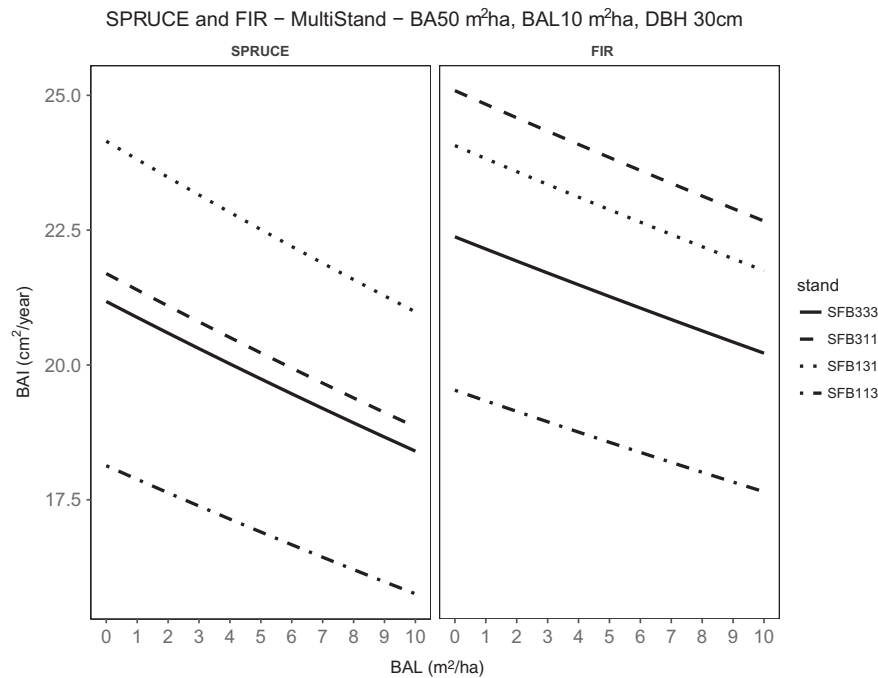


FIGURE 3 Predicted effect of increasing size-asymmetric competition (BAL) on a spruce and fir tree with DBH 30 cm in a stand with total basal area 50 m²/ha composed equally of spruce, fir and beech (SFB333, solid line, 16.67 m²/ha each), more spruce and less fir and beech (SFB311, dashed line, spruce 30 m²/ha, fir and beech 10 m²/ha each), more fir and less spruce and beech (SFB131, dotted line, fir 30 m²/ha, spruce and beech 10 m²/ha each), more beech and less spruce and fir (SFB113, dot-dashed line, beech 30 m²/ha, spruce and fir 10 m²/ha each). All other climatic and site variables were fixed at their mean (data in Supporting information Appendix S3)

but was reduced as soon as beech was present in the stand, even at low proportions (FSB8020 in Figure 2b). The interaction term $BA_{SS-spruce}:BA_{SS-beech}$ results in a slightly nonlinear effect of the competitor's proportions on the BAI of fir in the three-species mixture (Figure 2b). In the case of beech, both coefficients of inter-specific size-symmetric competition were lower than the intra-specific one, denoting positive SSME for beech when mixed with spruce and/or fir. The strongest increase of beech's growth was found when mixed with fir only, while the weakest increase was found in admixture with spruce only (Figure 2c). In the three-species mixture, SSME on beech BAI increased with increasing amounts of fir.

With regard to size-asymmetric competition, the final models for spruce and fir did not include species-specific indices. Individual tree growth of spruce and fir was found to decrease with increasing BAL but the effect of increasing size-asymmetric competition was only due to the total BAL coefficient (Figure 3). For beech, however, we found different effects on BAI depending on the species composition of the larger competitors (Figure 4, Table 2). The smallest growth reduction occurred when BAL was composed of spruce trees only, followed by the case when the pool of larger competitors consisted of 80% spruce and 20% fir (SF8020). Similar reductions were observed if larger competitors were only fir or spruce–fir in different proportions (SF5050, SF2080). Nonetheless, the highest reduction in beech BAI occurred when larger competitors were composed of beech, due to the higher intra-specific than inter-specific asymmetric competition. In the three-species mixture, the higher the proportions of beech in the larger competitors,

the more negatively was growth affected (Figure 4, dotted lines). When both spruce and fir were present among larger competitors, we detected the effect of the interaction term $BAL_{SS-spruce}:BAL_{SS-fir}$ (e.g. in Figure 4 beech BAI was more negatively affected in SF5050 and SF2080 than in F).

4 | DISCUSSION

The outcomes of this study illustrate that species-specific competition indices could be integrated into individual tree growth models to express the different modes of competition among species in mixed forests. We could also show that species interactions in temperate spruce–fir–beech forests differ depending on the mode of competition, and that although competitive interactions for fir and beech change from two- to three-species mixtures, this effect is weak compared to the effect due to the differences between intra- and inter-specific competition.

4.1 | Modes of competitive interactions in spruce–fir–beech forests

For all three investigated species we detected clear differences between intra- and inter-specific competition. This indicates the presence of mixing effects in two- and three-species mixtures of spruce, fir and beech. These effects, however, differed depending on the mode of competition.

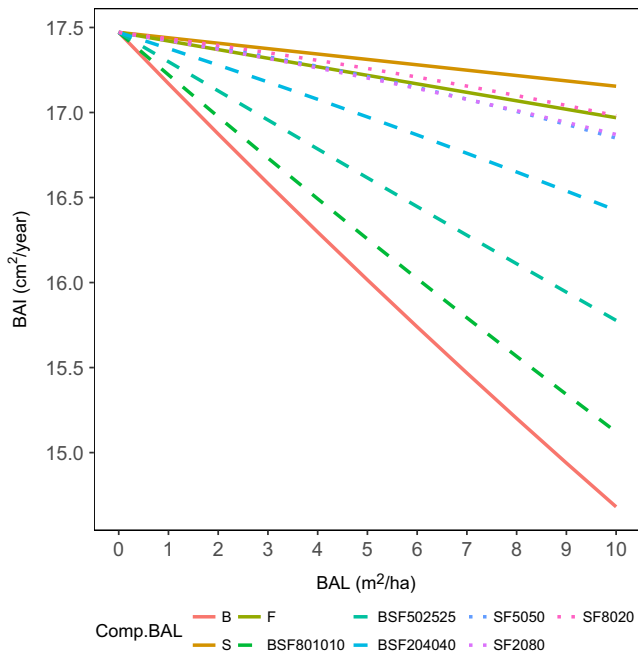


FIGURE 4 Predicted effect of increasing size-asymmetric competition (BAL) for beech when larger competitors are composed of: one species (solid lines; B = beech, F = fir, S = spruce), spruce and fir (dotted lines; SF5050: 50% spruce–50% fir; SF2080: 20% spruce–80% fir; SF8020: 80% spruce–20% fir); beech–spruce–fir (BSF801010: 80% beech–10% spruce–10% fir; BSF502525: 50% beech–25% spruce–25% fir; BSF204040: 20% beech–40% spruce–40% fir). BAI was calculated for a tree with DBH 30 cm in a stand with total basal area 50 m²/ha composed equally of spruce, fir and beech (16.66 m²/ha each). All other climatic and site variables were fixed at their mean (data in Supporting information Appendix S3)

In the case of spruce and fir, our results showed that individual tree growth of both species is larger in spruce–fir mixtures than in the respective monocultures. In particular, spruce benefited more in terms of growth than fir in spruce–fir mixtures (Figure 2a,b). This is consistent with results from previous studies where these two conifers were found to benefit from growing in the respective two-species mixture rather than in pure stands (Forrester et al., 2013 at single-tree level; Toigo et al., 2015 at stand-level). Vallet and Perot (2011) showed that fir generally grows better in spruce–fir mixtures than in pure stands, but Huber, Sterba, and Bernhard (2014) demonstrated that a positive complementarity occurred only under certain climatic and site conditions, underlining the importance of assessing mixing effects in relation to site variability (see further below). No evident differences between intra- and inter-specific size-asymmetric competition were found for spruce and fir. This indicates that interactions between spruce and fir are likely associated with size-symmetric competition. Therefore, although competition for light remains one of the prominent limiting factors for spruce and fir (variable BAL was yet highly significant), it seems that positive -competitive interactions for these two species might be due to a more efficient use of below-ground rather than above-ground resources. Forrester et al. (2013)

suggested that silver fir may have a competitive advantage in accessing soil water thanks to a better ability than spruce to develop deep root systems. In line with our results, Lebourgeois, Gomez, Pinto, and Merian (2013) suggested that positive effects of the presence of spruce on fir may be due to a reduced competition for water or improved soil water availability thanks to a more efficient vertical stratification of root systems (but see Forrester & Albrecht, 2014). A possible reason for the absence of significant SAME for spruce might be due to the characteristics of the data set on which our models were fitted. In most of the included stands, the largest trees were spruce (Supporting information Appendix S1: Figure S3), resulting in a BAL for spruce dominated by *intra-specific* competition. This may explain why we found no benefits from splitting BAL into species-specific components. For fir, the absence of significant SAME might be due to the large shade tolerance of this species, which may be less sensitive to the difference in crown morphology among species, as it is adapted to grow at low light levels (Bourdier et al., 2016). Several studies have found that canopy structuring in mixed stands can be one of the reasons for stand overyielding (Bauhus, van Winden, & Nicotra, 2004; Pretzsch, 2014). The fact that the crown structures of spruce and fir do not differ as much as that of beech might be another explanation why we did not detect above-ground complementarity between the two conifers.

When spruce and fir were admixed with beech we detected negative effects of increasing proportions of beech on individual tree growth of both conifers. Since only SSME were significant for spruce and fir, the negative effects of beech on the growth of the two conifers could be due to the competition between rooting systems and below-ground use rather than for above-ground resources. Several studies have indicated that beech has a higher ability to make morphological and physiological adjustments to its root system compared to competing species in mixed stands (Büttner & Leuschner, 1994; Curt & Prévosto, 2003). In particular, Bolte, Kampf, and Hilbrig (2013) demonstrated that beech can adopt a flexible root foraging strategy to access soil resources less exploited by the competing species, while spruce maintains a conservative strategy by keeping a shallow vertical fine root distribution in both pure and mixed spruce–beech stands. Also, Pretzsch et al. (2010) concluded that the reduction in growth of spruce admixed with beech on fertile sites can be caused by competition for root space and soil resources between these two species. Although we did not directly measure root systems, our outcomes support earlier findings that beech fine rooting may be facilitated in the presence of spruce, whereas the competitive pressure on spruce increases when mixed with beech (Bolte & Villanueva, 2006). Our results on spruce–beech stands also support the study of Toigo et al. (2015), who showed that these mixtures are more productive than the respective monocultures but that the observed stand-level overyielding was due to enhanced growth of beech to the detriment of spruce.

Unlike spruce–beech mixture, which is quite common in the literature, studies on fir–beech mixtures are rather scarce. Common ecological knowledge suggests that fir is the most capable conifer to compete with beech (Ellenberg, 1988), and those few investigations



on this mixture type concluded that fir's growth was positively affected by beech admixture (Bosela et al., 2015; Toigo et al., 2015). Lebourgeois et al. (2013) attributed a positive effect of beech on fir to the different strategies of water extraction by roots of the two species; however, these facilitative effects were detected only in drought-prone sites, which are absent in our study region (Table 1). Our results suggest that individual tree growth of fir in Switzerland responds negatively to increased proportions of beech, but only on the size-symmetric component. Since we did not investigate if this effect occurs only under particular site and soil conditions, and given that fir is not influenced by the species composition of larger competitors, our results do not disagree with previous findings showing over-yielding in fir-beech stands (Toigo et al., 2015). To better disentangle patterns of mixing effects between silver fir and beech, further investigations on this mixture type would be highly valuable, particularly considering interactions between competition and site conditions.

At constant amounts of stand basal area, our results indicate that the growth of beech in two- and three-species mixtures clearly benefits from an increasing admixture with spruce and fir. The model for beech was the only one including similar patterns for SSME and SAME. These results suggest that beech has a competitive advantage in mixtures for the use of both below- and above-ground resources (Pretzsch et al., 2010). Many studies demonstrated the low self-tolerance of beech and its severe intra-specific asymmetric competition due to high lateral expansion (Pretzsch, 2014; Pretzsch & Schütze, 2016). Our study not only confirms that beech is a strong self-competitor for above-ground resources but also highlights that it has strong below-ground competitive ability (Rewald & Leuschner, 2009; del Río, Condes, & Pretzsch, 2014). The fact that beech benefits from the presence of fir in the size-symmetric component (i.e. lower inter- than intra-specific competition for below-ground resources) might be explained by assuming that this broad-leaved species profits from the hydraulic redistribution of water taken up by the deep root system of silver fir (Magh et al., 2017). Furthermore, the differences between the intra- and inter-specific coefficients are larger for asymmetric than symmetric competition. This implies that the composition of larger competitors is very important for beech and suggests that how species are stratified is key in modulating the growth of this species (Pretzsch & Schütze, 2005). The influence of the species composition of competitors on beech growth is also confirmed by Bayer, Seifert, and Pretzsch (2013), who showed that crown morphological traits of conifers such as spruce do not change from pure to mixed stands but beech admixed with spruce can significantly increase its growing space by penetrating more crown space compared to monospecific beech stands.

Finally, as also shown by Coates et al. (2009) for North American temperate tree species, our results highlight the unbalanced feature of pair-wise competitive interactions for spruce, fir and beech (i.e. the effect of species A on B can be quite different than the effect of species B on A), particularly for size-symmetric competition (coefficients BA_{ss}). For example, the negative effect of beech size-symmetric competition on the growth of fir and spruce was much

stronger than the effect of fir and spruce size-symmetric competition on beech growth.

4.2 | Changes of competitive interactions from two- to three-species mixtures

With the exception of the meta-analysis of Pretzsch and Forrester (2017), we could not find much information in the literature on species interactions in three-species mixtures. Pretzsch and Forrester (2017) showed that productivity in spruce-fir-beech mixtures can be 120% of their respective monoculture, and that the productivity gain can be higher than in two-species mixtures. Their investigation, however, focused on the stand-level mean mixing effects rather than the individual tree level. At the species level, Pretzsch et al. (2013b) demonstrated that only silver fir does not benefit from growing in spruce-fir-beech mixtures. Analogously, our results suggest that an increase in productivity in a spruce-fir-beech mixture is likely due to enhanced growth of beech and – if the proportion of beech remains below a certain threshold – spruce. In contrast, the growth of fir was found to always be reduced in the three-species mixture, with stronger reductions at higher amounts of beech (Figure 2).

To our knowledge, our investigation is the first attempt to purposely explore changes in species interactions from two- to three-species mixtures. We found no significant changes in species interactions for spruce from two- to three-species mixtures, indicating that the relative proportions of the two other admixed species – fir and beech – do not have an influence on spruce growth. In contrast, in the case of fir, the interaction term between inter-specific indices of symmetric competition was included in the best model, implying that the relative proportions between amounts of basal area of spruce and beech in the three-species mixture significantly affect the growth of fir. However, this effect does not alter the main pattern of intra- and inter-specific size-symmetric competition for this species (Figure 2b). The effect of the interaction term was more evident for beech; at increasing BAL, beech growth was more negatively affected when larger competitors were composed of spruce and fir (in 50%/50% or 80%/20% proportions, respectively) rather than of fir alone. Nevertheless, these differences are evident only if larger competitors are composed of the two conifers. As soon as beech is present among the larger competitors, the effect of the interaction between $BAL_{ss,spruce}$ and $BAL_{ss,fir}$ is small compared to the differences between intra- and inter-specific competition, and only marginally affects patterns of SAME. Our results highlight the need to consider the interaction between the two other admixed species and the importance of vertical species stratification when modelling the complex structure, dynamics and species interactions in three-species tree mixtures.

4.3 | Methodological aspects

Several authors have demonstrated that species interactions change depending on site and climatic conditions (Forrester & Bauhus, 2016; Mina et al., 2018; Toigo et al., 2015) and others have concluded that

the mode of competition can vary spatially along ecological gradients (Hara, 1993; Pretzsch & Biber, 2010). Here we deliberately did not investigate how SSME and SAME are modulated by site and climatic conditions. We acknowledge that exploring interaction terms between competition indices and the other site-dependent variables could have revealed interesting patterns of SSME and SAME in relation to site conditions, thus we recommend further investigations on this aspect. Nonetheless, it is worth mentioning that our results are based on a representative data set encompassing a large geographic area, thus covering large parts of the ecological gradients of temperate Central European spruce–fir–beech forests. Our outcomes provide useful insights on mixing effects and how these can be explained depending on the different modes of competition. However, we focused on possible explanations of these effects on growth performance as our data set was not suitable for identifying the physiological mechanisms that lie behind competitive interactions. In addition, while above-ground competition involves one single resource (light), plants compete below-ground for a wide range of resources such as water, oxidation state, occupation of soil space and a range of nutrients (Casper & Jackson, 1997). Although our investigation was based on the broadly recognized concept of the symmetry of competition (Larocque, Archambault, & Delisle, 2011), we acknowledge the complexity of processes and mechanisms that drive competition symmetry (Schwinning & Weiner, 1998; Weiskittel et al., 2011). Finally, residuals in our models show some degree of heteroscedasticity (Supporting information Appendix S1: Figure S4). We acknowledge that this might warrant further investigations. However, since it likely did not affect the ecological interpretation of the results, we decided not to address this aspect further.

5 | CONCLUSIONS

Our results demonstrate the importance of considering the symmetry of competition alongside species competitive interactions in functions of individual tree models that aim to depict growth in mixed-species forests. Although we acknowledge the potential for further improvements, our approach could be integrated in forest scenario models fitted to nation-wide inventory data (Barreiro et al., 2016; Temperli, Stadelmann, Thurig, & Brang, 2017), allowing inference of whether complementary effects occur mainly at below- or above-ground level. Also, our analysis indicates that competitive interactions for spruce and fir are likely more relevant to the size-symmetric component and that being a strong self-competitor for both above-ground and below-ground resources, beech generally benefits from admixture with spruce and fir in temperate Central European mixed forests. Only for silver fir and beech did we find significant changes in species interactions from the two- to the three-species mixture, but these are not as prominent as effects due to differences between intra- and inter-specific competition. We recommend that forest productivity models – whether statistical or mechanistic – that aim to project growth in mixed-species systems should not only explicitly consider mixing effects but also the

symmetry of competition. Improved modelling of competitive interactions can help to better evaluate adaptation measures for mixed forests under global change stressors.

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REFERENCES

- Ammer, C. (2017). Unraveling the importance of inter- and intraspecific competition for the adaptation of forests to climate change. *Progress in Botany*, 78, 345–367.
- Barreiro, S., Schelhaas, M.-J., Kändler, G., Antón-Fernández, C., Colin, A., Bontemps, J.-D., ... Wikberg, P.-E. (2016). Overview of methods and tools for evaluating future woody biomass availability in European countries. *Annals of Forest Science*, 73, 823–837. <https://doi.org/10.1007/s13595-016-0564-3>
- Bauhus, J., Forrester, D. I., Gardiner, B., Jactel, H., Vallejo, R., & Pretzsch, H. (2017). Ecological stability of mixed-species forests. In H. Pretzsch, D. I. Forrester & J. Bauhus (Eds.), *Mixed-species forests: Ecology and management* (pp. 337–382). Berlin DE, Springer. <https://doi.org/10.1007/978-3-662-54553-9>
- Bauhus, J., van Winden, A. P., & Nicotra, A. B. (2004). Aboveground interactions and productivity in mixed-species plantations of *Acacia mearnsii* and *Eucalyptus globulus*. *Canadian Journal of Forest Research*, 34, 686–694. <https://doi.org/10.1139/x03-243>
- Bayer, D., Seifert, S., & Pretzsch, H. (2013). Structural crown properties of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in mixed versus pure stands revealed by terrestrial laser scanning. *Trees – Structure and Function*, 27, 1035–1047. <https://doi.org/10.1007/s00468-013-0854-4>
- Bolte, A., Kampf, F., & Hilbrig, L. (2013). Space sequestration below ground in old-growth spruce-beech forests – signs for facilitation? *Frontiers in Plant Science*, 4, 322.
- Bolte, A., & Villanueva, I. (2006). Interspecific competition impacts on the morphology and distribution of fine roots in European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.). *European Journal of Forest Research*, 125, 15–26. <https://doi.org/10.1007/s10342-005-0075-5>
- Bosela, M., Tobin, B., Seben, V., Petras, R., & Larocque, G. R. (2015). Different mixtures of Norway spruce, silver fir, and European beech modify competitive interactions in central European mature mixed forests. *Canadian Journal of Forest Research*, 45, 1577–1586. <https://doi.org/10.1139/cjfr-2015-0219>
- Bourdier, T., Cordonnier, T., Kunstler, G., Piedallu, C., Lagarrigues, G., & Courbaud, B. (2016). Tree size inequality reduces forest productivity:



- An analysis combining inventory data for ten European species and a light competition model. *PLoS ONE*, 11(3), e0151852. <https://doi.org/10.1371/journal.pone.0151852>
- Burnham, K. P., & Anderson, D. (2003). *Model selection and multimodel inference – A practical information-theoretic approach*. New York, NY: Springer.
- Büttner, V., & Leuschner, C. (1994). Spatial and temporal patterns of fine root abundance in a mixed oak-beech forest. *Forest Ecology and Management*, 70, 11–21. [https://doi.org/10.1016/0378-1127\(94\)90071-X](https://doi.org/10.1016/0378-1127(94)90071-X)
- Casper, B. B., & Jackson, R. B. (1997). Plant competition underground. *Annual Review of Ecology and Systematics*, 28, 545–570. <https://doi.org/10.1146/annurev.ecolsys.28.1.545>
- Cavard, X., Bergeron, Y., Chen, H. Y. H., Pare, D., Laganier, J., & Brassard, B. (2011). Competition and facilitation between tree species change with stand development. *Oikos*, 120, 1683–1695. <https://doi.org/10.1111/j.1600-0706.2011.19294.x>
- 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. *Journal of Ecology*, 97, 118–130. <https://doi.org/10.1111/j.1365-2745.2008.01458.x>
- Cordonnier, T., & Kunstler, G. (2015). The Gini index brings asymmetric competition to light. *Perspectives in Plant Ecology, Evolution and Systematics*, 17, 107–115. <https://doi.org/10.1016/j.ppees.2015.01.001>
- Curt, T., & Prévosto, B. (2003). Rooting strategy of naturally regenerated beech in Silver birch and Scots pine woodlands. *Plant and Soil*, 255, 265–279. <https://doi.org/10.1023/A:1026132021506>
- del Río, M., Condes, S., & Pretzsch, H. (2014). Analyzing size-symmetric vs. size-asymmetric and intra- vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. *Forest Ecology and Management*, 325, 90–98.
- Ellenberg, H. (1988). *Vegetation ecology of Central Europe*, 4th ed. Cambridge, UK: Cambridge University Press.
- Fares, S., Mugnozza, G. S., Corona, P., & Palahi, M. (2015). Sustainability: Five steps for managing Europe's forests. *Nature*, 519, 407–409. <https://doi.org/10.1038/519407a>
- Forrester, D. I. (2014). The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. *Forest Ecology and Management*, 312, 282–292. <https://doi.org/10.1016/j.foreco.2013.10.003>
- Forrester, D. I., & Albrecht, A. T. (2014). Light absorption and light-use efficiency in mixtures of *Abies alba* and *Picea abies* along a productivity gradient. *Forest Ecology and Management*, 328, 94–102. <https://doi.org/10.1016/j.foreco.2014.05.026>
- Forrester, D. I., & Bauhus, J. (2016). A review of processes behind diversity–productivity relationships in forests. *Current Forestry Reports*, 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. *Forest Ecology and Management*, 304, 233–242. <https://doi.org/10.1016/j.foreco.2013.04.038>
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., ... Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, 4, 1340. <https://doi.org/10.1038/ncomms2328>
- Hara, T. (1993). Mode of competition and size-structure dynamics in plant communities. *Plant Species Biology*, 8, 75–84. <https://doi.org/10.1111/j.1442-1984.1993.tb00059.x>
- Huber, M. O., Sterba, H., & Bernhard, L. (2014). Site conditions and definition of compositional proportion modify mixture effects in *Picea abies*–*Abies alba* stands. *Canadian Journal of Forest Research*, 44, 1281–1291. <https://doi.org/10.1139/cjfr-2014-0188>
- Kaufmann, E. (2001). Estimation of standing timber, growth and cut. In P. Brassel, & H. Lischke (Eds.), *Swiss National Forest Inventory: Methods and models of the second assessment* (pp. 162–196). Birmensdorf, CH: Swiss Federal Research Institute WSL.
- Knoke, T., Ammer, C., Stimm, B., & Mosandl, R. (2008). Admixing broad-leaved to coniferous tree species: A review on yield, ecological stability and economics. *European Journal of Forest Research*, 127, 89–101. <https://doi.org/10.1007/s10342-007-0186-2>
- Larocque, G. R., Archambault, L., & Delisle, C. (2011). Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. *Ecological Modelling*, 222, 2570–2583. <https://doi.org/10.1016/j.ecolmodel.2010.08.035>
- Larocque, G. R., Luckai, N., Adhikary, S. N., Groot, A., Bell, F. W., & Sharma, M. (2013). Competition theory – science and application in mixed forest stands: Review of experimental and modelling methods and suggestions for future research. *Environmental Reviews*, 21, 71–84. <https://doi.org/10.1139/er-2012-0033>
- Lebourgeois, F., Gomez, N., Pinto, P., & Merian, P. (2013). Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *Forest Ecology and Management*, 303, 61–71. <https://doi.org/10.1016/j.foreco.2013.04.003>
- Magh, R.-K., Grün, M., Knothe, V. E., Stubenazy, T., Tejedor, J., Dannenmann, M., & Rennenberg, H. (2017). Silver-fir (*Abies alba* MILL.) neighbors improve water relations of European beech (*Fagus sylvatica* L.), but do not affect N nutrition. *Trees*, 32, 337–348.
- Manso, R., Morneau, F., Ningre, F., & Fortin, M. (2015). Effect of climate and intra- and inter-specific competition on diameter increment in beech and oak stands. *Forestry*, 88, 540–551. <https://doi.org/10.1093/forestry/cpv020>
- Mina, M., Huber, M. O., Forrester, D. I., Thürig, E., & Rohner, B. (2018). Multiple factors modulate tree growth complementarity in Central European mixed forests. *Journal of Ecology*, 106, 1106–1119. <https://doi.org/10.1111/1365-2745.12846>
- Pinheiro, J., & Bates, D. (2000). *Mixed-effects models in S and S-PLUS*. Berlin, DE: Springer Science & Business Media. <https://doi.org/10.1007/978-1-4419-0318-1>
- Pretzsch, H. (2014). Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *Forest Ecology and Management*, 327, 251–264. <https://doi.org/10.1016/j.foreco.2014.04.027>
- Pretzsch, H., & Biber, P. (2010). Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. *Canadian Journal of Forest Research*, 40, 370–384. <https://doi.org/10.1139/X09-195>
- Pretzsch, H., Biber, P., Uhl, E., & Dauber, E. (2015). Long-term stand dynamics of managed spruce-fir-beech mountain forests in Central Europe: Structure, productivity and regeneration success. *Forestry*, 88, 407–428. <https://doi.org/10.1093/forestry/cpv013>
- Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.-P., ... Zingg, A. (2013a). Productivity of mixed versus pure stands of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. *European Journal of Forest Research*, 132, 263–280. <https://doi.org/10.1007/s10342-012-0673-y>
- Pretzsch, H., Bielak, K., Bruchwald, A., Dieler, J., Dudzinska, M., Ehrhart, H.-P., ... Nagel, J. (2013b). Species mixing and productivity of forests. Results from long-term experiments. German title: Mischung und Produktivität von Waldbeständen. Ergebnisse langfristiger ertragskundlicher Versuche: Aus dem Lehrstuhl für Waldwachstumskunde der Technischen Universität München. *Allgemeine Forst-Und Jagdzeitung*, 184, 177–196.
- Pretzsch, H., Block, J., Dieler, J., Dong, P. H., Kohnle, U., Nagel, J., ... Zingg, A. (2010). Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological

- gradient. *Annals of Forest Science*, 67, 712. <https://doi.org/10.1051/forest/2010037>
- Pretzsch, H., & Forrester, D. I. (2017). Stand dynamics of mixed-species stands compared with monocultures. In H. Pretzsch, D. I. Forrester & J. Bauhus (Eds.), *Mixed-species forests: Ecology and management* (pp. 117–209). Berlin, DE: Springer. <https://doi.org/10.1007/978-3-662-54553-9>
- Pretzsch, H., & Schütze, G. (2005). Crown allometry and growing space efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. *Plant Biology*, 7, 628–639. <https://doi.org/10.1055/s-2005-865965>
- Pretzsch, H., & Schütze, G. (2016). Effect of tree species mixing on the size structure, density, and yield of forest stands. *European Journal of Forest Research*, 135, 1–22. <https://doi.org/10.1007/s10342-015-0913-z>
- Reineke, L. H. (1933). Perfecting a stand-density index for evenaged forests. *Journal of Agricultural Research*, 46, 0627–0638.
- Rewald, B., & Leuschner, C. (2009). Belowground competition in a broad-leaved temperate mixed forest: Pattern analysis and experiments in a four-species stand. *European Journal of Forest Research*, 128, 387–398. <https://doi.org/10.1007/s10342-009-0276-4>
- Riofrio, J., del Rio, M., & Bravo, F. (2017). Mixing effects on growth efficiency in mixed pine forests. *Forestry*, 90, 381–392.
- Rohner, B., Waldner, P., Lischke, H., Ferretti, M., & Thürig, E. (2018). Predicting individual-tree growth of central European tree species as a function of site, stand, management, nutrient and climate effects. *European Journal of Forest Research*, 137, 29–34.
- Rohner, B., Weber, P., & Thürig, E. (2016). Bridging tree rings and forest inventories: How climate effects on spruce and beech growth aggregate over time. *Forest Ecology and Management*, 360, 159–169. <https://doi.org/10.1016/j.foreco.2015.10.022>
- Rothe, A., & Binkley, D. (2001). Nutritional interactions in mixed species forests: A synthesis. *Canadian Journal of Forest Research*, 31, 1855–1870. <https://doi.org/10.1139/x01-120>
- Schwinning, S., & Weiner, J. (1998). Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, 113, 447–455. <https://doi.org/10.1007/s004420050397>
- Seidl, R., Spies, T. A., Peterson, D. L., Stephens, S. L., & Hicke, J. A. (2016). Searching for resilience: Addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology*, 53, 120–129. <https://doi.org/10.1111/1365-2664.12511>
- Temperli, C., Stadelmann, G., Thürig, E., & Brang, P. (2017). Silvicultural strategies for increased timber harvesting in a Central European mountain landscape. *European Journal of Forest Research*, 136, 493–509. <https://doi.org/10.1007/s10342-017-1048-1>
- Thürig, E., Kaufmann, E., Frisullo, R., & Bugmann, H. (2005). Evaluation of the growth function of an empirical forest scenario model. *Forest Ecology and Management*, 204, 53–68. <https://doi.org/10.1016/j.foreco.2004.07.070>
- Toigo, M., Vallet, P., Perot, T., Bontemps, J. D., Piedallu, C., & Courbaud, B. (2015). Overyielding in mixed forests decreases with site productivity. *Journal of Ecology*, 103, 502–512. <https://doi.org/10.1111/1365-2745.12353>
- Traub, B., Meile, R., Speich, S., & Rösler, E. (2017). The data storage and analysis system of the Swiss National Forest Inventory. *Computers and Electronics in Agriculture*, 132, 97–107. <https://doi.org/10.1016/j.compag.2016.11.016>
- 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. *Journal of Vegetation Science*, 22, 932–942. <https://doi.org/10.1111/j.1654-1103.2011.01288.x>
- Wagenmakers, E. J., & Farrell, S. (2004). AIC model selection using Akaike weights. *Psychonomic Bulletin & Review*, 11, 192–196. <https://doi.org/10.3758/BF03206482>
- Weiner, J. (1990). Asymmetric competition in plant-populations. *Trends in Ecology & Evolution*, 5, 360–364. [https://doi.org/10.1016/0169-5347\(90\)90095-U](https://doi.org/10.1016/0169-5347(90)90095-U)
- Weiskittel, A. R., Hann, D. W., Kershaw, J. A., & Vanclay, J. K. (2011). Indices of competition. In A. R. Weiskittel, D. W. Hann, J. A. Kershaw & J. K. Vanclay (Eds), *Forest growth and yield modeling* (pp. 15–36). New York, NY: John Wiley & Sons. <https://doi.org/10.1002/9781119998518>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

APPENDIX S1 Additional figures and tables

FIGURE S1 Difference in temperature range for pure spruce plots including and excluding the sub-alpine vegetation zone

FIGURE S2 Ranges of species-specific basal area (BA_{SS}) for each target species growing in pure stands, two- and three-species mixture

FIGURE S3 Ranges of species-specific basal area of trees larger than the target tree (BAL_{SS}) growing in pure stands, two- and three-species mixture

FIGURE S4 Comparison of observed and predicted basal area increments of the selected models for the three species

TABLE S1 Number of sampling plots between two consecutive NFIs by altitudinal vegetation zone in Switzerland

TABLE S2 Models for BAI of spruce, fir and beech with different competition structures ranked according to their AICc

TABLE S3 Overview of the variables composing the fixed effects of the final models

APPENDIX S2 Additional information on the Swiss NFI, plots selection, explanatory variables, competition indices and model selection

APPENDIX S3 Stand/species composition scenarios with varying BA_{SS} and BAL_{SS} , including climatic and site variables and estimated BAI values (files in TXT format)

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