

## RESEARCH ARTICLE

# Multiple factors modulate tree growth complementarity in Central European mixed forests

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**Abstract**

1. Mixed species forests can often be more productive and deliver higher levels of ecosystem services and functions than monocultures. However, complementarity effects for any given tree species are difficult to generalize because they can vary greatly along gradients of climatic conditions and resource availability. Identifying the conditions where species diversity can positively influence productivity is crucial. To date, few studies have examined how growth complementarity across species and mixture types is modulated by stand and environmental factors, and fewer have considered more than one or two factors.
2. We investigated how complementarity effects for several major Central European tree species change with climatic and edaphic conditions, and with stand structural characteristics, including species composition. We used data from the Swiss National Forest Inventory, which is based on 3,231 plots of pure and mixed stands (19 mixture types) across a broad environmental gradient, to test (i) how mixing effects change depending on the identity of the admixed species and (ii) if complementarity consistently increases when environmental conditions become harsher.
3. The magnitude, whether positive or negative, of complementarity increased with increasing stand density and stand developmental stage, but no general pattern could be identified across mixture types. Complementarity for many species increased as drought intensity and temperature increased, but not for all species and mixture types. While soil conditions, nitrogen and site topography influenced complementarity for many species, there was no general pattern (increases and decreases were observed).
4. *Synthesis.* Our study indicates that complementarity varies strongly with stand density and stand development as well as with topographic, climatic and soil conditions. This emphasizes the need to account for site-dependent conditions when exploring mixture effects in relation to forest productivity. We found that under certain conditions (i.e. increasing drought, higher temperature), mixed forests can promote individual tree growth in Central European temperate forests. However, careful assessments depending on the species composing the stands are required under changing resource availability as well as under different levels of stand density and development.

**KEYWORDS**

climate, mixed species forests, mixing effects, modelling, National Forest Inventory, nonlinear mixed effect models, plant–plant interactions, species diversity

## 1 | INTRODUCTION

Most of the world's forests are composed of multiple species and disentangling the relationships between growth and diversity is currently one of the most crucial and challenging tasks for ecologists. Previous studies have demonstrated that higher tree species richness can lead to higher productivity (Liang et al., 2016; Paquette & Messier, 2011; Vilà et al., 2013) and that mixed stands can deliver higher level of ecosystem services and functioning than monocultures (Gamfeldt et al., 2013; Knoke, Ammer, Stimm, & Mosandl, 2008). Forests with a higher structural and species diversity may also be more resistant and resilient to biotic and abiotic disturbances (Jactel & Brockerhoff, 2007; Seidl, Spies, Peterson, Stephens, & Hicke, 2016). Thus, identifying the conditions under which diversity and species composition positively influence productivity is critical in the context of adapting forest management and conservation to changing environmental conditions (Ammer, 2017; Mina, Bugmann, et al., 2017; Nabuurs et al., 2013).

The fundamental mechanisms responsible for diversity effects in forests have been widely described in the literature as competition, facilitation and competitive reduction (Forrester & Bauhus, 2016; Pretzsch, Bielak, et al., 2013). The first two usually occur when the presence of a tree species in a mixture negatively or positively influences the growth of another, while the third type of interaction indicates lower interspecific competition due to a differentiation for resources among two or more species (Vandermeer, 1989). In practice, the single contribution of these three mechanisms in mixed forests is very difficult to differentiate and they are usually collectively described as complementarity (Loreau & Hector, 2001). Defined as the effect of species mixture on growth, complementarity effects for a given pair of species are difficult to generalize, as they often vary along spatial and temporal gradients of climatic conditions and resource availability (Forrester, 2014). Following the stress-gradient hypothesis, which is based on the competitive and facilitative interactions (Bertness & Callaway, 1994), complementarity might be expected to increase when conditions for growth become harsher (e.g. declining nutrient availability, intensifying water stress) due to an increase in facilitation and a decrease in competition.

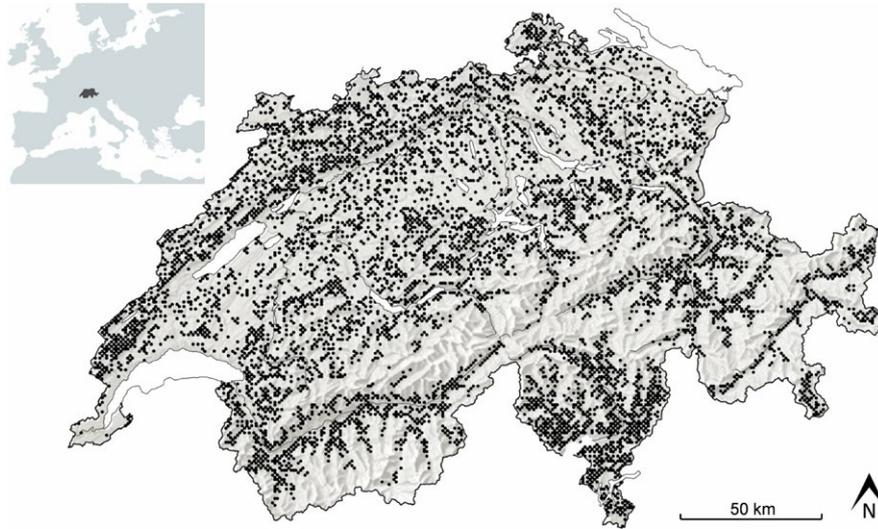
There are many climatic, edaphic and stand structural factors that can influence complementarity. Experimental plantations or carefully selected forest plots have often been used to look at one or two of these factors. For examining many factors, a much wider spatial extent is required. While this does not provide the same level of control of the conditions for any given plot, the higher numbers of plots can enable analyses of many factors and species combinations (Baeten et al., 2013; Forrester & Pretzsch, 2015; Vilà et al., 2013). The use of large-scale forest inventory data provides suitable alternatives for investigating patterns of complementarity on many mixture types

(Condes et al., 2017; Toigo et al., 2015). Given the systematic location of plots across large spatial extents, inventory data allow exploring a wide range of climatic, stand and site gradients. However, as mixture effects could be easily confounded with other drivers affecting productivity, appropriate modelling approaches are needed to disentangle complementarity from other biotic and abiotic factors (Condes & del Rio, 2015; Vallet & Perot, 2011). Many conclusions have been drawn on selected pairs of species (Condes, Del Rio, & Sterba, 2013; Huber, Sterba, & Bernhard, 2014; Pretzsch, Bielak, et al., 2013), relationships between species richness and productivity (Chamagne et al., 2016; Zhang, Chen, & Reich, 2012) or changes in complementarity with site fertility (Coates, Lilles, & Astrup, 2013; Toigo et al., 2015). Indices of site quality expressing the average effect of multiple resources and climatic factors in one variable are problematic when examining complementarity effects, as they do not reveal which factors change along the gradient and therefore influence the complementarity (Forrester & Bauhus, 2016). To date, few studies have examined how growth complementarity is affected by factors such as climate, soil condition, stand and topographic characteristics. Even fewer have considered more than one or two of these factors, although many factors are likely to be important for any given species combination. A comprehensive investigation for a variety of species and for a wide range of factors is lacking.

We take advantage of the data of the Swiss National Forest Inventory (NFI) to investigate how complementarity on individual tree growth varies with climate, stand properties and site conditions for the main tree species growing in Central European forests. Our analysis encompasses a large environmental gradient, and examines 19 two- and three-species mixtures. The aim was to disentangle individual tree growth complementarity on the main Central European tree species using large-scale forest inventory data by testing the hypotheses that (1) there is no general pattern for stand property effects on complementarity, for example with increases in stand density leading to increases in complementarity for some species combinations but decreases for others (Condes et al., 2013; Forrester, Kohnle, Albrecht, & Bauhus, 2013; Garber & Maguire, 2004); (2) complementarity mostly increases as growing conditions become harsher (Toigo et al., 2015), although opposite trends can also occur depending on the identity of the species composing the mixture (Forrester et al., 2016), especially where species interactions have been shown to reduce competition for light.

## 2 | MATERIALS AND METHODS

We used data from the Swiss NFI to study complementarity effects on individual tree growth. We chose those species with the largest



**FIGURE 1** Geographical location of the study region and distribution of the forest inventory plots across Switzerland (map modified with permission from Brändli, 2010; source digital height model: Federal Office of Topography swisstopo)

representation in the NFI: spruce (*Picea abies* L.), fir (*Abies alba* Mill.), larch (*Larix decidua* Mill.), pine (*Pinus sylvestris* L., *Pinus nigra* J.F. Arnold, *Pinus mugo arborea* Turra), beech (*Fagus sylvatica* L.), maple and ash (*Acer campestris* L., *Acer platanoides* L., *Acer pseudoplatanus* L., *Fraxinus excelsior* L. and *Fraxinus ornus* L.). These tree species are among the most widespread in Central European forests (Ellenberg, 1988). Our dataset covered the entire forest area of Switzerland (Figure 1) and encompassed a broad climatic and topographical gradient for temperate forests, with elevation ranging from 217 to 2,219 m a.s.l., mean annual temperatures between  $-0.3$  and  $12.9^{\circ}\text{C}$  and mean annual precipitation from 600 to 2,657 mm (Table 1).

## 2.1 | Forest inventory data

The Swiss NFI is based on terrestrial sampling on a  $1.4 \times 1.4$  km grid of permanent plots covering the entire country. In each forest plot, data were collected within two concentric circles of 200 and 500 m<sup>2</sup>, in which trees with diameter at breast height (DBH)  $\geq 12$  cm and  $\geq 36$  cm were measured respectively. Variables describing stand and site characteristics are assessed on a larger interpretation area of  $50 \times 50$  m around the plot (e.g. stand structure type; Keller, 2011). To date, a total of three surveys have been completed (NFI1 1983–1985, NFI2 1993–1995 and NFI3 2004–2006). The fourth inventory (NFI4) began in 2009 and will be completed by the end of 2017 (Abegg et al., 2014). Information on the sampling design and methods of the Swiss NFI can be found in Brassel and Lischke (2001), Lanz et al. (2010) and <http://www.lfi.ch/>. Our dataset was restricted to those sampling plots classified as accessible forest (without shrub forest) in at least two consecutive inventories. To minimize edge effects, we excluded plots that were not completely within the forest. This resulted in 3,400 plots between NFIs 1–2, 3,469 plots between NFIs 2–3 and 1,985 plots between NFIs 3–4 (NFI4 measurements until 2015). For each tree, basal area increment (BAI, cm<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>) was calculated from the DBHs at two consecutive NFIs and the number of vegetation

periods between them. After excluding the largest and the smallest 0.01% of the BAI values as outliers (BAI  $\leq -242$  cm<sup>2</sup> and  $\geq 295$  cm<sup>2</sup>), a total of 88,110 BAI observations were available for model fitting.

## 2.2 | Modelling approach

We used data from all four inventory campaigns to fit nonlinear mixed effect models (Pinheiro & Bates, 2000) with the package *nlme* in R 3.3.1 (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2017; R Core Team, 2017) for each species described above. The individual tree models included BAI 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). The functions accounted for the effect of site topography, stand characteristics, soil resources, management interventions, climate and nitrogen deposition and were further developed and broadly evaluated in the studies by Rohner and Thürig (2015) and Rohner et al. (in review). The functions followed the form:

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

where  $b_1$  and  $b_2$  are model coefficients,  $\epsilon$  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 ( $b_{\text{plot}}$ ):

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

where  $\beta_0$  is the estimated fixed intercept and  $\beta_{1, \dots, i}$  are model coefficients for each explanatory variable. Details on the original development of the functions, model fitting and selection are given in Appendix S1.

## 2.3 | Factors influencing tree growth

Tree variables were obtained directly from the NFI database (Traub, Meile, Speich, & Rösler, 2017). At the individual tree level, we considered

**TABLE 1** Overview of the dendrometric and climatic characteristics for the forest inventory plots in which the respective species is present. The number of plots and basal area increment (BAI) observations are the ones on which the final models for each species were fitted (multi-mixed plots excluded). The total represents the number of plots that were sampled in at least two consecutive inventories between NFI1 and NFI4

Species composition	Spruce	Fir	Pine	Larch	Beech	Maple/ash	Total
Number of plots	2,316	1,074	275	380	1,393	612	3,231
Number of BAI obs.	33,636	8,798	2,916	3,072	13,616	3,305	65,343
Mean BAI (cm <sup>2</sup> /year)	19.42 ± 19.13	27.53 ± 26.67	9.28 ± 10.08	17.11 ± 15.38	17.21 ± 17.63	14.97 ± 15.43	19.15 ± 19.77
Basal area (m <sup>2</sup> /ha)	41.27 ± 16.31	39.54 ± 14.16	34.1 ± 14.07	35.42 ± 16.17	35.72 ± 13.48	31.65 ± 13.95	38.44 ± 15.47
Elevation (m a.s.l.)	1,199 ± 424	906 ± 273	1,036 ± 497	1,558 ± 428	825 ± 264	797 ± 285	1,057 ± 423
Mean annual temperature (°C)	6.0 ± 2.2	7.5 ± 1.4	6.9 ± 2.7	4.3 ± 2.4	8.0 ± 1.3	8.2 ± 1.4	6.8 ± 2.2
Annual precipitation (mm)	1,409 ± 352	1,440 ± 262	1,085 ± 287	1,180 ± 401	1,412 ± 306	1,385 ± 298	1,384 ± 338

variables DBH and basal area of trees larger than the target tree (BAL, m<sup>2</sup>/ha), which was used as a proxy for competition within the forest plot. At the plot level, the arithmetic mean value of the 100 largest DBH per ha (DDOM, cm) was used to express stages of stand development as proposed in Brassel and Lischke (2001), and stand density was quantified using the stand density index (SDI), calculated using quadratic mean diameter, maximum stocking and an allometric coefficient according to Reineke (1933). Additionally, a categorical variable differentiated between stand structure types (TYP), even- (0) or uneven-aged forest (1). Variables expressing site topography were derived from digital elevation models and consisted of slope (SLP, in percentage), profile curvature (CURV, index between -2 and 2, where negative values indicate convex and positive denote concave curvature), northness index (NORTH, calculated from the plot aspect with  $\cos(2\pi \times \text{aspect}/360)$ , where 1 indicates a north-exposed plot, -1 a south-exposed plot) and eastness index (EAST,  $\sin(2\pi \times \text{aspect}/360)$ , where 1 indicates an east-exposed and -1 a west-exposed plot). As a measure of soil acidity, we used the pH value (PH) of the upper soil layer (below the humus layer), which had been determined in the laboratory after the first NFI from soil samples obtained in the field (Bachofen, Brändli, & Brassel, 1988). Management was considered with a continuous index expressing release effects at the plot level (RE). When an overstorey tree was removed, RE takes a value between 0 and 1 for each remaining tree on the plot, with the index being inversely proportional to the number of remaining trees (e.g. 0.1 if a tree was removed and 10 remained on the plot; see Rohner & Thürig, 2015).

Climate and nitrogen deposition data for each NFI plot were obtained from the climatology engineering office MeteoTest (Remund, Rihm, & Huguenin-Landl, 2016). Spatially interpolated historical series of temperatures (TEMP, in °C), moisture index (MI; ratio between actual and potential evapotranspiration ET<sub>a</sub>/ET<sub>p</sub>, ranging between 0 and

1, the lower the dryer) and solar radiation (SR, W/m<sup>2</sup>) were provided at monthly resolution for the reference period (1980–2015). We calculated the annual means of temperature, moisture index and solar radiation over the physiological years according to Lapointe-Garant et al. (2010) and subsequently averaged them over the inventory intervals (see Rohner, Weber, & Thürig, 2016). Available water holding capacity to a depth of 1 m (AWC, in mm) was also provided for each NFI plot (Remund, 2013). Elevation and mean annual precipitation were initially considered by Rohner and Thürig (2015) as explanatory variables but were later removed due to their high correlation with temperature and moisture index, respectively (see Appendix S1). Atmospheric nitrogen deposition data for each NFI plot (NDEP, kg N ha<sup>-1</sup> year<sup>-1</sup>) were derived from a combination of emission inventories, statistical dispersion models and spatially interpolated monitoring data from 5-year periods (Thimonier, Schmitt, Waldner, & Rihm, 2005). Values for the three reference years were associated with each NFI interval (1990 NFI1-2, 2000 NFI2-3 and 2010 NFI3-4).

## 2.4 | Tree species complementarity

To explore mixing effects on growth, we categorized NFI plots according to species composition. We considered *monospecific* those plots where the corresponding species accounted for 85% or more of the basal area. A plot was categorized as a *two-species mixture* when the two species represented 85% or more of the total basal area and each of the two species contributed at least 20% of the basal area. Similarly, a plot was classified as a *three-species mixture* when the three considered species represented 85% or more of the total basal area and each of the three species contributed at least 15% of the basal area. Plots that did not fall into one of these categories were categorized as “multi-mixed.” Based on these criteria,

**TABLE 2** Species composition of the Swiss NFI plots with the number of BAI observations for each mixture type. The mixtures with more than 100 observations (grey-shaded cells) were used as levels in the categorical variable CATMIX, while the ones with <100 observations were excluded

Species composition	Spruce	Fir	Larch	Pine	Beech	Maple/ash
Monospecific	21,976	2,180	1,543	1,558	5,514	888
Two-species mixture						
Beech-maple/ash	33	32	1	3	1,023	689
Beech-pine	12	9	0	272	438	9
Beech-larch	7	2	131	3	197	0
Fir-beech	106	1,456	2	3	1,611	73
Fir-larch	8	104	42	0	3	0
Fir-maple/ash	24	256	1	0	21	228
Spruce-beech	1,864	128	7	10	2,237	89
Spruce-pine	1,024	7	18	729	22	13
Spruce-larch	2,487	13	1,398	32	18	0
Spruce-fir	3,546	3,244	4	13	296	124
Spruce-maple/ash	795	27	0	0	28	600
Pine-larch	24	0	71	116	4	0
Three-species mixture						
Spruce-beech-maple/ash	309	26	0	6	343	299
Spruce-pine-beech	123	9	2	137	195	7
Spruce-pine-larch	143	1	76	104	0	0
Spruce-larch-beech	130	7	75	3	139	1
Spruce-fir-maple/ash	216	187	2	1	25	185
Spruce-fir-beech	917	961	2	7	1,068	61
Fir-beech-maple/ash	44	282	0	0	332	292

we created the multinomial categorical variable CATMIX to indicate the species composition of the NFI plot. To avoid problems of over-parameterization and convergence due to singularity errors, we retained only mixture categories with more than 100 observation points, resulting in a total of 19 mixture types (Table 2). Plots specified as “multi-mixed” were excluded from the dataset. To assess the difference in growth between pure and mixed stands, the selected models were fitted including CATMIX in the function  $f(V_1, \dots, V_i)$  (Table S1).

To investigate whether complementarity effects are modulated by stand characteristics and resource availability, we included interactions between variables expressing site and stand conditions (fixed effects in the function  $f(V_1, \dots, V_i)$ ) and the effect of mixing (CATMIX). We concentrated on ecologically meaningful and interpretable pairs of interaction terms and fitted them in separate models (Table S3). As there were cases in which all plots belonging to a given mixture did not experience any management (i.e., RE equal zero for all plots in a mixture caused non-convergence in the nonlinear functions), we avoided exploring interactions between CATMIX and RE, as well between CATMIX and the categorical variable TYP.

Following the approach by Forrester (2014), tree-level complementarity for each species was calculated with the following equation:

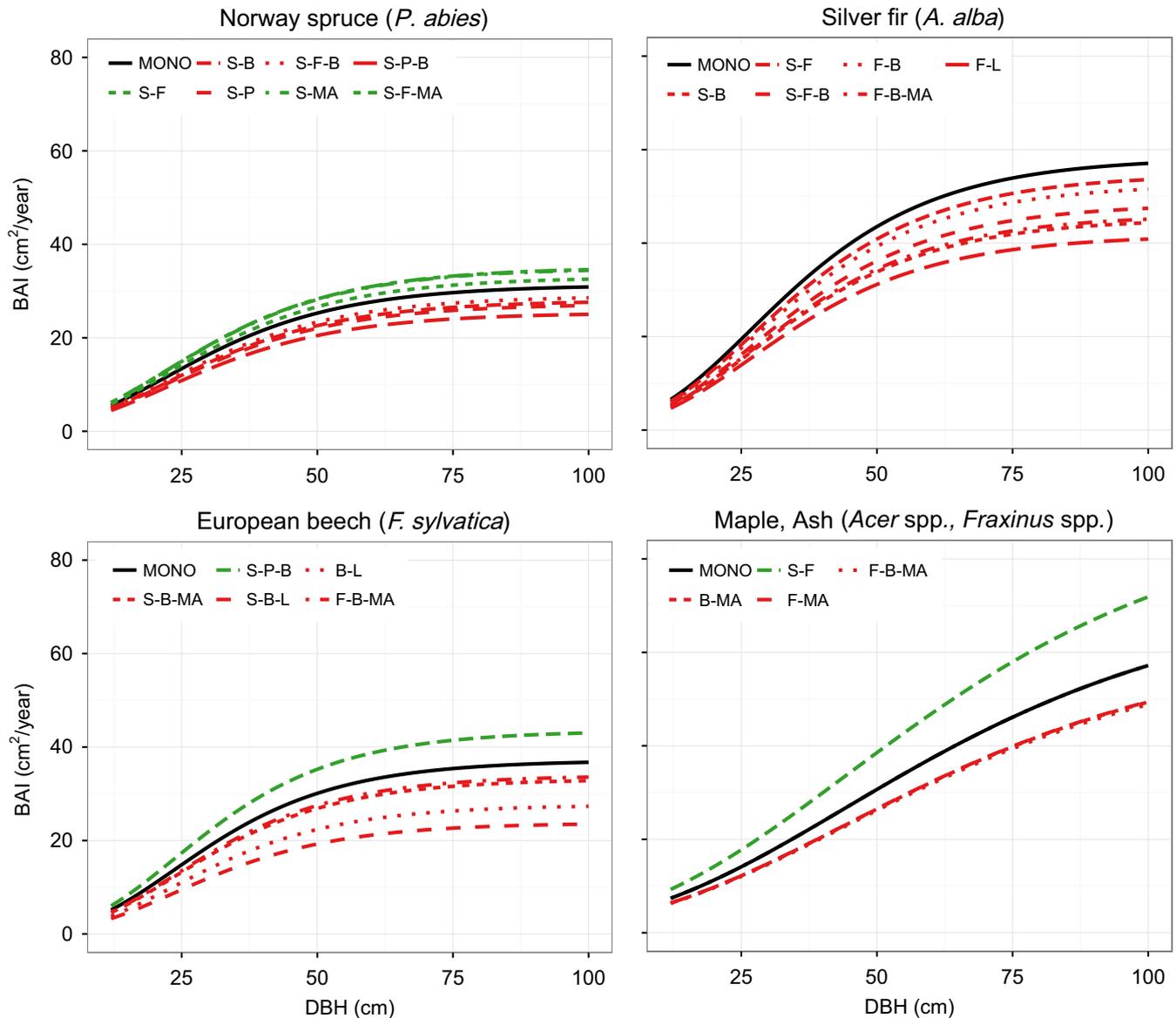
$$\text{Complementarity(\%)} = \frac{\text{BAI}_{\text{MIX}} - \text{BAI}_{\text{MONO}}}{\text{BAI}_{\text{MONO}}} \times 100 \quad (3)$$

where  $\text{BAI}_{\text{MIX}}$  is the BAI for a tree in a mixed stand and  $\text{BAI}_{\text{MONO}}$  the BAI for a tree in a monospecific plot of the same species, both predicted using the species-specific models (Equation 1). Complementarity was calculated for the increasing value of a single factor (e.g., BAL, TEMP), while all the other predictors were fixed at their mean. Thus, positive values of complementarity indicate positive mixing effects on individual BAI depending on stand conditions and resource availability. We considered significant interactions between CATMIX and other explanatory variables with  $p < .05$  and marginally significant interactions with  $p$ -values between .1 and .05. For evaluating the goodness-of-fit of the models, we calculated the relative root-mean-square error, the per cent bias and the Pearson correlation coefficients between observed and predicted values of BAI within the R package *hydroGOF* (Zambrano-Bigiarini, 2014).

### 3 | RESULTS

#### 3.1 | Factors influencing tree growth and mean mixture effects

Individual tree growth of the investigated species was affected differently by factors expressing stand conditions and resource availability. As previously confirmed by Rohner and Thürig (2015), some of them had a consistent positive or negative effect for all species,



**FIGURE 2** Relationship between basal area increment (BAI) and diameter at breast height (DBH) for spruce, fir, beech and maple/ash. The solid black line represents the growth in monospecific plots, while the dashed and dotted curves represent the growth in different mixtures (S, spruce; F, fir; P, pine; L, larch; B, beech; MA, maple/ash). All the other explanatory variables were fixed at their mean in the calculation of BAI. Only the mixtures with a significant difference in growth in comparison to monoculture were plotted (see Table S2). Remaining species in Figure S2

while the effect of others varied depending on the species (Figure S1). For instance, BAL, SDI, SLP and PH generally had a negative influence on tree growth, although their effect size differed among species. A minor negative effect of DDOM was observed for spruce and beech. Temperature had a uniform positive effect on growth of all species, although it was found to be non-significant for pine. Other factors positively influenced BAI, although with a lower effect size: NORTH for spruce and beech; MI for spruce, beech and fir; AWC for spruce and beech; SR for spruce. The release effect due to management positively affected BAI of spruce, beech and maple/ash. Only growth of pine was positively influenced by an uneven-aged structure (TYP = 1), while BAI of larch and maple/ash benefited from an even-aged structure. Higher amounts of nitrogen deposition had contrasting effects

depending on the species, with negative impacts on growth of spruce and fir, but beneficial effects for beech, pine and maple/ash.

Estimates of CATMIX indicated more negative (20) than positive (5) mixing effects on individual tree BAI. In another 21 cases, however, the effects were not significant (see Table S2). BAI of spruce was found to be higher in spruce–fir, spruce–maple/ash and spruce–fir–maple/ash stands, but lower when mixed with beech or pine, and in the three-species mixtures spruce–fir–beech and spruce–pine–beech (Figure 2). For silver fir, all six significant mixing responses were negative, with different effect sizes depending on the mixture type. Estimates of CATMIX for beech and maple/ash were mainly negative, but beech BAI was positively affected in beech–spruce–pine stands, while the growth of maple/ash was higher when present as a sporadic species

(<15% basal area) in a spruce–fir stand. Pine trees in spruce and beech stands and larch trees mixed with beech had a lower BAI than in the respective monospecific stands (Figure S2). Goodness-of-fit statistics for the six models are given in Table 3.

### 3.2 | Interactions between mixture effects and site variables

With the exception of larch, all investigated species showed significant changes in complementarity depending on stand characteristics, site topography, soil and climate conditions (Figure 3). Generally, the magnitude of the complementarity effects was amplified with increasing above-ground competition (BAL). For spruce and beech, contrasting trends in increasing or decreasing complementarity depending on the mixture type were detected (e.g. decreasing for spruce when mixed with fir, beech or maple/ash but increasing when mixed with larch; Figure 4a,b). Increasing stand density (SDI) was found to both increase and reduce complementarity, but, except for fir, not many interactions were found to be significant. For example, there was positive complementarity at higher stand densities for spruce when mixed with beech or pine, but complementarity declined for fir when mixed with beech, maple/ash or larch and for pine when mixed with larch or beech (Figure S3). The interactions between DDOM and CATMIX generally resulted in increasing complementarity with increasing DDOM, particularly for spruce. In spruce–beech stands, positive complementarity effects were detected for spruce at increasing DDOM, while an opposite trend was found for beech. Topographic characteristics (SLP, CURV, NORTH and EAST) significantly influenced complementarity, although they did not show a consistent modulating pattern across species. Nonetheless, complementarity for beech was positively affected by increasing slope, and in west- and south-oriented stands. Climatic factors also had a significant impact on complementarity for most of the species. In the majority of cases (11 out of 12), increasing drought (low values of MI) was associated with increasing complementarity effects for spruce and beech (Figures 3 and 4c,d for spruce and beech), and increasing temperature increased complementarity in 8 out of 11 significant interactions (Figure 4e,f for spruce and beech). Except for one mixture type (spruce–larch–beech, found only in 17 plots across Switzerland), interactions with solar radiation for spruce indicated an increase in complementarity with rising levels of solar

radiation. Soil conditions and nutrient availability also significantly affected complementarity. Complementarity for spruce and fir decreased from acidic to alkaline soils, while in the case of beech, complementarity increased with increasing soil alkalinity. In 15 out of 18 cases, higher levels of nitrogen deposition reduced complementarity. This trend was particularly clear for beech, in which complementarity declined with increasing NDEP in seven mixtures (Figure S3). Soil water holding capacity did not have a uniform effect on complementarity across species, as for example, it increased with higher AWC for spruce but decreased for beech.

## 4 | DISCUSSION

Our findings demonstrate that complementarity effects for the most common tree species growing in European temperate forests strongly vary with stand density, stand development, topographic, climatic and soil conditions. These results are in line with recent studies that emphasized the need to account for site-dependent conditions when exploring mixture effects in relation to forest productivity (Forrester & Bauhus, 2016; Jucker et al., 2016; Toigo et al., 2015). We could also confirm that the relationship between complementarity and resource availability can have different—sometimes opposing—trends depending on the species composition. As shown in our analysis, these trends can be identified using modelling approaches taking into account site-specific conditions.

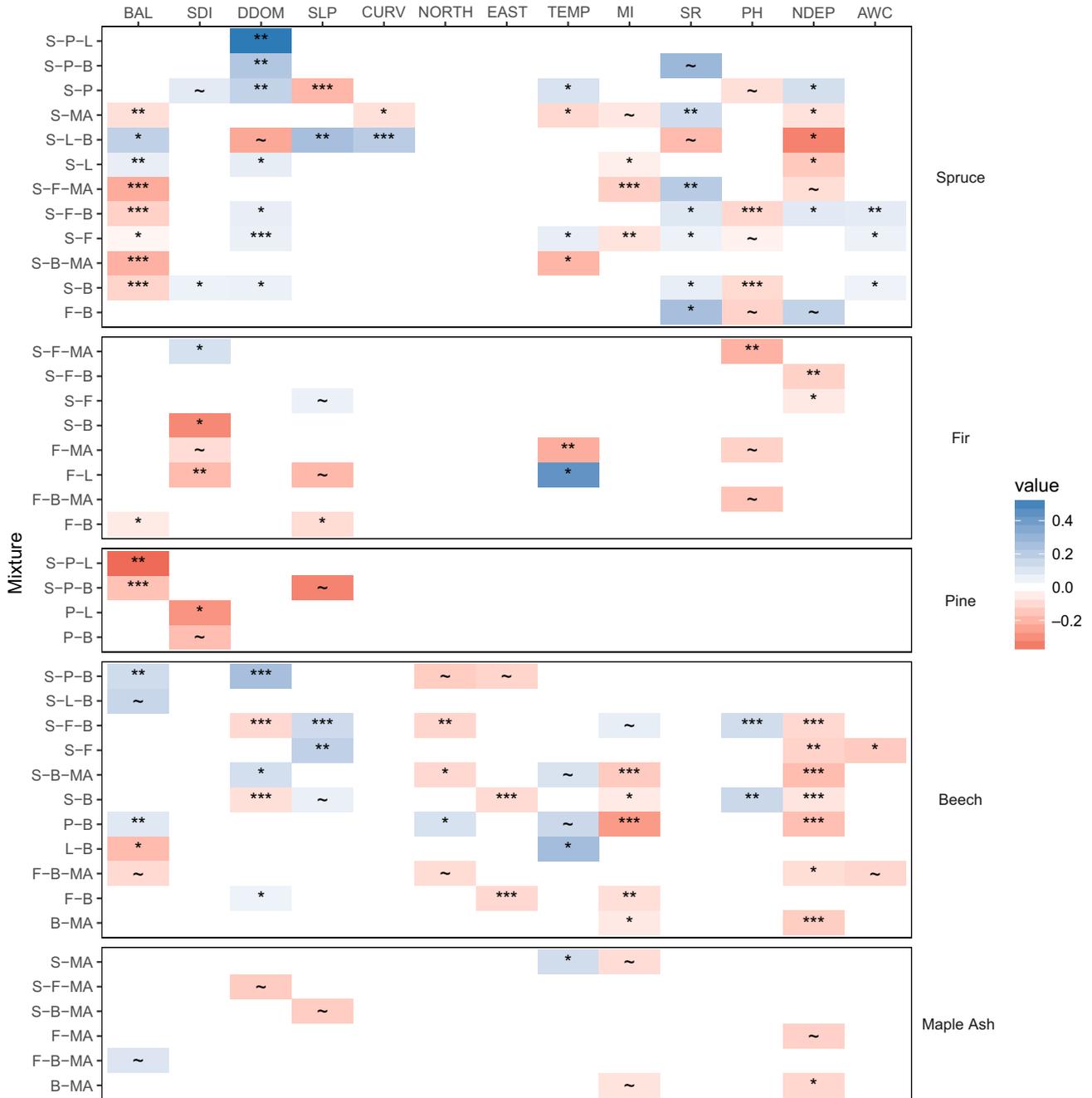
### 4.1 | Mean mixing effects

The effects of the site-specific variables on individual tree growth were generally plausible for the investigated species. These results confirm the finding by Rohner and Thürig (2015) and Rohner et al. (in review), where a detailed discussion of the effects of the single drivers on tree growth can be found (see also Appendix S2). Focusing on complementarity effects, mixing was only significant for 25 out of 45 mixture types. The lack of significance often resulted because of opposing effects under contrasting site conditions. Taking spruce and fir as an example, our results suggest that in general, there was a weak positive effect for spruce only when mixed together with fir and maple/ash compared to monospecific forests, while for fir there were only negative influences on growth when mixed with other species such as spruce, beech or larch. This is somewhat in contrast with the findings of Vallet and Perot (2011), who indicated positive effects on fir when mixed with spruce in France. However, these results are not directly comparable as they modelled growth at the stand level. Forrester et al. (2013) found that in German stands, often both spruce and fir benefited from growing in mixed rather than monospecific stands but that individual tree growth complementarity was strongly modulated by climate and stand density. Similarly, Huber et al. (2014) found contrasting positive and negative mixing effects for both species in Switzerland depending on site quality and climatic conditions.

Even within a given species combination, species interactions are often dynamic and vary greatly with resource availability and climatic

**TABLE 3** Goodness-of-fit as root-mean-square error (RMSE, in  $\text{cm}^2/\text{year}$ ), percentage bias (P-BIAS) and Pearson correlation coefficient ( $r$ ) for the six species-specific models, based on the fixed and the random effects and including CATMIX (Table S2)

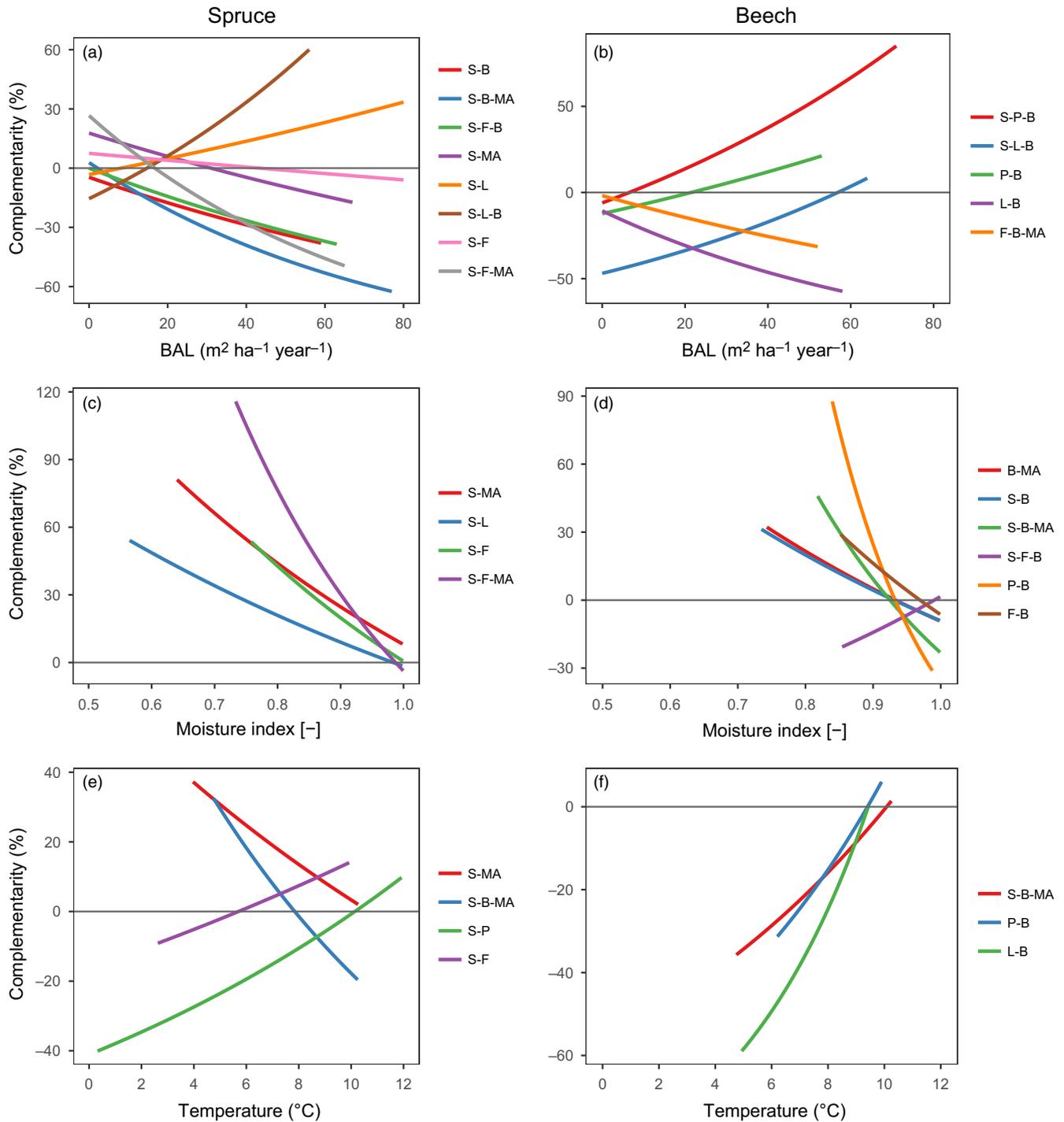
	RMSE	P-BIAS (%)	$r$
Spruce	12.56	1.7	.74
Fir	15.22	2.3	.82
Pine	6.72	3.2	.72
Larch	10.88	2.7	.73
Beech	10.17	2.4	.81
Maple/ash	8.51	3.1	.83



**FIGURE 3** Overview of the estimates for the interactions between site conditions and mixture variables. Positive estimates indicate increasing complementarity with increasing values of the variable (blue cells), while negative estimates denote an inverse relationship (red cells). Symbols for  $p$ -values:  $\sim p \leq .1$ ,  $* p \leq .05$ ,  $** p \leq .01$ ,  $*** p \leq .001$ . Legend for the tree species: S, spruce; F, fir; P, pine; L, larch; B, beech; MA, maple/ash. Larch is not displayed as target species due to the absence of significant estimates of the interaction terms. The formulation of all models is given in Table S3. Legend for the site variables: BAL: basal area of trees larger than the target tree; SDI: stand density index; DDOM: mean of the 100 largest diameters per ha; SLP: slope of the plot; CURV: profile curvature; NORTH: northness index; EAST: eastness index; TEMP: temperature; MI: moisture index (ETa/ETp); SR: global solar radiation; PH: soil pH; NDEP: nitrogen deposition; AWC: available soil water holding capacity

conditions. When such gradients were ignored, the mean mixing effects were only significant for approximately half of the investigated mixture types because positive effects at one end of the gradient neutralized negative effects at the other end. In contrast, when the gradient was considered, mixing was significant for many more mixture types (see significant patterns in Figures 3 and 4, Figure S3). In

line with a number of recent studies (Forrester et al., 2013; Huber et al., 2014; Toigo et al., 2015), our results give a clear indication that individual tree growth complementarity cannot be generalized over large gradients of site and stand factors, and it must be assessed in relation to them when aiming at inference across large-scale gradients.



**FIGURE 4** Changes in complementarity for spruce and beech in multiple mixture types depending on above-ground competition (BAL, a, b), moisture index (c, d) and temperature (e, f). The lines are restricted to the data range of each mixture type used for fitting the models. Remaining species and interactions as shown in Figure S3

## 4.2 | Factors modulating complementarity in mixed species forests

Our results for the interactions between stand and mixture variables supported our first hypothesis that the modulating effects of stand density and development stage are important to consider when examining complementarity patterns (Cavard et al., 2011; Forrester &

Pretzsch, 2015; Garber & Maguire, 2004). Depending on the mixture type, we showed that complementarity increased or decreased with increasing above-ground competition, stand density and stand development. A general pattern for these three variables across mixture types, however, could not be identified. As most of the previous investigations on the effects of stand characteristics on complementarity focused on one mixture type, only a part of our results could be

compared with other studies from the literature. For example, in the case of spruce and fir, we detected similar trends to those in Germany (Forrester et al., 2013), where complementarity in spruce–fir stands increased with stand density for both species (see Figure S3 for fir with SDI and spruce with DDOM). This was suggested to occur because the interaction between both species improved light absorption and/or light use efficiency, and this effect became more useful as stand density and competition increased. In contrast, complementarity for pine with beech declined as stand density increased (Figure S3), consistent with reductions in growth efficiency of pine admixed with beech as density increased (Condes et al., 2013). What our analyses clearly suggest is that the magnitude of complementarity, whether positive or negative, increased with increasing above-ground competition (Figure 4a,b), stand density and stand development.

Our findings for spruce, beech and maple/ash clearly indicated higher complementarity effects in different mixture types with increasing drought conditions (i.e. lower moisture index). This suggests that the species interactions in those mixtures reduced competition for water either by increasing availability, uptake or efficiency (Forrester & Bauhus, 2016). These species have also been shown to be less stressed by drought in certain mixtures in other regions within Europe (Forrester et al., 2016). Past studies indicated positive influences of species diversity by reducing sensitivity of fir to drought (Gazol & Camarero, 2016; Lebourgeois, Gomez, Pinto, & Merian, 2013); however, these effects could not be detected in our study, probably due to the limited number of very dry sites with the presence of fir in Switzerland. At increasing drought, complementarity for beech increased more sharply when mixed with pine rather than with fir, maple/ash or spruce. This may be due to the beech fine-root system that can out-compete pine roots throughout the soil layers in mature mixed stands (Curt & Prévosto, 2003). In spruce–beech forests, complementarity for beech increased at increasing drought, but this was not the case for spruce (Figure 4c,d) suggesting that in this mixture type, only beech trees are likely to benefit from interspecific interactions under increasing water stress. This can be explained by the higher drought tolerance of beech compared to spruce and to the higher efficiency of its roots system for exploiting soil layers (Bolte & Villanueva, 2006). In brief, these results indicate increasing complementarity effects for spruce, beech, maple and ash under increasing drought conditions, but still with different magnitude depending on the mixture type. Consequently, this implies that some but not all mixed species forests can reduce water stress. For example, complementarity for beech decreased with increasing drought in a three-species mixture spruce–beech–fir. This confirms that complementarity effects related to drought conditions should be investigated considering the species identity rather than using indices of species diversity (i.e. higher number of species does not necessarily denote lower susceptibility to drought; see Forrester et al., 2016).

Under changing temperature, complementarity patterns revealed a different trend. In four out of the six investigated species, complementarity mostly increased with increasing temperature (Figure 3). Although we found an overall positive effect of temperature on the growth of our investigated species (Figure S1), the

effect of temperature might be positive or negative depending on the location of the mixture (i.e. possible negative effect of higher temperatures at sites with a comparably low moisture index). In this regard, Condes and del Rio (2015) found that beech benefited from admixture of pine where climatic conditions were more favourable, while Forrester et al. (2013) reported an increasing complementarity for spruce mixed with fir at milder temperature. Huber et al. (2014) investigated stand increment and reported an increasing mixture effect with increasing site quality for spruce mixed with fir. When climatic conditions become more favourable, trees usually allocate a higher proportion of their growth above-ground, enlarging their crown leaf area (Litton, Raich, & Ryan, 2007; Poorter et al., 2012). In some forest communities, interactions between two or more species may enhance light absorption or light use efficiency, thus complementarity tends to increase along the temperature gradient (Forrester & Bauhus, 2016). In our case, complementarity for beech increased with increasing temperature when mixed with conifers such as pine, larch or spruce, while for conifers such as spruce and fir, complementarity increased with rising temperature only when mixed with shade intolerant conifers (e.g., pine, larch) but it decreased when mixed with beech and other broadleaved species. Following the concept described above, under more favourable climatic conditions, broadleaved species such as beech, maple and ash can develop larger leaf areas, thus competition for light increases to the detriment of conifers which are usually unable to develop large crown areas. Our findings confirm recent notions about facilitative or complementarity effects under increasing temperature (Forrester et al., 2013; Holmgren & Scheffer, 2010).

It is well known that due to their influence on water runoff and wind exposition, topographic factors such as slope and aspect can critically affect tree growth and forest productivity (Adams, Barnard, & Loomis, 2014; Fekedulegn, Hicks, & Colbert, 2003). To our knowledge, this is the first study demonstrating that topographic characteristics can also induce changes in complementarity effects, although a general trend across species and mixture types could not be identified.

Soil acidity was also responsible of altering complementarity for many of the investigated species. Essentially, our results indicate that the growth of beech benefits from mixture with increasing soil pH, while spruce and fir seem to grow better in mixtures than in monoculture on more acidic soils. It is well known that beech has a wide tolerance to soil acidity; it grows on a large variety of soils over Europe but not in the most acidic ones (Packham, Thomas, Atkinson, & Degen, 2012). Instead, spruce is most common on acidic soils (Caudullo, Tinner, & de Rigo, 2016). Among the most common European species, spruce and fir have the highest acidifying impact on upper soil pH (Augusto, Ranger, Binkley, & Rothe, 2002). Our results indicate that complementarity for beech becomes negative when present in minor proportions with spruce and fir. It is possible that high proportions of spruce and fir in a stand induce an acidification of the topsoil which may be unfavourable for beech, as confirmed by the fact that beech greatly benefited from admixture with the two conifers on alkaline soils (Figure S3). Further investigations including temporal series of pH

measurements—which were not available for our study—are required for unravelling mechanisms and relationships between soil acidification and overstorey composition. Studies focusing on this topic could provide useful guidelines for managing the acidifying impact of a tree species in mixed stands (Rothe & Binkley, 2001).

Regarding nitrogen deposition, previous studies found both positive and negative effects on tree growth due to increasing levels of this resource (Emmett, 1999; Ferretti et al., 2014; McNulty, Aber, & Newman, 1996). Given the complex spatial pattern of the crowns of different species enhancing through-fall quantity and chemistry, mixed stands have usually better nitrogen nutrition than monocultures (Augusto et al., 2002; Rothe & Binkley, 2001). In this regard, the presence of conifers in broadleaved stands may increase nitrogen nutrition availability, as coniferous species often have a higher intercepting rate of atmospheric elements than the broadleaves, thanks to their canopy structure, height and leaves shape (Balsberg-Pahlsson & Bergkvist, 1995). Our analysis shows a reduced complementarity for beech and maple/ash under increasing levels of nitrogen deposition, while a general pattern among mixture types could not be identified for spruce. A possible explanation for this phenomenon could be that at lower N-deposition levels, the presence of conifers such as spruce and fir may enhance N availability for beech, while at higher N-concentrations, this benefit is redundant (no deposition N is required) because there is already enough nitrogen. This trend is consistent with results from mixtures with N-fixing species, whose facilitative effects decline as soil N availability increases (Binkley, 2003; Bouillet et al., 2008; Boyden, Binkley, & Senock, 2005). This trend, however, was not confirmed by complementarity patterns for fir and the inconsistent trends detected across mixture types for spruce (Figure 3). As shown in past observations, there does not appear to be a general simplification about the effects of mixed stands on nitrogen nutrition, as they strongly depend on the mixture composition and on site characteristics (Augusto et al., 2002; Rothe & Binkley, 2001). It is worth mentioning that the spatially interpolated nitrogen deposition data used for this study were derived from a combination of emission inventories and statistical dispersion models and this should be considered when interpreting the coefficients for nitrogen deposition. Further research accounting for the varying proportions of the individual species in the mixture would be particularly helpful for drawing more accurate conclusions on nutritional interactions in mixed forests.

### 4.3 | Methodological aspects and recommendations for future research

Our analysis provides evidence about drivers influencing tree growth complementarity and suggests possible explanations. However, our approach based on available inventory data does not allow analysis of the underlying mechanisms and biological processes behind the mixing effects. Studies based on designed plantations would be useful for understanding these mechanisms (Mueller, Tilman, Fornara, & Hobbie, 2013; Williams, Paquette, Cavender-Bares, Messier, & Reich, 2017). Due to the limitation of the investigated NFI dataset to trees with DBH >12 cm, we recognize that our results are only valid for adult trees;

complementarity effects may be different of young tree communities. Our approach of grouping two or more species within the same model structure (e.g., pines but particularly for maple and ash) may have hindered the detection of some environmental effects. Thus, the results presented for these species need to be interpreted within these limitations of the approach. Nonetheless, we are confident that our study provided robust results concerning the effects of species mixture, as a large range of variables have been considered and integrated in the models in order to de-correlate from the influence of environmental and site conditions. Alternatively, simulations of complementarity effects from validated process-based models could be compared to forest inventory data. Such studies could be helpful to explain biochemical and ecophysiological interactions affecting complementarity in mixed species forests (Forrester & Tang, 2016; Pretzsch, Forrester, & Rotzer, 2015) and also to examine shifts in species composition and forest dynamics due to changing climate and management at various spatial and temporal scales (Mina, Bugmann, et al., 2017; Morin, Viner, & Chuine, 2008). We also acknowledge that the use of continuous instead of categorical variables could allow detecting mixing effects depending on different proportions of the species in a mixture. This approach is usually applied for two-species mixtures (Forrester et al., 2013; Huber et al., 2014) but further investigations on forests composed by three or more species would be highly valuable. Lastly, further development of the functions presented in this analysis could be integrated in state-of-the-art forest scenario models for estimating potential wood supply and for supporting management decisions (Pretzsch et al., 2015; Temperli, Stadelmann, Thürig, & Brang, 2017).

### 4.4 | Conclusive remarks and implications for forest management and conservation

Enhancing species diversity and promoting mixed forests has been increasingly proposed as a strategic approach for managing and conserving forests under climate change (Ammer, 2017; Brang et al., 2014; Keenan, 2015). We found that, under certain conditions, mixed forests can promote individual tree growth of the main species growing in Central European forests. Such outcomes are of high interest in the context of forest management and conservation, as they allow to identify under which set of conditions promoting species diversity can also help in fostering forest productivity. Although at increasing drought most of the investigated species would benefit from growing in mixed forests rather than in monoculture (Lebourgeois et al., 2013; Pretzsch, Schütze, & Uhl, 2013; but see Grossiord et al., 2014), our study does not fully confirm that complementarity generally increases when environmental conditions become harsher. We recommend careful assessments depending on species composition under changing temperature and drought regimes and soil conditions, because relationships between complementarity and resource availability can vary greatly among mixture types. Also, our analysis indicates that complementarity is not only contingent to climate but also to above-ground competition, developmental stage and stand density. This is particularly relevant in the framework of adapting forest management,

as competition, stand development or density can be directly modified through silvicultural interventions. Further modelling and experimental studies are required for disentangling ecological mechanisms behind complementarity, but efforts should also be targeted towards developing tools in support to forest ecosystem management and conservation.

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## AUTHORS' CONTRIBUTIONS

B.R., E.T., M.H. and M.M. conceived ideas and designed the methodology of the study; M.M. compiled and analysed the data; M.M. led the writing of the manuscript. All authors revised to the drafts critically and gave final approval for publication.

## DATA ACCESSIBILITY

Model outputs are archived in the Dryad Digital Repository <https://doi.org/10.5061/dryad.r8591> (Mina, Huber, Forrester, Thürig, & Rohner, 2017). Tables with the results of the four Swiss NFIs are freely available for download from the website <http://www.lfi.ch/resultate/>, while the complete list of available tree- and plot-level attributes can be found at <http://www.lfi.ch/dienstleist/katalog.php?lang=de>. The raw data from the Swiss NFI can be provided free of charge within the scope of a contractual agreement (<http://www.lfi.ch/dienstleist/daten-en.php>).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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