

The productivity of mixed mountain forests comprised of *Fagus sylvatica*, *Picea abies*, and *Abies alba* across Europe

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Mixed mountain forests of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst), and silver fir (*Abies alba* Mill.) cover a total area of more than 10 million hectares in Europe. Due to altitudinal zoning, these forests are particularly vulnerable to climate change. However, as little is known about the long-term development of the productivity and the adaptation and mitigation potential of these forest systems in Europe, reliable information on productivity is required for sustainable forest management. Using generalized additive mixed models this study investigated 60 long-term experimental plots and provides information about the productivity of mixed mountain forests across a variety of European mountain areas in a standardized way for the first time. The average periodic annual volume increment (PAI) of these forests amounts to $9.3 \text{ m}^3 \text{ ha}^{-1} \text{ y}^{-1}$. Despite a significant increase in annual mean temperature the PAI has not changed significantly over the last 30 years. However, at the species level, we found significant changes in the growth dynamics. While beech had a PAI of $8.2 \text{ m}^3 \text{ ha}^{-1} \text{ y}^{-1}$ over the entire period (1980–2010), the PAI of spruce dropped significantly from 14.2 to $10.8 \text{ m}^3 \text{ ha}^{-1} \text{ y}^{-1}$, and the PAI of fir rose significantly from 7.2 to $11.3 \text{ m}^3 \text{ ha}^{-1} \text{ y}^{-1}$. Consequently, we observed stable stand volume increments in relation to climate change.

Introduction

Mixed mountain forests of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst), and silver fir (*Abies alba*

Mill.; hereinafter referred to as beech, spruce, and fir, respectively) at elevations between ~600–1 400 m above sea level cover an area of more than 10 million hectares in Europe (Brus *et al.*, 2012; EUFORGEN, 2017). More than half of Central Europe's

surface area consists of mountain areas, which is where most of the existing forests are concentrated (CIPRA, 2007). Mixed mountain forests are of high ecological and (socio-) economic importance in Central and Eastern Europe due to their provision of various ecosystem goods and services (e.g. Ellenberg, 1988; Pretzsch et al., 2015; Mina et al., 2017). Connecting deciduous forests in lowlands and coniferous tree communities at high elevations, the coexistence of beech, spruce, and fir has lasted for many centuries locally, depending on the distance from glacial refugia (Magin and Mayer, 1959; Mosandl, 1984). As a consequence, mixed mountain forests provide habitat for a substantial diversity of plant and animal taxa (Hilmers et al., 2018).

Currently, there is a great interest in mobilizing and processing wood resources from mixed mountain forest areas (e.g. BAFU, 2015; Bayerische Staatsforsten AÖR, 2018). Previous investigations on the productivity of mixed mountain forests have concentrated mainly on mixtures of two of the three species and indicate that beech generally achieves higher growth rates when grown in mixtures with conifers, because intraspecific competition is reduced (Pretzsch et al., 2010; Bosela et al., 2015). Under certain conditions, spruce and fir also benefit from growing in two-species mixtures (Forrester et al., 2013).

Looking at three-species mixture of beech, spruce, and fir, Pretzsch et al. (2015) demonstrated an additional yield of about 20 per cent compared to neighbouring pure stands. But other studies show quite heterogeneous results, with complementarity effects strongly depending on climate, stand, and site conditions (Grossiord et al., 2014; Mina et al., 2018). Indeed, complementarity effects do not always favour beech and conifers in association (e.g. Conte et al., 2018).

Due to their altitudinal zoning, however, mountain forests are particularly susceptible to the effects of climate change (Theurillat and Guisan, 2001; Beniston, 2003; Pearson and Dawson, 2003; Scherler et al., 2016). The species-specific optimum habitats are severely restricted in their geographical distribution in mountain areas. Particularly vulnerable are beech-spruce-fir mixed mountain forests that occur in areas with species-specific suboptimal vitality. Here, climate change induced changes of environmental conditions

are likely to alter their competitiveness (McEvoy et al., 2013; Grace et al., 2014; Harvey et al., 2014). In addition, these forest systems may become more vulnerable in the future because of extensive bark beetle outbreaks and pathogens that profit from increased drought and higher temperatures under global change (Porta et al., 2008; Seidl et al., 2014). A number of studies report that in recent decades there have been more frequent problems with the natural regeneration of spruce and fir, ozone stress, and drought in mixed mountain forests (e.g. Ashmore et al., 1985; Ammer, 1996; Matyssek et al., 1997; Dell'Era et al., 1998; Ruehr et al., 2010; Hartl-Meier et al., 2014a; Pretzsch et al., 2015).

Against the background of the strong vulnerability of these ecosystems, the Agenda 2010 for Sustainable Development explicitly states that there needs to be an intensification of the implementation of concrete measures, sustainable processes, and strategies to strengthen the resilience of mountain areas (Mountain Partnership, 2017). Due to the restricted climatic conditions, mountain forests are well suited to analyze the influence of climate change over a relatively short period of time (Cudlin et al., 2017).

Large scale studies on mixed mountain forests and their productivity are rare and regionally limited (Preuhsler, 1981; Priezel and Christophel, 2014; Bosela et al., 2018, 2015; Pretzsch et al., 2015), but necessary to support management decisions that take environmental conditions and their possible future change into account. This paper uses a data set of a series of long-term experimental plots across mountain regions in Europe. It aims to improve the knowledge about site-specific productivity and growth trends in European mixed mountain forests, and addresses the following questions:

(Q1) How productive are mixed mountain forest systems in Europe currently and how has their productivity changed in recent decades with regard to climate change and anthropogenic influences?

(Q2) Is there a shift in species-specific productivity of beech, spruce or fir over recent decades?

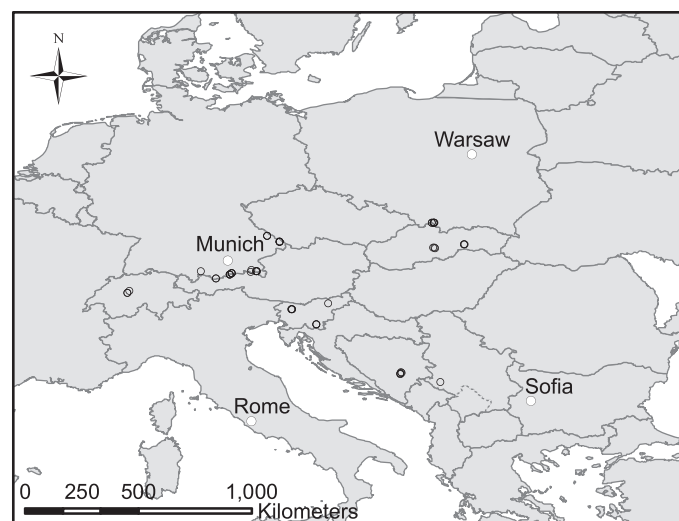


Figure 1 Geographic location of the 60 long-term mixed beech-fir-spruce mountain forest experimental plots (black points). Some experimental plots are not visible (overlaid) due to scaling.

Material and methods

Study area

Our data set covered most parts of the mountainous regions of Europe (Figure 1) and maps a wide climatic and topographic gradient for mixed mountain forests with elevations from 733 to 1443 m, mean annual temperatures from 4.4 to 8.5°C, and annual precipitation from 813 to 2818 mm (Figure 2; Table 1). The dominant parental material varies between slightly consolidated (e.g. unconsolidated deposits), moderately consolidated (e.g. sedimentary rocks), and intensively consolidated (e.g. igneous and metamorphic rocks) with medium to very high available water storage capacity, low to high base saturation, and very low to medium soil organic carbon contents (Panagos *et al.*, 2012).

Data

Sixty long-term experimental plots with a total of 222 observations between 1980 and 2010, consisting of beech, spruce, and fir, were investigated (Figure 1; Table 1). All trees with a diameter at breast height >7 cm were measured at every observation. Tree heights were measured on a subsample of trees. Thus, the volume of single trees and stands could be calculated by means of stand height curves and regionally adopted form factors. At least two of the three species (beech, spruce, and fir) had to be present and each species must have had a mixture portion of at least 20 per cent. On the experimental plots only low intensity thinning or no thinning was allowed. In this way, we avoided confounding growth trends with thinning effects.

Our study focused on the periodic annual increment at the stand level (PAI). To evaluate the stand characteristics, we followed the DESER-Norm 1993 by Johann (1993). Repeated observations at the stand level were carried out at intervals of several years, and enabled the calculation of PAI, giving the mean annual growth rates over longer time intervals. Between two observations at times t_1 and t_2 , the PAI was calculated from the difference between the wood volumes V_1 and V_2 of the remaining stand at both times plus the volume of trees which died (or were removed) between the observations.

$$PAI = (V_2 \text{ remaining} - V_1 \text{ remaining} + V_{\text{removed}}) / (t_2 - t_1)$$

Factors used to explain stand productivity

The growth of any tree and forest stand is age dependent. However, since most of the study plots under investigation are uneven-aged, it was not possible to create a useful metric regarding stand age. For this reason, we used the standing volume per hectare of the remaining stock (V) as a proxy for the development stage of the forest stands. Furthermore we used the stand density quantified by the stand density index (SDI; Reineke, 1933) to characterize the growing stock. To quantify the proportion of each species in the total stand with respect to the different space requirements of each individual species, the SDI values of spruce and fir were transformed into a comparable SDI referenced from beech following the model of Pretzsch and Biber (2016). Species proportions were logit transformed using the car package for R (Fox and Weisberg, 2011).

Since some of the experimental plots under investigation had a long time period between two consecutive observations (>20 years) we used the mean values of the stand characteristics (V , SDI) between the two observations (Assmann, 1961) instead of their values at the beginning of the period.

In addition to the location of each plot (latitude, longitude), variables representing terrain topography were derived from digital elevation models (European Union, Copernicus Land Monitoring Service, 2019) and

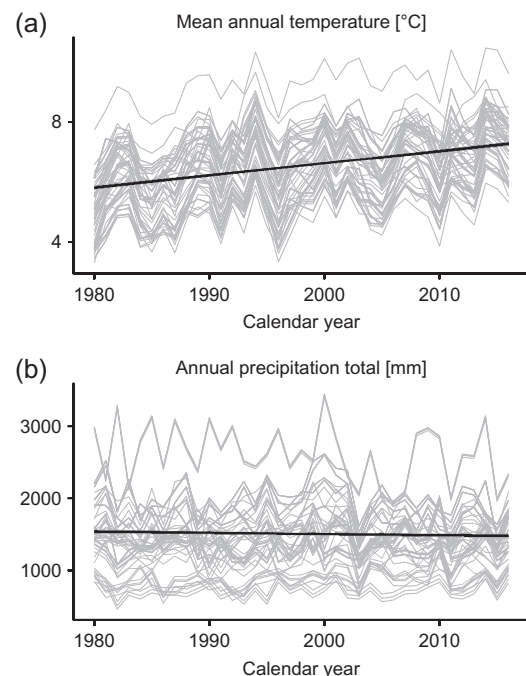


Figure 2 Mean annual temperature (a) and annual precipitation totals (b) of all 60 long-term mixed mountain forest experimental plots from 1980 to 2017. Climate data from the closest available stations to the experimental plots. For 34 out of the 60 plots an elevation correction was executed based on a lapse rate for temperature and a scaling factor for precipitation. Correction factors were defined based on 103 station measurements from Central Europe with diverse elevation levels (CRU database; Harris *et al.*, 2014). The black regression line is based on a linear model (a: estimate = 0.04, $P < 0.001$; b: estimate = -1.645 , $P = 0.06$).

consisted of slope inclination (in degrees), north index (calculated from slope orientation with $\cos(2\pi \times \text{slope orientation}/360)$, where 1 indicates a north-exposed plot, -1 indicates a south-exposed plot), and east index $\sin(2\pi \times \text{slope orientation}/360)$, where 1 indicates an east-exposed plot and -1 indicates a west-exposed slope orientation). As a measure of soil productivity we used the dominant parental material (three groups: slightly, moderately and intensively consolidated) and the available water storage capacity to a depth of 1 m (AWC) from the European Soil Database v2.0 (Panagos *et al.*, 2012).

Monthly data for mean temperature and precipitation total were collected from the closest available meteorological stations. For 34 out of the 60 plots, meteorological station based interpolated data were available. For the remaining 27 plots only station data itself were accessible and some of the stations were located further away (8.7 km on average) or at a different elevation. In order to improve the representativeness of the latter datasets, an elevation correction was used based on a lapse rate for temperature and a scaling factor for precipitation. Correction factors were defined using 103 station measurements from Central Europe with diverse elevation levels (CRU database; Harris *et al.*, 2014). Temperature and precipitation were aggregated to annual mean values (mean annual temperature and annual precipitation totals) and then again averaged for the respective recording intervals. To detect possible changes in the productivity of mixed mountain forests in Europe over the last 30 years, beyond the effect of the change in considered climate variables, we also took the calendar year into account.

Table 1 Main characteristics of the 60 investigated long-term mixed beech-fir-spruce mountain forest experimental plots from 1980 to 2010. Standard deviations are given in brackets. The respective tree species shares were calculated using transformed SDI values according to Pretzsch and Biber (2016)

	Country	Number of plots <i>N</i>	Total number of observations <i>N</i>	Number of observations per plot <i>N</i>	Elevation m a.s.l.	Mean annual temperature °C	Annual precipitation total mm	Volume m ³ ha ⁻¹	Basal area m ² ha ⁻¹	Periodic annual increment m ³ ha ⁻¹ y ⁻¹	Species share		
											Beech %	Spruce %	Fir %
mean [sd]	Bosnia and Herzegovina	5	14	2.8 [±0.45]	1185 [±113]	7.21 [±0.7]	1269 [±84]	381.5 [±72.8]	33.4 [±4.9]	9.3 [±2.1]	21.8 [±29.9]	33.2 [±19.2]	43.5 [±18.8]
min.—max.				2-3	1006-1291	6.2-8.5	1095-1387	248.8-501.0	26.6-41.2	6.0-11.9	0.2-71.6	10.7-64.9	16.3-71.4
mean [sd]	Germany	29	116	4.14 [±0.97]	984 [±186]	6.35 [±0.7]	1605 [±366]	532.5 [±206.8]	38.0 [±12.7]	8.6 [±3.0]	18.1 [±13.9]	45.0 [±15.4]	33.1 [±14.9]
min.—max.				2-6	743-1281	4.7-7.6	1109-2191	183-1178.5	9.6-73.5	3.1-15.1	0-60.8	9.6-77.5	2.6-63.9
mean [sd]	Poland	7	21	3	983 [±57]	5.5 [±0.4]	1434 [±66]	549.8 [±77.7]	39.2 [±3.4]	6.9 [±2.7]	54.9 [±15.8]	17.8 [±18.9]	27.1 [±10.3]
min.—max.				—	902-1087	4.8-6.4	1306-1550	438.8-713.7	35.4-45.7	1.5-11.0	22.0-77.4	4.7-64.2	11.3-44.9
mean [sd]	Serbia	1	2	2	1270	7.1 [±0.5]	1184 [±33]	652.5 [±91.9]	51.4 [±1.4]	13.2 [±1.0]	0.5 [±0.2]	44.5 [±1.5]	55.0 [±1.7]
min.—max.				—	—	6.8-7.5	1161-1208	587.5-717.5	50.4-52.4	12.5-13.9	0.3-0.6	43.5-45.6	53.8-56.2
mean [sd]	Slovakia	6	21	4.2 [±1.3]	775 [±45]	6.1 [±0.7]	922 [±96]	710.2 [±181.8]	43.8 [±7.4]	11.2 [±3.1]	38.7 [±16.3]	17.6 [±25.7]	42.3 [±16.7]
min.—max.				3-6	733-845	4.9-7.3	813-1200	445.1-985.2	33.9-55.7	3.1-15.6	11.0-63.4	0-62.8	14.7-69.1
mean [sd]	Slovenia	8	28	3.5 [±0.53]	1171 [±264]	5.9 [±1.2]	2247 [±513]	704.4 [±158.2]	47.2 [±7.1]	10.2 [±3.0]	47.4 [±17.7]	29.3 [±29.4]	21.6 [±19.3]
min.—max.				3-4	910-1443	4.4-7.8	1471-2818	433.5-1030.0	35.2-61.9	4.6-17.1	20.3-74.1	0-78.2	0-69.8
mean [sd]	Switzerland	4	20	5	897 [±5]	7.3 [±0.3]	1426 [±26]	404.5 [±104.4]	30.9 [±6.1]	12.3 [±2.6]	12.9 [±10.7]	27.6 [±7.4]	58.8 [±13.0]
min.—max.				—	890-899	6.9-7.7	1394-1479	215.8-721.7	18.9-49.2	6.2-15.9	5.1-41.6	11.4-36.7	22.6-74.4
mean [sd]	All	60	222	3.8 [±1.0]	995 [±201]	6.4 [±0.9]	1563 [±461]	552.7 [±198.9]	39.0 [±11.0]	9.3 [±3.2]	26.8 [±21.3]	35.5 [±21.6]	35.1 [±18]
min.—max.				2-6	733-1443	4.4-8.5	813-2818	183-1178.5	9.6-73.5	1.5-17.1	0-77.4	0-78.2	0-74.4

Modelling procedures

All analyses were performed in R 3.4.0 (R Core Team, 2018). To test the influence of the variables described above on the productivity of mixed mountain forests, we used a generalized additive mixed model (GAMM) with a Gaussian distribution using the package *mgcv* (Wood, 2011). The model included the periodic annual volume increment of the mixed forest plots as a dependent variable. By using a random factor (plot) as a grouping factor no pairs were taken into account twice. To account for potential autocorrelations, we treated plot geographical location as a two-dimensional non-linear smoother. Since climate change led to changes of the mean annual temperatures at same elevations (see Figure 2a), we also integrated the combination of elevation and mean annual temperature into the model as a two-dimensional smoother. If the term of the calendar year nevertheless remained significant, it was assumed that other factors besides the considered climate variables, such as late frost events, nitrogen inputs etc., influenced stand growth (cf. Pretzsch et al., 2014). The determination of the degrees of freedom of the nonparametric terms is part of the fitting process (Wood, 2011; Package *mgcv*; Tables S2-S4).

In order to investigate whether the productivity of the individual species (beech, spruce, and fir) has changed in recent decades, we extrapolated the species-specific stand values to one hectare. We used the species shares at the beginning of each period as a scaling factor, which we calculated from the transformed SDI values. Again, a generalized additive mixed model (GAMM) was applied by species with the scaled periodic annual volume increment as the dependent variable and a random factor (plot) was used as the grouping factor.

The model selection from the extensive models was carried out with a principal component analysis (PCA) and further supported by testing all possible mathematical models using all combinations of variables by Akaike information criterion (AIC; Barton, 2018). Explanatory variables, which were used as factors in the model, were tested for significance using the R-package *multcomp* (Hothorn et al., 2016).

Results

Trends in temperature and precipitation

When pooling the climate data of all experimental plots we found a significant positive trend of mean annual temperature over the last 30 years (Figure 2a). The analysis of the temperature development of each individual plot also showed a significant positive trend (Table S1). We found no significant trend of the annual precipitation totals in the last 30 years with the pooled dataset (Figure 2b). The detailed analyses of each experimental plot showed significant increases in precipitation only in 4 out of 60 experimental plots (Table S1).

Long term trend of productivity

The average periodic annual volume increment of mixed mountain forests in Europe amounts to $9.3 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$. The most important factors influencing stand productivity were the location of the plot (the further south the more productive), the interaction between elevation and temperature (with higher productivity at lower elevations), the consolidation of the dominant parental material (with a higher productivity on slightly consolidated parental material), and the volume of the remaining stand (positive effect; +). The calendar year had no significant influence on the periodic volume increment, indicating neither positive nor negative growth trends (Table 2, S2; Figure 3, S1).

Long term trend of species specific productivity

Beech showed growth rates of $8.2 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ over the entire investigation period with a slight, albeit not significant, increase in productivity. The most important factors influencing the volume increment of beech in mixed mountain forests were the consolidation of the dominant parental material (with highest productivity on moderately consolidated parental material) and the volume of the remaining stand (+). For beech, the model showed no significant influence of the calendar year on productivity over the last 30 years (Table 2, S3; Figure 4, S1).

At $7.2 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$, the periodic annual volume increment of fir was the lowest among the investigated tree species in the 1980s. However, the growth of fir rose significantly to $11.3 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ (+36 per cent) and was thus the most productive tree species in the mixed mountain forests of Europe at the end of the study period. On average, the annual volume increment of fir was $9.7 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ over the entire investigation period (1980–2010). For fir, we found the interaction between elevation and temperature (higher productivity with increasing mean annual temperature), the consolidation of the dominant parental material (the more consolidated the more productive), and the volume of remaining stand (+) as significant drivers of stand productivity. The calendar year had a significant positive influence on the productivity of the stands (Table 2, S4; Figure 4, S1).

At the beginning of the study period, the productivity of spruce was still about $14.2 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ and decreased to $10.8 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ (–23 per cent) in 2010. The mean periodic volume increment of spruce over the entire study period (1980–2010) in the mixed mountain forests was $11.6 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$. For spruce, the location of the plot (the more south, the more productive), the interaction of elevation and temperature (with decreasing productivity at higher elevations), the consolidation of the dominant parental material (with highest productivity on slightly consolidated parental material), and the volume of the remaining stand (+) were the most important factors influencing stand productivity. Spruce productivity declined significantly in recent decades (Table 2, S5; Figure 4, S1). However, although spruce showed a significant decline in productivity over the last 30 years, it was the most productive tree species in the triumvirate for almost the entire period under study. Therefore, a higher proportion of spruce in the stand also had a positive, albeit not significant, effect on the total productivity of the stand.

Discussion

For the first time, the productivity of mixed beech-spruce-fir mountain forests was analysed across a variety of European mountain areas in a standardized way. Our results show that despite a significant increase in annual mean temperature and stable precipitation, the average productivity of European mixed mountain forests has not changed significantly over the last decades. The studied mixed mountain forests showed constant volume growth during the last 30 years, amounting to $9.3 \text{ m}^3\text{ha}^{-1}\text{y}^{-1}$ (Q1). Thus, climate change seems to have no impact on the productivity of mixed mountain forests in Europe, at least within the time span of this study. At the tree species level, however, we found significant changes in the growth dynamics of the three species. Each species (beech, spruce, and fir) reacted to climate change in a different way. The PAI of spruce

decreased significantly while the PAI of fir increased significantly. The productivity of beech remained constant over the last 30 years (Q2). Thus, climate change has led to a shift in the competitive strength of the involved tree species. As a consequence, the proportion of tree species coexisting in the forest system has shifted in favour of beech in recent decades. After declines in the 1990s and 2000s, the proportion of fir trees has stabilized again since the 2010s (Figure S2). We found a significant influence of the interaction between elevation and temperature in the models for spruce, fir and the model of the total stand. For spruce and the total stand, productivity decreased with increasing elevation. In the case of spruce, we also observed declining productivity with warming temperature trends at higher elevations. With expected further increases in temperature, it can be assumed that the productivity of spruce at higher elevations will continue to decline. The productivity of fir increases with warming temperature trends at high elevations (Figure S1). Moreover, the calendar year had a negative effect for spruce and positive for fir, suggesting that other changing factors different than mean temperature are strengthening their productivity long term trends. PAI increases with a higher volume of the remaining stand in all cases (Tables S2–S5). This finding is in line with Pretzsch *et al.* (2015) who found a linear relationship between the volume of the remaining stand and its productivity in a study of mixed mountain forests in the Bavarian Alps.

European beech

Contrary to our expectations, results show that beech productivity did not change significantly in recent decades. Due to the warming in the last century and especially the most recent decades (Luterbacher *et al.*, 2004; Büntgen *et al.*, 2011) and the simultaneously high amount of precipitation, especially at

higher elevations (cf. Figure 2), the productivity of beech is expected to increase (cf. Aertsen *et al.*, 2014; Tegel *et al.*, 2014). Our study confirms that the productivity of beech in mixed mountain forests remained stable or increased slightly, albeit not significantly, throughout Europe between 1980 and 2010. This is consistent with published measurements (Pretzsch *et al.*, 2014; Tognetti *et al.*, 2014; Bosela *et al.*, 2016b) and model simulations (Hlásny *et al.*, 2011). On the other hand, our results contradict the study of Dittmar *et al.* (2003), who documented a decline of radial growth of beech at higher elevations at Central European scale, and Bosela *et al.* (2018) who, corresponding to a significant warming trend from 1990–2010, found an average decline in beech growth in Continental Europe over the last three decades. However, as trends in productivity on the stand level also depend on stand structure (e.g. density and size distribution) it is not possible to infer the stand level productivity trends from tree level trends.

Nevertheless, beech faces challenging environmental changes, especially in mountainous areas. Environmental changes in the Alpine regions are mainly characterized by acid and nitrogen deposits, and O₃ pollution (Brang, 1998; Flückiger and Braun, 1999; Smidt and Herman, 2004). Muzika *et al.* (2004), for example, found significant negative correlations between air pollutants (O₃, NO₂ and SO₂) and the growth of beech and spruce in the Carpathian Mountains. In addition, there are natural influences due to climate change such as late frost events and drought stress (Dittmar *et al.*, 2003; Jump *et al.*, 2006; Bontemps *et al.*, 2009), as well as biotic diseases, such as fungal infestation (Cherubini *et al.*, 2002). Furthermore, Dittmar and Elling (2007) found increasing crown transparency and reduced vitality in recent years based on long-term crown condition surveys of beech trees in mixed mountain forests of the Bavarian Alps. Although beech was exposed to these negative effects on tree growth, its productivity has remained unchanged in recent decades (Figure 4; Table 2). We assume, therefore, that the positive

Table 2 Estimated coefficients with standard error and p-values for the four final models for beech, spruce, fir, and beech-spruce-fir in mixture. Empty cells denote variables that are not included in the models because they were excluded from the model selection. Note that the proportion values of the respective tree species were logit transformed using the package car (Fox and Weisberg, 2011)

Variable	Beech		Spruce		Fir		Beech-Spruce-Fir	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
s(Latitude, Longitude)		0.446		< 0.001		0.521		0.272
s(Elevation, Temperature)		0.11		< 0.001		0.021		0.028
Precipitation								
Slope								
North exposition								
East exposition								
Available water capacity								
Dominant parental material		< 0.001		< 0.001		< 0.001		0.532
Volume	0.006 ± 0.002	0.006	0.007 ± 0.001	< 0.001	0.006 ± 0.001	< 0.001	0.006 ± 0.001	< 0.001
Calendar year	0.042 ± 0.038	0.265	−0.087 ± 0.039	0.026	0.064 ± 0.029	0.029	0.013 ± 0.023	0.574
Proportion beech							−0.445 ± 0.387	0.252
Proportion spruce							0.559 ± 0.517	0.281
Proportion fir							−0.658 ± 0.523	0.209
R ²	0.327		0.623		0.316		0.526	
RMSE	2.751		3.004		3.545		2.113	

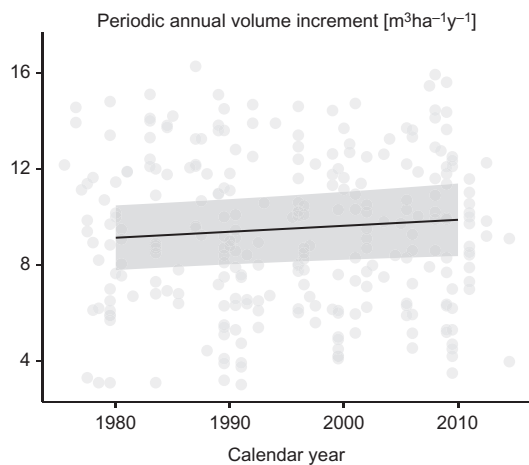


Figure 3 Periodic annual volume increment of the investigated long-term experimental plots of beech, spruce, and fir over the calendar year. The annual volume increment was predicted using a generalized additive mixed model (GAMM) with a random factor (plot) as the grouping variable. Predictor variables were the volume of the remaining stand, the interaction between latitude and longitude, the interaction between elevation and mean annual temperature, the dominant parental material, and the species proportions of the three tree species involved, beech, spruce, and fir. For the predictions, the prediction variables were kept constant at the mean value. The grey area indicates the standard error.

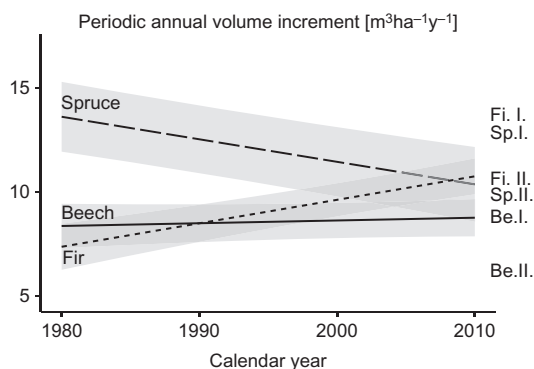


Figure 4 Periodic annual volume increment over the calendar year of the tree species beech, spruce, and fir in the long-term experimental forest plots. The periodic annual volume increment of the three tree species was scaled using the species share derived from SDI proportions. Estimation was done using a generalized additive mixed model (GAMM) with a random factor (plot) as the grouping variable. See table 2 for the predictor variables. For the prediction, the predictor variables were kept constant at the mean value. The grey area indicates the standard error. Stars show the mean annual volume increment of the first (I.) and second (II.) yield classes of the three tree species spruce (Sp.), fir (Fi.) and beech (Be.) at age 100 according to the yield tables of Hausser (1956), von Guttenberg (1915) and Wiedemann (1949).

effect of a warmer, but not drier, climate and the negative effects of substance discharges on beech growth, have so far compensated each other. Tognetti *et al.* (2014) did not observe an influence of marked drought periods on basal area increment in beech during the twentieth century; in the absence of climatic

stress, predictions that follow increasing atmospheric CO₂ concentration effects over water use efficiency, together with rising temperature and related factors (e.g. length of growing season), would increase or stabilize productivity in healthy trees.

Silver fir

Fir exhibited accelerating growth rates during the last few years. This is remarkable, as fir experienced a strong decline in growth across Europe caused by sulphur dioxide emissions in the years 1970–1990 (Diaci *et al.*, 2011; Uhl *et al.*, 2013; Büntgen *et al.*, 2014; Čavlović *et al.*, 2015) or low summer temperatures in the 1960s and 1970s (Bosela *et al.*, 2018, 2016a). Our study might provide additional evidence for this event, as the productivity of fir was the lowest among the analysed tree species at the beginning of the study period. Efforts to reduce emissions since the 1980s, combined with a warmer, but not drier, climate (cf. Figure 2; Diaci *et al.*, 2011; Uhl *et al.*, 2013; Büntgen *et al.*, 2014), have probably enabled the significant increase in fir productivity (Figure 4). These results are in line with studies by Bosela *et al.* (2018) and Büntgen *et al.* (2014), who also demonstrated an unprecedented increase in productivity in Central Europe's fir stands. However, a recent Europe-wide study on the growth of fir throughout the Holocene (Büntgen *et al.*, 2014) describes increasing radial growth in the Italian Alps and the Apennines until the turn of the millennium, but not beyond. Bosela *et al.* (2018) showed that fir populations in the southern parts of the Alps may have recently experienced growth limitation due to drought. Seemingly, fir populations close to the Mediterranean distribution limit already show a drought-induced growth depression, which will become even more critical in a warmer and drier future. However, there are indications that the sensitivity of fir to drought stress decreases when mixed with beech (Lebourgeois *et al.*, 2013; Metz *et al.*, 2016; Vitali *et al.*, 2017) or when the genetic diversity is high (Gazol and Camarero, 2016).

Norway spruce

As shown in the present and previous studies (e.g. Schöpfer *et al.*, 1997; Uhl *et al.*, 2013), the growth relation of spruce and fir in mixed mountain forests has changed significantly in recent decades (Figure 4). These results illustrate the importance of external factors on the competitive relationships between species and thus on their growth dynamics. With regard to resistance to emissions, spruce is mostly classified as particularly resistant, beech as less resistant, and fir as particularly sensitive (Rohmeder and von Schönborn, 1965). This may explain the superior productivity of spruce compared to fir in the 1980s. In the meantime, however, the reduction of the emission load and the recovery of fir have led to a direct improvement in fir's fitness and thus also an indirect improvement in the competitive relationship with spruce and beech (Elling *et al.*, 2009; Uhl *et al.*, 2013; Büntgen *et al.*, 2014; Bosela *et al.*, 2018). While the high PAI of spruce (Figure 4) in the 1980s was presumably favoured by the growing depression of fir (by allocating more resources to spruce in mixed stands that were previously available to fir), the recovery of fir is highly likely to have an effect on spruce's growth behaviour. Spruce is—without human intervention—

pushed back into its real niche by the resurgence of fir, which it held before the beginning of the emission load and weakening of fir (Uhl *et al.*, 2013). A further explanation for the significant decrease in spruce productivity at the stand level (Figure 4, Table 2) is the vulnerability of spruce to increasing summer droughts (Lévesque *et al.*, 2013; Zang *et al.*, 2014).

Effects of mixing

A number of recent studies show that species diversity has a positive effect on volume growth (Zhang *et al.*, 2012; Toïgo *et al.*, 2015). A higher number of species is also expected to mitigate the negative effects of extreme climatic events through higher growth resistance and resilience (Jucker *et al.*, 2014; Gazol and Camarero, 2016; Metz *et al.*, 2016). Although our study cannot directly estimate the benefit of mixed stands of beech, spruce, and fir in higher elevations, there are indications that the three tree species in mixed stands show no lower growth rates than monospecific pure stands. Thus, comparisons of the values from our study with the mean annual volume increment of the three tree species at age 100 from the yield tables for pure stands of Hausser (1956), von Guttenberg (1915), and Wiedemann (1949) show that beech and spruce are on average between the first and second yield class. However, due to the growth depressions at the end of the 20th century, the average PAI of fir is lower than the second yield class of the respective yield table. Other authors show significant increases in this mixture compared to monocultures. Pretzsch and Forrester (2017), for example, showed an average increase of 20 per cent in the productivity of mixed mountain forests compared to neighbouring pure stands. Mina *et al.* (2018) found that beech trees in temperate European mixed mountain forests generally benefit from the admixture of spruce and fir. Further studies on the mixing of at least two of the three species show, depending on site quality, clear increases in mixed stands of spruce and fir (Forrester *et al.*, 2013; Forrester and Albrecht, 2014) or beech and spruce (Pretzsch *et al.*, 2010) compared to monospecific pure stands.

Nevertheless, our results clearly indicate that growth in a mixture does not shield the three species from the effects of long-term changes in environmental conditions. For example, we show that the PAI of spruce has declined significantly over the last three decades under a number of conditions in Europe (Figure 4). At the stand level, however, Europe's mixed mountain forests appear to be stable (Figure 3; Table 2) and it is possible to achieve risk diversification by mixing the three tree species. These results are in line with the results of Hartl-Meier *et al.* (2014a, 2014b), who in their study on mixed mountain forests in the Northern Limestone Alps and the Berchtesgaden Alps come to the conclusion that mixed mountain forests can adapt well to temperature increases caused by climate change and that there may be no change in tree species composition.

Contribution of mixed mountain forests to ecosystem services

Our results show how productive mixed mountain forests are in Europe and that they have not yet experienced productivity declines under the conditions of climate change. With reference

to FOREST EUROPE's six overarching criteria for sustainable forest management, we can state that mixed mountain forests in Europe make a significant contribution to the conservation of forest resources and to securing their contribution to the global carbon cycle (C sequestration), especially since large parts of European forests are located in mountain areas (CIPRA, 2007). In addition to this fact, mixed mountain forests can also make a significant contribution to maintaining the production function of European forests. In the past, parts of our investigated forests were thinned, albeit only slightly, and were able to maintain their productivity (production function) despite management.

However, in the face of climate change and in order to fulfil the Paris climate agreement (UNFCCC, 2015), there is currently a high pressure on these forests. In order to meet these challenges, it is particularly important to develop strategies to enhance the adaptation (resilience) and mitigation potential of these forests in the future. One example is the management guideline for mountain forests of the Bavarian State Forests AöR (Bayerische Staatsforsten AöR, 2018). Nevertheless, considering different stand and site conditions, and also regional and elevation dependent magnitude of climate change, management options for mixed mountain forests to fulfil future ecosystem services should be regionally adopted at the local scale (Mina *et al.*, 2017).

Conclusion

According to our results, European mixed mountain forests have so far been stable in terms of volume growth in relation to climate change. The reduction of volume increment of one species was compensated by higher volume increments of another species. Although they grow under the same conditions, spruce and fir have shown remarkably different growth patterns over the last 30 years. While fir has responded positively to recent warming, spruce productivity has declined significantly, suggesting that at constant rainfall, fir is less susceptible to warmer conditions than spruce. There is some support for the use of mixed forests as a strategy for adapting to climate change. We show that a more diverse tree species composition can help to compensate to some extent for the effects of climatic and anthropogenic changes. The productivity of the tree species involved in this forest system is subject to constant fluctuations. In order to maintain a stable system prepared for future changes a balanced mix of the three tree species is recommended. Even if maintaining regeneration and a good share of spruce, especially in the application of selective forestry, will be more difficult in the future. Our results indicate that it is possible to develop a sustainable forest management system to maintain the resilience of the forests and thus ensure the continuous provision of ecosystem goods from mixed mountain forests and at the same time minimize the effects of climate-induced changes on mixed mountain forests.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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