Contrasting effects of environmental change factors on the radial growth of co-occurring European beech and fir trees across Europe

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Contrasting effects of environmental change on the radial growth of co-occurring beech and fir trees across Europe

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HIGHLIGHTS

- European fir and beech growth accelerated during the last century.
- Beech growth declined in northern Europe since 2000.
- Fir growth rates increased over most of Europe since 1980.
- Growth-climate responses were similar for most tree social classes.
- Climate sensitivity of both species was not affected by forest management.

GRAPHICAL ABSTRACT
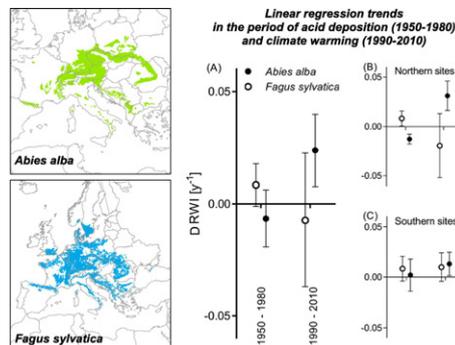
ARTICLE INFO

ABSTRACT

Under predicted climate change, native silver fir (*Abies alba*) and European beech (*Fagus sylvatica*) are the most likely replacement species for the Norway spruce (*Picea abies*) monocultures planted across large parts of continental Europe. Our current understanding of the adaptation potential of fir-beech mixed forests to climate change is limited because long-term responses of the two species to environmental changes have not yet been comprehensively quantified. We compiled and analysed tree-ring width (TRW) series from 2855 dominant, co-dominant, sub-dominant and suppressed fir and beech trees sampled in 17 managed and unmanaged mixed beech-fir forest sites across Continental Europe, including Bosnia and Herzegovina, Germany, Italy,

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Romania and Slovakia. Dendroecological techniques that combine various detrending methods were used to investigate variation in radial growth of co-occurring fir and beech trees. Coincidental with peak SO_2 emissions, the growth of silver fir declined between 1950 and 1980 at most sites, whereas beech growth increased during this period. Correspondent to a significant warming trend from 1990–2010, average beech growth declined, but silver fir growth increased. Long-term growth patterns and growth-climate sensitivity of fir and beech trees did not significantly differ between managed and unmanaged forests. Multi-decadal changes in the growth rate of all vertical tree classes were similar. In contrast to previous indications of limited drought susceptibility of beech mixed stands, this study suggests that the mixture of tree species in forest stands does not necessarily prevent growth depressions induced by long-term environmental change. Our results further imply that forest management does not necessarily alter their sensitivity to environmental changes.

1. Introduction

Beech (*Fagus sylvatica* L.) is Europe's most abundant forest species (Ellenberg, 1996). Naturally distributed across most of continental Europe, it either grows in pure broad leaved forests or in mixtures with conifer species. Beech has been increasingly used to convert conifer monocultures to mixed stands, reflecting the current transition of forest management strategies to accommodate non-productive forest functions and adapt to climate change (Knoke et al., 2008; Tarp et al., 2000). Silver fir (*Abies alba* Mill.) is a coniferous species native to Europe, with a geographical distribution similar to that of beech, but largely limited to the Alpine and the Carpathian arcs. There are indications that silver fir might be more suitable to future European climate as it grew well under warmer-than-present conditions during the mid-Holocene (Tinner et al., 2013; Ruosch et al., 2016). Today, mixed fir-beech forests represent an important forest ecosystem forming an essential part of central and south-eastern European landscapes (EEA, 2006).

Since the mid-19th century or even earlier, a large proportion of European beech-fir forests was converted to conifer monocultures of Norway spruce (*Picea abies* L. Karst.) (Spiecker et al., 2004). However, considerable areas of Norway spruce forests in central Europe suffered from acid deposition during the second half of the 20th century (Ulrich, 1995). Today, in many locations it is clear that Norway spruce is becoming increasingly susceptible to the more frequent summer droughts induced by climate change (Lévesque et al., 2013; Zang et al., 2014), as well as the devastating effects of severe windstorms and subsequent bark beetle outbreaks (Hlásny and Turčáni, 2013; Jönsson et al., 2009). Therefore, the introduction of appropriate replacement species, such as beech and fir, has become a key task (IPCC, 2014).

Despite recent publications describing the growth of silver fir and European beech (Bosela et al., 2016b; Büntgen et al., 2014; Cavin and Jump, 2016; Dittmar et al., 2003; Gazol et al., 2015; Pretzsch et al., 2014), relatively little is known about how these species react to environmental changes when growing in mixed stands (Vitali et al., 2017). Recent evidence shows that beech (Bosela et al., 2015), but also fir to some extent (Toïgo et al., 2015), may reach higher stem growth productivity in mixed stands. There are suggestions that growth sensitivity of silver fir and European beech to summer droughts decreases when growing in mixed stands (Lebourgeois et al., 2013; Metz et al., 2016; Vitali et al., 2017), but this has neither been tested nor confirmed under varying natural conditions across different parts of Europe. A higher diversity of tree species has been shown to potentially stimulate radial stem growth by better niche utilisation, but also via improved resistance and resilience at a forest ecosystem level (Gazol et al., 2016; Jucker et al., 2014; Metz et al., 2016; Paquette and Messier, 2011; Ruiz-Benito et al., 2014; Vitali et al., 2017). Nevertheless, we still lack unequivocal evidence supporting the notion that growing in mixed stands mitigates some of the negative long-term effects of rising temperatures, often associated with increased frequency and/or severity of droughts. A detailed understanding of the relationship between diversity and ecosystem productivity and stability is indeed crucial for advising the policy-forming processes at national and international levels.

To further complicate the picture, most dendroecological data that describe growth-climate relationships in European forests originate from western Europe and tend to consider only dominant and co-dominant trees (Büntgen et al., 2014; Cavin and Jump, 2016; Nehrbass-Ahles et al., 2014; Pretzsch et al., 2014). Yet, it is possible that populations of the same species inhabiting the eastern part of their distributional range possess different sensitivity levels to environmental factors due to genetic variation (Bosela et al., 2016a).

A Europe-wide investigation of species-specific growth dynamics in mixed forest stands affected by contrasting environmental factors is so far lacking. To fill this gap, we compiled a database of tree-ring width (TRW) samples from managed and unmanaged European mixed beech-fir forests covering most of the regions where these two species co-occur. Our aim was to test the following hypotheses: (H1) do radial growth patterns of beech and fir in mixed forests vary geographically, (H2) does tree status within the canopy or (H3) forest management interventions affect long-term variation in annual growth, and finally (H4) was the growth behaviour of co-occurring beech and fir similarly affected by the 1970–1990 period of heavy pollution and the warming during recent decades?

2. Material and methods

2.1. Tree-ring sampling

A network of 17 beech-fir mixed forest stands located in five European countries was used to compile 2855 core samples (Fig. 1). Taking in Slovakia, Romania, Bosnia & Herzegovina, Italy and Germany, the network covers a large part of Europe's natural distribution range of mixed beech-fir forests. The sites were allocated to 8 regional groups, reflecting differences in post-glacial recolonization from different forest refugia, but also current climatic conditions (Tables 1 and S1). The following selection criteria were followed at all sites to ensure reasonable comparability of observations: 1) growing conditions were characterised by mesic soils and mean annual precipitation in excess of 800 mm year^{-1}, 2) no forest management interventions were carried out for at least 30 years prior to sampling, 3) specimens of both species were present in all four social classes, as described by Oliver & Larson (1996; dominant, co-dominant, sub-dominant and suppressed), 4) all trees above a registration threshold within a fixed-area plot were marked and then either all or a randomly selected subset were cored. A single location in Slovakia where managed beech-fir stands are found in close vicinity to unmanaged stands was used to investigate the impact of forest management on growth-climate sensitivity.
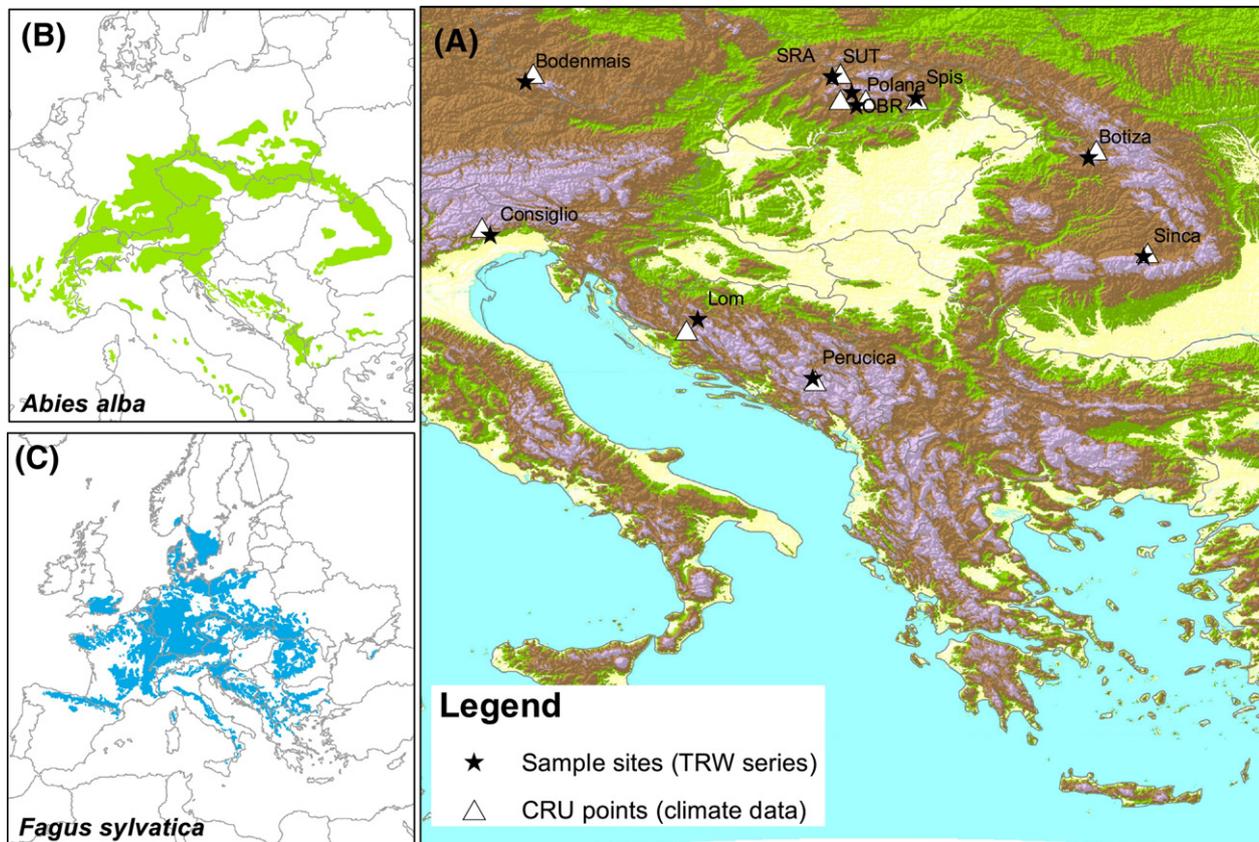
Fig. 1. a) Sampling sites used in the study, with corresponding Climate Research Unit (CRU) climate data points; b) current distribution of *Abies alba* and c) current distribution of *Fagus sylvatica*. (Source: EUFORGEN).

2.2. Tree-ring standardisation

Four standardisation techniques were applied to remove age-related trends from raw TRW measurements, all aim to preserve the effects of environmental signals at inter-annual to multi-decadal timescales. The following detrending methods were used and compared in this study;

a) Modified Exponential Function (MEF, Fritts, 2001). The MEF method was first applied to individual tree TRW series, followed by the calculation of ring-width indices (RWI) defined as the ratio between raw measurements and corresponding MEF function values. Mean RWI chronologies for each site were calculated as bi-weight robust means of all individual tree series (Cook and Kairiukstis, 2013)

b) cubic Smoothing Spline with 50% frequency response cut-off at 100 years (SS; Cook, 1985). This setting was used to preserve the inter-annual to multi-decadal growth fluctuations (Büntgen et al., 2008). The SS standardisation was applied in the same manner as the MEF approach, the only variation was the use of a different function.

c) Regional Curve Standardisation (RCS; Briffa and Melvin, 2011). RCS detrending was applied to individual tree data, but only after the exclusion of all partial-length TRW series where it was not possible to estimate the number of rings from the beginning of the core to the pith (Table 1). For example, this includes data series where the beginning of the core was too far from the pith and no ring arc was visible (Briffa and Melvin, 2011). Raw TRW series were aligned by cambial age (ring number from bark to pith), followed by mean TRW calculation for each series. A smoothing spline with a 50% frequency response cut-off at 10% maximum cambial age curve wavelength (i.e. the Regional Curve (RC)) was then fitted to mean TRW series. RWIs were calculated as ratios between individual series and the smoothed RC. Individual RWI series were re-aligned by

calendar dates. The final site chronology was then developed by using bi-weight robust means.

d) Korf growth function (Korf; Korf, 1939). Multi-decadal growth changes may be underestimated by common detrending methods in even-aged forests (Briffa and Melvin, 2011). To counter this tendency we applied a growth function developed by Korf (1939). Raw TRW series were aligned by age and the mean curve was calculated. Then, in contrast to the RCS method, regression parameters of the Korf function were estimated from the first 50 years of the mean curve only. An extrapolation to the full length of the curve was then carried out, assuming that the first 50 years indicate both growth culmination and decline. RWI series at each site were then calculated as the ratio between raw TRW and estimated Korf's function. Bi-weight robust mean was used to develop a mean site chronology as in previous methods, and Korf standardisation was used only on sites where growth culmination was clearly visible.

Most dendrochronological studies report site chronologies developed from data describing the dominant trees only (Nehrbass-Ahles et al., 2014), an approach which may not capture the growth history of the whole stand. To shed light on this issue, at each site we developed a mean site chronology for both species from a sample of the 15 largest trees only (hereafter "dominant trees") and compared it to that covering all measured individuals.

2.3. Growth variability and sensitivity assessments

Growth trends describing several predefined periods were compared to identify effects of known environmental factors. The predefined periods, such as the decades characterised by heavy air

Table 1

Brief description of site location, total number of tree-ring width series used per site (N1) and the number of tree-ring width series that intercepted the pith or were sufficiently close to estimate the number of rings to the ptith (N2). Time span is the minimum and maximum calendar year of the site chronology. B&H denotes Bosnia and Herzegovina, Alt denotes altitude in m a.s.l.

Country	Species	Locality (abr.)	N1	N2	Time span	Mountain range	Long	Lat	Alt
B & H	Abies	Lom	158	158	1583–2005	Western Dinaric Mts	16.47	44.45	1350
B & H	Fagus	(bh_lom)	440	440	1625–2005				
B & H	Abies	Perucica b1	44	43	1786–2006	Eastern Dinaric Mts	18.71	43.3	1200
B & H	Fagus	(bh_perb1)	81	75	1595–2006				
B & H	Abies	Perucica b2	76	69	1663–2007				
B & H	Fagus	(bh_perb2)	70	63	1509–2007				
B & H	Abies	Perucica f1	118	109	1686–2006				
B & H	Fagus	(bh_perf1)	35	27	1614–2006				
B & H	Abies	Perucica f2	82	71	1702–2007				
B & H	Fagus	(bh_perf2)	64	60	1703–2007				
Germany	Abies	Bodenmais	28	–	1820–1995	Bavarian Forest	13.1	49.09	800
Germany	Fagus	(de)	21	–	1821–1995				
Italy	Abies	Cansiglio	140	140	1931–2012	Southern Alps	12.42	46.1	1100
Italy	Fagus	(it)	205	184	1856–2012				
Romania	Abies	Botiza	54	25	1774–2013	Eastern Carpathians	24.09	47.61	1050
Romania	Fagus	(ro_bo)	67	23	1614–2013				
Romania	Abies	Sinca	281	184	1665–2013	Southern Carpathians	25.17	45.67	1140
Romania	Fagus	(ro_si)	163	101	1556–2013				
Slovakia	Abies	Polana	22	22	1860–2010	Western Carpathians	19.57	48.62	760
Slovakia	Fagus	(sk_p)	58	58	1867–2010				
Slovakia	Abies	Spis S1	20	20	1896–2010		20.73	48.77	760
Slovakia	Fagus	(sk_s1)	19	19	1881–2010				
Slovakia	Abies	Spis S2	36	36	1794–2010		20.73	48.77	760
Slovakia	Fagus	(sk_s2)	33	33	1811–2010				
Slovakia	Abies	Spis S3	59	59	1820–2011		20.67	48.79	760
Slovakia	Fagus	(sk_s3)	14	14	1821–2011				
Slovakia	Abies	Spis S4	24	24	1848–2010		20.72	48.76	830
Slovakia	Fagus	(sk_s4)	26	26	1898–2010				
Slovakia	Abies	OBR	25	21	1805–2013	Western Carpathians	19.47	48.88	887
Slovakia	Fagus	(sk_obr)	146	120	1740–2014				
Slovakia	Abies	SRA	57	57	1783–2013		19.11	49.19	1048
Slovakia	Fagus	(sk_sra)	133	133	1717–2013				
Slovakia	Abies	SUT	29	28	1814–2013		19.09	49.18	1029
Slovakia	Fagus	(sk_sut)	27	24	1761–2013				

pollution in Europe (1950–1990) and the unprecedented climate warming (1980–2000, resp. 1990–2010), were selected on the basis of published descriptions of major environmental issues and trends (Bosela et al., 2016a, 2016b; Büntgen et al., 2014; Gazol et al., 2015; Jump et al., 2006; Linares and Camarero, 2012). Simple linear regression was used to describe growth trends within selected periods; regression coefficients denoting the slope were then used to compare tree growth between the periods and between regional groups of sites. In this comparison, we applied generalized additive models using "gamm" function in "mgcv" R package (Wood, 2011) to filter out inter-annual high frequency variation and preserve multi-decadal growth trends. The "gamm" function used Generalized Cross Validation (GCV) to estimate the smoothing parameter. Populations of regression parameters describing individual site RWI series were assessed for differences between species, regional groups, time periods and detrending methods by ANOVA. All populations were tested for normality of distribution and equality of variance; no conversion of data was necessary. Bonferroni correction was used in pair-wise comparisons, and differences were considered significant at $p < 0.05$.

Monthly temperature means, precipitation totals and drought indices (scPDSI – self-calibrated Palmer Drought Severity Index) were obtained from gridded CRU TS 3.10 database (http://www.cru.uea.ac.uk/data/) via Climate Explorer (http://climexp.knmi.nl/) (Dai, 2011; Harris et al., 2014; Mitchell and Jones, 2005). Data from half-degree lat/lon grid points nearest to each study site were used to analyse the relationship between growth of both species and climate variation at each site (Fig. 1). Radial growth responses to climate (standardised mean chronologies) were quantified by Pearson's correlation coefficients computed over 31-yr moving window segments to investigate temporal changes in the climate-growth relationships (Büntgen et al., 2010; Wilson and Elling, 2004). Bootstrapping was applied to calculate 95%

confidence intervals of the correlation coefficients using the 'bootRes' R package (Zang and Biondi, 2013). The significance of the correlation was then tested using 95% percentile range method (Dixon, 2002).

Correlation coefficients describing the relationship between site chronologies and climate variables were analysed by principal component analysis (PCA). PCA was performed with the "hclust" function in the R Stats package (R Development Core Team, 2008). The distance matrix was computed using the Euclidian measure. The "dendextent" package (Galili, 2015) was used to visualise PCA results. Ward Hierarchical Clustering was used to interpret growth trend responses to climate. Findings from the Ward clustering were then compared with PCA grouping in a 2-dimmensional space.

3. Results

Regional growth trends identified by the four detrending methods applied in this study show a wide variation of growth between sites, species and time periods across Europe (Fig. 2), yet a certain amount of generalisation is possible (Table 2). Beech growth accelerated between the 1950s and 1980s in the more 'northern' forests, loosely defined as those above 47°N parallel. Growth acceleration in the north was followed by a slow decline in annual ring width, with the exception of the Bavarian forest where beech growth accelerated continuously since about the 1940s (Fig. 2, Table 2).

At the 'southern' sites, mid-century acceleration has slowed down or even decreased. At the Cansiglio site in northern Italy, we observed the earliest onset of this decline starting in the 1950s. While forming the same forest stands in a mixture with beech, fir has shown very different growth patterns during the last century (H1). A decline of fir growth rate was observed between the1950s and 1980s in most locations apart from the populations in the southern Carpathians, which
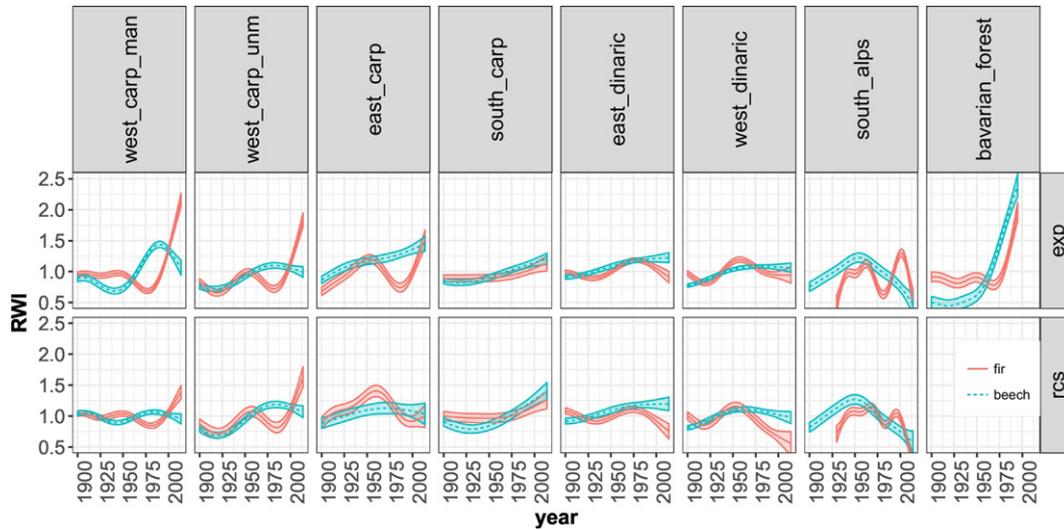
Fig. 2. Mean ring-width index (RWI) chronologies of silver fir and European beech after modified exponential (exp) and Regional Curve Standardisation (RCS) techniques for aggregate sites (west_carp_man: managed stands in western Carpathians, west_carp_unm – unmanaged forests in western Carpathians, east_carp: eastern Carpathians, south_carp: southern Carpathians, east_dinaric: eastern Dinaric, west_dinaric, south_alps: southern Alps, Bavarian Forest). Generalized Additive Model (GAM) was applied to filter out the inter-annual variation and preserve multi-decadal changes. The shaded bands denote 95% confidence intervals.

exhibited a slight acceleration of growth during this period (Fig. 2). This period of fir decline was followed by a rapid acceleration of growth in the 'north', and a steep decline in the 'south', again with the exception of the southern Carpathians.

A comparison of growth trends created from dominant trees only or all trees above a DBH threshold (H2) did not show any effect of canopy position (Fig. S5). Regression parameters denoting the slope of the fit were not affected by tree social status in any of the time periods under consideration, nor for beech (p = 0.128 to 0.516) or fir (p = 0.336 to 0.990). Similarly, we did not find any difference in annual growth between managed stands and old-growth unmanaged forests in the western Carpathians when comparing mean RWI growth trends

within each of the time periods under consideration (H3, p = 0.063 to 0.441), indicating that factors other than forest management affect long-term growth trends in beech and fir. We made use of the pre-defined periods of environmental stress to explore whether beech and fir respond differentially to acid deposition (1950–1980) and accelerating climate change (1990–2010). We found a strong interaction between species and time period (H4; p < 0.001) when comparing mean growth rates in these two periods. Considering all sites used in this study (Fig. 3a), fir RWI y^{-1} was smaller than that of beech in the period 1950–1980 but the growth trends of these two species reversed by 1990–2010. An interesting observation emerged when considering the more northern and southern sites separately; the relationship between

Table 2
A comparison of detrending methods applied to tree-ring width data describing radial growth of European beech (*Fagus sylvatica*) and Silver fir (*Abies alba*) in two time periods characterised by different environmental conditions. Linear regression was fitted to data detrended by Modified exponential function (MEF), smoothing spline (SS), regional curve standardisation (RCS) and Korf growth function (Korf). Coloured cell backgrounds denote a negative regression trend. Stars denote significance level of regression fit at: *** - <0.001, ** - <0.01, * - <0.05. Empty cells represent a non-significant fit, and a dash is used in cases where regression was not possible to fit.

Locality	European beech								Silver fir							
	MEF		SS		RCS		Korf		MEF		SS		RCS		Korf	
	1950-80	1990-10	1950-80	1990-10	1950-80	1990-10	1950-80	1990-10	1950-80	1990-10	1950-80	1990-10	1950-80	1990-10	1950-80	1990-10
de	***	-		-	-	-	-	-	*	-	***	-	-	-	-	-
sk_p	***		**			***			***	***	***		***		***	***
sk_s1	***	**		**			*	*	***	***	***	***	**		***	***
sk_s2	***	***	***	***		***	***	***	***	***	***	***	***	***	**	***
sk_s3	***		***	*	***		***	*		***	***	***	***	***		***
sk_s4	***	**	**	**			***		***	***	***	***			***	***
sk_obr	***	***		**		**				***	**	***		***		***
sk_sra	***		*		***		-	-	**	***	***	***	**	***	**	***
sk_sut	*	*		**	**	**		-	***	***	***	***	**	***	***	***
ro_bo		*			**		-	-	***	***	***	***				***
ro_si	*		**	*	*	***			*	**	***	**	**		**	

environmental factors and the rate of radial growth was not affected by species in the south (p = 0.359; Fig. 3c), but there was a strong effect in the north (p < 0.001, Fig. 3b). There was no difference between the trends identified by the four standardisation methods in 1950–80 (p = 0.249) and only the Korf standardisation method differed from the other three in 1990–2010 (p = 0.004).

Differential response of fir and beech growth to environmental change was confirmed by a PCA testing as well as by a cluster analysis for the strength of relationship between previous- and current-year temperature, precipitation and PDSI and tree growth (Fig. 4). Fir growth at the southern sites was mainly influenced by drought (scPDSI), whereas temperature was the most dominant driver of tree ring width at the northern sites. There was considerable variation between individual sites in observed effects of climate on fir and beech growth, however a very similar grouping of tree populations and sites was achieved by cluster analysis (Fig. 5).

In a further attempt to contrast the growth behaviour of the two species within the sampled range of sites, we calculated correlation coefficients between RWI and current-year summer temperature and drought over the century-long time period (Fig. 6). Fig. S6 shows a large temporal variation of correlation coefficients over the past century. On average, a negative correlation between RWI and drought dominates in the south, while a positive correlation with temperature is present in the north.

4. Discussion

4.1. European beech

Published literature describing the dendroecology of European beech at European and regional scales does not paint a clear picture; there is evidence of (i) either increased or decreased growth rates of beech in the last two decades in Central Europe (Dittmar et al., 2003; Pretzsch et al., 2014), and (ii) either increased or decreased radial growth of beech at the southern edge of distribution (Jump et al., 2006; Tegel et al., 2014). Our study confirms that beech growth rates have increased during the period between 1950 and 1980 across
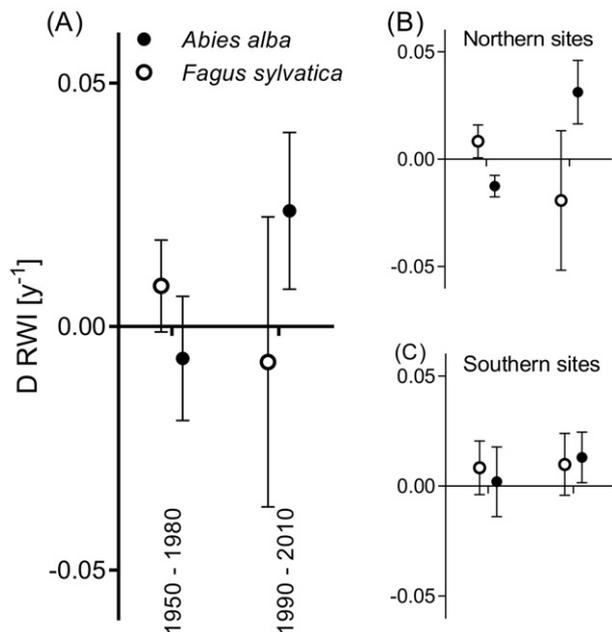
Europe, an observation which is in line with published measurements (Bosela et al., 2016b; Hlásny et al., 2011; Pretzsch et al., 2014) and model simulations (Hlásny et al., 2011). However, our results contradict those of Dittmar et al. (2003), who in a Europe-wide study found no detectable increase of beech growth in Europe, but documented a decline of the rate of growth at high altitudes in central Europe. Interestingly, the authors found that high summer temperatures favoured radial growth at the expense of vertical growth. Existing studies and observations presented in this paper suggest a positive effect of increasing summer temperature at higher latitudes or altitudes on beech growth. Thus, given the summer period warming observed in the last century (Büntgen et al., 2011; Luterbacher, 2004) and predicted warming across Europe (IPCC), it seems reasonable to expect further acceleration of beech growth at the northern edge of its distribution. A recent Europe-wide study documents an increased basal area increment in the last decades in beech forests in temperate and continental core regions of the species distribution range (Cavin and Jump, 2016). Our study adds evidence suggesting that the growth decline in the southern localities started in mid-20th century and continues until today. However, a recent increase in beech radial increments in some Mediterranean beech-fir forests (Tegel et al., 2014) suggests strong regional differences, probably related to regional climate or site productivity (Aertsen et al., 2014; Bosela et al., 2016b), which limit any broad extrapolation of our results.

Hacket-Pain et al. (2016) found no clear spatial pattern in the drought sensitivity of European beech, indicating that the populations from the southern and northern range edges respond to summer drought equally. In contrast, we found a strong spatial pattern in the growth responses to summer temperature and to drought. While radial growth of the species generally did not respond to summer drought in central Europe (Germany, Slovakia and Romania), it became highly responsive in the Balkan Peninsula (Bosnia & Herzegovina, except for the Lom site). Our study thus supports existing observations showing that some southern European beech populations are increasingly suffering from summer drought (Linares and Camarero, 2012; Piovesan et al., 2008). Not only can we confirm the same trends, but we are also able to pinpoint the onset and the severity of the decline allowing for investigation of site-specific reasons for growth modification. For example, unlike beech trees in Perucica, which were sensitive to drought, the population in the Lom site in the same climatic zone was non-responsive to sc-PDSI. Trees at the Lom site were substantially younger than those at Perucica (Fig. S1), growth plasticity of a younger population of beech might thus explain the difference – as outlined by the age-related climate response hypothesis (Carrer and Urbinati, 2004; Primicia et al., 2015).

4.2. Silver fir

Silver fir experienced a severe growth decline in Europe during 1970–1990, driven by sulphur dioxide emissions (Büntgen et al., 2014), an event often referred to as Europe-wide fir dieback (Cramer, 1984; Larsen, 1986; Meyer, 1957). Our study provides tree-ring width evidence of this event; however, it is not possible to exclude the possibility that lower summer temperatures during this period might have contributed to the growth depression (Fig. S2). In contrast to other studies, our investigation shows that the growth of silver fir did not decline in the eastern part of its distribution range during this period (southern Carpathians and partly eastern Dinaric Mts.). It has been suggested that the greater genetic diversity of the Balkan populations helps the species mitigate effects of changing environmental conditions (Bosela et al., 2016a), and this study supports that suggestion. Increased genetic diversity, but also a greater functional diversity of forest stands where it occurs, have been shown to increase the capacity of silver fir to tolerate drought (Gazol et al., 2016). The latter relationship is indicative of the need to understand the implications of ecosystem diversity for species performance and production stability.
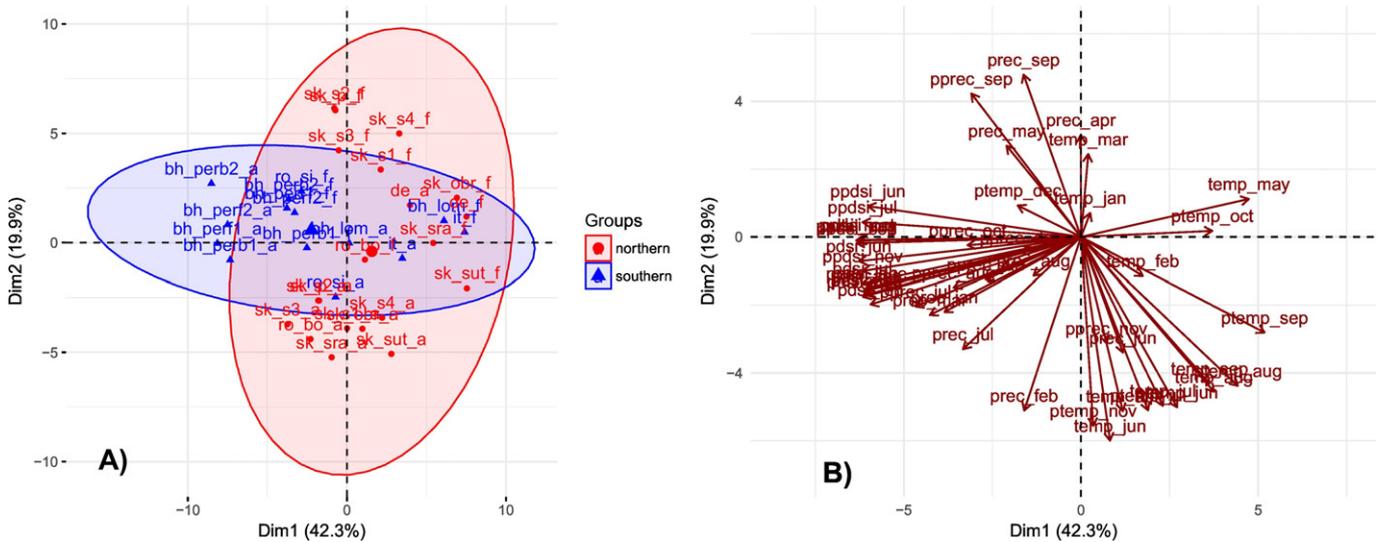

Fig. 3. Linear regression trends of silver fir and European beech ring-width indices (RWI) in two distinct time periods of acid deposition (1950–1980) and climate warming (1990–2010). Dots indicate average RWI change per annum representing the whole range of stands considered in this study (A) or in two sub-sets according to geographical location (B and C). Error bars denote standard deviation.

Fig. 4. Principal component analysis (PCA) of growth-climate responses of silver fir and European beech across Europe: a) dissimilarities between the study localities and species and indication of northern and southern sites in the ordination space; b) ordination of contributing climate variables. The matrix of the correlation coefficients between site chronologies (produced by smoothing spline with 70% cut-off at 10-year segments) and climate variables (temperature, precipitation and sc-Palmer Drought Index) was used as an input to the PCA. Abbreviations in labels: bh – Bosnia & Herzegovina, it – Italy, ro – Romania, sk – Slovakia, per – Perucica; a – silver fir and b – European beech; temp – monthly temperature, ptemp – monthly temperature in the previous year, prec – monthly precipitation, pprec – monthly precipitation in the previous year, pdsi – sc-Palmer drought index, ppdsi – monthly sc-Palmer drought index in the previous year.

Following the period of growth decline, silver fir experienced a rapid recovery reaching unprecedented levels across most of its distributional range, coincidental with successful pan-European effort to limit acid deposition. Even at the Cansiglio site (Italy) characterised by warm and dry conditions, the growth pattern almost exactly followed that seen in Slovakia until around 1995–2000, when at Cansiglio it turned to another decline. This finding brings a new angle to a recent Europe-wide study of silver fir growth throughout the Holocene. Büntgen et al. (2014) showed an increasing radial increment of fir trees growing in Italian Alps and Apennines until 2000, but did not indicate growth trends after that year. Our observations from the Cansiglio site indicate that fir populations in the southern parts of the Alps may have recently experienced a drought-stress related growth decline (Fig. 6a).

4.3. Long-term patterns of radial growth

For the first time, to our knowledge, this study compares growth pattern response to climate between managed and unmanaged forests. We were able to make this comparison only for a series of sites in the western Carpathians, however a pattern typical for many other sites where these two species co-exist emerges. There was no discernible difference between tree growth in managed and unmanaged forests, but beech RWIs were positive during 1950–1980 while those of fir were negative. By 1990–2010, the pattern reversed; RWIs describing fir growth were positive as the species recovered both in managed and unmanaged forests, but those depicting beech growth declined to negative values. Again, this observation underlines the effect of long-term
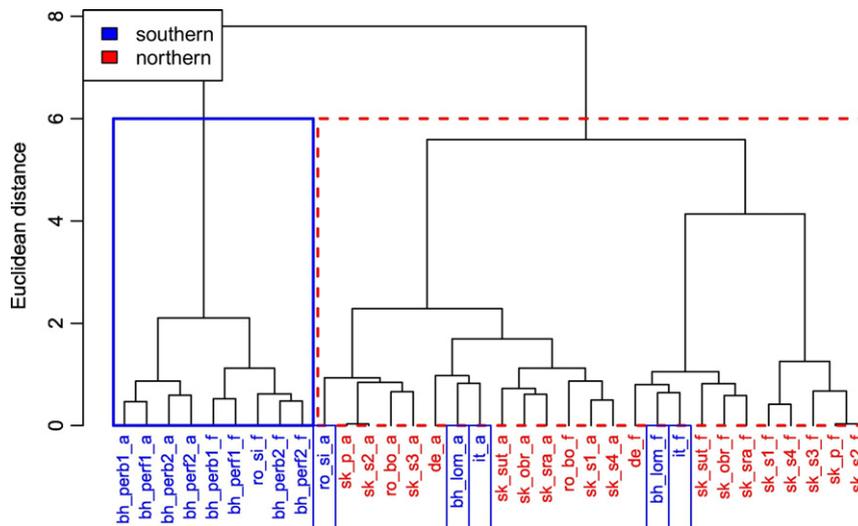

Fig. 5. Dissimilarities in climate responses of silver fir and European beech across European sites using hierarchical clustering. The analysis shows a differentiation between northern (red and dashed-line rectangle) and southern (blue and solid-line rectangle) populations of fir and beech. The southern sites that were clustered within the northern cluster are highlighted by a blue rectangle around the labels. Abbreviations in the x-axis label: bh – Bosnia & Herzegovina, it – Italy, ro – Romania, sk – Slovakia, per – Perucica; a – silver fir and b – European beech.
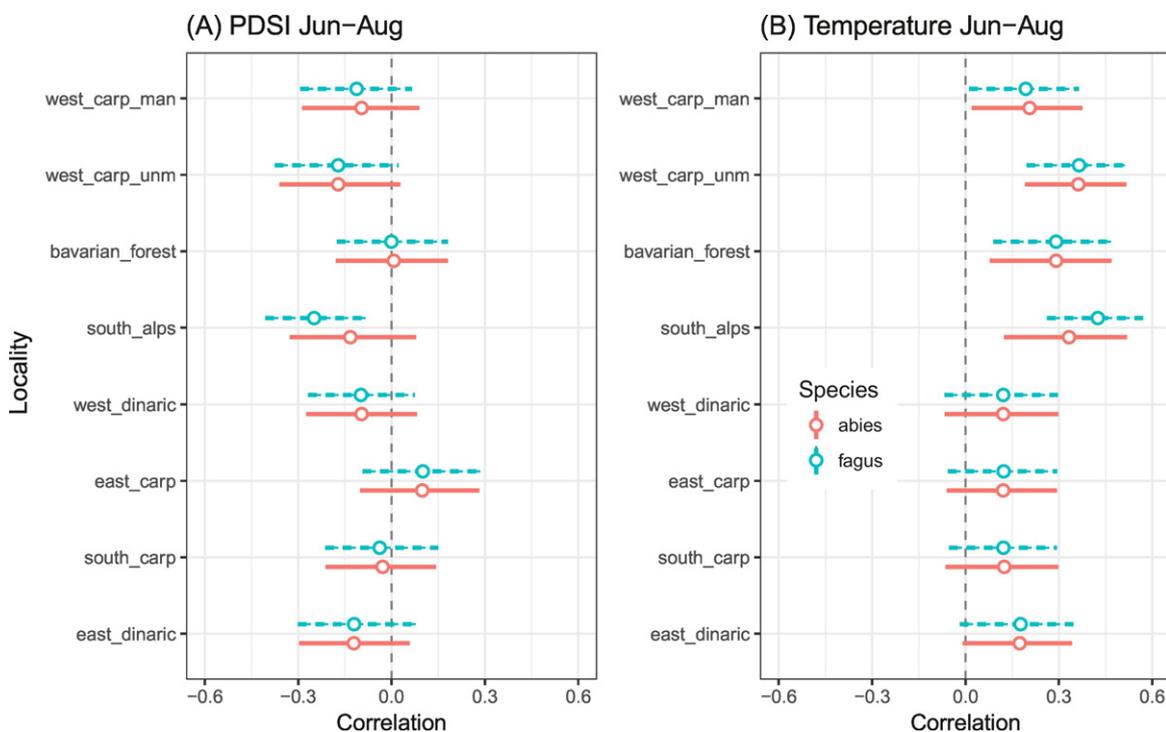
Fig. 6. Correlation between the site ring-width index (RWI) chronologies and mean temperature (a) and sc-Palmer Drought Index (PDSI) (b) during the period of June to August in silver fir (green dashed lines) and European beech (red solid lines) in different localities across Europe (west_carp_man: managed stands in western Carpathians, west_carp_unm – unmanaged forests in western Carpathians, east_carp: eastern Carpathians, south_carp: southern Carpathians, east_dinaric: eastern Dinaric, west_dinaric, south_alps: southern Alps, Bavarian Forest). RWI were obtained after detrending by modified negative exponential function; bootstrapped correlation was computed over the whole period of about 110 years; values shown represent mean and 95% confidence intervals.

environmental conditions on tree-ring width, which seems to override even the effect of forest management designed to stimulate bole wood productivity.

While our observations of European beech show a wide variation of growth patterns driven by several factors, the results for European silver fir are quite consistent. A number of recent studies provides evidence that diversity, whether species or functional, has a positive effect on tree growth (Toïgo et al., 2015; Zhang et al., 2012). Higher diversity is also believed to mitigate the negative impacts of extreme climate events through higher growth resistance and resilience (e.g. Jucker et al., 2014; Gazol et al., 2016; Metz et al., 2016). Although our study cannot directly estimate the benefits of growing in a diverse stand, the results clearly indicate that growing in a mixture does not shield the two species from impacts of long-term changes in environmental conditions. For example, we show that beech growth has been declining over the last two decades in both managed and unmanaged forests and across a range of conditions in Europe, regardless of the species composition and forest structure. The same holds true for fir's unusual radial increment patterns, whereby long-term changes of environmental conditions seem to prevail over local ecology. In this context, any calculation of resistance and resilience indices based on RWI must take into account multi-decadal trends as these form the 'background' against which tree growth must be considered.

5. Conclusions

Our study shows that state-of-the-art dendroecologicial techniques can unravel complex environmental factors that influence species-specific tree growth trends. Although growing under the same conditions, European beech and silver fir exhibited remarkably different growth patterns over the last half a century. While fir responded positively to the recent warming, beech growth has declined across our

range of sites, suggesting that fir is less susceptible to warmer and drier conditions than beech. A comparison of growth patterns between managed and unmanaged mixed beech-fir forests revealed that the long-term growth patterns were the same, suggesting only a limited scope for tree growth stimulation by active forest management. There is some support for the use of mixed forests as an adaptation strategy to climate change. We show that a higher tree species diversity might help mitigate the effects of short-term climatic events such as drought and acidification, but may not prevent mixed forests from the long-term consequences of climate change. Thus, any effort to convert Norway spruce monocultures to preserve long-term growth at the forest ecosystem level should consider a purposeful decision to utilise both beech and fir as replacement species. Further scientific effort should be directed towards investigating effects of various management interventions designed to aid the adaptation of beech-fir ecosystems to future climate change.

Authors' contributions

MB conceived the ideas and MB, ML, DC and RS designed methodology. MB and ML analysed data. MB, ML and UB wrote the manuscript. All

authors collected data, contributed critically to the drafts and gave final approval for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2017.09.092.

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