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Long-term effects of environmental change and species diversity on tree radial growth in a mixed European forest

Michal Bosela[a], *Ladislav Kulla*[b], *Joerg Roessiger*[b], *Vladimír Šebeň*[b], *Laura Dobor*[c], *Ulf Büntgen*[d,e,f], *Martin Lukac*[c,g]

[a] *Faculty of Forestry, Technical University in Zvolen, T.G. Masaryka 24, 960 53 Zvolen, Slovakia*

[b] *National Forest Centre, Forest Research Institute, T.G. Masaryka 22, 960 92 Zvolen, Slovakia*

[c] *Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 00 Praha 6 – Suchdol, Czech Republic*

[d] *Department of Geography, University of Cambridge, Cambridge, CB2 3EN, UK*

[e] *Swiss Federal Research Institute, 8903 Birmensdorf, Switzerland*

[f] *CzechGlobe & Department of Geography, Masaryk University, 61137 Brno, Czech Republic*

[g] *School of Agriculture, Policy and Development, University of Reading, Reading, RG6 6AR, UK*

Running head: Complex climate response of beech, fir, spruce and pine

Keywords: atmospheric pollution, climate warming, drought stress, European forests, plant–climate interactions, species diversity, tree growth

Corresponding author: Michal Bosela, ybosela@tuzvo.sk, +421 45 5206 310

Abstract

Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*), silver fir (*Abies alba*) and Scots pine (*Pinus sylvestris*) typically co-occur in European forests, but show contrasting response to climate and environmental change. Sustainable forest management therefore depends on species- and regional-specific information. Here, we use tree-ring width measurements of 334 beech, 280 fir, 144 spruce and 63 pine trees from 75 inventory plots in Slovakia to assess the predominant climatic factors that control radial stem growth of Europe's economically most important forest species. All four species exhibit significant shifts in stem growth over the past 100 years. Ring width patterns were, however, not significantly affected by tree species diversity and site elevation. The resistance, resilience and recovery of all species to the extreme summer droughts between 1950 and 2003 suggest that spruce is the species most unsuitable for the predicted warmer and drier future. Silver fir may benefit from warmer conditions, although we cannot conclude that it will not suffer from predicted increased frequency of climate extremes. Forest management in this locality should aim to avoid significant loss of forest cover by replacing Norway spruce monocultures with mixed stands of silver fir and European beech.

Introduction

Anthropogenic climate change has been identified as an important driver of functioning and productivity of forest ecosystems, which contribute to the global carbon cycle (Ciais et al., 2005; Frank et al., 2015; Parmesan et al., 2003). Many tree species are expected to experience range shifts accompanied by population extinctions within a specific locality in the medium to distant future (IPCC, 2014; Lenoir et al., 2009; Thomas et al., 2004). Local forests are, however, primarily affected by intra- and inter-specific competition (Coomes and Allen, 2007), forest management (Bosela et al., 2016b; Johnson and Curtis, 2001), as well as nitrogen deposition (Solberg et al., 2009) and pollution (Wang et al., 2016). With reference to a long history of (mis)management of European forests, only few existing forest ecosystems resemble their natural state (Sabatini et al., 2018).

Norway spruce (*Picea abies* Karst.), European beech (*Fagus sylvatica* L.), silver fir (*Abies alb*a Mill.) and Scots pine (*Pinus sylvestris* L.) are among the most ubiquitous tree species frequently cooccurring in many areas covering Europe's temperate zone (San-Miguel-Ayanz et al., 2016). Norway spruce is currently one of the economically most important species, which has traditionally been used to replace beech and beech-fir forests across Central Europe to increase income from timber production (Spiecker et al., 2004). However, this species has been shown to be prone to summer drought (Pretzsch et al., 2013; Zang et al., 2014), windstorms (Seidl et al., 2014), and bark beetle outbreaks (Hlásny and Turčáni, 2013), especially when grown in monocultures. Both beech and fir, on the other hand, are known to respond positively to temperature increases (Pretzsch et al., 2014), except for populations at the trailing edge of their current distribution (Jump et al., 2006; but see Tegel et al. (2014)). Silver fir has also been suggested to be less sensitive to extreme drought than spruce (Vitali et al., 2017), and may play an important role in maintaining the vigour of central European forest ecosystem services under warmer-than-present conditions (Ruosch et al., 2016). Being the most widespread across Europe, Scots pine is another important contributor to ecological and economic functioning and productivity of current forests (Matías et al., 2017; Matías and Jump, 2012), where the species naturally co-occurs with Norway spruce (Pretzsch et al., 2015).

There are indications that mixed-species forests possess a higher potential for resistance, resilience and recovery in the face of changing climate conditions (Isbell et al., 2015; Metz et al., 2016), and thus may constitute a viable alternative to monocultures. Species growing in mixed forests were recently suggested to be less sensitive to rapid warming and/or drying (Pretzsch et al., 2013), and also produce more timber than their monospecific equivalents (Pretzsch and Schütze, 2009; Toïgo et al., 2015). Tree species diversity, however, is not the only determinant of forest sensitivity to climate. In fact, the long-term productivity of forest ecosystems is a result of several interacting factors, such as the genetic diversity of populations (Bosela et al., 2016a), their position within the current geographical distribution of the species (Jump et al., 2006), and/or the level of intra- and inter-specific competitive stress (Paquette and Messier, 2011). In addition, the climate sensitivity of individual trees as well as their populations varies along altitudinal and edaphic gradients (Dittmar et al., 2003; Jump et al., 2006; Tegel et al., 2014), thus exhibiting distinct regional differences (Babst et al., 2013).

Predicted changes in the productivity, as well as survival and competitive behaviour of forest tree species will be relevant for adapting their management practices to future environmental and climatic changes (Kirilenko and Sedjo, 2007). A set of new silvicultural management strategies must therefore be developed to safeguard the provision of ecosystem services, including timber production. Forest management mainly operates at stand or even sub-stand level and requires information relating to local conditions. Therefore, to be truly informative for management, regional investigations using appropriate sampling designs may be preferable to inference on the basis of generalised observations (Law, 2015). Should climate change force a large-scale transformation of Norway spruce monocultures in Europe, mixtures of Silver fir, European beech and Scots pine, among other species, may be well-suited to certain localities. Similar tree mixtures are likely to perform differently across a wide range of ecological settings with varying climate conditions, information that relates forest productivity to climate variability must therefore be tailored to local scales to support evidence-based management decisions.

Aiming to generate species-specific information about basal area growth relevant for local forest management, this study reconstructs historical growth-climate responses of Europe's four aforementioned forest tree species: Norway spruce, European beech, silver fir and Scots pine. We consider a variety of mixed stands growing between 366 and 1150 m a.s.l. within an area of 2,128 hectares in Slovakia, and analyse interactive effects of climate, altitude and the level of stand diversity on long-term radial stem growth changes as well as the resilience to major European heat waves in 821 trees. We hypothesise that, at our study site, Norway spruce is the most susceptible species to increasing temperature and drought (H1), and that species diversity (H2) and stand level competition (H3) modify the long-term climate sensitivity of tree growth.

Material and Methods

Study area

The study area of 2,128 hectares is located in the Slovakian part of the Carpathian Mountains (Fig. 1). A single-tree selection management system (individual mature trees removal in support of natural regeneration) has been applied to all forest stands in this locality since the 1950s (Saniga and Bruchánik, 2009), and the area is listed by the Pro Silva foundation that promotes continuous-cover forestry and sustainable forest management (www.prosilva.org). With the exception of some valley bottoms, the area was almost fully forested at the point of conversion to the individual selection system, and the conversion has resulted in a further increase in forest cover (Fig. S1). The area, in which 11 different tree species were recorded, is characterised by heterogeneous topography between 366 and 1150 m a.s.l. on phylit-derived cambisol soils. Mean annual temperature is around 5 °C and annual precipitation totals are approximately 950 mm. The area is dominated by mixed forests of European beech, silver fir, Norway spruce, and Scots pine, with a minor admixture of ash (*Fraxinus excelsior* L.), sycamore (*Acer pseudoplatanus* L.) and larch (*Larix decidua* Mill.). Forests in the area are characterised by a high spatial variability of stand ages, mean stand diameters, species composition and stand densities (Table 1). Potential productivity of the species investigated in this study, as indicated by the site index (locally defined as stand height at standard age of 100 years), is broadly similar (Table 1).

Table 1 Description of forest stands found on the 75 inventory plots utilised for tree core sampling in this study (mean across all sites ± standard deviation).

	Species				
Variable	Beech	Pine	Fir	Spruce	Total
Species proportion (%)[1]	40±30	61±17	49±31	18±20	-
Mean stand diameter (mm)	243±100	435±76	358±127	279±143	295±102
Mean stand height (m)	22±7	31±3	28±8	23±9	26±7
Stand density (n trees ha^{-1})	315±350	163±98	167±130	205±400	604±463
Stand volume (m^3 ha^{-1})	133±127	292±141	230±210	55±52	389±232
Age (years)[2]	77±44	114±46	90±41	77±27	-
Site index (m)[3]	30±10	30±4	30±13	29±9	-
Proportion of plots containing a specific mixture	Beech-Fir-Spruce 53%	Beech-Fir 24%	Beech-Fir-Spruce-Pine 8%	Beech-Spruce 5%	
	Fir-Spruce 3%	Fir 3%	Beech 1%	Spruce 1%	
	Other 2%				

Footnote: [1]proportion of species at a site, based on tree volume; [2]mean age weighed by basal area; [3] defined as mean stand height at the age of 100 years (Halaj and Petráš, 1998).

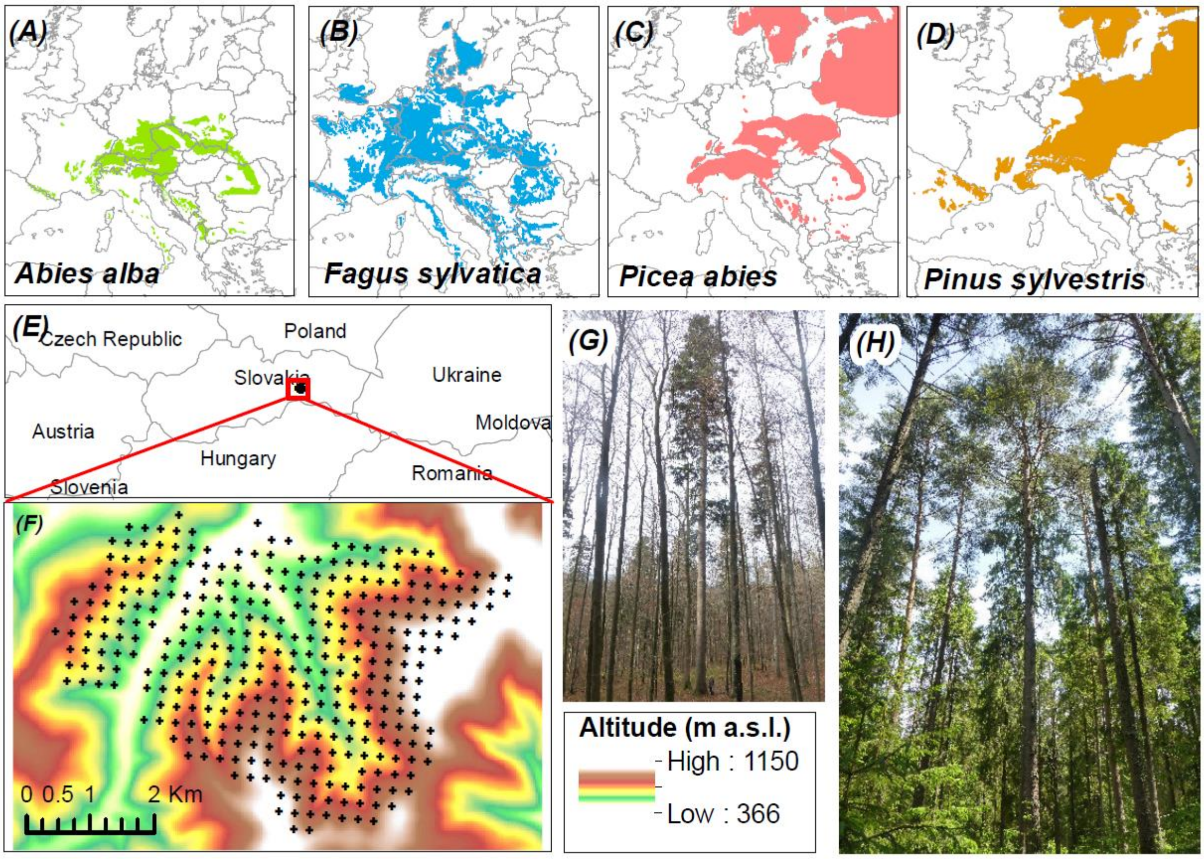

Figure 1 Distribution of silver fir (A), European beech (B), Norway spruce (C) and Scots pine (D) in Europe; (E) location of the study area in Slovakia; (F) spatial distribution of all inventory (sampling) plots; (G) mixture of beech, spruce and fir; (H) mixture of pine, spruce and beech

Inventory plots

Forest inventory plots (IP) were established in 2014, when a regular grid of 250 × 250 m was superimposed over the study area. A total of 344 variable-sized circular plots, with a radius ranging from 5 to 20 m to include 20–30 trees, were centered on the intersection points of the grid. Diameter at breast height (DBH), height and crown length of all trees within each plot were measured in 2014. We calculated the Shannon Diversity Index (SDI; Shannon 1948) to describe tree species diversity of each IP, taking into account the overall tree species presence. SDI was preferred to other indices as it accounts for both species richness and species evenness (Purvis and Hector, 2000). Tree species dominance within each plot was classified as: pure (% proportion of volume >75%), mixed (% proportion of volume 25–75%) and admixed (% proportion of volume <25%). Crown quality, an indicator of tree vigour and past competition interactions, was visually assessed for each tree (A – well developed and symmetrical crown with defoliation not exceeding 30%; B – middle developed crown under higher inter-tree competition with defoliation between 30 and 60%; C – less developed, sparse and/or damaged crown with defoliation above 60%). All plots were assigned to two altitudinal categories: lower (≤800 m a.s.l.) and higher (>800 m a.s.l.).

Tree-ring data

Radial increment cores were collected at each IP of a coarser 500 × 500 m grid. This coarser grid included 75 out of 344 IPs. Sample trees for coring were selected to cover the range of investigated species, mixture types, diameter range and vertical tree classes (dominant, co-dominant, sub-dominant and suppressed trees). The mean proportion of trees selected for coring within each IP (i.e. plot sampling intensity) ranged from 47% for beech to 78% for pine. In contrast to most published dendroecological studies which collected data from dominant trees only, in all we considered 821 tree-ring width (TRW) series from all vertical tree classes on each IP to avoid bias related to tree size (e.g. Nehrbass-Ahles *et al.* 2014). A single core sample from each tree was taken at the height of 1.3 m in 2015. Core samples were subsequently air-dried in the laboratory, mounted on wooden slats and sanded to facilitate the detection of individual ring boundaries. TRW were measured using a LINTAB device (Rinntech, Heidelberg, Germany) and cross-dated by common dendrochronological techniques (Cook and Kairiukstis, 1990) coded in R package “dplR” (Bunn, 2010). The frequency distributions of DBH of all cored trees within mixture and altitude categories are shown in the Supplementary Figures S2 and S3.

Climate indices

For growth-climate response analyses, we used daily weather station measurements, gridded monthly observations (CRU TS4.01; Harris *et al.* 2014), and output from the MTClim model (Mountain Microclimate Simulation Model; Hungerford *et al.* 1989). Observed meteorological data from two weather stations in the surrounding area (the first station at 583 m a.s.l and the second at 1242 m a.s.l) were recalculated for two elevational zones within the study area at 600 m a.s.l and 1000 m a.s.l, by using output from the MTClim model at daily resolution. While local meteorological observations were available for 1961–2006, the CRU dataset extends over the 1901–2016 period. Monthly time-series were derived from daily MTClim simulations and distance-weighted averages of the closest four CRU gridpoints were fitted to the climate of the two elevational zones based on the common period 1961-2006. Distributions of monthly temperature and precipitation time-series were then separately fitted by the quantile-quantile mapping method for each month (Piani et al., 2010). Correction factors obtained by the comparison were applied to the CRU data to obtain climate data outside the overlaping period. Finally, we combined the corrected CRU and observational data to a time-series for both elevational zones which covers the period of 1901–2016.

Resilience, resistance and recovery measures

To quantify effects of major summer droughts on the growth of the four forest species, we calculated resistance, resilience and recovery indices from our TRW data (Lloret et al., 2011). We combined the information obtained from local weather station data and reviewed recent publications (Ciais et al., 2005; Parry et al., 2012; Spinoni et al., 2015) to identify years with abnormal summer droughts. Here, resistance is defined as the capacity to retain pre-disturbance growth during a disturbance event, calculated as the ratio of growth rate during to that before an extreme event. Resilience is defined as the capacity to return to pre-disturbance growth levels, estimated by the ratio of post-disturbance growth to that prior to the event. Finally, recovery describes the ability of tree growth to recover from a disturbance-driven suppression, expressed as the ratio of increment after over that during disturbance event. We calculated all three indices for all sampled trees to describe the reaction of tree species to major European heat waves and drought spells in the period of 1950–2003. We used a period of three years before and after the events to quantify these indices (e.g. Gazol *et al.* 2016). We further used Tukey's multiple comparisons using "glht" function in "multcomp" R package (Hothorn et al., 2008) to test for statistical significance of the differences between species and altitudinal and mixture categories (Dushoff et al., 2019).

Mixed-effects models

A transformation of TRW into basal area increment (BAI) was employed to remove biases of productivity estimates inherent to TRW data (Bouriaud et al., 2005). Tree productivity expressed as BAI captures the addition of volume to circular stems and therefore better represents overall tree growth (Biondi and Qeadan, 2008).

We used generalised additive mixed models (GAMM) in R package "mgcv" (Wood and Wood, 2014) to compare the BAI patterns of the four species in the mixture and altitudinal categories along the study period. The GAMM was preferred over linear models to explore non-linear BAI patterns via a mixed-effects model setting. This GAMM function uses the Bayesian approach of spline smoothing (Wahba, 1983, Silverman, 1985). Since BAI is usually positively correlated to DBH, DBH was used as a covariate in the models to remove its effect and to preserve temporal changes due to other factors. Tree identity was nested within sample plot and used as a random factor to estimate between-plot variation. We used a standard DBH of 22 cm to compare century-long BAI patterns among the species and categories.

Furthermore, a linear mixed-effects model (LMER) in the R package "lme4" (Bates et al., 2015) was applied to estimate the effects of DBH, spring and summer temperature, as well as precipitation (Fig. S4), and the crown length-to-height ratio or crown quality classes, representing indicators of past competition and tree vigour (Drobyshev et al., 2007) on annual BAI variation. Between-variable interaction terms were used to assess how the effect of one factor varies along the levels of another factor.

Three model alternatives (*a*-*c*) were used to test the effects of climate, competition and species diversity on BAI variation:

In the first alternative (a), competition was expressed by the ratio between crown length and total tree height and species diversity (mixture) by the proportion of the species basal area from the total stand basal area:

$$(a)\ BAI_{ij} = b_0 + b_1 ln(dbh_{ij}) + b_2 ln(dbh_{ij}) \times T_{jun\text{-}aug} + b_3\, CR_{ij} + b_4\, T_{jun\text{-}aug} \times CR_{ij} + b_2 ln(dbh_{ij}) \times T_{mar\text{-}may} + b_2 ln(dbh_{ij}) \times P_{jun\text{-}aug} + b_2 ln(dbh_{ij}) \times P_{mar\text{-}may} + SPprop + SPprop \times T_{jun\text{-}aug} + (1|\ IDPlot_j/IDTree_{ij}) \qquad (Eq.\ 1)$$

In the second alternative (b), Shannon diversity index was used to express tree species diversity:

$$(b)\ BAI_{ij} = b_0 + b_1 ln(dbh_{ij}) + b_2 ln(dbh_{ij}) \times T_{jun\text{-}aug} + b_3\, CR_{ij} + b_4\, T_{jun\text{-}aug} \times CR_{ij} + b_2 ln(dbh_{ij}) \times T_{mar\text{-}may} + b_2 ln(dbh_{ij}) \times P_{jun\text{-}aug} + b_2 ln(dbh_{ij}) \times P_{mar\text{-}may} + H' + H' \times T_{jun\text{-}aug} + (1|\ IDPlot_j/IDTree_{ij}) \qquad (Eq.\ 2)$$

The third alternative (c) included Shannon diversity index as in (b), but the level of competition was expressed by crown quality classes. The crown quality classes are more complex than the simple crown length-height ratio because it also reflects crown foliage (density, defoliation) as well as the shape of crown:

$$(c)\ BAI_{ij} = b_0 + b_1 ln(dbh_{ij}) + b_2 ln(dbh_{ij}) \times T_{jun\text{-}aug} + b_3\, CQ_{ij} + b_4\, T_{jun\text{-}aug} \times CQ_{ij} + b_2 ln(dbh_{ij}) \times T_{mar\text{-}may} + b_2 ln(dbh_{ij}) \times P_{jun\text{-}aug} + b_2 ln(dbh_{ij}) \times P_{mar\text{-}may} + H' + H' \times T_{jun\text{-}aug} + (1|\ IDPlot_j/IDTree_{ij}) \qquad (Eq.\ 3)$$

Where

dbh_{ij} – breast height diameter of the i^{th} tree on j^{th} plot

$T_{jun\text{-}aug}$ – mean temperature anomaly of the June-August period (anomaly calculated against the mean summer temperature in the period of 1901 – 1980 used as the reference climate before the recent climate warming)

$T_{mar\text{-}may}$ – mean temperature anomaly of the March-May period (anomaly calculated against the mean summer temperature in the period of 1901 – 1980 used as the reference climate before the recent climate warming)

$P_{jun\text{-}aug}$ – precipitation totals of the June-August period (anomaly calculated against the mean summer temperature in the period of 1901 – 1980 used as the reference climate before the recent climate warming)

$P_{mar\text{-}may}$ – precipitation totals of the March-May period

CR_{ij} - ratio between crown length and total tree height of the i^{th} tree on j^{th} plot

SPprop – species proportion calculated from tree basal area

H' – Shannon's diversity index

CQ_{ij} – qualitative classes of crown status of the i^{th} tree on j^{th} plot (A=1, B=2 and C=3)

Tree identity nested within sample plot was used as a random factor in all model variants. Marginal effects of interaction terms were calculated using the "effect" function in R "effects" package (Fox et al., 2015). When calculating the individual interaction effects, all remaining covariates were set to the mean. A "sjp.int" function in "sjPlot" R package (Lüdecke and Schwemmer, 2017) was used for visualisation of the effects. Both mean and standard deviation were used as moderator variables when plotting the interaction effects.

Results

Over the last 100 years, each of the four tree species investigated in this study exhibited very contrasting BAI patterns (Fig. 2 and 3). At the beginning of the 20th century, spruce revealed the fastest growth rate (app. 35±3.3 $cm^2\ yr^{-1}\ tree^{-1}$), but following a steady decline the species became the least productive in the early 2000s (H1, app. 7.5±2.1 cm^2 yr^{-1} tree^{-1}). A relatively high initial BAI of the silver fir trees dipped between 1950 and 1980, but following a recent recovery it now reaches the highest values among the four species (app. 20.5±2.5 cm^2 yr^{-1} tree^{-1}). Beech experienced a slow but steady BAI increase during the 20th century, without any discernible variation of growth. Compared to the other major species growing in this locality, beech was the second most productive since the start of the 21st century (app. 15.8±1.2 cm^2 yr^{-1} tree^{-1} in 2014). Finally, pine trees exhibited a slow BAI decline over the last 100 years, becoming the second least productive species in the region after spruce (app. 9±3 cm^2 yr^{-1} tree^{-1} in 2014). Interestingly, no differences in the mean long-term BAI patterns were observed between trees growing at various levels of species mixture (Fig. 2). We found that at the beginning of 20th century, fir and beech were growing better at lower elevations while spruce grew better at higher elevations. By the end of the 20th century, however, their growth rates in the two altitudinal categories were found to be nearly identical (Fig. 3).

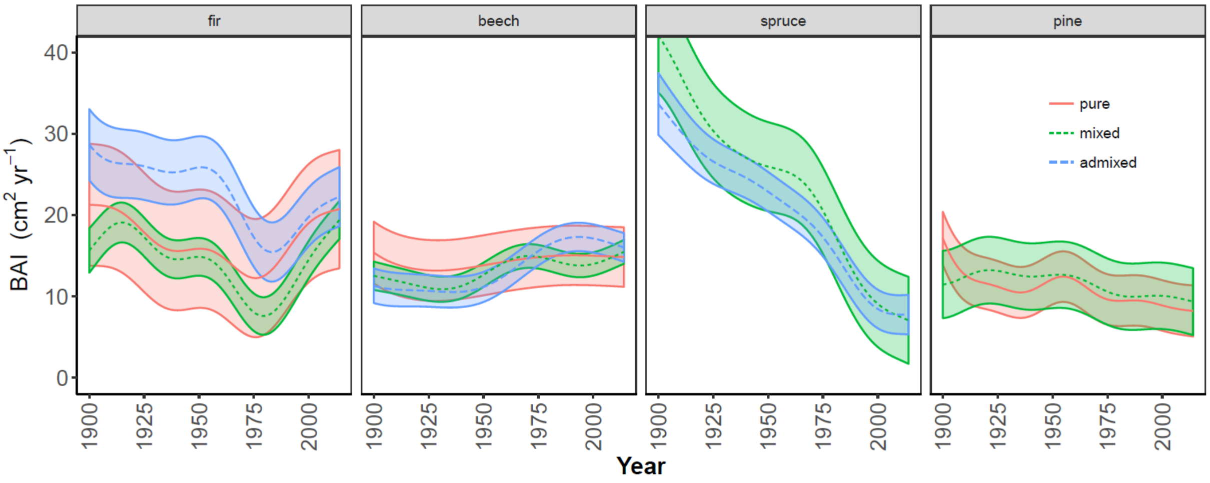

Figure 2 Individual tree Basal Area Increment (BAI) of fir, beech, spruce and pine trees normalised to standard DBH of 22 cm. Lines represent smoothed mean of trees classified as growing in a pure or mixed stand, or as an admixture, bands represent 95% confidence intervals.

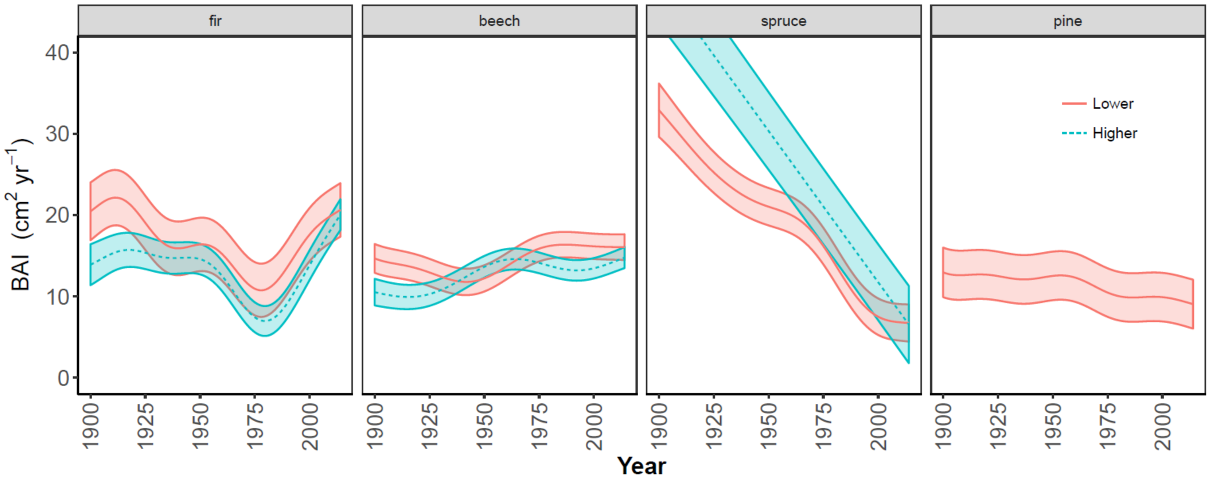

Figure 3 Individual tree Basal Area Increment (BAI) of fir, beech, spruce and pine trees normalised to standard DBH of 22 cm categorised by altitude (Lower – below 800 m a.s.l. and Higher – above 800 m a.s.l.). Lines represent smoothed mean, bands represent 95% confidence interval.

Mixed-effects modelling shows that climatic and forest stand characteristics considered in this study explain 47–72% of the variability in tree BAI over the last century (Table S1). Fir and beech trees revealed positive responses to summer temperature and precipitation, whereas the responses were negative for spruce and pine in the region (Fig. 4). We found strong effect of tree size on the BAI-climate responses, but differing among the species (Fig. 4, Fig. S7 and S8). Large-sized fir trees showed strong increase of BAI as a reaction to the increase in summer temperature, whereas small-DBH trees revealed a decline. Spruce experienced a contrasting pattern. Strong decline of BAI along a temperature gradient was found for large trees whereas small trees showed no trend. Unlike temperature, we found smaller differences between the species regarding the effect of DBH on BAI responses to summer precipitation (Fig. S8).

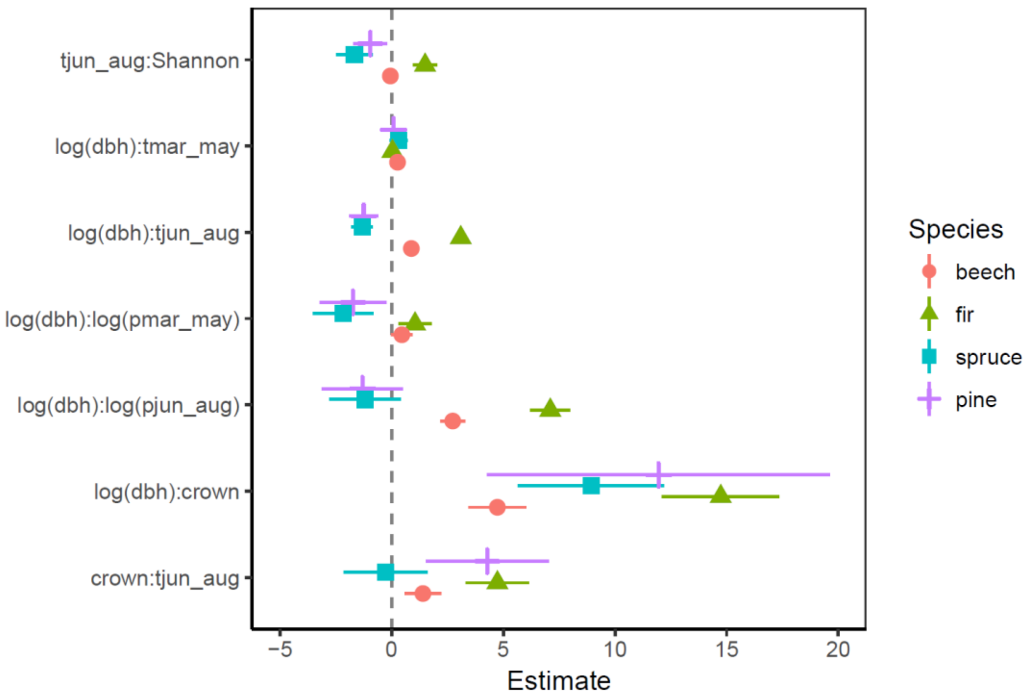

Figure 4 Regression coefficients of a linear mixed-effects model contrasting how current year basal area increment of four tree species is affected by competition, climate and species diversity. The competition is represented by crown length-to-tree height ratio and species diversity by the Shannon's diversity index. Since the interpretation of the main effects when testing interaction terms can be misleading, only the estimates of the interaction terms are presented. The whiskers denote the 99% confidence intervals.

We found significant effect of tree species diversity (expressed by Shannon's index) on BAI and BAI-climate responses (Table S1, Fig. 4). For fir and beech, higher diversity meant greater BAI (Fig. S9). However, the opposite effect was found for spruce and pine. At lower temperatures, BAI was larger when species diversity was higher, but at higher temperatures growth was faster in less diverse stands.

Crown size affected the BAI and BAI-climate responses. In general, larger crowns were associated with greater BAI, but the effects of crown on the growth-climate sensitivity differed among the species, from no effect in spruce to the greatest effects in pine and fir (Fig. S10).

Further, we found large variability in resilience indices among the species. Fir trees showed the strongest recovery but were found less resistant than beech (Fig. 5 and 6). The two altitudinal zones had greater effect on species resilience than species mixture (Table S2 and S3). Spruce was found to be the least resilient and the least resistant among studied species (Table S2).

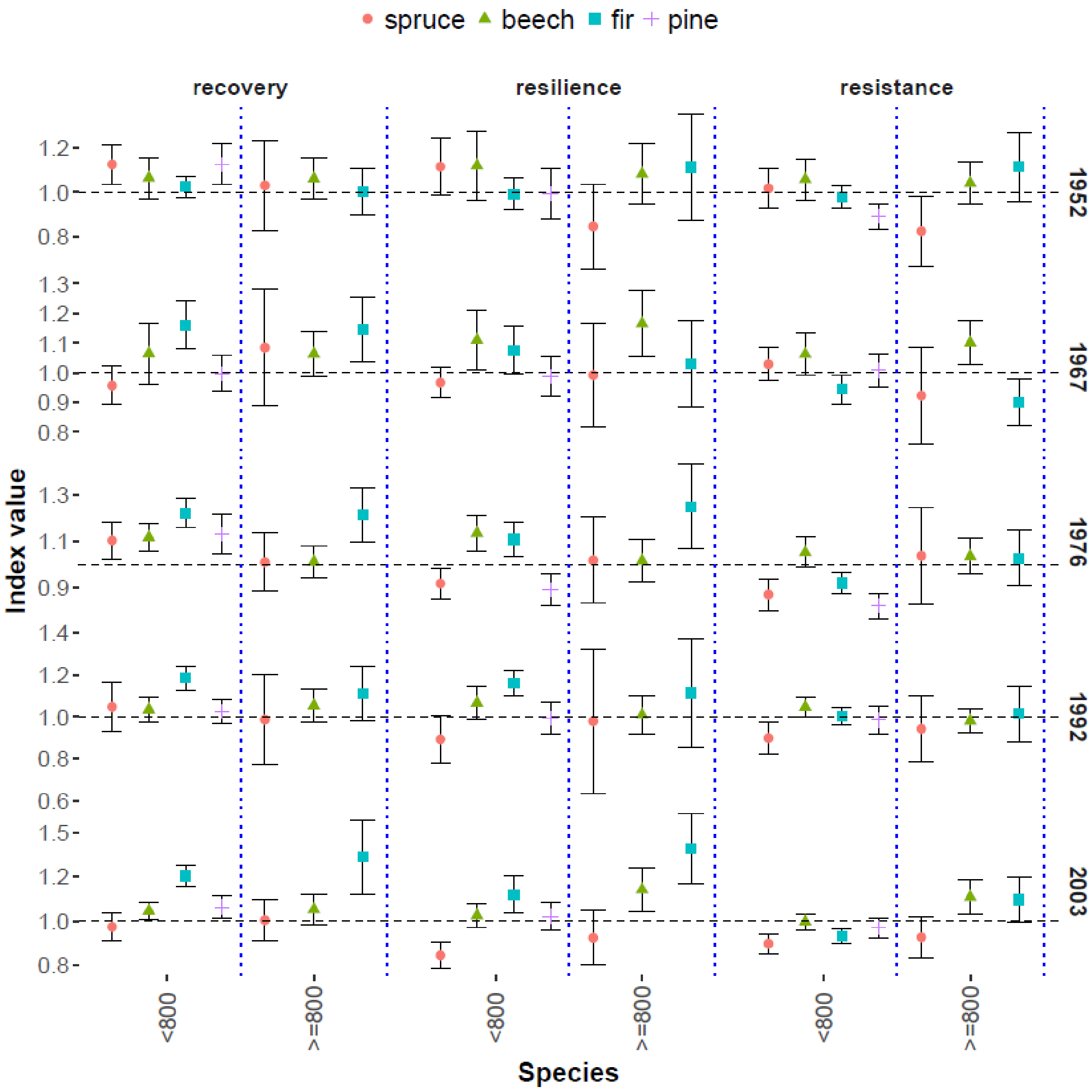

Figure 5 Recovery, resilience and resistance of the BAI of the four species at the two altitudinal categories (<800 and ≥800 m a.s.l.). The whiskers denote 95% confidence intervals.

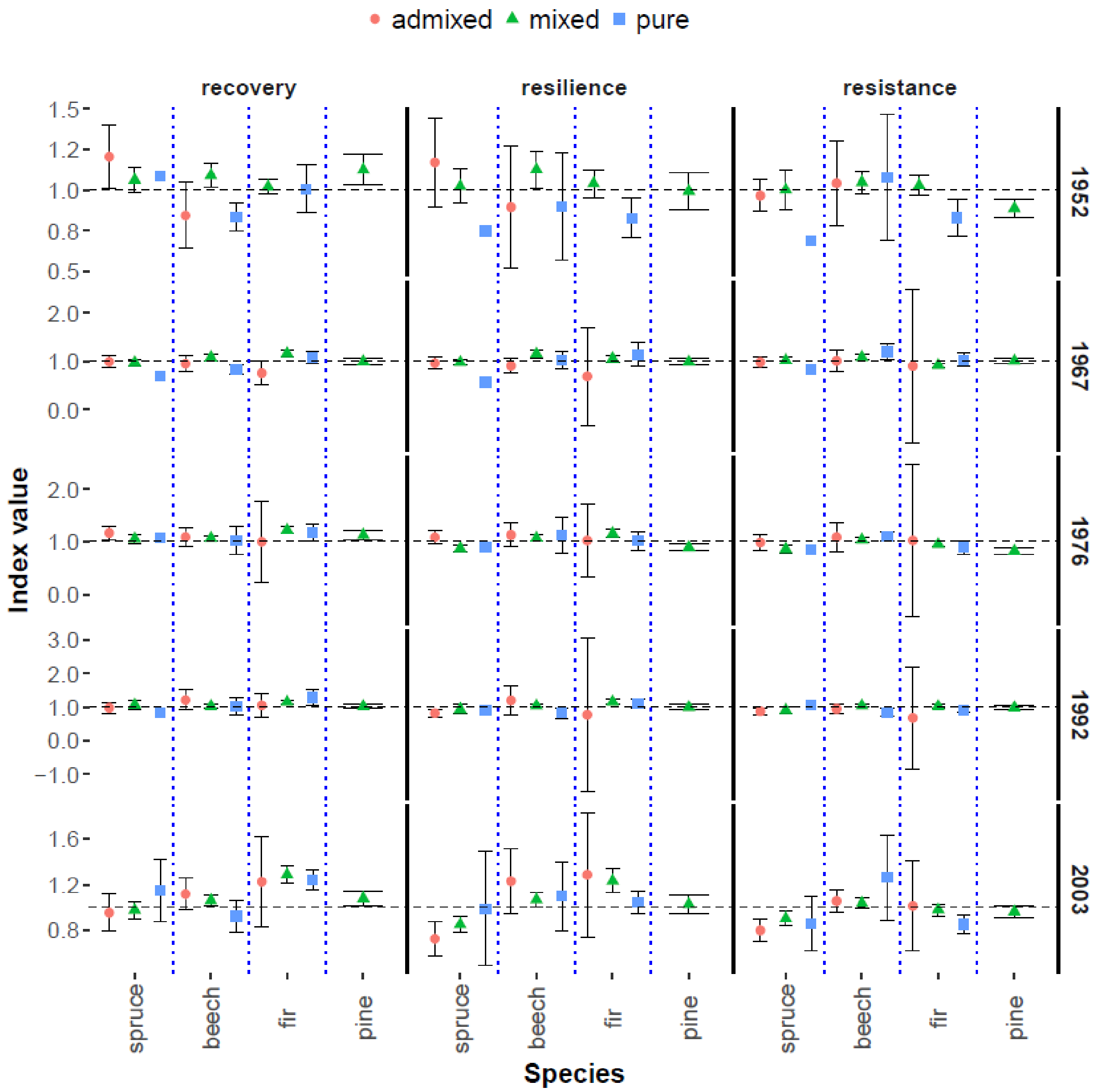

Figure 6 Recovery, resilience and resistance of the BAI of the four species in the three species mixture categories (<800 and >800 m a.s.l.). The whiskers denote 95% confidence intervals.

In summary, this study shows that over the past century a) Norway spruce was the most sensitive to changing conditions, b) thus far, silver fir benefitted from climate warming and rapid reduction of air pollution, c) species mixture had only small effect on long-term growth changes and trees resilience to drought events in the period 1952–2003, but d) species diversity played crucial role in driving BAI responses to climate changes.

Discussion

Recent studies that describe effects of climate change on growth of European tree species paint a very unclear picture. A range of responses is reported, for example (i) both enhanced and reduced growth of spruce after the rapid reduction of air pollution in 1990s (Cienciala et al., 2017; Hauck et al., 2012; Jonard et al., 2012; Kolář et al., 2015); (ii) both increased and decreased growth rates of beech in Central Europe during the last two decades (Dittmar et al., 2003; Pretzsch et al., 2014) and at the southern edge of its distribution range (Jump et al., 2006; Tegel et al., 2014); and (iii) both faster and slower growth rate of Scots pine across Europe (Castagneri et al., 2015; Matías et al., 2017). Spatial and temporal variability of growth patterns uncovered so far calls for a strong focus on local- and regional-scale investigations. A detailed description of growth patterns within a given locality can yield information valuable to foresters, especially when used in conjunction with climate change predictions for the area in question. In order to devise a sampling strategy and to test its potential for generating data fully representative of local populations and to serve as a basis for management recommendations (Babst et al., 2018; Nehrbass-Ahles et al., 2014), we overlaid a systematic distribution of sample plots across an area covering an entire forest management unit.

European beech

So far, beech trees in the region have benefited from recent environmental change, especially at the lower altitude. No sign of a decrease in radial growth rate was identified by this investigation, which is in line with other recent studies from Central Europe, based either on data from long-term forest inventories (Bosela et al., 2016b; Pretzsch et al., 2014) or on growth simulations (Hlásny et al., 2011). However, a recent Europe-wide study showed that beech growth rates have been declining on many sites across its distribution in the past 20–30 years (Bosela et al., 2018). Beech is considered a drought-sensitive species, likely to be limited by increasing frequency or severity of summer droughts (Di Filippo et al., 2007). However, mean resistance, resilience and recovery indices, covering extreme drought events in the period between 1950 and 2003, show that beech was not negatively affected by these events at our location – values of all indices are higher than one. Remarkably, and contrary to our expectations, the resilience and recovery of beech BAI at lower altitude was higher than that at higher elevations (Fig. 5). Tree mixture did not modify the response of beech to extreme drought (H2, Fig. 6). Similarly, the facilitation effect of inter-specific interactions was not confirmed in a recent study of González de Andrés *et al.* (2017b). The authors explained the lack of facilitation at their Mediterranean site by severe competition for water preventing any manifestation of the beneficial effect of a mixture with Scots pine. In contrast to the Mediterranean, the region of our study is normally well-supplied with water, but still no beneficial effect of admixture was found in beech. Interestingly, the copious natural regeneration of beech across the researched area (Fig. S11) suggests suitable site conditions for this species at the present.

There is evidence within the region that intensively managed beech forests growing on less-productive sites have experienced a recent decrease of growth rates (Bosela et al., 2016b), however the current study does not confirm this. Beech growing at lower altitudes (<800 m a.s.l.) reacted positively to increasing spring and summer temperature and summer precipitation (Fig. 3), which is in agreement with observations from other parts of beech distribution in Europe (Cavin and Jump, 2016; Dittmar et al., 2003; Hacket-Pain et al., 2016). A recent tree-ring investigation by Kolář et al. (2017) from beech-dominated forests in the Czech Republic, growing in similar climate conditions to the current study, shows that spring temperature and summer water availability are the most influential factors driving radial growth of beech. However, contrary to our study, they did not find any relationship between radial growth and summer temperature, suggesting a regional variation in climate sensitivity.

Silver fir

Paleoecological records suggest that silver fir was growing under significantly warmer conditions than those experienced by its current populations in Europe (Büntgen et al., 2014; Ruosch et al., 2016; Tinner et al., 2013). Recent studies exploring radial growth of European silver fir consistently confirm a strongly negative effect of SO_2 emissions, which peaked during 1970–90 and caused a large-scale growth depression across Europe (Büntgen *et al.* 2014, Bošel'a et al., 2014; Elling et al., 2009). Our results confirm this trend, the coincidence of the period of minimum growth and that of peak pollution is stark. The reduction of acid deposition, along with the observed 'warming-without-drying' change of climatic conditions allowed fir to recover (Büntgen et al., 2014) and, in central Europe, to reach growth rates nearly as high as those at the beginning of the 20th century (Fig. 2).

Recent evidence suggests that silver fir may grow even better and have lower climate sensitivity when growing in a mixture with other tree species (Lebourgeois et al., 2013), overyielding when compared to pure fir alternatives (Toïgo et al., 2015). However, our results do not support this hypothesis, data describing fir growth in the post-acidification recovery at the beginning of the 21st century do not show any difference between trees growing in pure and mixed stands (H2, Fig. 2). Vitali *et al.* (2017) have shown that fir trees growing at lower altitude in South-Western Germany are more drought-prone when compared to those at higher altitudes. They also assessed fir drought sensitivity by focusing on drought events of 1976 and 2003 using resilience and recovery as response variables. Our results corroborate those of Vitali *et al.* (2017), fir trees at higher altitude (>800m) had higher resilience and resistance indices that those growing lower down. Recovery, however, was the same at both elevations considered in this study. In 2003, we saw a positive effect of increasing tree mixture on all three indices, fir trees growing in mixed and admixed stands shown higher recovery, resilience and resistance to drought than those in monoculture (H2, Fig.6).

Scots pine

Confirming recent findings (Castagneri et al., 2015; González de Andrés et al., 2017a; Matías et al., 2017), radial growth of Scots pine in our study area was found to be positively correlated with late winter and spring temperature, as well as with precipitation in June (Fig. S4). Moreover, LMER analysis revealed high sensitivity of this species to increasing summer temperature and drought (Fig. 4). Scots pine has been shown to benefit from increasing spring temperature, but it also experiences summer drought-related stress (González de Andrés et al., 2017a; Matías et al., 2017; Thabeet et al., 2009). Scots pine responses to climate change vary across latitudinal and altitudinal gradients (Matías et al., 2017), however. While trees from northern populations respond positively to increasing summer temperature, the opposite effect was observed in southern Mediterranean. Similarly, trees growing at high-altitude sites react positively to summer temperature, whereas negative effects prevail in lower-altitude populations (Matías et al., 2017).

Due to the distribution of pine in our area, we could describe long-term variation of its BAI only at elevations of less than 800 m a.s.l. Radial growth of pine trees in the study region showed a mildly decreasing trend over the past century (Fig. 3), indicating that environmental conditions at low elevation correspond to those at the trailing edge of Scots pine distribution in Europe. Similarly, Matías *et al.* (2017) predict that radial growth of pine will decrease at low-altitude sites in the near future. Increasing summer temperature (Fig. S5) may be the reason behind the decreases of growth rate of this species (González de Andrés et al., 2017a). It is also possible that the negative BAI trend of Scots pine in our study area was partly caused by the change of management towards single tree selection forest management. Pine, as the most light demanding of investigated species, is likely to be negatively affected by increasingly closed canopy. Negative impact of the change of forest management on this species is supported by the very low cover of pine regeneration compared to the vigorous regrowth of beech, fir and spruce (Fig. S11). Extreme climatic events could play a contributing role, resilience and resistance indices describing BAI reaction to the 1976 drought are significantly smaller than 1 and so is the resistance index in 1952 (Fig. 5).

Norway spruce

Tree ring width records show that, at the beginning of the 20th century, Norway spruce was by far the most productive of the four species in this region. Spruce radial growth was more than twice that of pine or beech and considerably higher than that of fir. This did not last, we observed a continuous decline of spruce growth, with no detectable change of trend due to increasing pollution (1970–90) or subsequent clean up (mid 1990's onwards). Norway spruce at this location did not benefit from an extensive transition to single tree selection management either, resulting in the lowest current productivity of all considered species. A leading thesis posits that Norway spruce is the least adapted to climate warming and drying when compared to the other species considered here, spruce has been suggested to be more drought-sensitive than co-occurring silver and Douglas fir (Vitali et al., 2017). Indeed, spruce has repeatedly been shown to be limited by summer drought, possibly due to its shallow root system (Kolář et al., 2017). This leads to beech, but also fir, outperforming spruce trees in competition for soil nutrients and available water which has been reduced due to recent climate change (Bolte and Villanueva, 2006).

Our observations of continuous decline of Norway spruce radial growth are in contradiction with several studies that report its recovery following the reduction of air pollution in the

1990s (Cienciala et al., 2018; Hauck et al., 2012; Kolář et al., 2015). There is no clear explanation for this interesting finding, the most likely is a combination of several factors of rapid environmental change which renders the area unsuitable for Norway spruce. Despite significant reduction of atmospheric pollution loading after 1990, concentration of heavy metals such as mercury and arsenic remains high in the upper soil layer (Fig. S12-S14; Čurlík and Šefčík, 2012). In this region, a relatively high amount of sulphur was found in spruce needles (Maňkovská, 1991) and trees were heavily affected by both Honey fungus (*Armilaria mellea* (Vahl) P. Kumm) and bark beetle (*Ips typographus* L.) (Jakuš, 1998). Although we can exclude the bark beetle, having cored only trees with no sign of attack, it has been argued that spruce weakened by pollution and biological agents is more susceptible to climate warming and drought stress (Cienciala et al., 2017). Some recent studies show that spruce not affected by air pollution and soil contamination can benefit from warmer but not drier conditions (Cienciala et al., 2018; Kolář et al., 2015). This suggests that trends described at continental scale may not be applicable to all populations and local environmental factors must always be considered.

Over the last century, the growth rate of spruce populations has collapsed along the entire altitudinal gradient considered in this study (500–1100 m a.s.l.). Hlásny *et al.* (2011) modelled tree growth under climate change and suggested that spruce productivity will increase at elevations of over 1,200 m a.s.l.in Central Europe by the end of the 21st century. Looking at resilience and resistance indices describing effects of 1976, 1992 and 2003 droughts on Norway spruce at both higher and lower elevations (Fig. 5), predictions of future spruce productivity at high elevation might need to be reconsidered in locations where the species seems to inhabit an increasingly unsuitable climatic envelope.

Conclusions

Our results show significant shifts in radial growth of four tree species during the last hundred years or so. At the beginning of the 20th century, the population of Norway spruce in the study area started as the most productive, only to end up as the least productive today. Silver fir and European beech have responded positively to recent environmental change, suggesting much better productive potential under near-future climate. We saw limited evidence of the positive role of tree species diversity in increasing tree productivity, apart from much better recovery, resistance and resilience of fir BAI in relation to the 2003 drought when growing in mixtures. The study highlights the utility of dendrochronological studies for investigating future suitability of species and the need to carry out such studies with regional or local focus as observations from large-scale trends are not likely to be replicated across distributional ranges of tree species.

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Supplementary Material

Table S1 Analysis of variance of the linear mixed-effect model (Eq. 2) for the four species. R^2 total includes the variance explained by the random factor while R^2 fixed is the variance explained solely by the fixed factors. AIC is the Akaike Information Criterio.

Table S2 Multiple comparisons of linear mixed model to test the differences in resilience, resistance and recovery indices between species within altitudinal zones. The LME included interaction between species and altitudinal zones. Tukey test using “glth” function in “multcomp” R package was used.

Table S3 Multiple comparisons of linear mixed model to test the differences in resilience, resistance and recovery indices between mixture variants for the four species. The LME included interaction between species and altitudinal zones. Tukey test using “glth” function in “multcomp” R package was used.

Figure S1 Aerial photography of the study area taken in 1950 and 2013 to compare changes in forest cover during the intervening period.

Figure S2 Diameter at breast height (DBH) distribution of European beech, Scots pine, Silver fir and Norway spruce trees growing at the site in defined mixture types.

Figure S3 Diameter at breast height (DBH) distribution of European beech, Scots pine, Silver fir and Norway spruce trees growing at the site split by altitude category (Lower – below to 800 m a.s.l. and Higher – above 800 m a.s.l.)

Fig. S4 Responses of silver fir (A1: lower, A2: higher altitude); European beech (B1: lower, B2: higher altitude); Norway spruce (C1: lower, C2: higher altitude) and Scots pine (D1: lower altitude) to climate variation. Modified exponential function (MEF) was used to remove non-climatic variation from the TRW series. Ring-width indices (RWI) were then obtained for individual TRW series by calculating the ratio between ring width and the fitted values of the MEF. Finally, bootstrapped correlation function in R package "bootRes" (Zang and Biondi, 2013) was used to identify significant responses. Fir trees was found to be significantly driven by summer temperature and drought (sc-Palmer Drought Index). No differences in responses were observed between the contrasting altitudinal categories. Spruce trees at the lower altitudes (<800 m a.s.l.) were found to negatively respond to summer temperature of the year in which the tree ring is formed as well as to summer temperature of the previous year. The species negatively reacted to summer drought of the previous year. In contrast, spruce at higher elevations showed no reaction to climate variation. Pine trees were found to positively respond to late winter temperatures (January to March) and June precipitation totals.

Figure S5 Long-term trends of temperature and precipitation with identification of major abrupt climate events (high temperature and less precipitation at the same time) at the higher (1000 m a.s.l.) and lower (600 m a.s.l.) elevations above sea level during the study period.

Figure S6 Regression coefficients of a linear mixed-effects model contrasting how current year basal area increment of four tree species is affected by competition, climate and species diversity. The competition is represented by crown quality classes and species diversity by the Shannon's diversity index. Since the interpretation of the main effects when testing interaction terms can be misleading, only the estimates of the interaction terms are presented. The whiskers denote the 99% confidence intervals.

Figure S7 Interactive effects of diameter at breast height (DBH) and temperature (jun-aug) on basal area increment (BAI) of silver fir, European beech, Norway spruce and Scots pine.

Figure S8 Interactive effects of diameter at breast height (DBH) and summer precipitation (jun-aug) on basal area increment (BAI) of silver fir, European beech, Norway spruce and Scots pine.

Figure S9 Interactive effects of Shannon's diversity index and temperature (jun-aug) on basal area increment (BAI) of silver fir, European beech, Norway spruce and Scots pine.

Figure S10 Interactive effects of crown quality index (0-1) and temperature (jun-aug) on basal area increment (BAI) of silver fir, European beech, Norway spruce and Scots pine.

Figure S11 Proportion of plots with regeneration of each species (left axis) and the average cover of regeneration within the plots where it occurred (right axis). Natural regeneration was visually assessed on each of 344 sample plots at the time of taking core samples.