

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

Article

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

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13

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

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

17

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19 **Abstract**

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

35 **Introduction**

36 Anthropogenic climate change has been identified as an important driver of functioning and
37 productivity of forest ecosystems, which contribute to the global carbon cycle (Ciais et al.,
38 2005; Frank et al., 2015; Parmesan et al., 2003). Many tree species are expected to experience
39 range shifts accompanied by population extinctions within a specific locality in the medium to
40 distant future (IPCC, 2014; Lenoir et al., 2009; Thomas et al., 2004). Local forests are,
41 however, primarily affected by intra- and inter-specific competition (Coomes and Allen,
42 2007), forest management (Bosela et al., 2016b; Johnson and Curtis, 2001), as well as
43 nitrogen deposition (Solberg et al., 2009) and pollution (Wang et al., 2016). With reference to
44 a long history of (mis)management of European forests, only few existing forest ecosystems
45 resemble their natural state (Sabatini et al., 2018).

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

60 the most widespread across Europe, Scots pine is another important contributor to ecological
61 and economic functioning and productivity of current forests (Matías et al., 2017; Matías and
62 Jump, 2012), where the species naturally co-occurs with Norway spruce (Pretzsch et al.,
63 2015).

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

78 Predicted changes in the productivity, as well as survival and competitive behaviour of forest
79 tree species will be relevant for adapting their management practices to future environmental
80 and climatic changes (Kirilenko and Sedjo, 2007). A set of new silvicultural management
81 strategies must therefore be developed to safeguard the provision of ecosystem services,
82 including timber production. Forest management mainly operates at stand or even sub-stand
83 level and requires information relating to local conditions. Therefore, to be truly informative
84 for management, regional investigations using appropriate sampling designs may be

85 preferable to inference on the basis of generalised observations (Law, 2015). Should climate
86 change force a large-scale transformation of Norway spruce monocultures in Europe,
87 mixtures of Silver fir, European beech and Scots pine, among other species, may be well-
88 suited to certain localities. Similar tree mixtures are likely to perform differently across a wide
89 range of ecological settings with varying climate conditions, information that relates forest
90 productivity to climate variability must therefore be tailored to local scales to support
91 evidence-based management decisions.

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

102

103 **Material and Methods**

104 **Study area**

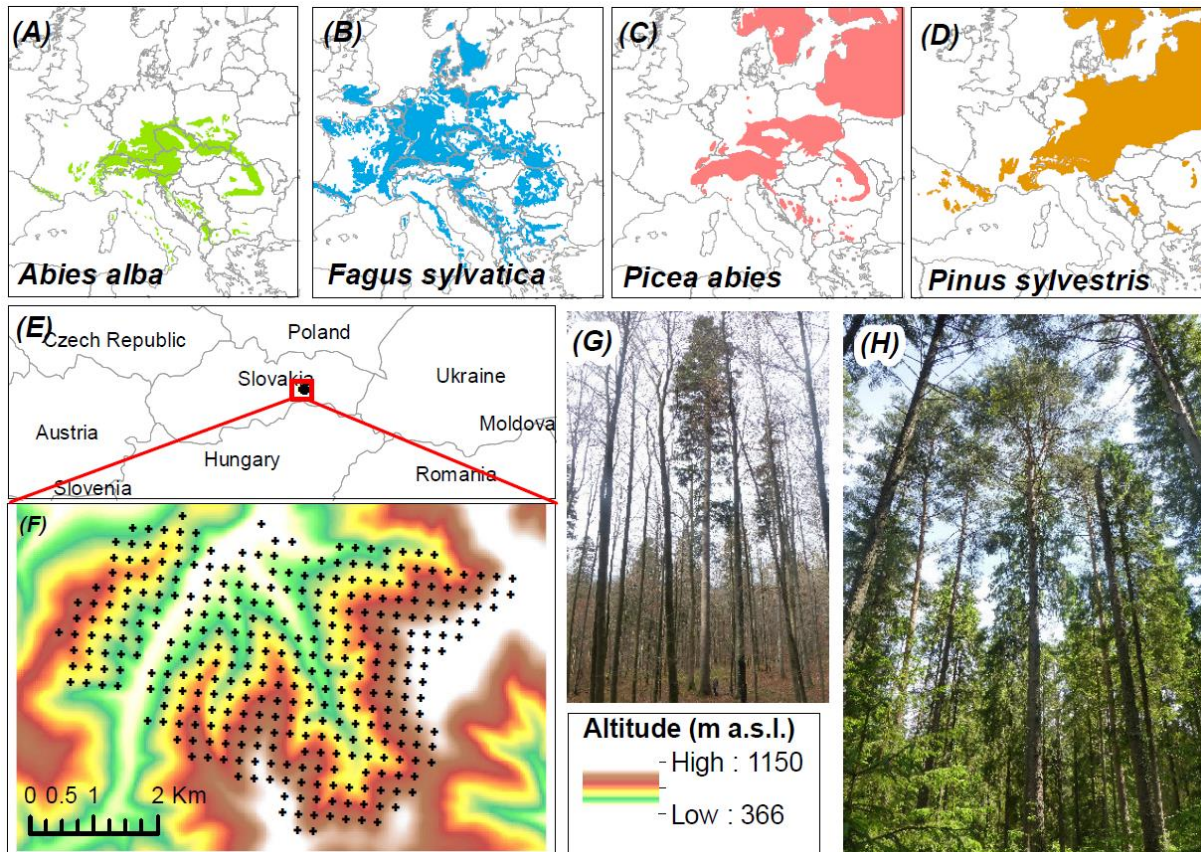
105 The study area of 2,128 hectares is located in the Slovakian part of the Carpathian Mountains
106 (Fig. 1). A single-tree selection management system (individual mature trees removal in
107 support of natural regeneration) has been applied to all forest stands in this locality since the
108 1950s (Saniga and Bruchánik, 2009), and the area is listed by the Pro Silva foundation that

109 promotes continuous-cover forestry and sustainable forest management (www.prosilva.org).
 110 With the exception of some valley bottoms, the area was almost fully forested at the point of
 111 conversion to the individual selection system, and the conversion has resulted in a further
 112 increase in forest cover (Fig. S1). The area, in which 11 different tree species were recorded,
 113 is characterised by heterogeneous topography between 366 and 1150 m a.s.l. on phylit-
 114 derived cambisol soils. Mean annual temperature is around 5 °C and annual precipitation
 115 totals are approximately 950 mm. The area is dominated by mixed forests of European beech,
 116 silver fir, Norway spruce, and Scots pine, with a minor admixture of ash (*Fraxinus excelsior*
 117 L.), sycamore (*Acer pseudoplatanus* L.) and larch (*Larix decidua* Mill.). Forests in the area
 118 are characterised by a high spatial variability of stand ages, mean stand diameters, species
 119 composition and stand densities (Table 1). Potential productivity of the species investigated in
 120 this study, as indicated by the site index (locally defined as stand height at standard age of 100
 121 years), is broadly similar (Table 1).

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

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

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



126

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

130

131 **Inventory plots**

132 Forest inventory plots (IP) were established in 2014, when a regular grid of 250×250 m was
 133 superimposed over the study area. A total of 344 variable-sized circular plots, with a radius
 134 ranging from 5 to 20 m to include 20–30 trees, were centered on the intersection points of the
 135 grid. Diameter at breast height (DBH), height and crown length of all trees within each plot
 136 were measured in 2014. We calculated the Shannon Diversity Index (SDI; Shannon 1948) to
 137 describe tree species diversity of each IP, taking into account the overall tree species
 138 presence. SDI was preferred to other indices as it accounts for both species richness and
 139 species evenness (Purvis and Hector, 2000). Tree species dominance within each plot was

140 classified as: pure (% proportion of volume >75%), mixed (% proportion of volume 25–75%)
141 and admixed (% proportion of volume <25%). Crown quality, an indicator of tree vigour and
142 past competition interactions, was visually assessed for each tree (A – well developed and
143 symmetrical crown with defoliation not exceeding 30%; B – middle developed crown under
144 higher inter-tree competition with defoliation between 30 and 60%; C – less developed, sparse
145 and/or damaged crown with defoliation above 60%). All plots were assigned to two altitudinal
146 categories: lower (≤ 800 m a.s.l.) and higher (> 800 m a.s.l.).

147 **Tree-ring data**

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

163 **Climate indices**

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

179 **Resilience, resistance and recovery measures**

180 To quantify effects of major summer droughts on the growth of the four forest species, we
181 calculated resistance, resilience and recovery indices from our TRW data (Lloret *et al.*, 2011).
182 We combined the information obtained from local weather station data and reviewed recent
183 publications (Ciais *et al.*, 2005; Parry *et al.*, 2012; Spinoni *et al.*, 2015) to identify years with
184 abnormal summer droughts. Here, resistance is defined as the capacity to retain pre-
185 disturbance growth during a disturbance event, calculated as the ratio of growth rate during to
186 that before an extreme event. Resilience is defined as the capacity to return to pre-disturbance
187 growth levels, estimated by the ratio of post-disturbance growth to that prior to the event.
188 Finally, recovery describes the ability of tree growth to recover from a disturbance-driven

189 suppression, expressed as the ratio of increment after over that during disturbance event. We
190 calculated all three indices for all sampled trees to describe the reaction of tree species to
191 major European heat waves and drought spells in the period of 1950–2003. We used a period
192 of three years before and after the events to quantify these indices (e.g. Gazol *et al.* 2016). We
193 further used Tukey’s multiple comparisons using “glht” function in “multcomp” R package
194 (Hothorn *et al.*, 2008) to test for statistical significance of the differences between species and
195 altitudinal and mixture categories (Dushoff *et al.*, 2019).

196 **Mixed-effects models**

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

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

211 Furthermore, a linear mixed-effects model (LMER) in the R package “lme4” (Bates *et al.*,
212 2015) was applied to estimate the effects of DBH, spring and summer temperature, as well as

213 precipitation (Fig. S4), and the crown length-to-height ratio or crown quality classes,
 214 representing indicators of past competition and tree vigour (Drobyshev et al., 2007) on annual
 215 BAI variation. Between-variable interaction terms were used to assess how the effect of one
 216 factor varies along the levels of another factor.

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

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

$$\begin{aligned}
 222 \quad (a) \quad BAI_{ij} = & b_0 + b_1 \ln(dbh_{ij}) + b_2 \ln(dbh_{ij}) \times T_{jun-aug} + b_3 CR_{ij} + b_4 T_{jun-aug} \times CR_{ij} + \\
 223 \quad & b_2 \ln(dbh_{ij}) \times T_{mar-may} + b_2 \ln(dbh_{ij}) \times P_{jun-aug} + b_2 \ln(dbh_{ij}) \times P_{mar-may} + SPprop + \\
 224 \quad & SPprop \times T_{jun-aug} + (1/IDPlot_j/IDTree_{ij}) \quad (Eq. 1)
 \end{aligned}$$

225

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

$$\begin{aligned}
 228 \quad (b) \quad BAI_{ij} = & b_0 + b_1 \ln(dbh_{ij}) + b_2 \ln(dbh_{ij}) \times T_{jun-aug} + b_3 CR_{ij} + b_4 T_{jun-aug} \times CR_{ij} + \\
 229 \quad & b_2 \ln(dbh_{ij}) \times T_{mar-may} + b_2 \ln(dbh_{ij}) \times P_{jun-aug} + b_2 \ln(dbh_{ij}) \times P_{mar-may} + H' + H' \times T_{jun-} \\
 230 \quad & aug + (1/IDPlot_j/IDTree_{ij}) \quad (Eq. 2)
 \end{aligned}$$

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

$$\begin{aligned}
 235 \quad (c) \quad BAI_{ij} = & b_0 + b_1 \ln(dbh_{ij}) + b_2 \ln(dbh_{ij}) \times T_{jun-aug} + b_3 CQ_{ij} + b_4 T_{jun-aug} \times CQ_{ij} + \\
 236 \quad & b_2 \ln(dbh_{ij}) \times T_{mar-may} + b_2 \ln(dbh_{ij}) \times P_{jun-aug} + b_2 \ln(dbh_{ij}) \times P_{mar-may} + H' + H' \times T_{jun-} \\
 237 \quad & aug + (1/IDPlot_j/IDTree_{ij}) \quad (Eq. 3)
 \end{aligned}$$

238 Where

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

240 $T_{\text{jun-aug}}$ – mean temperature anomaly of the June-August period (anomaly calculated against the mean
 241 summer temperature in the period of 1901 – 1980 used as the reference climate before the
 242 recent climate warming)

243 $T_{\text{mar-may}}$ – mean temperature anomaly of the March-May period (anomaly calculated against the mean
 244 summer temperature in the period of 1901 – 1980 used as the reference climate before the
 245 recent climate warming)

246 $P_{\text{jun-aug}}$ – precipitation totals of the June-August period (anomaly calculated against the mean summer
 247 temperature in the period of 1901 – 1980 used as the reference climate before the recent climate
 248 warming)

249 $P_{\text{mar-may}}$ – precipitation totals of the March-May period

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

251 $SPprop$ – species proportion calculated from tree basal area

252 H' – Shannon’s diversity index

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

254

255 Tree identity nested within sample plot was used as a random factor in all model variants.

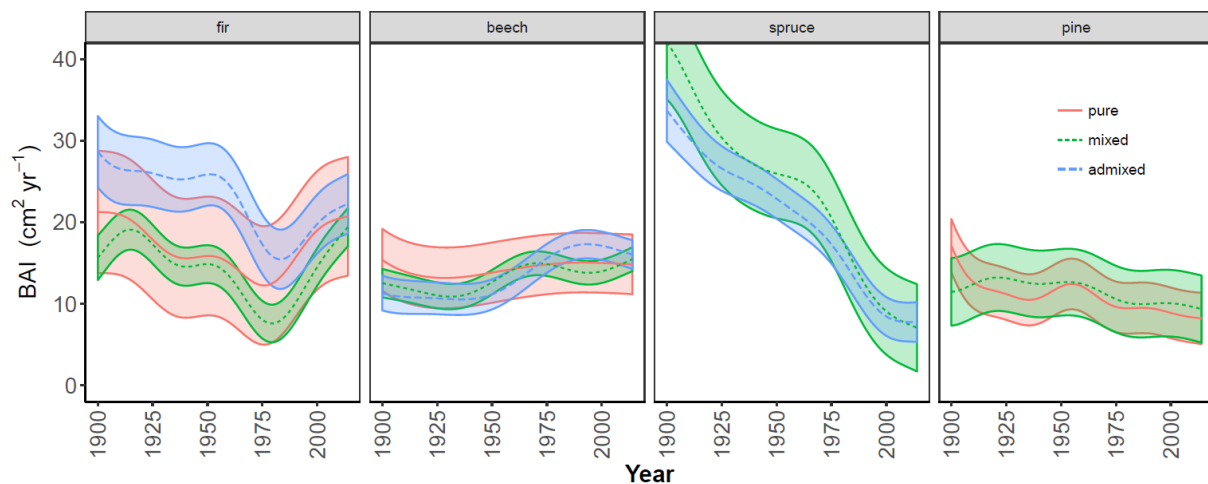
256 Marginal effects of interaction terms were calculated using the “effect” function in R “effects”
 257 package (Fox et al., 2015). When calculating the individual interaction effects, all remaining
 258 covariates were set to the mean. A “sjp.int” function in “sjPlot” R package (Lüdecke and
 259 Schwemmer, 2017) was used for visualisation of the effects. Both mean and standard
 260 deviation were used as moderator variables when plotting the interaction effects.

261

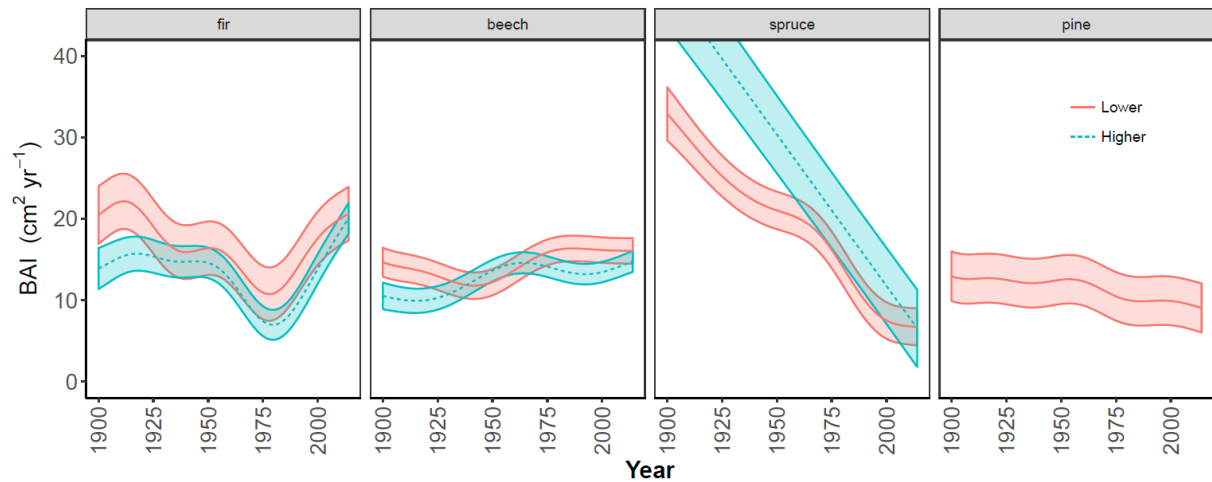
262 **Results**

263 Over the last 100 years, each of the four tree species investigated in this study exhibited very
 264 contrasting BAI patterns (Fig. 2 and 3). At the beginning of the 20th century, spruce revealed
 265 the fastest growth rate (app. $35 \pm 3.3 \text{ cm}^2 \text{ yr}^{-1} \text{ tree}^{-1}$), but following a steady decline the species

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



279
 280 **Figure 2** Individual tree Basal Area Increment (BAI) of fir, beech, spruce and pine trees normalised to
 281 standard DBH of 22 cm. Lines represent smoothed mean of trees classified as growing in a pure or
 282 mixed stand, or as an admixture, bands represent 95% confidence intervals.

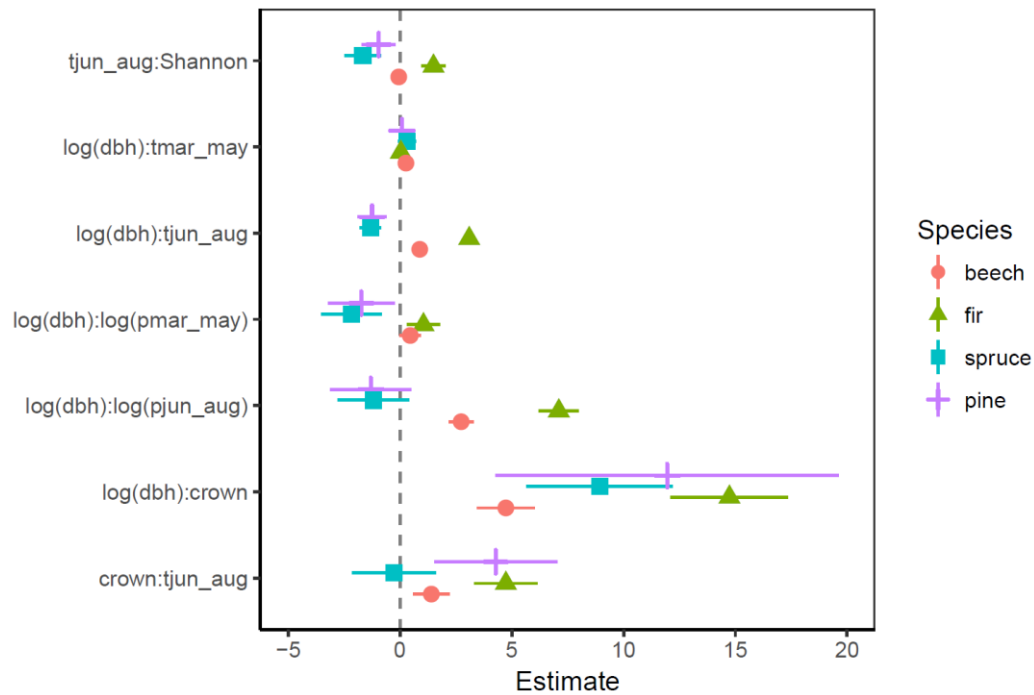


283

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

287

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



299

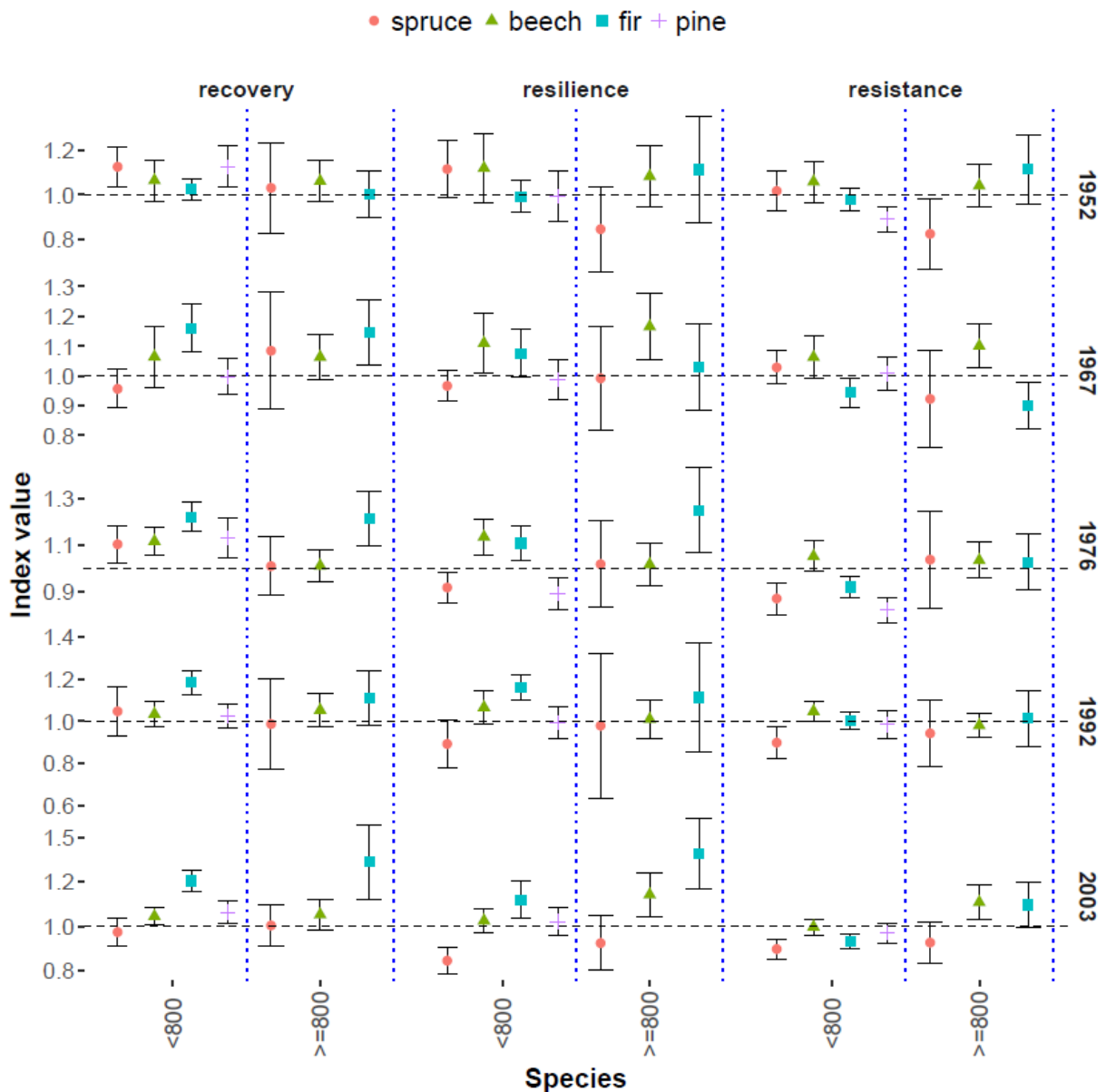
300 **Figure 4** Regression coefficients of a linear mixed-effects model contrasting how current year basal
 301 area increment of four tree species is affected by competition, climate and species diversity. The
 302 competition is represented by crown length-to-tree height ratio and species diversity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

306

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

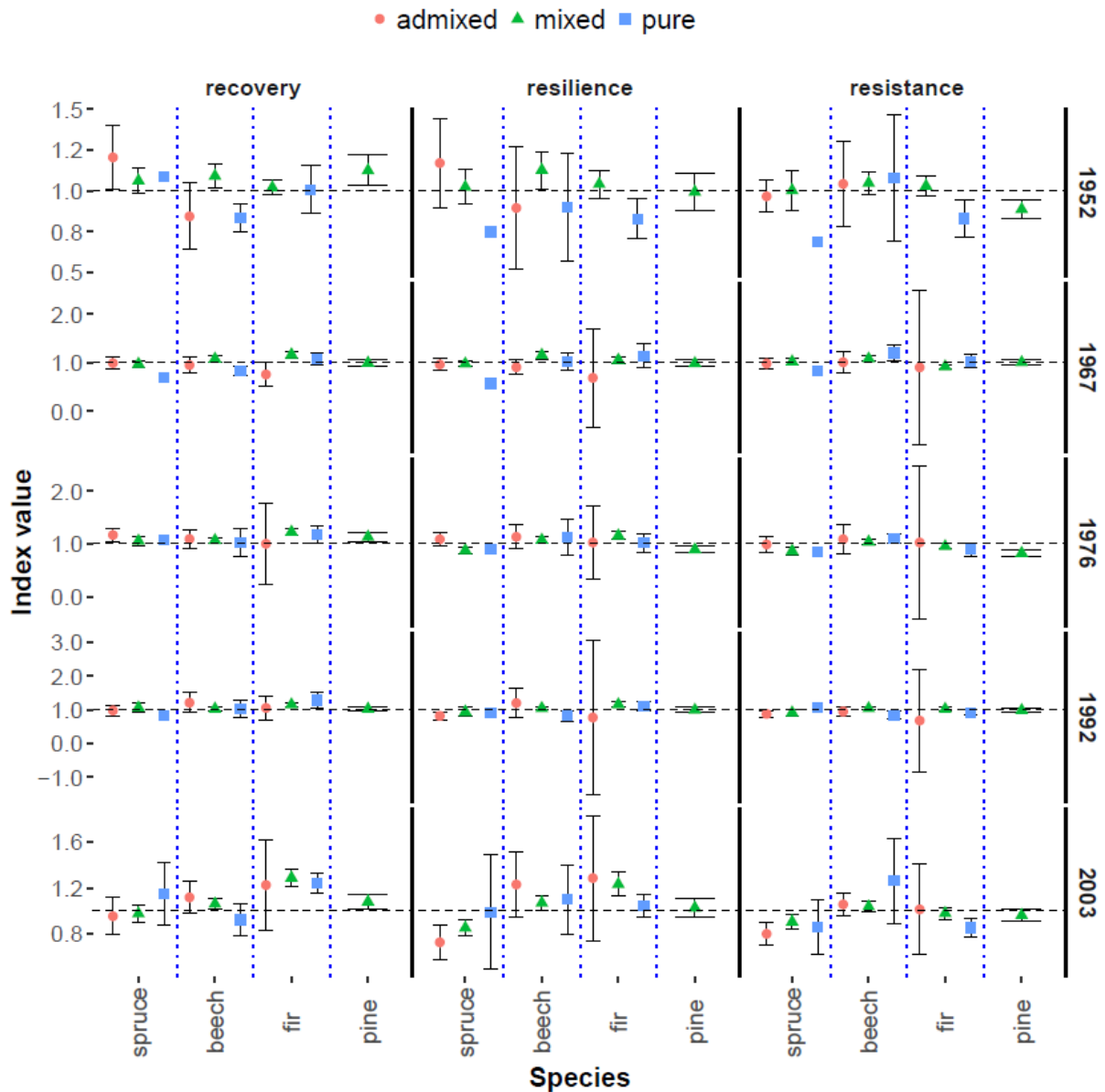
312 Crown size affected the BAI and BAI-climate responses. In general, larger crowns were
 313 associated with greater BAI, but the effects of crown on the growth-climate sensitivity
 314 differed among the species, from no effect in spruce to the greatest effects in pine and fir (Fig.
 315 S10).

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



321

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



324

325 **Figure 6** Recovery, resilience and resistance of the BAI of the four species in the three species

326 mixture categories (<800 and >800 m a.s.l.). The whiskers denote 95% confidence intervals.

327 In summary, this study shows that over the past century a) Norway spruce was the most

328 sensitive to changing conditions, b) thus far, silver fir benefitted from climate warming and

329 rapid reduction of air pollution, c) species mixture had only small effect on long-term growth

330 changes and trees resilience to drought events in the period 1952–2003, but d) species

331 diversity played crucial role in driving BAI responses to climate changes.

332

333 **Discussion**

334 Recent studies that describe effects of climate change on growth of European tree species
335 paint a very unclear picture. A range of responses is reported, for example (i) both enhanced
336 and reduced growth of spruce after the rapid reduction of air pollution in 1990s (Cienciala et
337 al., 2017; Hauck et al., 2012; Jonard et al., 2012; Kolář et al., 2015); (ii) both increased and
338 decreased growth rates of beech in Central Europe during the last two decades (Dittmar et al.,
339 2003; Pretzsch et al., 2014) and at the southern edge of its distribution range (Jump et al.,
340 2006; Tegel et al., 2014); and (iii) both faster and slower growth rate of Scots pine across
341 Europe (Castagneri et al., 2015; Matías et al., 2017). Spatial and temporal variability of
342 growth patterns uncovered so far calls for a strong focus on local- and regional-scale
343 investigations. A detailed description of growth patterns within a given locality can yield
344 information valuable to foresters, especially when used in conjunction with climate change
345 predictions for the area in question. In order to devise a sampling strategy and to test its
346 potential for generating data fully representative of local populations and to serve as a basis
347 for management recommendations (Babst et al., 2018; Nehrbass-Ahles et al., 2014), we
348 overlaid a systematic distribution of sample plots across an area covering an entire forest
349 management unit.

350 **European beech**

351 So far, beech trees in the region have benefited from recent environmental change, especially
352 at the lower altitude. No sign of a decrease in radial growth rate was identified by this
353 investigation, which is in line with other recent studies from Central Europe, based either on
354 data from long-term forest inventories (Bosela et al., 2016b; Pretzsch et al., 2014) or on
355 growth simulations (Hlásny et al., 2011). However, a recent Europe-wide study showed that
356 beech growth rates have been declining on many sites across its distribution in the past 20–30

357 years (Bosela et al., 2018). Beech is considered a drought-sensitive species, likely to be
358 limited by increasing frequency or severity of summer droughts (Di Filippo et al., 2007).
359 However, mean resistance, resilience and recovery indices, covering extreme drought events
360 in the period between 1950 and 2003, show that beech was not negatively affected by these
361 events at our location – values of all indices are higher than one. Remarkably, and contrary to
362 our expectations, the resilience and recovery of beech BAI at lower altitude was higher than
363 that at higher elevations (Fig. 5). Tree mixture did not modify the response of beech to
364 extreme drought (H2, Fig. 6). Similarly, the facilitation effect of inter-specific interactions
365 was not confirmed in a recent study of González de Andrés *et al.* (2017b). The authors
366 explained the lack of facilitation at their Mediterranean site by severe competition for water
367 preventing any manifestation of the beneficial effect of a mixture with Scots pine. In contrast
368 to the Mediterranean, the region of our study is normally well-supplied with water, but still no
369 beneficial effect of admixture was found in beech. Interestingly, the copious natural
370 regeneration of beech across the researched area (Fig. S11) suggests suitable site conditions
371 for this species at the present.

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

381 growth of beech. However, contrary to our study, they did not find any relationship between
382 radial growth and summer temperature, suggesting a regional variation in climate sensitivity.

383 **Silver fir**

384 Paleoecological records suggest that silver fir was growing under significantly warmer
385 conditions than those experienced by its current populations in Europe (Büntgen et al., 2014;
386 Ruosch et al., 2016; Tinner et al., 2013). Recent studies exploring radial growth of European
387 silver fir consistently confirm a strongly negative effect of SO₂ emissions, which peaked
388 during 1970–90 and caused a large-scale growth depression across Europe (Büntgen *et al.*
389 2014, Bošel'a et al., 2014; Elling et al., 2009). Our results confirm this trend, the coincidence
390 of the period of minimum growth and that of peak pollution is stark. The reduction of acid
391 deposition, along with the observed 'warming-without-drying' change of climatic conditions
392 allowed fir to recover (Büntgen et al., 2014) and, in central Europe, to reach growth rates
393 nearly as high as those at the beginning of the 20th century (Fig. 2).

394 Recent evidence suggests that silver fir may grow even better and have lower climate
395 sensitivity when growing in a mixture with other tree species (Lebourgeois et al., 2013),
396 overyielding when compared to pure fir alternatives (Toïgo et al., 2015). However, our results
397 do not support this hypothesis, data describing fir growth in the post-acidification recovery at
398 the beginning of the 21st century do not show any difference between trees growing in pure
399 and mixed stands (H2, Fig. 2). Vitali *et al.* (2017) have shown that fir trees growing at lower
400 altitude in South-Western Germany are more drought-prone when compared to those at higher
401 altitudes. They also assessed fir drought sensitivity by focusing on drought events of 1976 and
402 2003 using resilience and recovery as response variables. Our results corroborate those of
403 Vitali *et al.* (2017), fir trees at higher altitude (>800m) had higher resilience and resistance
404 indices that those growing lower down. Recovery, however, was the same at both elevations

405 considered in this study. In 2003, we saw a positive effect of increasing tree mixture on all
406 three indices, fir trees growing in mixed and admixed stands shown higher recovery,
407 resilience and resistance to drought than those in monoculture (H2, Fig.6).

408 **Scots pine**

409 Confirming recent findings (Castagneri et al., 2015; González de Andrés et al., 2017a; Matías
410 et al., 2017), radial growth of Scots pine in our study area was found to be positively
411 correlated with late winter and spring temperature, as well as with precipitation in June (Fig.
412 S4). Moreover, LMER analysis revealed high sensitivity of this species to increasing summer
413 temperature and drought (Fig. 4). Scots pine has been shown to benefit from increasing spring
414 temperature, but it also experiences summer drought-related stress (González de Andrés et al.,
415 2017a; Matías et al., 2017; Thabeet et al., 2009). Scots pine responses to climate change vary
416 across latitudinal and altitudinal gradients (Matías et al., 2017), however. While trees from
417 northern populations respond positively to increasing summer temperature, the opposite effect
418 was observed in southern Mediterranean. Similarly, trees growing at high-altitude sites react
419 positively to summer temperature, whereas negative effects prevail in lower-altitude
420 populations (Matías et al., 2017).

421 Due to the distribution of pine in our area, we could describe long-term variation of its BAI
422 only at elevations of less than 800 m a.s.l. Radial growth of pine trees in the study region
423 showed a mildly decreasing trend over the past century (Fig. 3), indicating that environmental
424 conditions at low elevation correspond to those at the trailing edge of Scots pine distribution
425 in Europe. Similarly, Matías *et al.* (2017) predict that radial growth of pine will decrease at
426 low-altitude sites in the near future. Increasing summer temperature (Fig. S5) may be the
427 reason behind the decreases of growth rate of this species (González de Andrés et al., 2017a).
428 It is also possible that the negative BAI trend of Scots pine in our study area was partly

429 caused by the change of management towards single tree selection forest management. Pine,
430 as the most light demanding of investigated species, is likely to be negatively affected by
431 increasingly closed canopy. Negative impact of the change of forest management on this
432 species is supported by the very low cover of pine regeneration compared to the vigorous
433 regrowth of beech, fir and spruce (Fig. S11). Extreme climatic events could play a
434 contributing role, resilience and resistance indices describing BAI reaction to the 1976
435 drought are significantly smaller than 1 and so is the resistance index in 1952 (Fig. 5).

436 **Norway spruce**

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

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

453 1990s (Cienciala et al., 2018; Hauck et al., 2012; Kolář et al., 2015). There is no clear
454 explanation for this interesting finding, the most likely is a combination of several factors of
455 rapid environmental change which renders the area unsuitable for Norway spruce. Despite
456 significant reduction of atmospheric pollution loading after 1990, concentration of heavy
457 metals such as mercury and arsenic remains high in the upper soil layer (Fig. S12-S14; Čurlík
458 and Šefčík, 2012). In this region, a relatively high amount of sulphur was found in spruce
459 needles (Maňková, 1991) and trees were heavily affected by both Honey fungus (*Armillaria*
460 *mellea* (Vahl) P. Kumm) and bark beetle (*Ips typographus* L.) (Jakuš, 1998). Although we can
461 exclude the bark beetle, having cored only trees with no sign of attack, it has been argued that
462 spruce weakened by pollution and biological agents is more susceptible to climate warming
463 and drought stress (Cienciala et al., 2017). Some recent studies show that spruce not affected
464 by air pollution and soil contamination can benefit from warmer but not drier conditions
465 (Cienciala et al., 2018; Kolář et al., 2015). This suggests that trends described at continental
466 scale may not be applicable to all populations and local environmental factors must always be
467 considered.

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

476

477 **Conclusions**

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

489

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496

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768

769 **Supplementary Material**

770 **Table S1** Analysis of variance of the linear mixed-effect model (Eq. 2) for the four species.

771 R^2 total includes the variance explained by the random factor while R^2 fixed is the variance
772 explained solely by the fixed factors. AIC is the Akaike Information Criterion.

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

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

781

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

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

786 **Figure S3** Diameter at breast height (DBH) distribution of European beech, Scots pine, Silver
787 fir and Norway spruce trees growing at the site split by altitude category (Lower – below to
788 800 m a.s.l. and Higher – above 800 m a.s.l.)

789 **Fig. S4** Responses of silver fir (A1: lower, A2: higher altitude); European beech (B1: lower,
790 B2: higher altitude); Norway spruce (C1: lower, C2: higher altitude) and Scots pine (D1:
791 lower altitude) to climate variation. Modified exponential function (MEF) was used to remove

792 non-climatic variation from the TRW series. Ring-width indices (RWI) were then obtained for
793 individual TRW series by calculating the ratio between ring width and the fitted values of the
794 MEF. Finally, bootstrapped correlation function in R package “bootRes” (Zang and Biondi,
795 2013) was used to identify significant responses. Fir trees was found to be significantly driven
796 by summer temperature and drought (sc-Palmer Drought Index). No differences in responses
797 were observed between the contrasting altitudinal categories. Spruce trees at the lower
798 altitudes (<800 m a.s.l.) were found to negatively respond to summer temperature of the year
799 in which the tree ring is formed as well as to summer temperature of the previous year. The
800 species negatively reacted to summer drought of the previous year. In contrast, spruce at
801 higher elevations showed no reaction to climate variation. Pine trees were found to positively
802 respond to late winter temperatures (January to March) and June precipitation totals.

803 **Figure S5** Long-term trends of temperature and precipitation with identification of major
804 abrupt climate events (high temperature and less precipitation at the same time) at the higher
805 (1000 m a.s.l.) and lower (600 m a.s.l.) elevations above sea level during the study period.

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

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

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

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

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

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

824