

Climate change threatens on endangered relict Serbian spruce

Matteo Dell'Oro^{1,2*}; Milan Mataruga³; Ute Sass-Klaassen¹; Patrick Fonti²

¹ Forest Ecology and Forest Management Group, Wageningen University, Wageningen, Netherlands

² Swiss Federal Institute for Forest Snow and Landscape Research WSL, Birmensdorf, Switzerland

³ Faculty of forestry, University of Banja Luka. Bosnia and Herzegovina

* Corresponding author: matte.dello@hotmail.it

Abstract:

The increase in length and severity of drought events predicted for Southeast Europe are expected to engender important changes to its remaining native forest. To take informed management decision promoting their conservation, it is important to better understand their responses to environmental disturbances.

In this study we analyze tree-ring growth responses over a network of 15 sites of Serbian spruce (*Picea omorika*), an endemic relict conifer species of the Balkan region — with a natural range restricted to the canyon of the Drina river at the border between Serbia and Bosnia Herzegovina — and that has already shown signs of decline and dieback likely induced by climate change.

Tree-ring analyses spanning the common period from 1974 to 2016 have proved a strong growth reduction in the last 30 years and highlighted a negative growth response to summer drought, although the strength of the response differed among individuals, where younger trees and trees growing at lower altitude suffered more from drought.

Management practice, such as inter- and intra-specific thinning to reduce competition for water resources and enhance survival of seedlings, together with assisted natural regeneration and migration to more suitable habitats are recommended for the conservation of this relict species. The measures are even more necessary considering that this species is more vulnerable than others due to its weak capacity to naturally regenerate and compete.

Key words: *Picea omorika*, Global warming, Balkan region, Relict species, tree rings

32 Introduction

33 The Mediterranean Basin represents one of the most important hotspots of biodiversity on Earth (Médail
34 and Quézel, 1999; Fady-Welterlen, 2005). However, a rapid economic development, an increasing human
35 population and climate-change-induced environmental disturbances are creating unprecedented pressures
36 on the natural resources in the area. The Balkan region, hosting 7500 plant species, of which one third is
37 endemic (Aleksić and Geburek, 2014), including some relict tree populations, does not escape this threat.
38 General increase in temperature and decrease in precipitation together with the increased frequency and
39 severity of drought events represent a new threat for many tree species on the Balkan. Moreover, this region
40 is expected to undergo highest impacts in Europe, since the frequency, length and severity of droughts events
41 are expected to be stronger (Ivetić and Devetaković, 2016) in areas already coping with water scarcity
42 (Laušević et al., 2008). According to the IPCC (Intergovernmental Panel on Climate Change) scenario for
43 Bosnia and Herzegovina mean annual temperature will increase by 2,4 to 4 °C by the end of this century with
44 a 0 to -30% decline in precipitation regimes compared to the period 1961-1990 (UNDP , 2016).

45 These changes in climate are expected to strongly affect native forest ecosystems and first evidences of such
46 changes have already been already reported since the middle of the 19th century (Lindner et al., 2010). More
47 recently, signs of reduced growth and dieback have been mainly observed in coniferous tree species as spruce
48 and pine (Ivetić and Aleksić, 2016). These diebacks are often related to insect calamities, such as bark beetles,
49 which are suggested to be triggered by the ongoing climate change (e.g.; Allen et al., 2010). It is in particular
50 suggested, that drought periods, such the recent summer droughts in 2015 and 2018, lead to a physiological
51 weakening and enhanced susceptibility to disease and pests (Ivetić and Aleksić, 2016). Yet, little is known
52 about the long-term response to changing climate and climate extremes of relict and endangered native
53 forest trees species of in the Balkan region (Aleksić and Geburek, 2014).

54 Serbian spruce (*Picea omorika*) is one of these endemic and endangered relict conifer species. Its natural
55 range is restricted around the course of the Drina river, between Western Serbia and Eastern Bosnia and
56 Herzegovina (Ballian et al., 2016; Ivetić and Aleksić, 2016). Its actual habitat is restricted to hardly accessible
57 steep and rocky slopes mostly facing north, east and west on lime stone and serpentine bedrock at an
58 elevation ranging from 800 to 1500 m (Wardle, 1956; Ballian et al., 2016) characterized by a continental
59 climate with cold and snowy winter and by hot and dry summers. Few authors who have morphologically
60 and ecologically described the species (Ostojić and Dinić, 2009; Nikolić et al., 2015; Ballian et al., 2016; Ivetić
61 and Aleksić, 2016) characterised it as very heliophile and ideally requiring at least mean annual temperature
62 between 4 and 6 °C and yearly precipitation around 1000 mm. Due to anthropogenic factors such as forest
63 clearing or wildfires, together with poor competition capacity, physiological stress to global warming and a
64 higher susceptibility to disease, have strongly contributed to fragmentate the habitat of the species. For these
65 reasons, Serbian spruce has been officially listed on the red list of threatened species (Mataruga et al., 2011;

66 Aleksić and Geburek, 2014; IUCN, 2018). In the past few years Serbian spruce has also been in the focus of
67 several investigations, mostly genetic, oriented at clarifying the available genetic information and for
68 promoting its conservation (Ballian et al., 2006; Nasri et al., 2008; Aleksić et al., 2009; Aleksić and Geburek,
69 2014). In fact, Serbian spruce can for example hybridize with Sitka spruces (*Picea sitchensis* x *omorika*) and
70 display better juvenile frost resistance and vigour at poor sites (Ivetić and Aleksić, 2016). Current
71 conservation measures include both an assisted natural regeneration by removal of competitors to enhance
72 seedlings survival, and an assisted migration.

73 Conservation measures would much benefit by complementary knowledge of Serbian spruce's susceptibility
74 to future climate conditions. Since these native forests have hardly been considered for an active
75 management, there is very little information on the growth ecology of the species. In this study we use tree-
76 ring width measurements to assess climate-growth relationships of Serbian spruce at 15 sites along its native
77 range along the Drina river canyon with the aim of i) characterizing the long-term growth trend of populations
78 of different age, ii) identifying the main climatic drivers limiting growth within its native range, iii) quantifying
79 the vulnerability to extreme (drought) events among ages and locations.

80

81 **Materials and methods**

82

83 **Study area, site locations and sampling**

84 This study has been performed in the native area of occurrence of Serbian spruce (*Picea omorika*), at the
85 border between Serbia and Bosnia and Herzegovina (Fig. 1a). A total of 17 unmanaged stands were selected
86 across the native area and on different elevation (from 845 to 1541 m asl; Table 1). The climate of the area
87 is characterized by a continental climate characterized by mean annual temperature of 7-8 °C and well
88 distributed precipitation totaling ~950 mm (Fig. 1b). Over the last 100 years an increase of the annual
89 average temperature is observed while precipitation was slightly decreasing (Fig. 1c).

90 Sampling has been performed from June to August, 2018 on 11 to 35 dominant and healthy trees per sites.
91 In total 325 wood cores were collected at 1.3 m stem height using an increment borer. Cores were labelled
92 and stored in plastic straws and delivered to the Swiss Federal Institute for Forest, Snow and Landscape
93 Research WSL for further processing (i.e. surface preparation to increase the tree rings visibility and
94 measurement the annual increments). After this, only 15 out of 17 population were considered in further
95 analyses since sites 9 and 17 (Plistina and Bozurevac) were discarded due to insufficient number of replicates.

96

97 **Tree-ring width measurements and chronology building**

98 Tree-ring width (TRW) was measured on each collected core with a Lintab digital positioning table connected
99 to the TSAP-Win software (both RinntechH, 2010). Time series were first visually cross-dated and its quality
100 checked with the software Cofecha (Holmes, 1983). Site chronologies have been successively calculated by
101 removing non-climatic signal using a 10-year spline function applied to each time series to only maintain high
102 frequency variation. The obtained ring-width indices (RWI) have been averaged into a chronology for each
103 site.

104 To assess the common variation among individual detrended time-series at each site, we calculated, i) the
105 Gleichläufigkeit (Glk; which represents the percentage of common signs of year-to-year growth change
106 between series, Eckstein and Bauch, 1969), ii) the inter-series correlation (calculated as the average between
107 each series and a master chronology), and iii) the mean correlation between trees (r_{bar} , calculated as the
108 mean Pearson correlation coefficient of the tree-ring width time series at a site). Chronology building and
109 quality assessment have been performed using the R package *dp/R* (Bunn, 2008). Additionally, the mean ring
110 width and tree age (by considering the pith offsets) were also determined.

111

112 **Assessing growth responses to climate**

113 To identify the main climatic drivers of tree growth we assessed climate response analyses using the R (R
114 Core Team, 2018) package *Treeclim* (Biondi and Waikul, 2004; Zang and Biondi, 2015) by applying a
115 bootstrapped response function where the RWI chronologies are used as the dependent variable and the
116 monthly climatic data are the independent variables. The analyses only considered the period with sufficient
117 replicates, i.e. for the period 1974 to 2016.

118 As climatic variable we considered the monthly mean temperature, precipitation sum and the standardize
119 precipitation evapotranspiration index (SPEI) with a time-scale of three months. SPEI is a multiscale drought
120 index combining temperature and precipitation data, based on monthly water balances (Vicente-Serrano et
121 al., 2010). Temperature and precipitation were retrieved from the high-spatially resolved (30 arc sec) data
122 from CHELSA (Karger et al., 2017) and extended prior to 1979 (extended-CHELSA) by applying a transfer
123 function with the lower resolved Climatic Research Unit data (CRU, 0.5 degree; Harris et al., 2014) of the
124 corresponding grid cell. Site coordinates were assessed by averaging the longitude and latitude of the trees
125 belonging to the same population. The SPEI was calculated with the R package *SPEI* on the length of three
126 months (SPEI3) using the previously extracted CHELSA temperature and precipitation data. For the
127 calculation, we included only the monthly climate variables from June of the previous year to September of
128 the current year as well as the monthly average from March to May and from June to August. The significance
129 of the correlation coefficients was calculated by assessing the 95% confidence levels based on 1000 random
130 samplings with replacements.

131

132 **Analysis of growth responses to extreme years**

133 Growth responses to extreme drought events were assessed by comparing the changes in growth during the
134 extreme events and in the following years. Trees were categorised in three classes according to elevation
135 (LOW = 800 to 1000 m asl., MIDDLE = 1000 to 1200 m asl., and HIGH = 1200 to 1500 m asl.) and age: (YOUNG
136 < 80 years, MEDIUM = 81 to 160 years, and OLD > 161 years). Negative pointer years were selected when at
137 least 50% of trees featured a tree-ring width index decline of at least 40% compared to the average previous
138 five years using the R package *pointRes* (Van der Maaten-Theunissen et al., 2015). The response to extreme
139 years was assessed using the resilience parameters of Lloret et al., (2011), as:

140 - $Resistance = Dr/PreDr$

141 - $Recovery = PostDr/Dr$

142 - $Resilience = PostDr/PreDr$

143 where *PreDr* is the average tree-RWI five years before the drought year, *Dr* the tree-RWI in the drought year
144 and *PostDr* the average tree-RWI in the five years after the drought year.

145

146 **Results**

147

148 **Growth characteristics**

149 The 15 tree-ring width chronologies indicate that large differences in age and growth rates exist between
150 sites (Fig. 2a). The stand age ranged from 40-55 (1, 2, 3, 7, 8, 10, 12, 15, 16), to 120-150 years old stands (5
151 and 6). Few sites showed quite heterogeneity in tree age (4, 11, 13,14, Table 1). The average annual radial
152 growth ranged from a minimum of 0.92 mm (6) to a maximum of 2.27 mm (15) (Table 2) and in general it
153 was higher for younger stands (e.g.; 1, 3, 15, 16) than older stands (e.g.; 4, 5, 6, 11). The age-aligned regional
154 growth curves indicated that Serbian spruce generally reached a maximum growth rates at around 20 years
155 (Fig. 2b). Although few young (10, 15, 16) and old stands (4, 6, 11) clearly showed higher and respectively
156 lower maximum growth rates than average, all young stand seemed to experience a steeper and more
157 persistent growth decline than older ones. However, this difference could be related to the establishment
158 after a forest fire, when light availability in the beginning is high and after 20 years competition leads to
159 strong growth declines. Indeed, Fukarek (1951) mentions the occurrrnece of numerous forest fire in 1946-
160 1947 decimating the Serbian spruce populations. In older stands, the situation is most likely different since
161 we see a much slower juvenile growth indicating establishment e.g. in smaller gaps.

162 The similarity in growth patterns of trees within each site is consistently high. The Gleichläufigkeit values are
163 > 61%, denoting strong common signs of year-to-year growth change between the series of the same sites.

164 Moreover, both the inter-series correlation and the R_{bar} varied little among sites and showed strong values,
165 ranging between 0.47 and 0.69 for the inter-series correlation and between 0.36 and 0.63 for the R_{bar} . Sites
166 which are geographically close and/or belong to the same altitudinal band showed similar growth (see Fig.
167 3). The lowest correlation ($r=0.12$) was found between the young low-elevation stand at site 5 and the old
168 high-elevation stand at site 8.

169

170 **Climate-growth responses**

171 The climate-growth analysis over the common period from 1974 to 2016 indicated that Serbian spruce
172 growth is strongly related to summer conditions (Fig. 4a). The growth responses to precipitation and SPEI
173 were similarly strong. Correlation with SPEI showed higher absolute coefficients compared to correlation
174 with temperature, which is only significant for the summer (JJA). All the sites have a significant positive
175 correlation with SPEI3 in August (average drought index June, July and August) and precipitation in summer,
176 with coefficients values also above 0.6 ($p<0.05$), meaning that smaller rings are formed during drier
177 conditions. The composite chronology showed a positive, but non-significant relation with temperature in
178 the early growing season and a negative significant relation with summer mean temperature.

179 The climate-growth correlation on a 25-years moving window (Fig. 4b) indicated an increase of the SPEI3
180 correlation of September (water availability in July, August and September), which is significant from the
181 1980ies until present. This correlation was also highly significant at the beginning of the last century, then it
182 started to decrease around the 1930ies and 40ies, to increase again in the 1980ies. This means that trees
183 seem to have a longer growing season but at the same time are experiencing more drought during summer.
184 Also, the increase in correlation coefficient in April and May indicates the trees benefit, in terms of growth,
185 from the higher temperature during the first part of the growing season. The same conclusions can be drawn
186 looking at the temperature-growth correlation on the 25-years moving window, where an increase in the
187 negative influence of summer months appears for the last 50 years, as well as an increase in the negative
188 influence of May. Regarding the precipitation-growth correlation, positive and significance values for spring
189 and summer months indicate that growth is higher when precipitation regime are high.

190 All study sites show positive and significant correlation with SPEI3 in August, which represents the strongest
191 climate signal obtained in the results, considering the sites singularly (Fig. 4c). Regarding the altitude, it is not
192 possible to establish a clear climate-growth correlation gradient along the elevation, since population in
193 middle of the altitude orders misshape the decreasing gradient. Still, in general sites at lower elevations (1,
194 3, 15, 16) tend to show a stronger relationship with SPEI3, as well as with temperature, in comparison to sites
195 at more elevated sites (4, 10, 13, 14). Considering the single sites, 5 and 11 show lower – though still
196 significant - positive relationship with SPEI3, meaning that they seem to be less susceptible to summer

197 drought in comparison to other low and middle elevation sites. Site 5 is the northernmost one, while 11 is
198 the is the furthest southwest-located.

199

200 **Resilience to extreme events**

201 When considering all the trees, only 2012 was revealed as an extreme negative growth year, in which the
202 majority of trees featured at least a 40% growth decline. However, Fig 1c and literature (Hodzic et al., 2011)
203 suggest other extreme years (1990, 2000, 2003) in the Bosnia and Herzegovina climate's history. If computing
204 the analysis on trees grouped into three distinct elevation groups, the drought year 2012 clearly emerged as
205 a negative pointer year for the low-elevation sites. Although according to Van der Maaten-Theunissen et al.
206 (2015) the year 2012 cannot be strictly considered a pointer year for middle and high elevations trees, Llorets
207 resilience components (Llorets et al. 2011) calculated among elevation and age classes indicated the
208 presence of significant differences among groups (Kruskal-Wallis, $p < 0.05$) (Fig. 5). In general, the resistance
209 of low elevation trees to the 2012 dry summer conditions were significantly lower than that of middle and
210 high elevation trees (both $p < 0.05$). However, resistance to drought did not significantly differed between
211 middle and high elevation trees ($p = 0.247$). These analyses also indicate that the resistance of younger trees
212 was significantly lower than for more aged trees. Significance differences have also been observed regarding
213 the recovery, specifically indicating that old trees recover slower than young trees ($p < 0.05$.) However, low
214 resistance and high recovery could also be an indication of strong plasticity.

215

216 **Discussion**

217 Serbian spruce growth - and supposedly also establishment - is closely related to short-term and long-term
218 dynamics in climate, mainly related to water availability during summer. This relationship expressed by high
219 correlations with precipitation and the SPEI3 in the summer from June to August was consistently found in
220 all 15 studied relict populations. Among populations there was a tendency that Serbian spruce at lower
221 elevation show a stronger negative growth response to summer drought in comparison to those growing at
222 higher elevations (Fig. 4c). This elevation trend is in line with findings for the other spruce species growing in
223 South-Eastern Europe, such as Norway spruce (*Picea abies*) in Serbia (Castagneri et al., 2014) as well as *Pinus*
224 *peuce* and *Pinus heldreichii* in Bulgaria (Panayotov et al., 2010). Levanič et al. (2009) found that mainly
225 increasing summer temperature deteriorates radial growth of low elevation Norway spruce in South-Eastern
226 Europe by enhancing evapotranspiration and hence drought stress. Drought stress has, however, also been
227 observed, although with minor impact, at high-elevation sites indicating that, despite tree growth in
228 mountain environment is often positively related to warmer conditions, has still led to increased
229 evapotranspiration (Jolly et al., 2005; Savva et al., 2006).

230 The assessment of long-term variation in climate-growth relationships (Fig. 4b) proved the short-term
231 acclimation potential of Serbian spruce. Past periods with summer droughts, e.g. 1945 to 1955 (Fig. 1c & d)
232 and consecutive wetter and cooler period until 1980, when the recent warming initiated, are reflected by
233 synchronous stronger links or weaker dependencies on summer conditions. The fact that young populations
234 established in the relative wetter and cooler period in the 1960ies and 70ies (Fig. 2) could indicate the
235 regeneration potential of Serbian spruce, at least in the past. After a period with heavy droughts between
236 1945 and 1955 with lot of forest fires (Fukarek, 1951) the forest has recovered showing the its potential
237 under improved climate conditions (low SPEI in the 1960ies and generally higher rainfall). However, under
238 future conditions with increasing drought this might not be possible. The young trees showed a strong growth
239 decline in the recent period which seems stronger than the growth decline of older trees to the dry conditions
240 in the 1940ies and 1950ies – and which might indicate that they indeed suffered from recent climate change.

241 The recent period with enhanced temperature and drought frequency starting in 1980 resulted again in a
242 stronger relationship between growth and summer conditions, comparable to the situation in the 1940ies
243 and 50ies. The SPEI3, indicating drought intensity in the summer months (JJA) reached unprecedented low
244 values in 1990, 2000, 2003 and especially 2012 (Fig. 1d) causing – for 2012 – strong growth depressions,
245 specifically in young spruces and trees at low altitude (Fig. 5). However, trees in all age (but especially young
246 trees) and elevation categories had the ability to fast recover.

247 Although we found differences in the climate-growth correlation between the studied sites, the
248 environmental variables used in the analysis were not sufficient to explore specific site-related reasons
249 beyond the explained general trends related to altitude and tree age. Low elevation sites may have indeed,
250 a generally higher growth rate, because of the warmer conditions during the growing season, which generally
251 favor growth in mountainous areas. But at the same time higher temperature, especially during summer can
252 cause water shortage and hence induce drought stress at lower elevation sites. Indeed, the soil observations
253 from the field work indicate very underdeveloped soil, probably due to the erosion process during the years.

254 However, the extreme drought event in 2012 does not seem to have much influenced the Serbian spruce
255 populations, since almost all the trees completely recovered in the years following the event (resilience).
256 Also, differences in soil depth, nutrient levels, stand density, presence of other competing species are all
257 factors which would be to consider to assess sites-specific differences.

258 Interestingly, site 6 showed an unusual growth trend in the past two and a half decades, which apparently is
259 paralleling the increasing in temperature trend (Fig. 3a). This would lead to the conclusion that this site
260 (Strugovi), may have adapted better and faster to the current climate change, relatively to the other ones.
261 However, a better explanation of this unusual trend can be related to fire taking place in Strugovi during
262 1992-1993 (Mataruga et al., 2011), which, burning down a great part of the forest, may have enhanced the
263 growth of the survived trees. In fact, as literature reports, Serbian spruce is a high shade-intolerant (Tucić

264 and Stojković , 2001; Tucić et al., 2005; Ivetić and Aleksić, 2016). In particular, Tucić and Stojković (2001)
265 reported a low additive genetic variation for plasticity in shade-avoidance traits, leading this species to
266 predominate open sites, although its growth may be later on suppressed by other shade-tolerant species.

267 Overall, these results confirm that the recent changes in climate conditions — along with fires, competition
268 and low migration rate — form a potential threat to the survival of this endangered forest species. Indeed,
269 consequently to its small populations size and the lack of regeneration combined with the slow migration
270 potential and speed, already constituted a broad set of threats for the conservation of the species in its
271 natural habitat. An increased frequency of longer periods with high summer temperature in South Eastern
272 Europe occurring during the last few decades (Ivetić and Devetaković, 2016) add a new element reducing the
273 growth resilience of the species. Five out of seven among the greatest heat waves in the period 1961-2010
274 have occurred between 2000 and 2010 and summer 2012 was recorded by most regional weather station as
275 the hottest summer since climate measurements (WMO, 2013; Sippel and Otto, 2014). The increased
276 drought stress might likely explain the reported increased susceptibility to insect attack and fungal diseases
277 (Ivetić and Aleksić, 2016) associated with warm and dry years.

278 This new threat is expected to further increase in the near future. According to local climate model, due to a
279 combination of increasing temperature and decreasing precipitations in the next future (Ivetić and
280 Devetaković 2016), the pressure on Serbian spruce natural distribution area is expected to increase. In
281 additional, warmer and drier summers will even have greater repercussion, since compared to other conifer
282 species, it is often restricted to steep, sun exposed sites with shallow soils stimulating the formation of a
283 superficial and branched roots system (Panayotov et al., 2010; Ballian et al., 2016). Changes in climate are
284 being faster than Serbian spruce actual capability of adapt or migrate. Considering other obstacles, such as
285 habitat fragmentation, soil's lack of depth and nutrients, and general geography and topography, this species
286 will face a hard time to survive in such condition (Ivetić and Devetaković, 2016; Ivetić and Aleksić, 2016). This
287 scenario thus represents a big challenge for the conservation of this endangered relict species.

288 Serbian spruce has been already successfully and widely planted outside of its place of origin for both
289 ornamentals and forestry purposes. In Estonia it has been categorized as fast growing and cold resistant
290 species for valuable timber production, while in Southern Finland its performance was assessed as “good”
291 and considered a potential species for forestry (Sander and Meikar, 2009) and in Czech Republic its growth
292 rate has equaled those of the domestic Norway spruce (Kral, 2002). However, more active measures are
293 required to promote in situ conservation. These includes assisted natural regeneration, removal of
294 competitors to enhance seedlings survival, and preparation of new sites in less drought exposed conditions.

295

296 **References**

- 297 Aleksić, J.M., Schueler, S., Mengl, M., Geburek, T., 2009. EST-SSRS developed for other *Picea* species amplify
298 in *Picea omorika* and reveal high genetic variation in two natural populations. *Belgian Journal of Botany*. 89-
299 95.
- 300 Aleksić, J.M., Geburek, T., 2014. Quaternary population dynamics of an endemic conifer, *Picea omorika*, and
301 their conservation implications. *Conservation Genetics*. 15, 87-107.
- 302 Allen, C.D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Gonzalez, P., 2010. A
303 global overview of drought and heat-induced tree mortality reveals emerging climate change risks for
304 forests. *Forest ecology and management*. 259, 660-684.
- 305 Ballian, D., Longauer, R., Mikić, T., Paule, L., Kajba, D., Gömöry, D., 2006. Genetic structure of a rare European
306 conifer, Serbian spruce (*Picea omorika* (Pančić) Purk.). *Plant Syst Evol*. 260, 53–63.
- 307 Ballian, D., Ravazzi, C., Caudullo, G., 2016. *Picea omorika* in Europe: distribution, habitat, usage and
308 threats. *European Atlas of Forest Tree Species*. Publications Office of the European Union, Luxembourg. 157.
- 309 Biondi, F., Waikul, K., 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in
310 tree-ring chronologies. *Comput. Geosci*. 30, 303–311.
- 311 Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia*. 26, 115–124.
- 312 Castagneri, D., Nola, P., Motta, R., Carrer, M., 2014. Summer climate variability over the last 250 years
313 differently affected tree species radial growth in a mesic *Fagus–Abies–Picea* old-growth forest. *Forest*
314 *ecology and management*. 320, 21-29.
- 315 Eckstein, D., Bauch, J., 1969. Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur
316 Analyse seiner Aussagesicherheit. *Forstwissenschaftliches Centralblatt*. 88, 230-250.
- 317 Fady-Welterlen, B., 2005. Is there really more biodiversity in Mediterranean forest ecosystems? *Taxon*. 54,
318 905–910.
- 319 Fukarek, P., 1951: Staništa Pančićeve omorike nakon šumskih požara 1946/47. *Godine, Šumarski list*, br.1-2.
320 61-71.
- 321 Harris, I., Jones, P.D., Osborn, T.J. and Lister, D.H., 2014. Updated high-resolution grids of monthly climatic
322 observations - the CRU TS3.10 Dataset. *International Journal of Climatology*. 34, 623-642.
- 323 Hodzic, S., Markovic, M., Custovic, H., 2011. Drought conditions and management strategies in Bosnia and
324 Herzegovina. In *Proceedings of the 1st Regional Workshop on Capacity Development to Support National*
325 *Drought Management Policies for Eastern European Countries*. 42.
- 326 Holmes, R. L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree -Ring*
327 *Bulletin*. 43, 69 -78
328
- 329 IUCN 2018. The IUCN Red List of Threatened Species. Version 2018-2. <http://www.iucnredlist.org>.
330
- 331 Ivetić, V., Aleksić, J. M., 2016. Response of rare and endangered species *Picea omorika* to climate change:
332 The need for speed. *Reforesta*. 1, 81-89.
- 333 Ivetić, V., Devetaković, J., 2016. Reforestation challenges in Southeast Europe facing climate
334 change. *Reforesta*. 1, 178-220.

- 335 Jolly, W.M., Dobbertin, M., Zimmermann, N.E., Reichstein, M., 2005. Divergent vegetation growth responses
336 to the 2003 heat wave in the Swiss Alps. *Geophys Res Lett* 32 (Art. No. L18409).
- 337 Karger, D.N., Conrad, O., Böhrer, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Kessler, M., 2017. Climatologies
338 at high resolution for the earth's land surface areas. *Scientific data*. 4, 170122.
- 339 Král, D., 2002. Assessing the growth of *Picea omorika* [Panč.] Purkyně in the Masaryk Forest Training Forest
340 Enterprise at Křtiny *Journal of Forest science*. 48, 388–398.
- 341 Laušević, R., Jones-Walters, L., Nieto, A., 2008. Climate change and biodiversity in South-East Europe –
342 impacts and action. REC, Szentendre, Hungary; ECNC, Tilburg, the Netherlands. 67.
- 343 Levanič, T., Gričar, J., Gagen, M., Jalkanen, R., Loader, N. J., McCarroll, D., Robertson, I., 2009. The climate
344 sensitivity of Norway spruce [*Picea abies* (L.) Karst.] in the southeastern European Alps. *Trees*. 23, 169.
- 345 Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Lexer, M. J., 2010.
346 Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest ecology
347 and management*. 259, 698-709.
- 348 Lloret, F., Keeling, E. G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth
349 episodes in old ponderosa pine forests. *Oikos*. 120, 1909-1920.
- 350 Mataruga, M., Isajev, V., Gardner, M., Christian, T., Thomas, P., 2011. *Picea omorika*. The IUCN Red List of
351 Threatened Species.
- 352 Médail, F., Quézel, P., 1999. Biodiversity hotspots in the Mediterranean Basin: setting global conservation
353 priorities. *Cons. Biol*. 13, 1510–1513.
- 354 Nasri, N., Bojovic, S., Vendramin, G. G., Fady, B., 2008. Population genetic structure of the relict Serbian
355 spruce, *Picea omorika*, inferred from plastid DNA. *Plant Systematics and Evolution*. 271, 1-7.
- 356 Nikolić, B., Bojović, S., Marin, P. D., 2015. Variability of morpho-anatomical characteristics of the needles of
357 *Picea omorika* from natural populations in Serbia. *Plant Biosystems-An International Journal Dealing with all
358 Aspects of Plant Biology*. 149, 61-67.
- 359 Ostojić, D., Dinić, A., 2009. Experimental phytocoenological investigations of Serbian spruce (*Picea omorika*
360 /Pančić/ Purkyně) natural regeneration in the national park Tara. *Šumarstv.*, 23-35.
- 361 Panayotov, M., Bebi, P., Trouet, V., Yurukov, S., 2010. Climate signal in tree-ring chronologies of *Pinus peuce*
362 and *Pinus heldreichii* from the Pirin Mountains in Bulgaria. *Trees*. 24, 479-490.
- 363 R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical
364 Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 365 Rinntech H, 2010. TSAP-WIN TM: Time series analysis and presentation for dendrochronology and related
366 applications. <http://www.rinntech.com>, Heidelberg, Germany.
- 367
- 368 Sander, H., Meikar, T., 2009. Exotic coniferous trees in Estonian forestry after 1918. *Forst und Jagdzeitung*.
369 158.
- 370
- 371 Savva, Y., Oleksyn, J., Reich, P.B., Tjoelker, M.G., Vaganov, E.A., Modrzynski, J., 2006. Interannual growth
372 response of Norway spruce to climate along an altitudinal gradient in the Tatra Mountains, Poland. *Trees*. 20,
373 735-746.
- 374
- 375 Sippel, S., Otto, F.E., 2014. Beyond climatological extremes-assessing how the odds of hydrometeorological
376 extreme events in South-East Europe change in a warming climate. *Climatic Change*. 125, 381-398.

377
378 Tucić, B., Stojković, B., 2001. Shade avoidance syndrome in *Picea omorika* seedlings: a growth-room
379 experiment. J Evol Biol. 14, 444–455.

380 Tucić, B., Pemac, D., Ducić, J., 2005. Life history responses to irradiance at the early seedling stage of *Picea*
381 *omorika* (Pancic) Purkynhe: adaptiveness and evolutionary limits. Acta Oecologica-International J. Ecol. 27,
382 185-195.

383 UNDP, 2016. Third national communication and second biennial update report on greenhouse gas emissions
384 of Bosnia and Herzegovina under the United Nations framework convention on climate change. UNDP,
385 Sarajevo.

386 Van der Maaten-Theunissen, M., Van der Maaten, E., Bouriaud, O., 2015. pointRes: An R package to analyze
387 pointer years and components of resilience. Dendrochronologia. 35, 34-38.

388 Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global
389 warming: the standardized precipitation evapotranspiration index. Journal of climate. 23, 1696-1718.

390 Wardle, P., 1956. *Picea omorika* in its natural habitat. Forestry: An International Journal of Forest
391 Research. 29, 91-117.

392 WMO (World Meteorological organization), 2013. WMO statements on the status of global climate in 2012.
393 WMO-No. 1118

394 Zang, C., Biondi, F., 2015. treeclim: an R package for the numerical calibration of proxy-climate
395 relationships. Ecography. 38, 431-436.

396
397

398 **TABLES**

399

400 **Table 1: Site names, sampling depth, mean elevation, geographical location and age range.**

Site name	Site ID	N of trees	Elevation [m]	Latitude [decimal degrees]	Longitude [decimal degrees]	Age range [years]
Perišin Gaj	1	29	948	43.85910	19.18797	40-57
Starogorske stijene	2	19	1160	43.91499	19.16403	34-55
Suvi Do	3	27	935	43.85932	19.17326	35-55
Panjak	4	11	1290	43.99898	19.14943	59-130
Tisovljak	5	19	1039	44.07286	19.09082	53-243
Strugovi	6	17	974	43.97844	19.20715	68-128
Šarena bukva	7	11	1061	44.01897	19.19293	22-54
Borov vrh	8	14	1047	44.01689	19.20147	36-48
Grad	10	23	1198	44.00212	19.22175	36-50
Radomišlje	11	29	1122	43.46225	18.61265	49-180
Vijogor	12	23	1121	43.65015	19.12427	42-141
Gostilj	13	35	1173	43.85674	19.33362	44-132
Veliki stolac	14	29	1242	43.92315	19.28002	44-190
Karaula Štula	15	24	915	43.92976	19.28252	43-58
Vidikovac	16	15	861	43.93219	19.27914	45-55

401 Population 9 and 17 were not measured and included in the analyses due to lack of replicates

402

403

404 **Table 2: Tree-ring characteristics**

Site name	Site ID	MRW (mm)	Glk	Inter-series correlation	R_{bar}
Perišin Gaj	1	1.95	0.70	0.63	0.53
Starogorske stijene	2	1.79	0.67	0.55	0.42
Suvi Do	3	1.67	0.67	0.54	0.42
Panjak	4	1.17	0.72	0.62	0.50
Tisovljak	5	1.10	0.64	0.58	0.41
Strugovi	6	0.92	0.65	0.58	0.42
Šarena bukva	7	1.86	0.66	0.47	0.36
Borov vrh	8	1.67	0.71	0.56	0.55
Grad	10	2.14	0.68	0.66	0.52
Radomišlje	11	0.99	0.61	0.54	0.31
Vijogor	12	1.74	0.62	0.53	0.36
Gostilj	13	1.45	0.63	0.58	0.37
Veliki stolac	14	1.49	0.64	0.60	0.39
Karaula Štula	15	2.27	0.73	0.67	0.56
Vidikovac	16	2.01	0.77	0.69	0.63

405 MRW = Mean ring width, Glk = Gleichläufigkeit, inter-series correlation (calculated on ring width index), and r_{bar} = mean correlation
406 between trees (calculated on 10-years spline detrended timeseries, i.e. on the tree-ring width index).

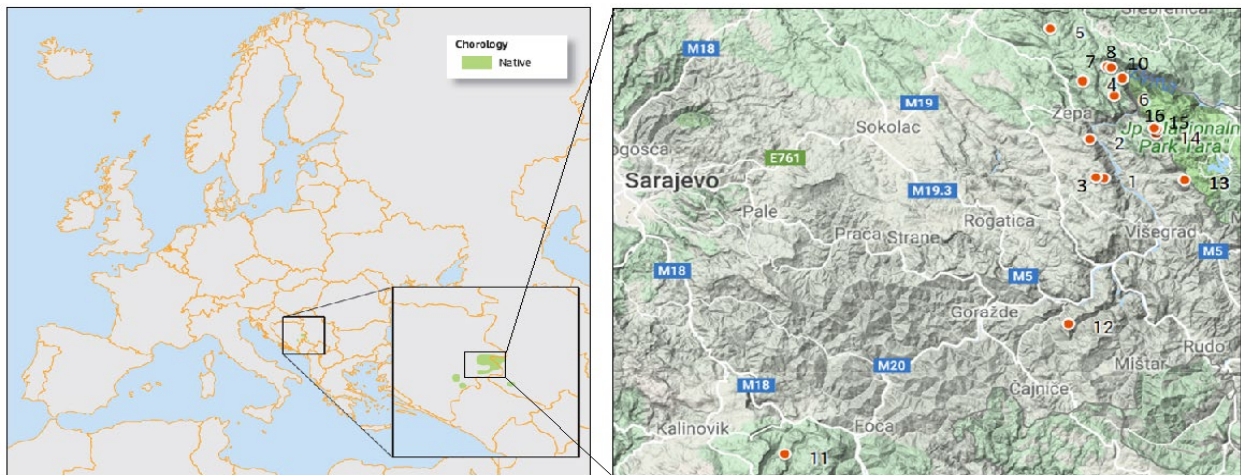
407

408

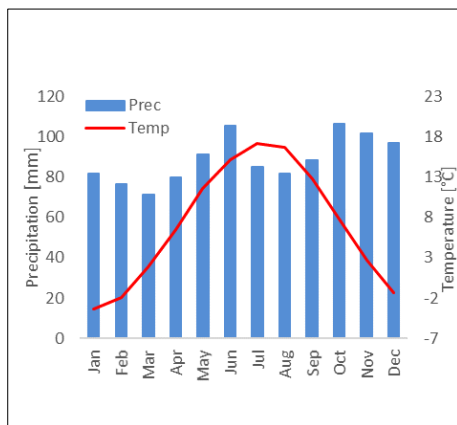
FIGURES

Fig. 1: Sites location and regional climate characteristics. a) Location of the study area and sampled sites; b) Climate diagram of the period 1901-2017; c) Average yearly temperature and precipitation of the period 1901-2017. d) Average yearly temperature and precipitation SPEI3 of the period 1901-2017. b) and c) have been obtained from averaged CHELSA-extended gridded data (Karger et al., 2017) at all 15 sites.

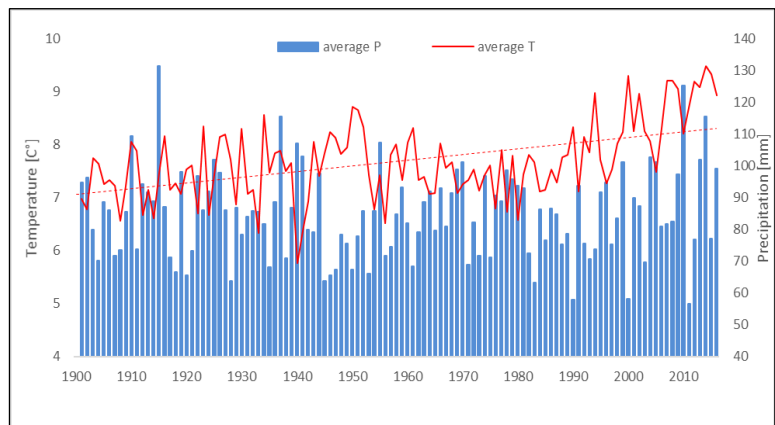
a)



b)



c)



d)

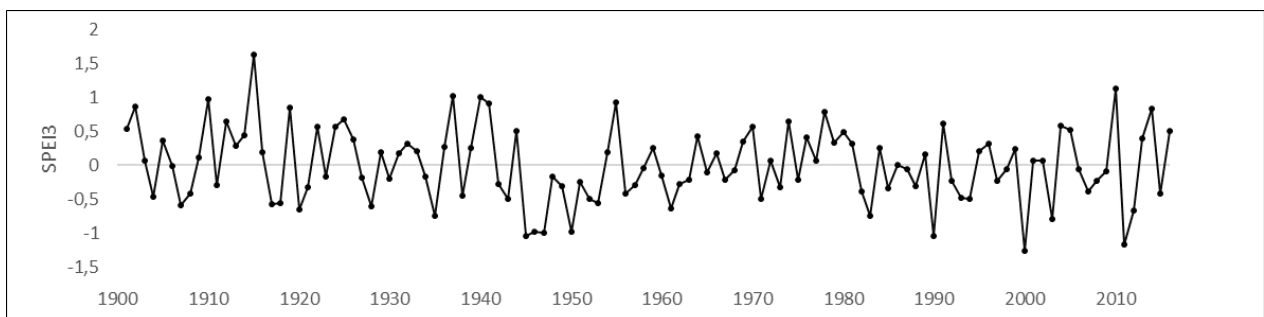
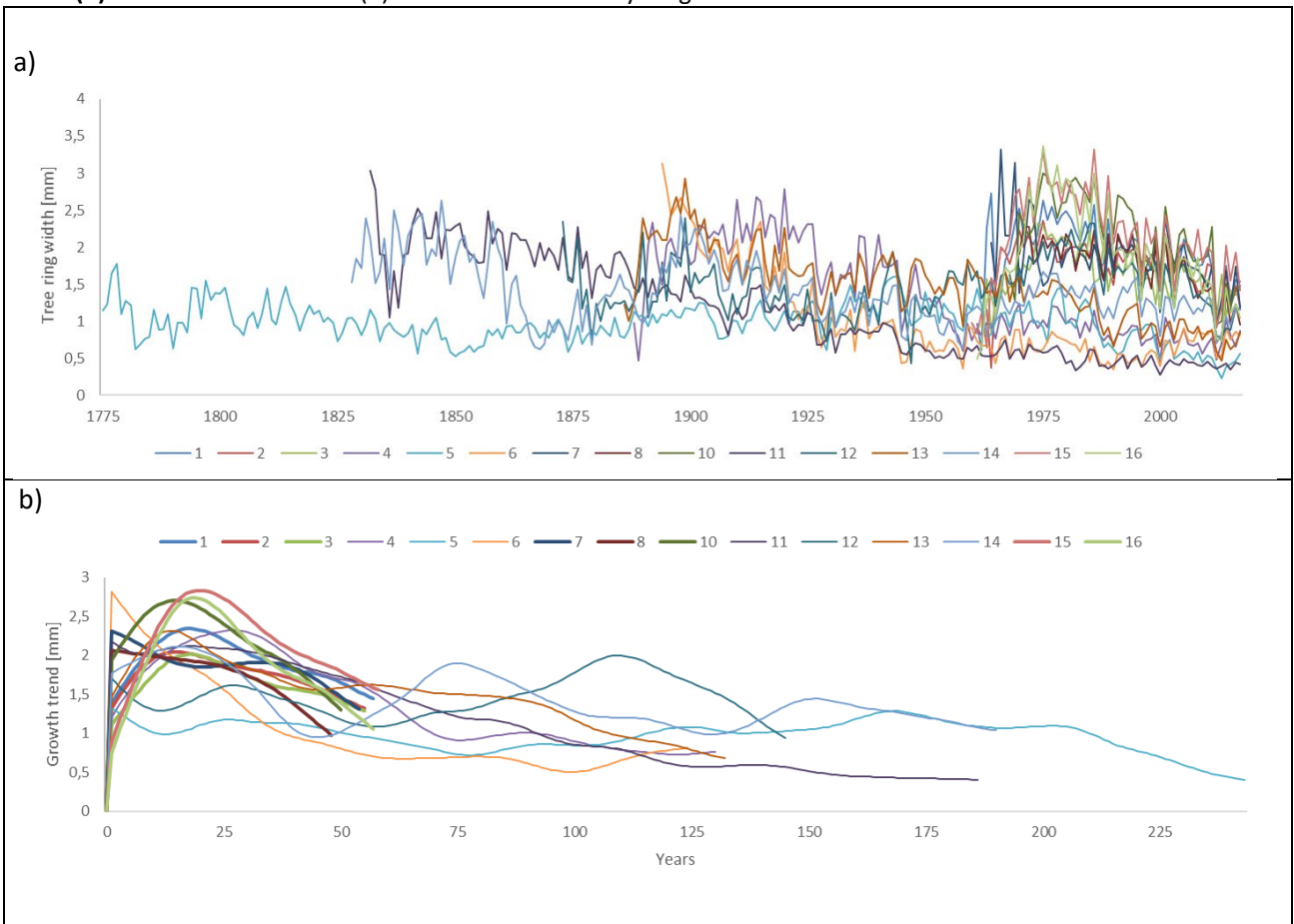


Fig. 2 Tree-ring width chronologies (a) and age-aligned regional growth curves of the 15 sampled Serbian spruce sites (b). Thick and thin lines in (b) differentiate old and young sites.

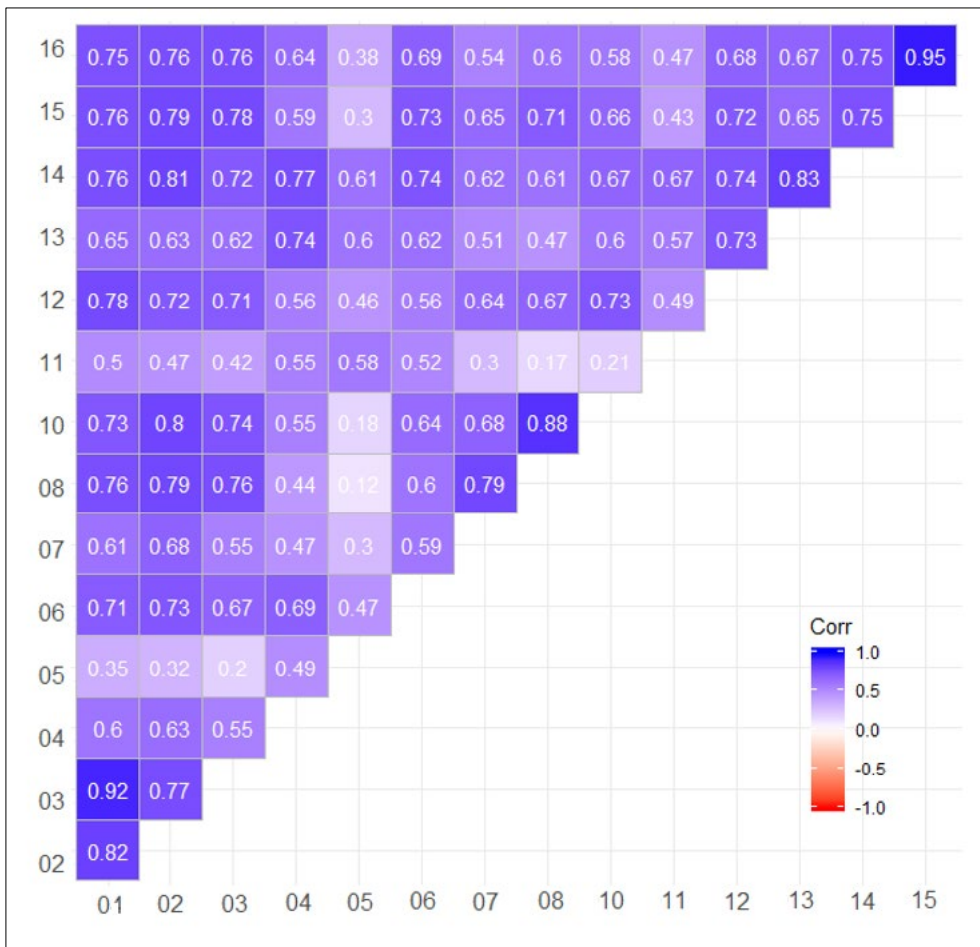


409

410

411
412

Fig. 3: Correlation matrix among the ring-width site chronologies

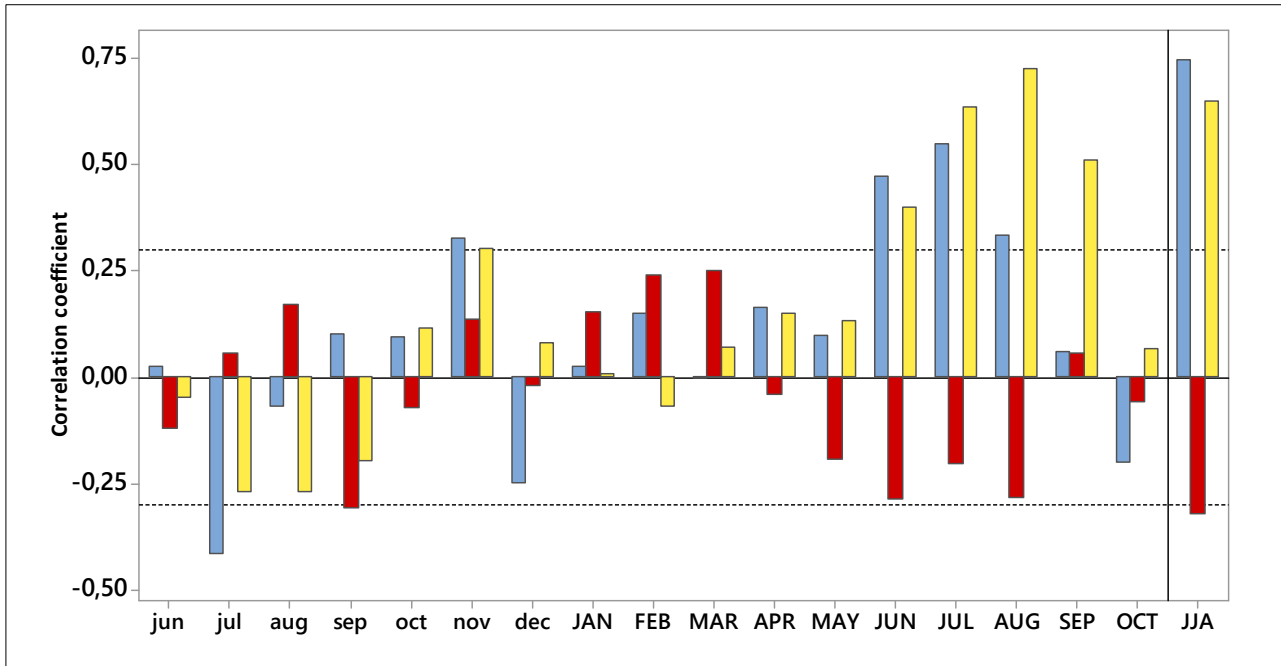


413
414

415

416 **Fig. 4 Climate growth relationships.** a) *Bootstrapped climate correlation for the period 1974-2016 for the species for*
 417 *the composite of the 10-years detrended chronologies with precipitation sum (blue), monthly mean temperature (red)*
 418 *and drought index SPEI3 (yellow). JJA indicates the summer mean correlation (June, July and August). Dashed*
 419 *horizontal lines represent the threshold of significance ($p < 0.05$). b) *Moving window correlation (25 years wide) of*
 420 *climate-growth responses over the period 1906-2016 for the species for the composite of the 10-years detrended*
 421 *chronologies. Climate parameter are precipitation, temperature and SPEI3. Asterisk indicates significance ($p < 0.05$). c) *Climate-growth responses for each individual site chronologies over the period 1974-2016 for the strongest climatic*
 422 *signal obtained in the analyses (SPEI3 in August). Dashed horizontal lines represent the threshold of significance*
 423 *($p < 0.05$). Site are ordered on their mean elevation and vertical line separate the results for elevation classes (800-1000,*
 424 *1000-1200 and 1200-1500 m).***

426 a)



427

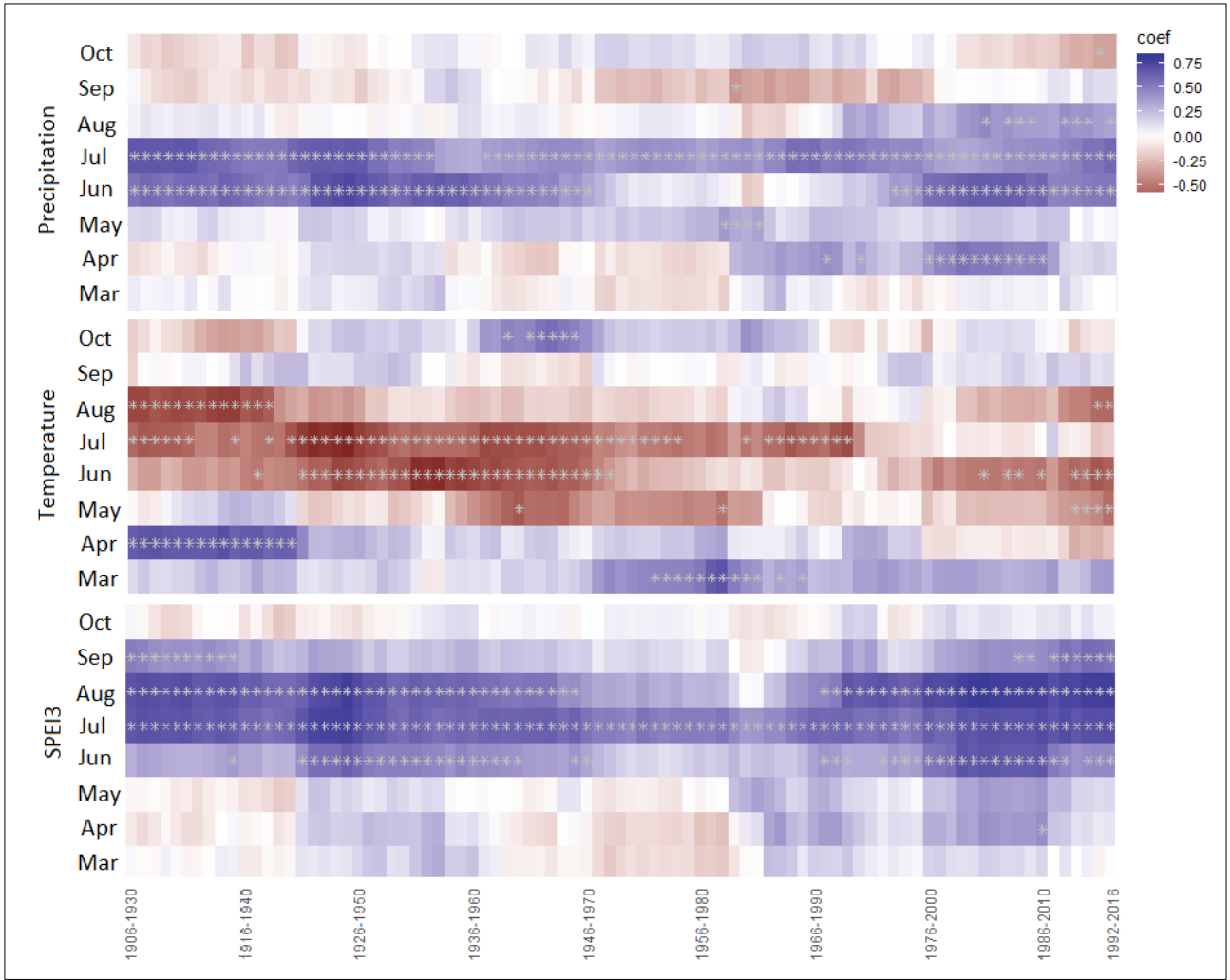
428

429

430

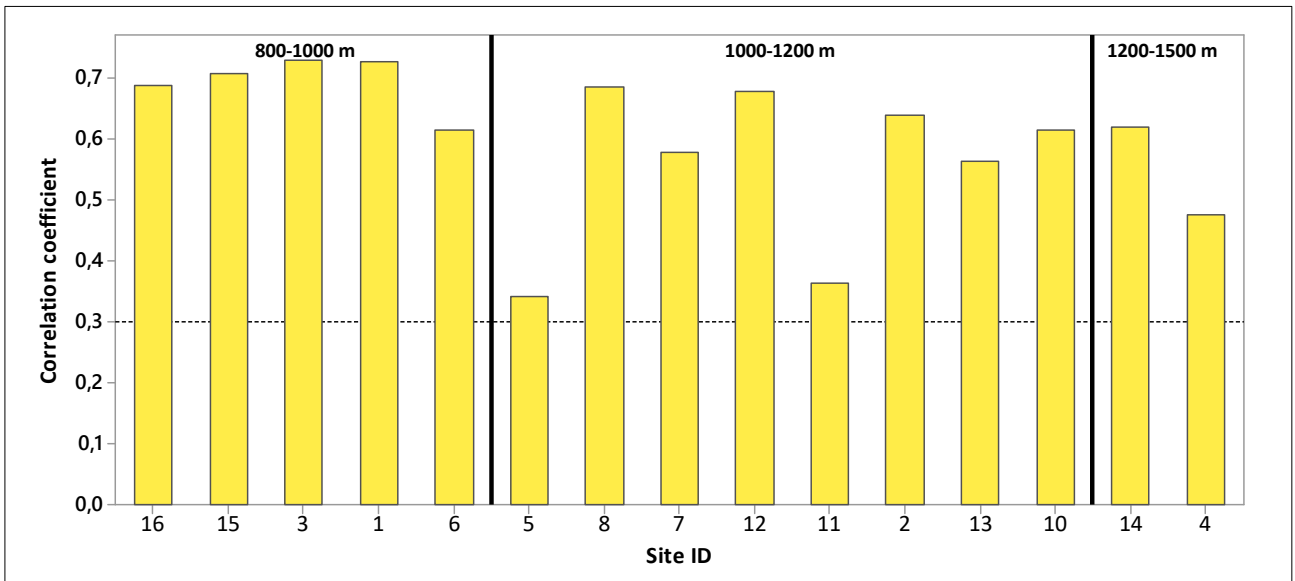
431

432 b)



433

434 c)



435

436

437

438

Fig. 5 Box plots representing the three resilience components of Llorets et al. (2011) resistance, recovery, resilience of the individual trees grouped per elevation (a) and age (b) as a response to the drought year 2012. L = 800 to 1000 m asl., M = 1000 to 1200 m asl., and H = 1200 to 1500 m asl.; Y < 80 years, M = 81 to 160 years, and O > 161 years). The horizontal dashed line indicates the value 1, indicating no changes with respect to the reference.

