**Distinct effects of climate warming on populations of silver fir (Abies alba) across Europe**

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## Distinct effects of climate warming on populations of silver fir (Abies alba) across Europe

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5   Antonio Gazol[1], J. Julio Camarero[1], Emilia Gutiérrez[2], Ionel Popa[3], Laia Andreu-

6   Hayles[4], Marc Macias-Fauria[5], Renzo Motta[6], Elena Muntán[2], Paola Nola[7], Gabriel

7   Sangüesa-Barreda[1], Carlo Urbinati[8] and Marco Carrer[9]

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9   [1]Instituto Pirenaico de Ecología (IPE-CSIC). Avda Montañana 1005. Zaragoza 50059, Spain.
10  [2]Dept. d'Ecologia, Universitat de Barcelona, Avda. Diagonal 643, 08028 Barcelona, Spain.
11  [3]Forest Research and Management Institute, Calea Bucovinei 73 bis, 725100 Câmpulung
12  Moldovenesc, Romania.
13  [4]Tree-Ring Laboratory, Lamont-Doherty Earth Observatory of Columbia University, 61 Route
14  9W, Palisades, NY 10964, USA
15  [5]Long-term Ecology Laboratory, Biodiversity Institute, Department of Zoology, University of
16  Oxford, Oxford, UK .
17  [6]Universitá degli Studi di Torino, Dip. Agroselviter, 10095 Grugliasco, Italy.
18  [7]Universitá. degli Studi di Pavia, Dip. Ecologia del Territorio, Via S. Epifanio 14, 27100 Pavia,
19  Italy.
20  [8]Universitá Politecnica delle Marche, Dip. SAPROV, Via Brecce Bianche, 60131 Ancona, Italy.
21  [9]Universitá degli Studi di Padova, Dip. TeSAF, 35020 Legnaro, Italy.
22

23  Corresponding author:

24  J. Julio Camarero

25  Instituto Pirenaico de Ecología (IPE-CSIC).

26  Avda Montañana 1005. Zaragoza 50059, Spain.

27  Tel. (+34) 976 369393, Fax: 976 716019

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28    **Abstract**

29    Climate change can modify mid to long term forest growth across a tree

30    biogeographical range. In the Mediterranean basin, the predicted increase in aridity is

31    expected to cause growth decline for several temperate tree species that are in the rear-

32    edge (southernmost limit) of their distribution area. Empirical evidence suggests that the

33    forecasted growth decline seems to be site- and species-specific, but few studies have

34    considered the response of a species along its entire distribution range. We study growth

35    trends and response to climate of silver fir (*Abies alba*) populations across its southern

36    distribution limit in Europe. More than 1300 trees from 111 populations located across

37    Spain, Italy and Romania were used to describe growth trends using basal area

38    increment and to characterize year-to-year growth responses to climate using ring-width

39    indices. We found significant contrasting patterns of basal area increments among sites.

40    Populations located out of the Mediterranean area (northern Italy, Romania) have

41    shown a clear growth improvement over the last two decades, whereas most of those

42    located in Spain and southern Italy display a marked growth decline since the 1980s.

43    Most populations in the southwestern distribution limit are strongly affected by spring-

44    summer water deficit, whereas those located in northern Italy and Romania are more

45    sensitive to late winter and early spring temperatures. The increase in aridity driven by

46    rising temperatures observed in southwestern Europe is causing growth decline in some

47    silver fir populations portending their die-off, whilst in more temperate area warming is

48    driving growth improvement. The forecasted increase in the duration and severity of

49    drought stress will likely trigger multiple die off events in the majority of

50    Mediterranean silver-fir populations.

51    **Key words:** *Abies alba*, basal area increment, climate warming, dendroecology,

52    drought stress.

53

**Introduction**

54

55 Global-warming consequences on ecosystems represent a challenge for human well-

56 being (Nelson et al. 2013). Air temperature has risen by 0.13º C per decade for the latter

57 half of the last century (IPCC 2013), inducing changes in the geographic distribution

58 and performance of animal and plants (Taberlet and Cheddadi 2002). Warming trends

59 influence vegetation patterns by modifying the start and duration of the growing season,

60 and higher air temperatures alter growth responses to climate (Wolkovich et al. 2012).

61 How plant populations face these changes depend in their plasticity and ability to

62 acclimatize to new environmental conditions (Nicotra et al. 2010). Therefore, far from

63 being homogenous the consequences of warming on species performance vary across

64 the species distribution range (Vila et al. 2008; Carrer et al. 2010). This geographical

65 variability is illustrated by tree populations located at the lower latitudinal limit (rear

66 edge) margin of the species distribution area which are particularly sensitive to climate

67 oscillations (Hampe and Petit, 2005).

68 Many European tree species such as silver fir (*Abies alba* Mill.) or Scots pine

69 (*Pinus sylvestris* Ll.) reach its rear edge in the Mediterranean region, a climate change

70 hotspot (Luterbacher et al. 2012). There, warming is predicted to amplify aridity

71 through increased vapour pressure deficit leading to exacerbated soil moisture deficit

72 (Piñol et al. 1998, Giorgi and Lionello 2008, IPCC 2013). Recent drought events have

73 caused widespread growth decline, decreasing productivity and inducing forest die-off

74 of Mediterranean forests both in dry sites (Sarris et al., 2007; Thabeet et al. 2009;

75 Dorman et al. 2013; Vicente-Serrano et al., 2013) but also in mesic sites (Jump et al.,

76 2006; Linares and Camarero, 2012a, 2012b; Castagneri et al. 2014). Conversely, other

77 authors have reported growth improvements of tree species in Mediterranean sites

78 (Tegel et al. 2014). These findings are further complicated in mixed stands where each

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79  tree species can respond with different intensity to similar climate drivers (Bouriaud and

80  Popa 2009; Castagneri et al. 2014). Such contrasting findings confirm that long-term

81  growth responses of trees to climate are highly contingent on local climatic conditions

82  including warming trends and precipitation regimes. For instance, Vila *et al*. (2008)

83  reported that Scots and Aleppo (*Pinus halepensis* Mill.) pines performed differently

84  along an altitudinal gradient depending on how site conditions buffered the effects of

85  regional climatic factors. This local contingency of growth responses to climate is

86  further complicated because present growth patterns across the range of tree species

87  were also shaped by past events including land use (Camarero et al. 2011) or long-term

88  genetic and phenotypic variability due to postglacial gene flow (Liepelt et al. 2009).

89      The consequences of warming-induced drought on forest growth and the

90  determination of those tree species and populations that will be the most affected are

91  still under debate. For example, in Iberian conifer forests drought stress adversely

92  influenced growth and survival of those species most vulnerable to xylem cavitation

93  (Sánchez-Salgero et al. 2012) or those populations living in the driest sites (Andreu-et

94  al. 2007, Martínez-Vilalta et al. 2008, del Río et al. 2014) or near the species' rear edge

95  (Macias et al. 2006). Other authors have emphasized how remarkable is the capacity of

96  tree populations from drought-prone areas to cope with water shortage by changing

97  growth dynamics, wood anatomy and water use efficiency (WUE) (Alla and Camarero

98  2012; Linares and Camarero 2012b, Granda et al. 2013). Despite the plasticity of tree

99  species to tolerate drought stress, and the potential increase of WUE as a result of an

100  increase in atmospheric $CO_2$ concentrations (Norby et al. 1999), water-demanding tree

101  species such as silver fir should respond negatively to the increase in aridity, especially

102  near the species rear edge.

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103        In a recent study, Büntgen et al. (2014) showed that silver-fir secondary growth

104    has increased considerably during the last 20 years across central Europe, whereas there

105    was a noticeable growth decline across drought-prone Mediterranean sites. Consistently,

106    different patterns of tree growth have been reported between northern and southern

107    silver-fir populations in Italy (Carrer et al. 2010). Die-off episodes of silver fir forests

108    have been described for the past five centuries across Europe but their incidence varies

109    geographically and it seems to be increasing during the 20th century, particularly in SW

110    (Spanish Pyrenees, see Camarero et al. 2011) and SE locations (Slovenia, see Bigler et

111    al. 2004). Could such silver-fir growth decline portend drought- or heat-induced die-off

112    (*sensu* Allen et al., 2010)? Several authors report long-term growth declines in some

113    rear-edge silver fir populations (Linares and Camarero 2012a, Büntgen et al. 2014),

114    where summer water deficit, a major driver of silver fir growth (Pasho et al. 2011), has

115    increased considerably (Giorgi and Lionello 2008). Nevertheless, growth responses to

116    water deficit can be mediated by several different factors including phenotypic plasticity

117    among populations as a consequence of local acclimatization. Thus, to fully understand

118    how silver fir responds to climate warming studies across the entire distribution range

119    are required to disentangle biogeographical imprints in growth patterns.

120        Here we compile an extensive network of tree-ring width chronologies to

121    characterize the spatiotemporal trends of silver-fir growth across its southern

122    distribution limit in Romania, Italy and Spain. The main objective of our study is to

123    describe the geographical patterns in silver fir growth across its rear edge and ascertain

124    its main climatic drivers. We hypothesize that silver fir growth across the European

125    continent is declining and could become locally extinct in specific drought-prone

126    regions of its rear-edge distribution range as a local response to warming-induced

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127  drought stress. To achieve our objective, we combined nonlinear additive modeling of

128  long-term growth trends with dendrochronological analyses.

129

130  **Material and methods**

131  *Study area and species*

132  Silver fir is a highly productive conifer growing in sites with mesic conditions and deept

133  soils, and showing very sensitive to high vapour pressure deficit or atmospheric drought

134  (Aussenac 2002), showing a wide distribution across central and southern Europe where

135  it forms pure or mixed stands, mainly coexisting with European beech (*Fagus sylvatica*

136  L.), Norway spruce (*Picea abies* (L.) Karst.) or Scots pine (Peterken et al. 1996). The

137  distribution range of silver fir extends from the Pyrenees (southwestern edge) to

138  mountainous regions in southern Poland. It is one of the biggest tree species and

139  dominates tree assemblages in moist and productive sites from central Europe, the

140  Balkans, France, northern Spain, Italy and Romania (Brus et al. 2011). Silver fir is

141  usually dominating in sites under temperate to continental conditions with positive

142  summer water balance (**Supporting Information, Fig. S1**). In those sites a clear

143  warming trend has observed throughout the past century, and that rise in air

144  temperatures has intensified since the 1980s **(Supporting Information, Fig. S2).**

145      We collected wood samples of 1338 silver fir trees from 111 sites located in

146  Spain (46 sites), Italy (52 sites) and Romania (13 sites) (**Fig. 1; Supporting**

147  **Information, Table S1**). A detailed description of the different study sites can be found

148  elsewhere (Macias et al. 2006; Carrer et al. 2010; Camarero et al. 2011; Linares and

149  Camarero 2012a, 2012b). The study area covers a vast extension and includes a wide

150  longitudinal gradient (from 1.05º W to 26.69º E) over the rear-edge distribution limit of

151  the species.

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152

*Field sampling and dendrochronological methods*

153  *Field sampling and dendrochronological methods*

154  In each site, at least 10 dominant or co-dominant standing trees were randomly selected.

155  We also determined the geographical location (latitude, longitude) of each site. We

156  characterized radial-growth trends of silver-fir using dendrochronology (Fritts 2001).

157  Secondary growth was measured in two to three radial cores per tree, which were

158  extracted at breast height on the cross-slope sides of the trunk with an increment borer

159  whenever possible. Wood samples were sanded until tracheids were visible and then

160  visually cross-dated. Once dated, we measured the tree-ring widths to the nearest 0.01

161  mm using a binocular scope and the LINTAB measuring device (Rinntech, Germany).

162  The accuracy of visual cross-dating and measurements were checked with the program

163  COFECHA which calculates moving correlations between each individual series and

164  the mean site series (Holmes 1983).

165  To quantify the short-term growth responses to climate, first we standardized

166  and detrended the tree-ring width series to remove age or size trends and their temporal

167  autocorrelation (Briffa and Melvin 2011). We fit negative exponential or linear

168  functions and 30-year long splines to the tree-ring width series. These relatively short

169  splines allow removing growth trends in periods longer than decades, withholding the

170  high-frequency (mainly annual) growth variability. Then, we applied autoregressive

171  models to model and eliminate the temporal (usually first-order) autocorrelation.

172  Finally, we obtained the residual growth-index series, which we averaged following a

173  hierarchical approach from tree to site (chronology) levels. These detrended and

174  residual site chronologies of growth indices ($RWI_{site}$) were built using the program

175  ARSTAN (Cook 1985).

176    To characterize the growth series at the site level we calculated several

177  dendrochronological statistics either considering mean series of raw data (AC, first-

178  order autocorrelation which measures the serial persistence of growth) or residual

179  (RWI$_{site}$) growth indices (MS, mean sensitivity, a measure of year-to-year growth

180  variability; rbt, mean correlation between trees which evaluates the similarity in growth

181  variability among trees; PC1, variance explained by the first principal component; Fritts

182  2001). If a reliable time span is defined as the period showing values of Expressed

183  Population Signal (EPS) over 0.85 (Wigley et al. 1984), 85% of all site chronologies

184  cover the period 1900-1998 and show EPS values over the 0.85 threshold value

185  (**Supporting Information, Table S1**).

186    In those sites (Spain, 40 sites; Italy, 43 sites; and Romania, 5 sites) where tree

187  diameter at breast height (dbh; measured at 1.3 m) and bark thickness data were

188  available for all trees tree-ring width series were converted into basal area increment

189  (BAI) to describe long-term growth trends. The calculation of BAI allows removing the

190  geometrical constraint of adding a volume of wood to a stem of increasing radius

191  (Biondi and Qaedan, 2008). For each site, the mean BAI site series was calculated

192  considering all sampled trees.

193

194  *Cimate data*

195  Monthly climate data (mean temperature, total precipitation) were interpolated for those

196  0.5º grids including each sampled stand and corresponding to the CRU TS 3.1 data set

197  (Harris et al. 2014). We also calculated the monthly water balance (P-PET) as the

198  difference between precipitation (P) and potential evapotranspiration (PET) following

199  Hargreaves and Samani (1982). Climatic data were obtained from the Royal

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200 Netherlands Meteorological Institute "Climate Explorer" web page

201 ([http://climexp.knmi.nl](http://climexp.knmi.nl)).

202       To evaluate the growth indices responses to drought we used the Standardized

203 Precipitation–Evapotranspiration Index (SPEI), which is a multiscalar drought index

204 useful to quantify the responses of forests to water deficit at several time scales

205 (Vicente-Serrano et al., 2010). Positive and negative SPEI values correspond to wet or

206 dry conditions, respectively. SPEI data were obtained for the same grids as climate data

207 but considering the entire region where silver fir was present in each country. These

208 data were downloaded from the SPEIbase web page

209 (http://sac.csic.es/spei/database.html).

210

211 *Statistical methods*

212     *1. Long term trends in silver fir growth*

213 To analyze the spatiotemporal trend in silver fir growth we used Generalized Additive

214 Mixed Models (GAMM; Wood 2006). GAMM is a flexible semi parametric method to

215 characterize non-linear patterns observed between the response variable and one or

216 several explanatory variables (Wood 2006; Augustin et al. 2009).

217       We considered silver-fir growth trend (BAI) across Europe as a result of non-

218 linear interactions between the spatial location and the temporal trend. The latitude and

219 longitude of each site were used to reflect the spatial structure of BAI trends and

220 calendar year (hereafter termed "year") was used to reflect temporal BAI trends. The

221 variable year can reflect ontogeny as well as trends in growth induced by drivers such as

222 rising atmospheric $CO_2$ concentrations, air temperatures and local disturbances. The

223 final GAMM was of the form:

224       $\log (\text{BAI}_i + 1) = tp\,(x_i, y_i, \text{year}_i) + s\,(\text{dbh}_i) + s\,(\text{stand age}_i) + Z_i B_i + \varepsilon_i$     (1)

225    In this model, BAI of site $i$ is modelled as a function of a spatiotemporal additive model

226    including a three-way interaction between calendar year and the $x_i$ (latitude) and

227    (longitude) $y_i$ coordinates and two variables reflecting site productivity (mean $dbh_i$,

228    diameter at breast height) and ontogeny (stand $age_i$). A tensor product smoother ($tp$) is

229    used to model the space x time interaction, and cubic regression splines ($s$) allow

230    modelling stand basal area and age (Augustin et al. 2009). In addition, since BAI

231    represents multiple measurements performed in different trees from each site, site

232    identity ($Z_iB_i$) was regarded as a random effect. We also included in the model an error

233    term ($\varepsilon_i$) with an AR1 ($p = 1$, $q = 0$) correlation structure. In this study $BAI_i$ showed a

234    skewed distribution, therefore we log-transformed this variable (log x +1).

235

236    *2.  Climatic drivers of silver-fir growth*

237    Residual site chronologies of tree-ring widths ($RWI_{site}$) were correlated with

238    monthly climatic variables (temperature, precipitation and P-PET) for the period 1902-

239    1994. We considered the correlations calculated for the temporal window including

240    from July of the previous year up to October of the year of growth. In addition, to detect

241    the effects of climate on growth extremes we calculated the percentage of narrow and

242    wide ring-width indices at country scale for the aforementioned period by determining

243    the relative frequency of sites showing indices below and above the 5th and 95th

244    percentiles of country-wide values, respectively (**Supporting Information, Fig. S3**).

245    Those country-wide frequencies were related to the same climatic variables

246    aforementioned but extending the temporal window from prior January up to concurrent

247    December. The SPEI was related to a mean residual site chronology calculated for each

248    country and considering the window from January to December since the SPEI is based

249    on cumulative water deficits. The Pearson correlation coefficient was used to test for the

250   strength and significance of the associations between growth indices and climate

251   variables or the SPEI. To get a better understanding of the geographical differences of

252   growth-indices responses to climate, the Pearson correlation coefficients obtained by

253   relating growth indices and climate variables (temperature, precipitation, P-PET) were

254   also correlated with site latitude and longitude.

255

256   **Results**

257   *Spatiotemporal trends in basal area increment*

258   Since 1950 BAI widely varied along the study region being characterized by growth

259   decreases in most Spanish sites and growth increases in most Romanian and Italian sites

260   (**Fig. 2**). The model proposed to describe growth trends accounted for 70% of the

261   variation in BAI (**Table 1**) and was statistically reliable (**Supporting Information, Fig.**

262   **S4**). Across Europe, silver-fir BAI in low latitude and longitude sites (i.e. Spain and

263   southern Italy) increased from the 1950s to the late 1970s, and then decreased until

264   nowadays. Conversely, at high latitudes and longitudes (Alps, northern Apennines and

265   Romania), silver fir BAI decreased from the 1950s to early 1980s and then this trend

266   reversed during the last decades showing a recent growth enhancement. During the

267   1990s, silver fir BAI trends were markedly negative in most Spanish sites, whilst they

268   were mainly clearly positive in Romania and northern Italy (**Fig. 2**).

269

270   *Dendrochronological characteristics of the silver fir network*

271   The dendrochronological statistics for the silver fir chronologies differed between

272   countries (**Table 2**; site values are displayed in **Supporting Information, Table S2)**.

273   Mean ring width was $2.00 \pm 0.75$ mm (mean $\pm$ SD) and it was significantly ($P < 0.05$)

274   higher in Romania than in Spain and Italy, and the same pattern was observed for the

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275    tree dbh (**Table 2**). The tree-ring width data showed no clear geographical pattern along

276    the latitudinal and longitudinal gradients, but it was negatively correlated with site

277    elevation ($r = -0.48$; $P < 0.05$). The mean sensitivity was $0.16 \pm 0.04$, and it was

278    significantly ($P < 0.05$) higher in Spain than in Romania and Italy. In general, the mean

279    sensitivity decreased with site latitude ($r = -0.37$; $P < 0.05$), longitude ($r = -0.37$; $P<$

280    $0.05$) and also elevation ($r = -0.23$; $P < 0.05$). The variance explained by the first axis of

281    the PCA for the residual chronologies of each site varied between 66% and 25%

282    accounting for a mean of $39.0 \pm 8.0\%$ in variance. These values tend to be higher in

283    Spain than in Italy and Romania, respectively (**Table 2**). The fraction explained by the

284    PC1 was negatively correlated with site elevation ($r = -0.45$; $P < 0.05$).

285        The first principal component of a PCA calculated on the covariance matrix

286    comparing all residual chronologies ($RWI_{site}$) accounted for 28% of variation and it

287    showed a clear biogeographical pattern with Romanian and Spanish sites located apart

288    along that axis (**Fig. 3**). The scores of that first component were negatively related to

289    site longitude ($r = -0.84$; $P < 0.05$) and to a lesser extent with site latitude ($r = -0.32$; $P$

290    $< 0.05$). The second component explained a lower percentage of the variance (8.6%),

291    and it was related to site differences among chronologies from the same region.

292

293    *Climatic drivers of silver fir growth*

294    In general, we found a significant influence of the previous year climate conditions on

295    silver fir ring-width indices (**Figs. 4, 5 and 6**). Wide ring-width indices showed a

296    marked positive response to current June and July precipitation in Spain in response to

297    the higher aridity in the region as compared with the other countries. The percentage of

298    wide rings was positively related with the precipitation of July (only in Romania) and

299    August prior to the growth year. Similarly, they were negatively related with the

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300   temperature of prior August and September, and also October in Spain. In addition,

301   silver fir in Romania showed significant responses to winter climate conditions, with

302   higher temperatures from December to March promoting the formation of wider rings

303   (**Fig. 4**). Cold winter conditions from December to February induced the formation of

304   narrow rings, particularly in Romania and Italy.

305       Concerning the responses to the SPEI drought index, the mean Spanish

306   chronology showed a stronger sensitivity to previous summer-autumn drought than

307   those from Italy and Romania (**Fig. 5**). In Spain, narrow rings are former when dry

308   conditions occur in the previous summer, whereas in Italy, this pattern is less clear. In

309   contrast, the Romanian narrow growth indices are more strongly related to spring (May)

310   dry conditions (compare **Figs. 4 and 5**).

311       The aforementioned country-wide patterns were corroborated when the analyses

312   were done at the site scale using site chronologies of growth indices (RWI$_{site}$) (**Fig. 6**)

313   showing clearly that the precipitation and the water balance (P-ETP) of June to

314   September during the year previous to growth are consistent drivers of silver-fir growth

315   along its entire distribution range (**Fig. 6**). However, in Spain silver-fir growth is

316   particularly dependent on sufficient precipitation and a positive water balance (P-PET)

317   from June to July during the year of growth. Further, the relevance of current spring-

318   water balance for silver-fir growth in Spain has increased in the second half of the past

319   century (see **Supporting Information, Fig. S5**)

320       Consequently, the correlation between BAI and the water balance from June to

321   July decreased significantly with latitude and longitude, whereas that with June

322   temperature increased (**Table 3, Fig. 7**). The higher sensitivity of the Mediterranean

323   (Spain, Southern Italy) silver fir populations to water availability contrasted with the

324   noticeable responsiveness of Romanian populations to temperature. There was a marked

13

325   increase in the strength of the relationship between temperature and growth with

326   latitude and longitude (mostly in cold months; **Table 3**). In this sense, we found a

327   strong correlation between growth response to temperature in December, January and

328   March and longitude. The strength of the relationship between previous summer climate

329   conditions and growth evidences the presence of a consistent response to climate across

330   most of the silver fir distribution area. However, there are also seasonal differences

331   between sites since the strength of the relationship between previous July water balance

332   and growth indices increased with latitude and longitude, whereas that with the water

333   balance during the previous autumn decreased.

334

335   **Discussion**

336   We found evidence for both, common climatic signals affecting silver-fir growth along

337   its southern distribution limit, and contrasting responses to recent climate trends of

338   populations from southwestern and northern regions. On one hand, we found a

339   generalized warming-driven decline in growth of many silver fir populations located in

340   the southwestern (Spain) and southernmost (Italy) limits of the species distribution area

341   **(Fig. 2**). Remarkably, this declining pattern contrasts with the recent improvement in

342   growth reported for silver fir populations located in central Europe (Büntgen et al.

343   2014) and in other wet sites located elsewhere (northern Italy, Romania). Warmer

344   temperatures are plausibly exacerbating drought stress across the species rear-edge,

345   mainly in the western Spanish Pyrenees and southern Italy, while enhancing wood

346   production and carbon uptake in mesic areas **(Figs. 5, 6 and 7**). On the other hand, our

347   results concur with previous studies indicating the remarkable sensitivity of silver fir to

348   the water balance at the end of the previous growing season across Europe (Rolland et

349   al. 1999, Tardif et al. 2003, Lévesque et al. 2013).

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350    Our empirical analysis of the growth trends and response to climate suggest that

351    the water balance, and particularly the difference between the evaporative demand by

352    the atmosphere and the available water to evaporate, determine those contrasting growth

353    trends (**Table 3**, **Figs. 6 and 7**). The examined climate-growth relationships either

354    considering extreme (wide and narrow) rings or average growth series (**Figs. 4 and 6**),

355    offered us a complete picture of the main drivers of silver fir year-to-year growth

356    variability across its distribution area. But we also found marked geographical

357    differences in long-term growth patterns, with eastern populations displaying a strong

358    sensitivity to winter temperatures and southwestern populations mainly responding to

359    water availability (**Fig. 6**). Interestingly, our results indicate that populations in the

360    southwestern distribution limit (i.e. Spain) were much more sensitive to the previous

361    fall (October) and current spring-summer (June, July) water balance than the rest of

362    populations. These results clearly indicate that the recent increase in aridity caused by

363    rising temperatures is driving silver fir growth decline in Spain (**Fig. 7**), which is the

364    most drought-prone region across the rear edge of the species distribution area (**Fig.**

365    **S1**).

366    Long-term basal area increment trends increased from the 1950s to the mid-

367    1970s in Spain due to the presence of favorable climatic conditions for growth such as

368    wet and cool summers (Macias et al. 2006, Camarero et al. 2011). This trend has been

369    also observed for other mountain forests of the study region such as those dominated by

370    pine species (Andreu et al. 2007, Martinez-Vilalta et al. 2008, Galván et al. 2012). In

371    the Mediterranean Basin, that decade was characterized by mild temperatures and high

372    precipitation regimes that favored tree growth (Sarris et al. 2007). Contrastingly, during

373    approximately the same period, silver-fir populations of central Europe showed a

374    marked growth decline that was associated with increasing sulfur emissions ($SO_2$) and

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375  also local drought events (Büntgen et al. 2014). The reduction in pollution since the

376  early 1980s was followed by a substantial recover of silver fir growth in central Europe

377  and the Carpathians as spring and summer temperatures rose (Elling et al. 2009, Bošela

378  et al. 2014). The spatiotemporal pattern of silver-fir growth has reversed during the last

379  two decades with a marked decline in southern Europe and a notable growth

380  improvement in central and Eastern Europe (**Fig. 2**). Populations of drought-sensitive

381  tree species such as silver fir inhabiting Mediterranean areas may display genotypic and

382  phenotypic adaptations allowing them to override water deficit (Carrer et al. 2010).

383  From our results it can be interpreted that silver-fir populations in Europe show a clear

384  biogeographical zonation.

385       The declines in growth reported in this study suggest that a warming-related

386  higher evaporative demand and lower available soil moisture could trigger die-off

387  (Williams et al. 2013). In fact, the associations observed between growth and the

388  evapotranspiration deficit in this and other studies were higher than those observed with

389  other climatic variables such as mean temperature or total precipitation (Camarero et al.,

390  2011; Linares and Camarero, 2012a). Atmospheric drought not only caused growth

391  decline but also increased water-use efficiency, i.e. the carbon uptake rate per water

392  lost. We argue that temperature may be enhancing silver-fir growth and productivity of

393  forests located in mesic sites while xeric sites are more sensitive to changes in water

394  availability mediated by rising evaporative demand. This is demonstrated by the high

395  correlation observed between the influence of temperature on growth and latitude and

396  longitude (**Fig. 7**). As we move eastwards, the importance of the previous winter and

397  early spring temperatures as growth drivers increase. Conversely, southwestern

398  populations in Spain are more strongly linked with the water balance and the

399  precipitation in late spring and early summer (June, July), confirming their sensitivity to

16

400    drought. Regarding the influence of inter-annual climate on growth, similar results were

401    obtained by de Luis *et al.* (2013) for a typically Mediterranean tree species, since they

402    found that growth of Aleppo pine was positively affected by warming in cold regions

403    and negatively by aridity in warm-dry regions. Since most die-off episodes of silver-fir

404    forests have been detected in xeric sites near the southernmost distribution limit of the

405    species in Europe such as the Pyrenees, our findings confirm that long-term growth

406    declines portend drought-triggered die-off (Camarero et al. 2011).

407         The origin of the silver fir growth decline and subsequent die-off episodes is the

408    result of interacting local conditions and regional climate variations (Bigler et al. 2004),

409    but the occurrence of severe drought events and increasingly warmer temperatures in

410    northern Spain during the 1980s and 1990s seems to be the main triggering factor in the

411    case of the Pyrenean populations (see **Supporting Information, Fig. S2**). Extreme

412    climatic events such as severe drought have low frequency by definition but they can

413    have important implications on tree growth if they trigger extreme growth reductions

414    (Babst et al. 2012; Carrer *et al.* 2012). Our analyses demonstrate that silver fir growth is

415    very sensitive to extreme drought events as can be interpreted from the strong influence

416    of previous year precipitation and temperature on the frequency of extremely narrow

417    rings. Thabeet et al. (2009) also showed how two consecutive and severe droughts

418    during the 2000s caused Scot pine growth decline in France. In addition, during periods

419    of low rainfall trees depend more strongly on cumulative precipitation and deep soil

420    water reserves (Sarris et al. 2007). Therefore, in drought-prone sites or in sites with low

421    water retention capacity prolonged drought periods can have negative consequences on

422    tree growth (Dorman et al. 2013). Rainfall amounts, particularly in summer and fall, are

423    much higher and temperatures relatively milder in northern Italy and Romania as

424    compared with Spain. That is probably the reason why the severe droughts starting in

17

425    the 1980s caused such negative consequences on those marginal sites regions that

426    represent the driest limit of the species distribution range in Spain.

427          Paleoecology provides recent contrasting views on the future responses of

428    European silver fir forests to global warming. This debate emerges from the confronting

429    opinions on the future of this species in Europe based on pollen and macrofossils

430    reconstructions of the species' climatic niche. Some studies have forecasted range

431    contractions under global-warming scenarios (Maiorano et al. 2013), whereas others

432    expect no contractions in response to a much warmer climate than today (summer

433    temperatures increasing up to +7°C), as long as precipitation does not fall below 700

434    mm (Tinner et al. 2013). This apparent conflict may be caused by two different sources

435    distorting the species' climatic niche. First, millennia of human impacts have greatly

436    diminished the realized climatic niche of silver fir (Tinner et al. 2013). Second, the rear

437    or warm edges of the silver fir range could show very different responses to climate

438    warming as a function of water availability and atmospheric drought (Aussenac 2002).

439    For instance, no silver fir growth decline has been observed in the wet upland areas of

440    Italy, where the species is still abundant today excluding the southernmost relict

441    populations, while decline and forest die-off persist in the western Pyrenees (Camarero

442    et al. 2011). Our findings prove that Pyrenean silver-fir die-off is a response to climate

443    warming and ongoing drought stress.

444          High levels of gene diversity occur in silver-fir rear-edge populations

445    corresponding to former glacial refugia (e.g., Pyrenees, Balkans, Italy), while allelic

446    richness declines in those populations forming the leading edge in central Europe

447    (Terhürne-Berson et al. 2004). Furthermore, comparing paleobotanic and genetic data

448    have allowed demonstrating that Calabrian (southern Italy) and Pyrenean silver-fir

449    populations are well differentiated from Carphatian and Alpine-central European

18

450    populations (Liepelt et al. 2009). Such elevated genetic diversity and ecological

451    plasticity of silver fir, which is widely distributed and grows under very contrasting

452    climatic conditions, guarantees its conservation at regional or continental scales.

453    Nonetheless, our findings portend impending local extinction and community shifts

454    (e.g., silver fir replaced by European beech or Scots pine) in some western Pyrenean

455    populations with negative consequences on ecosystem services given the high

456    productivity of silver fir (decreased productivity with reduced carbon uptake and wood

457    production, increased water yields and local temperatures linked to reduced

458    evapotranspiration, altered biodiversity patterns, etc.). Furthermore, some of the less

459    vulnerable Pyrenean populations derived from those refugia lineages could store

460    adaptive genetic or morphologic features determining the species fate in future drier and

461    warmer conditions.

462        The results provided here demonstrate that climate conditions during the

463    summer of the year previous to growth drive silver-fir growth though the control of

464    prior late summer water deficit and atmospheric drought. However, we also found

465    strong biogeographical imprints in silver-growth and response to climate. In the long

466    term, warmer conditions, and the subsequent increase in aridity, are causing growth

467    decline and triggering die-off of some Pyrenean silver-fir forests despite improved

468    water-use efficiency in response to rising concentrations of atmospheric $CO_2$ (Linares

469    and Camarero, 2012b; Lévesque et al. 2013). Conversely, warmer conditions may favor

470    the growth and expansion of populations in temperate sites such as those from northern,

471    central and eastern Europe. Our findings concur with the view that warming-induced

472    drought stress could be one of the ultimate drivers of forest die-off episodes worldwide

473    even in mesic sites such as mountain fir forests (Allen et al., 2010). Further, we concur

474    with the view of a prominent role of increasing air temperature as amplifiers of drought-

19

475    induced growth decline (Williams et al., 2013). Overall, we speculate that some silver

476    fir populations from southwestern Europe will not override the forecasted increase in

477    aridity during this century. There are plausible reasons to think that the geographical

478    range of silver fir in Europe will firstly shrink in the southwestern limit of the species

479    distribution area.

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668

669    **Tables**

670

671    **Table 1.** Results of the Generalized Additive Mixed Model (GAMM) to characterize

672    silver-fir basal-area increment trends across its European rear edge. The type of

673    regression spline used for each variable, the estimated degrees of freedom (*edf*), the

674    estimated *F* statistic and its associated probability (*P*) are also shown. The model

675    accounted for 70% of the variation in basal-area increment.

676

| Factor | Variable | Spline | *edf* | *F* | *P* |
|---|---|---|---|---|---|
| Spatiotemporal trend | Latitude, longitude and Year | tensor product | 29.9 | 7.18 | < 0.01 |
| Tree ontogeny | Age | cubic regression | 1 | 85.00 | < 0.01 |
| Tree size | Diameter at 1.3 m | cubic regression | 2.4 | 86.60 | < 0.01 |

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679  **Table 2.** Summary of the structural features (dbh, diameter at breast height; mean age)

680  and dendrochronological statistics (calculated for the period 1990−1998) obtained for

681  the studied silver fir forests in each country. The mean (SD) and range (minimum −

682  maximum) are shown. Abbreviations are as follows: MRW, mena tree-ring width; MS,

683  mean sensitivity; AC, first-order autocorrelation; rbt, correlation between trees; and

684  PC1, fraction explained by the first Principal Component. Superscript letters correspond

685  to the comparison of country values using Dunnett's Modified Tukey-Kramer Pairwise

686  Multiple Comparison test (Dunnett 1980), whereas different letters indicate the presence

687  of significant differences ($P < 0.05$) between countries. Site values are available in the

688  **Supporting Information, Table S2**.

689

|  | Spain | | Italy | | Romania | |
|---|---|---|---|---|---|---|
|  | Mean (SD) | Range | Mean (SD) | Range | Mean (SD) | Range |
| Dbh (cm) | 56.0 (13.1)[b] | 26.5 − 81.8 | 63.0 (17.3)[ab] | 41.0 − 112.2 | 74.0 (10.3)[a] | 65.0 − 90.2 |
| Age (years) | 112 (45) | 58 − 259 | 213 (85) | 117 − 533 | 260 (82) | 113 − 375 |
| MRW (mm) | 2.19 (0.76)[a] | 0.89 − 3.67 | 1.69 (0.62)[b] | 0.54 − 3.07 | 2.54 (0.69)[a] | 1.90 − 4.25 |
| MS | 0.19 (0.05)[a] | 0.10 − 0.30 | 0.14 (0.02)[c] | 0.08 − 0.21 | 0.16 (0.02)[b] | 0.12 − 0.19 |
| AC | 0.29 (0.15)[b] | -0.12 − 0.61 | 0.29 (0.14)[b] | 0.09 − 0.65 | 0.39 (0.10)[a] | 0.23 − 0.57 |
| rbt | 0.40 (0.09)[a] | 0.25 − 0.63 | 0.31 (0.06)[b] | 0.20 − 0.47 | 0.31 (0.08)[b] | 0.19 − 0.47 |
| PC1 (%) | 0.44 (0.08)[a] | 0.31 − 0.66 | 0.36 (0.06)[b] | 0.25 − 0.50 | 0.36 (0.07)[b] | 0.26 − 0.50 |

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692 **Table 3.** Biogeographical variability in the climate-growth relationships based on site
693 growth indices (RWI$_{site}$) observed across the silver-fir study sites. For each month (from
694 July of the year previous to growth –$y_{-1}$– up to October of the year of growth – $y$) the
695 Pearson moment correlation coefficients obtained between the climate-growth indices
696 correlation (see Fig. 6) and site latitude or longitude are shown. Significant values ($P <$
697 0.05) are in bold. The water balance (P-PET) is the difference between precipitation (P)
698 and potential evapotranspiration (PET).

699

| Year | Month | Temperature | | Precipitation | | P−PET | |
|---|---|---|---|---|---|---|---|
| | | Latitude | Longitude | Latitude | Longitude | Latitude | Longitude |
| Year | Jul. | **-0.44** | -0.12 | 0.21 | **0.49** | **0.25** | **0.48** |
| previous | Aug. | **0.29** | -0.17 | 0.09 | **0.41** | -0.04 | **0.30** |
| to growth | Sep. | 0.14 | 0.10 | -0.10 | -0.10 | -0.13 | -0.07 |
| ($y_{-1}$) | Oct. | **0.38** | **0.35** | -0.12 | **-0.47** | -0.18 | **-0.35** |
| | Nov. | **0.61** | 0.17 | -0.18 | -0.02 | **-0.39** | **-0.25** |
| | Dec. | **0.51** | **0.72** | **0.32** | -0.04 | 0.02 | **-0.40** |
| Year of | Jan. | **0.44** | **0.73** | -0.21 | 0.02 | **-0.44** | **-0.36** |
| growth ($y$) | Feb. | 0.10 | -0.12 | -0.14 | -0.12 | **-0.24** | -0.20 |
| | Mar. | **0.36** | **0.86** | **0.45** | **0.34** | 0.10 | -0.22 |
| | Apr. | -0.20 | -0.12 | **0.47** | 0.19 | **0.44** | 0.11 |
| | May. | **-0.32** | **-0.43** | 0.06 | 0.21 | 0.10 | **0.27** |
| | Jun. | -0.09 | **-0.23** | -0.09 | **0.24** | **-0.44** | -0.22 |
| | Jul. | **0.61** | 0.01 | **-0.44** | **-0.49** | **-0.49** | **-0.44** |
| | Aug. | **0.30** | **-0.33** | **-0.38** | -0.15 | **-0.44** | -0.07 |
| | Sep. | -0.09 | **-0.63** | -0.07 | 0.18 | -0.05 | **0.31** |
| | Oct. | **0.47** | 0.17 | **-0.34** | 0.01 | **-0.36** | -0.01 |

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