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

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

4

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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

## 54 **Introduction**

55 Global-warming consequences on ecosystems represent a challenge for human well-  
56 being (Nelson et al. 2013). Air temperature has risen by 0.13° 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* L.) 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

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<sub>2</sub> 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.

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 20<sup>th</sup> 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

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 deep  
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 1.05° W to 26.69° E) over the rear-edge distribution limit of  
151 the species.

152

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 *Climate data*

195 Monthly climate data (mean temperature, total precipitation) were interpolated for those  
196  $0.5^\circ$  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

200 Netherlands Meteorological Institute “Climate Explorer” web page  
201 (<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<sub>2</sub> concentrations, air temperatures and local disturbances. The  
223 final GAMM was of the form:

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

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,  
228 diameter at breast height) and ontogeny (stand age). 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 ( $Z_i B_i$ ) 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 5<sup>th</sup> and 95<sup>th</sup>  
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

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

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

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).

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<sub>2</sub>) and



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

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

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 Carpathian and Alpine-central European

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 through 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<sub>2</sub> (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-

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.

480

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489

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667

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	<i>edf</i>	<i>F</i>	<i>P</i>
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

677

678

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, mean 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) <sup>b</sup>	26.5 – 81.8	63.0 (17.3) <sup>ab</sup>	41.0 – 112.2	74.0 (10.3) <sup>a</sup>	65.0 – 90.2
Age (years)	112 (45)	58 – 259	213 (85)	117 – 533	260 (82)	113 – 375
MRW (mm)	2.19 (0.76) <sup>a</sup>	0.89 – 3.67	1.69 (0.62) <sup>b</sup>	0.54 – 3.07	2.54 (0.69) <sup>a</sup>	1.90 – 4.25
MS	0.19 (0.05) <sup>a</sup>	0.10 – 0.30	0.14 (0.02) <sup>c</sup>	0.08 – 0.21	0.16 (0.02) <sup>b</sup>	0.12 – 0.19
AC	0.29 (0.15) <sup>b</sup>	-0.12 – 0.61	0.29 (0.14) <sup>b</sup>	0.09 – 0.65	0.39 (0.10) <sup>a</sup>	0.23 – 0.57
rbt	0.40 (0.09) <sup>a</sup>	0.25 – 0.63	0.31 (0.06) <sup>b</sup>	0.20 – 0.47	0.31 (0.08) <sup>b</sup>	0.19 – 0.47
PC1 (%)	0.44 (0.08) <sup>a</sup>	0.31 – 0.66	0.36 (0.06) <sup>b</sup>	0.25 – 0.50	0.36 (0.07) <sup>b</sup>	0.26 – 0.50

690

691

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

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