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

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5 Antonio Gazol¹, J. Julio Camarero¹, Emilia Gutiérrez², Ionel Popa³, Laia Andreu-
6 Hayles⁴, Marc Macias-Fauria⁵, Renzo Motta⁶, Elena Muntán², Paola Nola⁷, Gabriel
7 Sangüesa-Barreda¹, Carlo Urbinati⁸ and Marco Carrer⁹

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9 ¹Instituto Pirenaico de Ecología (IPE-CSIC). Avda Montañana 1005. Zaragoza 50059, Spain.

10 ²Dept. d'Ecologia, Universitat de Barcelona, Avda. Diagonal 643, 08028 Barcelona, Spain.

11 ³Forest Research and Management Institute, Calea Bucovinei 73 bis, 725100 Câmpulung
12 Moldovenesc, Romania.

13 ⁴Tree-Ring Laboratory, Lamont-Doherty Earth Observatory of Columbia University, 61 Route
14 9W, Palisades, NY 10964, USA

15 ⁵Long-term Ecology Laboratory, Biodiversity Institute, Department of Zoology, University of
16 Oxford, Oxford, UK .

17 ⁶Università degli Studi di Torino, Dip. Agroselviter, 10095 Grugliasco, Italy.

18 ⁷Università degli Studi di Pavia, Dip. Ecologia del Territorio, Via S. Epifanio 14, 27100 Pavia,
19 Italy.

20 ⁸Università Politecnica delle Marche, Dip. SAPROV, Via Breccie Bianche, 60131 Ancona, Italy.

21 ⁹Università 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

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 CO₂ 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 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

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° 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 CO₂ 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 _{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 ($Z_i B_i$) was regarded as a random effect. We also included in the model an error
233 term (ε_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 ± 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 ± 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 (SO₂) 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 CO₂ (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) ^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 |

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. | -0.44 | -0.12 | 0.21 | 0.49 | 0.25 | 0.48 |
| | Aug. | 0.29 | -0.17 | 0.09 | 0.41 | -0.04 | 0.30 |
| | Sep. | 0.14 | 0.10 | -0.10 | -0.10 | -0.13 | -0.07 |
| | 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 |
| Year of growth (y) | Dec. | 0.51 | 0.72 | 0.32 | -0.04 | 0.02 | -0.40 |
| | Jan. | 0.44 | 0.73 | -0.21 | 0.02 | -0.44 | -0.36 |
| | 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 | |

700