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Abstract

Climate change can modify mid to long term forest growth across a tree biogeographical range. In the Mediterranean basin, the predicted increase in aridity is expected to cause growth decline for several temperate tree species that are in the rear-edge (southernmost limit) of their distribution area. Empirical evidence suggests that the forecasted growth decline seems to be site- and species-specific, but few studies have considered the response of a species along its entire distribution range. We study growth trends and response to climate of silver fir (*Abies alba*) populations across its southern distribution limit in Europe. More than 1300 trees from 111 populations located across Spain, Italy and Romania were used to describe growth trends using basal area increment and to characterize year-to-year growth responses to climate using ring-width indices. We found significant contrasting patterns of basal area increments among sites. Populations located out of the Mediterranean area (northern Italy, Romania) have shown a clear growth improvement over the last two decades, whereas most of those located in Spain and southern Italy display a marked growth decline since the 1980s. Most populations in the southwestern distribution limit are strongly affected by spring-summer water deficit, whereas those located in northern Italy and Romania are more sensitive to late winter and early spring temperatures. The increase in aridity driven by rising temperatures observed in southwestern Europe is causing growth decline in some silver fir populations portending their die-off, whilst in more temperate area warming is driving growth improvement. The forecasted increase in the duration and severity of drought stress will likely trigger multiple die off events in the majority of Mediterranean silver-fir populations.

Key words: *Abies alba*, basal area increment, climate warming, dendroecology, drought stress.

Introduction

Global-warming consequences on ecosystems represent a challenge for human well-being (Nelson et al. 2013). Air temperature has risen by 0.13º C per decade for the latter half of the last century (IPCC 2013), inducing changes in the geographic distribution and performance of animal and plants (Taberlet and Cheddadi 2002). Warming trends influence vegetation patterns by modifying the start and duration of the growing season, and higher air temperatures alter growth responses to climate (Wolkovich et al. 2012). How plant populations face these changes depend in their plasticity and ability to acclimatize to new environmental conditions (Nicotra et al. 2010). Therefore, far from being homogenous the consequences of warming on species performance vary across the species distribution range (Vila et al. 2008; Carrer et al. 2010). This geographical variability is illustrated by tree populations located at the lower latitudinal limit (rear edge) margin of the species distribution area which are particularly sensitive to climate oscillations (Hampe and Petit, 2005).

Many European tree species such as silver fir (*Abies alba* Mill.) or Scots pine (*Pinus sylvestris* Ll.) reach its rear edge in the Mediterranean region, a climate change hotspot (Luterbacher et al. 2012). There, warming is predicted to amplify aridity through increased vapour pressure deficit leading to exacerbated soil moisture deficit (Piñol et al. 1998, Giorgi and Lionello 2008, IPCC 2013). Recent drought events have caused widespread growth decline, decreasing productivity and inducing forest die-off of Mediterranean forests both in dry sites (Sarris et al., 2007; Thabeet et al. 2009; Dorman et al. 2013; Vicente-Serrano et al., 2013) but also in mesic sites (Jump et al., 2006; Linares and Camarero, 2012a, 2012b; Castagneri et al. 2014). Conversely, other authors have reported growth improvements of tree species in Mediterranean sites (Tegel et al. 2014). These findings are further complicated in mixed stands where each

tree species can respond with different intensity to similar climate drivers (Bouriaud and Popa 2009; Castagneri et al. 2014). Such contrasting findings confirm that long-term growth responses of trees to climate are highly contingent on local climatic conditions including warming trends and precipitation regimes. For instance, Vila *et al*. (2008) reported that Scots and Aleppo (*Pinus halepensis* Mill.) pines performed differently along an altitudinal gradient depending on how site conditions buffered the effects of regional climatic factors. This local contingency of growth responses to climate is further complicated because present growth patterns across the range of tree species were also shaped by past events including land use (Camarero et al. 2011) or long-term genetic and phenotypic variability due to postglacial gene flow (Liepelt et al. 2009).

The consequences of warming-induced drought on forest growth and the determination of those tree species and populations that will be the most affected are still under debate. For example, in Iberian conifer forests drought stress adversely influenced growth and survival of those species most vulnerable to xylem cavitation (Sánchez-Salgero et al. 2012) or those populations living in the driest sites (Andreu-et al. 2007, Martínez-Vilalta et al. 2008, del Río et al. 2014) or near the species' rear edge (Macias et al. 2006). Other authors have emphasized how remarkable is the capacity of tree populations from drought-prone areas to cope with water shortage by changing growth dynamics, wood anatomy and water use efficiency (WUE) (Alla and Camarero 2012; Linares and Camarero 2012b, Granda et al. 2013). Despite the plasticity of tree species to tolerate drought stress, and the potential increase of WUE as a result of an increase in atmospheric CO_2 concentrations (Norby et al. 1999), water-demanding tree species such as silver fir should respond negatively to the increase in aridity, especially near the species rear edge.

In a recent study, Büntgen et al. (2014) showed that silver-fir secondary growth has increased considerably during the last 20 years across central Europe, whereas there was a noticeable growth decline across drought-prone Mediterranean sites. Consistently, different patterns of tree growth have been reported between northern and southern silver-fir populations in Italy (Carrer et al. 2010). Die-off episodes of silver fir forests have been described for the past five centuries across Europe but their incidence varies geographically and it seems to be increasing during the 20th century, particularly in SW (Spanish Pyrenees, see Camarero et al. 2011) and SE locations (Slovenia, see Bigler et al. 2004). Could such silver-fir growth decline portend drought- or heat-induced die-off (*sensu* Allen et al., 2010)? Several authors report long-term growth declines in some rear-edge silver fir populations (Linares and Camarero 2012a, Büntgen et al. 2014), where summer water deficit, a major driver of silver fir growth (Pasho et al. 2011), has increased considerably (Giorgi and Lionello 2008). Nevertheless, growth responses to water deficit can be mediated by several different factors including phenotypic plasticity among populations as a consequence of local acclimatization. Thus, to fully understand how silver fir responds to climate warming studies across the entire distribution range are required to disentangle biogeographical imprints in growth patterns.

Here we compile an extensive network of tree-ring width chronologies to characterize the spatiotemporal trends of silver-fir growth across its southern distribution limit in Romania, Italy and Spain. The main objective of our study is to describe the geographical patterns in silver fir growth across its rear edge and ascertain its main climatic drivers. We hypothesize that silver fir growth across the European continent is declining and could become locally extinct in specific drought-prone regions of its rear-edge distribution range as a local response to warming-induced

drought stress. To achieve our objective, we combined nonlinear additive modeling of long-term growth trends with dendrochronological analyses.

Material and methods

Study area and species

Silver fir is a highly productive conifer growing in sites with mesic conditions and deept soils, and showing very sensitive to high vapour pressure deficit or atmospheric drought (Aussenac 2002), showing a wide distribution across central and southern Europe where it forms pure or mixed stands, mainly coexisting with European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst.) or Scots pine (Peterken et al. 1996). The distribution range of silver fir extends from the Pyrenees (southwestern edge) to mountainous regions in southern Poland. It is one of the biggest tree species and dominates tree assemblages in moist and productive sites from central Europe, the Balkans, France, northern Spain, Italy and Romania (Brus et al. 2011). Silver fir is usually dominating in sites under temperate to continental conditions with positive summer water balance (**Supporting Information, Fig. S1**). In those sites a clear warming trend has observed throughout the past century, and that rise in air temperatures has intensified since the 1980s **(Supporting Information, Fig. S2).**

We collected wood samples of 1338 silver fir trees from 111 sites located in Spain (46 sites), Italy (52 sites) and Romania (13 sites) (**Fig. 1; Supporting Information, Table S1**). A detailed description of the different study sites can be found elsewhere (Macias et al. 2006; Carrer et al. 2010; Camarero et al. 2011; Linares and Camarero 2012a, 2012b). The study area covers a vast extension and includes a wide longitudinal gradient (from 1.05º W to 26.69º E) over the rear-edge distribution limit of the species.

Field sampling and dendrochronological methods

In each site, at least 10 dominant or co-dominant standing trees were randomly selected. We also determined the geographical location (latitude, longitude) of each site. We characterized radial-growth trends of silver-fir using dendrochronology (Fritts 2001). Secondary growth was measured in two to three radial cores per tree, which were extracted at breast height on the cross-slope sides of the trunk with an increment borer whenever possible. Wood samples were sanded until tracheids were visible and then visually cross-dated. Once dated, we measured the tree-ring widths to the nearest 0.01 mm using a binocular scope and the LINTAB measuring device (Rinntech, Germany). The accuracy of visual cross-dating and measurements were checked with the program COFECHA which calculates moving correlations between each individual series and the mean site series (Holmes 1983).

To quantify the short-term growth responses to climate, first we standardized and detrended the tree-ring width series to remove age or size trends and their temporal autocorrelation (Briffa and Melvin 2011). We fit negative exponential or linear functions and 30-year long splines to the tree-ring width series. These relatively short splines allow removing growth trends in periods longer than decades, withholding the high-frequency (mainly annual) growth variability. Then, we applied autoregressive models to model and eliminate the temporal (usually first-order) autocorrelation. Finally, we obtained the residual growth-index series, which we averaged following a hierarchical approach from tree to site (chronology) levels. These detrended and residual site chronologies of growth indices (RWI_{site}) were built using the program ARSTAN (Cook 1985).

To characterize the growth series at the site level we calculated several dendrochronological statistics either considering mean series of raw data (AC, first-order autocorrelation which measures the serial persistence of growth) or residual (RWI_{site}) growth indices (MS, mean sensitivity, a measure of year-to-year growth variability; rbt, mean correlation between trees which evaluates the similarity in growth variability among trees; PC1, variance explained by the first principal component; Fritts 2001). If a reliable time span is defined as the period showing values of Expressed Population Signal (EPS) over 0.85 (Wigley et al. 1984), 85% of all site chronologies cover the period 1900-1998 and show EPS values over the 0.85 threshold value (**Supporting Information, Table S1**).

In those sites (Spain, 40 sites; Italy, 43 sites; and Romania, 5 sites) where tree diameter at breast height (dbh; measured at 1.3 m) and bark thickness data were available for all trees tree-ring width series were converted into basal area increment (BAI) to describe long-term growth trends. The calculation of BAI allows removing the geometrical constraint of adding a volume of wood to a stem of increasing radius (Biondi and Qaedan, 2008). For each site, the mean BAI site series was calculated considering all sampled trees.

Cimate data

Monthly climate data (mean temperature, total precipitation) were interpolated for those 0.5º grids including each sampled stand and corresponding to the CRU TS 3.1 data set (Harris et al. 2014). We also calculated the monthly water balance (P-PET) as the difference between precipitation (P) and potential evapotranspiration (PET) following Hargreaves and Samani (1982). Climatic data were obtained from the Royal

Netherlands Meteorological Institute "Climate Explorer" web page (http://climexp.knmi.nl).

To evaluate the growth indices responses to drought we used the Standardized Precipitation–Evapotranspiration Index (SPEI), which is a multiscalar drought index useful to quantify the responses of forests to water deficit at several time scales (Vicente-Serrano et al., 2010). Positive and negative SPEI values correspond to wet or dry conditions, respectively. SPEI data were obtained for the same grids as climate data but considering the entire region where silver fir was present in each country. These data were downloaded from the SPEIbase web page (http://sac.csic.es/spei/database.html).

Statistical methods

1. *Long term trends in silver fir growth*

To analyze the spatiotemporal trend in silver fir growth we used Generalized Additive Mixed Models (GAMM; Wood 2006). GAMM is a flexible semi parametric method to characterize non-linear patterns observed between the response variable and one or several explanatory variables (Wood 2006; Augustin et al. 2009).

We considered silver-fir growth trend (BAI) across Europe as a result of non-linear interactions between the spatial location and the temporal trend. The latitude and longitude of each site were used to reflect the spatial structure of BAI trends and calendar year (hereafter termed "year") was used to reflect temporal BAI trends. The variable year can reflect ontogeny as well as trends in growth induced by drivers such as rising atmospheric CO_2 concentrations, air temperatures and local disturbances. The final GAMM was of the form:

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

In this model, BAI of site i is modelled as a function of a spatiotemporal additive model including a three-way interaction between calendar year and the x_i (latitude) and (longitude) y_i coordinates and two variables reflecting site productivity (mean dbh_i, diameter at breast height) and ontogeny (stand age_i). A tensor product smoother (*tp*) is used to model the space x time interaction, and cubic regression splines (*s*) allow modelling stand basal area and age (Augustin et al. 2009). In addition, since BAI represents multiple measurements performed in different trees from each site, site identity (Z_iB_i) was regarded as a random effect. We also included in the model an error term (ε_i) with an AR1 (p = 1, q = 0) correlation structure. In this study BAI_i showed a skewed distribution, therefore we log-transformed this variable (log x +1).

2. Climatic drivers of silver-fir growth

Residual site chronologies of tree-ring widths (RWI_{site}) were correlated with monthly climatic variables (temperature, precipitation and P-PET) for the period 1902-1994. We considered the correlations calculated for the temporal window including from July of the previous year up to October of the year of growth. In addition, to detect the effects of climate on growth extremes we calculated the percentage of narrow and wide ring-width indices at country scale for the aforementioned period by determining the relative frequency of sites showing indices below and above the 5th and 95th percentiles of country-wide values, respectively (**Supporting Information, Fig. S3**). Those country-wide frequencies were related to the same climatic variables aforementioned but extending the temporal window from prior January up to concurrent December. The SPEI was related to a mean residual site chronology calculated for each country and considering the window from January to December since the SPEI is based on cumulative water deficits. The Pearson correlation coefficient was used to test for the

strength and significance of the associations between growth indices and climate variables or the SPEI. To get a better understanding of the geographical differences of growth-indices responses to climate, the Pearson correlation coefficients obtained by relating growth indices and climate variables (temperature, precipitation, P-PET) were also correlated with site latitude and longitude.

Results

Spatiotemporal trends in basal area increment

Since 1950 BAI widely varied along the study region being characterized by growth decreases in most Spanish sites and growth increases in most Romanian and Italian sites **(Fig. 2**). The model proposed to describe growth trends accounted for 70% of the variation in BAI (**Table 1**) and was statistically reliable (**Supporting Information, Fig. S4**). Across Europe, silver-fir BAI in low latitude and longitude sites (i.e. Spain and southern Italy) increased from the 1950s to the late 1970s, and then decreased until nowadays. Conversely, at high latitudes and longitudes (Alps, northern Apennines and Romania), silver fir BAI decreased from the 1950s to early 1980s and then this trend reversed during the last decades showing a recent growth enhancement. During the 1990s, silver fir BAI trends were markedly negative in most Spanish sites, whilst they were mainly clearly positive in Romania and northern Italy (**Fig. 2**).

Dendrochronological characteristics of the silver fir network

The dendrochronological statistics for the silver fir chronologies differed between countries (**Table 2**; site values are displayed in **Supporting Information, Table S2)**. Mean ring width was 2.00 ± 0.75 mm (mean ± SD) and it was significantly ($P < 0.05$) 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 ± 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

temperature of prior August and September, and also October in Spain. In addition, silver fir in Romania showed significant responses to winter climate conditions, with higher temperatures from December to March promoting the formation of wider rings (**Fig. 4**). Cold winter conditions from December to February induced the formation of narrow rings, particularly in Romania and Italy.

Concerning the responses to the SPEI drought index, the mean Spanish chronology showed a stronger sensitivity to previous summer-autumn drought than those from Italy and Romania (**Fig. 5**). In Spain, narrow rings are former when dry conditions occur in the previous summer, whereas in Italy, this pattern is less clear. In contrast, the Romanian narrow growth indices are more strongly related to spring (May) dry conditions (compare **Figs. 4 and 5**).

The aforementioned country-wide patterns were corroborated when the analyses were done at the site scale using site chronologies of growth indices (RWI_{site}) (**Fig. 6**) showing clearly that the precipitation and the water balance (P-ETP) of June to September during the year previous to growth are consistent drivers of silver-fir growth along its entire distribution range (**Fig. 6**). However, in Spain silver-fir growth is particularly dependent on sufficient precipitation and a positive water balance (P-PET) from June to July during the year of growth. Further, the relevance of current spring-water balance for silver-fir growth in Spain has increased in the second half of the past century (see **Supporting Information, Fig. S5**)

Consequently, the correlation between BAI and the water balance from June to July decreased significantly with latitude and longitude, whereas that with June temperature increased (**Table 3, Fig. 7**). The higher sensitivity of the Mediterranean (Spain, Southern Italy) silver fir populations to water availability contrasted with the noticeable responsiveness of Romanian populations to temperature. There was a marked

increase in the strength of the relationship between temperature and growth with latitude and longitude (mostly in cold months; **Table 3**). In this sense, we found a strong correlation between growth response to temperature in December, January and March and longitude. The strength of the relationship between previous summer climate conditions and growth evidences the presence of a consistent response to climate across most of the silver fir distribution area. However, there are also seasonal differences between sites since the strength of the relationship between previous July water balance and growth indices increased with latitude and longitude, whereas that with the water balance during the previous autumn decreased.

Discussion

We found evidence for both, common climatic signals affecting silver-fir growth along its southern distribution limit, and contrasting responses to recent climate trends of populations from southwestern and northern regions. On one hand, we found a generalized warming-driven decline in growth of many silver fir populations located in the southwestern (Spain) and southernmost (Italy) limits of the species distribution area **(Fig. 2**). Remarkably, this declining pattern contrasts with the recent improvement in growth reported for silver fir populations located in central Europe (Büntgen et al. 2014) and in other wet sites located elsewhere (northern Italy, Romania). Warmer temperatures are plausibly exacerbating drought stress across the species rear-edge, mainly in the western Spanish Pyrenees and southern Italy, while enhancing wood production and carbon uptake in mesic areas **(Figs. 5, 6 and 7**). On the other hand, our results concur with previous studies indicating the remarkable sensitivity of silver fir to the water balance at the end of the previous growing season across Europe (Rolland et 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_2) 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 Carphatian 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 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-

induced growth decline (Williams et al., 2013). Overall, we speculate that some silver fir populations from southwestern Europe will not override the forecasted increase in aridity during this century. There are plausible reasons to think that the geographical range of silver fir in Europe will firstly shrink in the southwestern limit of the species distribution area.

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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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Table 2. Summary of the structural features (dbh, diameter at breast height; mean age) and dendrochronological statistics (calculated for the period 1990−1998) obtained for the studied silver fir forests in each country. The mean (SD) and range (minimum – maximum) are shown. Abbreviations are as follows: MRW, mena tree-ring width; MS, mean sensitivity; AC, first-order autocorrelation; rbt, correlation between trees; and PC1, fraction explained by the first Principal Component. Superscript letters correspond to the comparison of country values using Dunnett's Modified Tukey-Kramer Pairwise Multiple Comparison test (Dunnett 1980), whereas different letters indicate the presence of significant differences ($P < 0.05$) between countries. Site values are available in the **Supporting Information, Table S2**.

	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

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

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**
	Dec.	**0.51**	**0.72**	**0.32**	-0.04	0.02	**-0.40**
Year of growth (y)	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