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

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ABSTRACT

Aim Climate change is expected to modify growth trends of forests around the world. However, this modification may vary in strength and intensity across a species' biogeographical range. Here, we study European populations of silver fir (*Abies alba*) across its southern distribution limits in Spain, Italy and Romania. We hypothesized that growth trends of silver fir will differ across its distribution range, with a marked decline in growth in drought-prone regions near the species' southernmost biogeographical limits.

Location Europe (Spain, Italy, Romania).

Methods We collected tree-ring data from at least 1300 silver fir trees located in 111 sites. The dataset was used to assess and model growth trends, quantified as changes in basal area increment, and to determine how growth responds to climate.

Results We found contrasting patterns of basal area increments among countries and sites. Populations of silver fir located outside the Mediterranean area (e.g. northern Italy, Romania) have shown a clear increase in growth over the last two decades, whereas most populations in Spain and southern Italy have displayed a marked decline in growth since the 1980s. The growth of silver fir forests at the south-western distribution limit is severely constrained by low spring–summer water availability, whereas growth of silver fir forests in non-Mediterranean areas is limited by cold conditions in late winter to early spring.

Main conclusions Climate warming is distinctly modifying growth patterns and responses to climate in silver fir across most of the species' European distribution area. In south-western Europe the reduction in growth of many populations is related to an observed increase in aridity, whereas in more temperate areas warming is enhancing growth. Our results confirm a decline in the growth of silver fir at its south-western distribution limits as a consequence of climate warming.

Keywords

Abies alba, basal area increment, biogeographical range, climate warming, dendroecology, drought stress, Italy, longitudinal gradient, Romania, Spain.

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INTRODUCTION

The direct and indirect effects of global warming on forest ecosystems represent a challenge for human well-being in the near future (Nelson *et al.*, 2013). Air temperature rose by 0.13 °C per decade during the latter half of the last century (IPCC, 2013), inducing changes in the geographical

distribution and performance of animal and plant species (Taberlet & Cheddadi, 2002). Warming trends can influence vegetation patterns by modifying the start and duration of the growing season, and abrupt air temperature increase can alter growth responses (Wolkovich *et al.*, 2012). The resistance of plant species or populations will depend upon their ability to acclimatize to new environmental conditions

(Nicotra *et al.*, 2010). Therefore, far from being uniform the effects of climate warming on species' performance may vary across the distribution range (Vila *et al.*, 2008; Carrer *et al.*, 2010). Special attention must be paid to tree populations located at the lower latitudinal limit of the species' distribution area, which is particularly sensitive to climate oscillations (Hampe & Petit, 2005).

The distribution range of woody plants is ultimately determined by the availability of water (Stephenson, 1990; O'Brien, 2006). Tree species dominant in boreal and temperate areas of Europe, such as silver fir (*Abies alba* Mill.) or Scots pine (*Pinus sylvestris* L.), reach their southern limit in the Mediterranean region, a climate change hotspot (Luterbacher *et al.*, 2012). In this region, warming is predicted to enhance aridity, exacerbating soil moisture deficit with the increase in vapour pressure deficit (Giorgi & Lionello, 2008; IPCC, 2013). Recent drought events have caused a widespread decline in growth, decreasing productivity and inducing forest die-off of Mediterranean forests, both at dry sites (Sarris *et al.*, 2007; Thabeet *et al.*, 2009; Vacchiano *et al.*, 2012; Dorman *et al.*, 2013) and in mesic environments (Jump *et al.*, 2006; Linares & Camarero, 2012a,b; Castagneri *et al.*, 2014). Conversely, other authors have reported growth improvements of tree species in Mediterranean sites (Tegel *et al.*, 2014). Responses in mixed stands are even more complicated: each tree species can respond to similar climate drivers with different intensity (Bouriaud & Popa, 2009; Castagneri *et al.*, 2014).

These contrasting findings may indicate that local factors such as topography or geographical location can modify the climatic impact on tree growth and performance (O'Brien, 2006; Austin & Van Niel, 2011). For instance, Vila *et al.* (2008) reported that Scots pine (*P. sylvestris*) and Aleppo pine (*Pinus halepensis* Mill.) performed differently along an elevational gradient depending on how site conditions buffered the effects of regional climatic factors. However, this local contingency of climate–growth responses may also be a consequence of past events such as long-term genetic and phenotypic variability as a result of post-glacial gene flow (Liepelt *et al.*, 2009) and also of land-use changes (Motta & Garbarino, 2003; Camarero *et al.*, 2011; Tinner *et al.*, 2013). The relevance of environmental and historical factors as determinants of climatic impacts on forest growth has been revealed by studies combining species distribution models and palaeoecological data (Svenning & Skov, 2004; Tinner *et al.*, 2013). In this sense, tree ring data provide a continuous and long-term assessment of the performance of tree species and populations, which allows the response to recent climate change to be understood (e.g. Büntgen *et al.*, 2014).

There is particular interest in discovering how ecologically and economically valuable species such as silver fir will cope with recent climate trends (Maiorano *et al.*, 2013; Tinner *et al.*, 2013). Silver fir is the tallest tree in Europe and in many regions forms mixed stands with other species (Aussenac, 2002). Its southern distribution limit is in mountainous areas of the Iberian Peninsula and Italy where it can form

mixed stands with Mediterranean tree species (Carrer *et al.*, 2010). Species distribution models suggest that the current distribution range of silver fir was determined by historical land use and that this obscures potential impacts of climate change (Svenning & Skov, 2004; Tinner *et al.*, 2013; Di Pasquale *et al.*, 2014). However, there are several discrepancies on whether the recent rise in temperature alone or in combination with a reduction in the amount of precipitation will lead to a contraction of the species' distribution range (Alba-Sánchez *et al.*, 2010; Maiorano *et al.*, 2013). Interestingly, dendroecological studies have provided evidence for a growth decline of silver fir in the Iberian Peninsula (Linares & Camarero, 2012a) and south-eastern European mountains (Diaci *et al.*, 2011), probably as a consequence of the increase in summer water deficit in those areas (Giorgi & Lionello, 2008). Furthermore, recent studies suggest a different response of the species along its distribution range. For instance, Büntgen *et al.* (2014) showed that radial growth of silver fir increased considerably during the last 20 years across central Europe, whereas there was a noticeable growth decline in drought-prone Mediterranean sites. Indeed, different patterns of tree growth have been reported between northern and southern populations of silver fir in Italy (Carrer *et al.*, 2010). The study of growth trends and responses to climate of silver fir across its biogeographical range could increase our knowledge about the potential impacts of climate change on silver fir populations.

Here we compiled an extensive network of tree-ring width chronologies of silver fir in Romania, Italy and Spain. We described the geographical patterns of the growth of silver fir across Europe and assessed its climatic sensitivity. Nonlinear additive modelling was applied to long-term growth trends obtained through dendrochronological methods. It is finally hypothesized that this species could become locally extinct in some drought-prone regions, especially near the southern limit of its distribution range where growth decline has been severe.

MATERIALS AND METHODS

Study area and species

Silver fir is a highly productive conifer growing in sites with mesic conditions and deep soils, and shows a strong sensitivity to high vapour pressure deficit or atmospheric drought (Aussenac, 2002). It has 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.) H.Karst.) or Scots pine (*P. sylvestris*) (Peterken, 1996). The distribution range of silver fir extends from the Pyrenees (south-western edge) to mountainous regions in southern Poland. It is one of the tallest tree species and dominates tree assemblages in moist and productive sites across central Europe, the Balkans, France, northern Spain, Italy and Romania (Brus *et al.*, 2011). Silver fir is the dominating tree species under temperate to

continental conditions with positive summer water balance. A clear warming trend has been observed in those sites throughout the past century, and the rise in air temperature has intensified since the 1980s (see Appendix S1 in Supporting Information).

We collected wood samples from 1338 silver fir trees at 111 sites: 46 in Spain, 52 in Italy and 13 in Romania (Fig. 1, and see Appendix S2). 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 & Camarero, 2012a,b). The study area covers wide latitudinal and longitudinal gradients from 38.15° to 47.69° N and from 1.05° W to 26.69° E.

Field sampling and dendrochronological methods

At each site, at least 10 dominant or co-dominant standing trees were randomly selected and the latitude and longitude of each site was recorded. Secondary growth was measured in two to three radial cores per tree, which were extracted with an increment borer at breast height (1.3 m) on the cross-slope sides of the trunk whenever possible (Fritts, 2001). Wood samples were sanded until tracheids were visible and then visually cross-dated. Once dated, we measured the tree-ring widths using a binocular microscope and either Aniol or LINTAB measuring devices (Rinntech, Heidelberg, Germany) to the nearest 0.01 mm. The accuracy of visual cross-dating and measurements was checked with the COFECHA program, which calculates moving correlations between each individual series and the mean site series (Holmes, 1983).

To quantify the short-term growth responses to climate, we standardized and detrended the tree-ring width series to remove age/size trends (Briffa & Melvin, 2011). We fitted negative exponential or linear functions and 30-year long splines to the tree-ring width series. These relatively short splines allow growth trends in periods longer than decades to be removed, retaining the high-frequency (mainly annual) growth variability. We applied autoregressive models to characterize and then to eliminate the temporal (usually first-order) autocorrelation of the detrended series in order to obtain the residual series. Finally, the individual series were averaged following a hierarchical approach from tree to site (chronology) levels. These detrended and residual site chronologies of ring-width indexes for each site (hereafter, RWI_{site}) were built using the ARSTAN program (Cook, 1985).

To characterize the growth series at site level we calculated several dendrochronological statistics considering either series of raw data in each site (AC, first-order autocorrelation that measures the serial persistence of growth; 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, fraction of variance explained by the first principal component, which estimates the degree of growth variations shared by trees in the same

site; Fritts, 2001). Note that these analyses were carried out at the site level to compare the results across sites. 85% of all site chronologies covered the period 1900–1998 and showed expressed population signal (EPS) values over 0.85. This threshold value is used to determine that a chronology is reliable (Wigley *et al.*, 1984).

To represent the geographical variation of the growth of silver fir across space and time we conducted a principal components analysis (PCA) using the entire network of residual site chronologies (RWI_{site}). The PCA was created using the variance–covariance matrix of all residual ring-width chronologies, in which the columns are the sites and the rows are years. Note that this analysis was carried out at the network level. The PCA scores thus illustrate the variation in ring-width indices across space and time.

Tree-ring width series were converted into basal area increment (BAI) to describe long-term growth trends in sites (Spain, 40 sites; Italy, 43 sites; and Romania, 5 sites) with diameter at breast height (d.b.h.; measured at 1.3 m) and bark thickness data available for all trees. The BAI calculation removes the geometrical constraint of adding a volume of wood to a stem of increasing radius (Biondi & Qaedan, 2008). The BAI was obtained as:

$$BAI = \pi(r_t^2 - r_{t-1}^2) \quad (1)$$

where r_t and r_{t-1} are the squared stem radial increments at the end and beginning of a given annual ring corresponding to rings formed in years t and $t-1$, respectively. For each site, the mean BAI site series was calculated using all sampled trees older than 100 years.

Climate data

Monthly climate data (mean temperature, total precipitation) were interpolated for the 0.5° grids including each sampled stand and corresponding to the CRU TS 3.1 dataset (Harris *et al.*, 2014). This dataset contains information on monthly temperature and precipitation data that has been checked and tested for homogeneity. It thus provides a reliable climatic data source for the entire 20th century across the whole study region. We are aware that a 0.5° spatial resolution may be too coarse for some mountain forests where topography induces local changes in precipitation. Furthermore, there were usually few meteorological stations in remote mountain areas prior to the 1950s. However, to the best of our knowledge the CRU climatic dataset is the best available dataset to test long-term changes in growth as related to climate in several countries. Based on this gridded dataset, we also calculated the monthly water balance (P – PET) as the difference between precipitation (P) and potential evapotranspiration (PET) following Hargreaves & Samani (1982). Climatic data were obtained from the Royal Netherlands Meteorological Institute ‘Climate Explorer’ web page (<http://climexp.knmi.nl>).

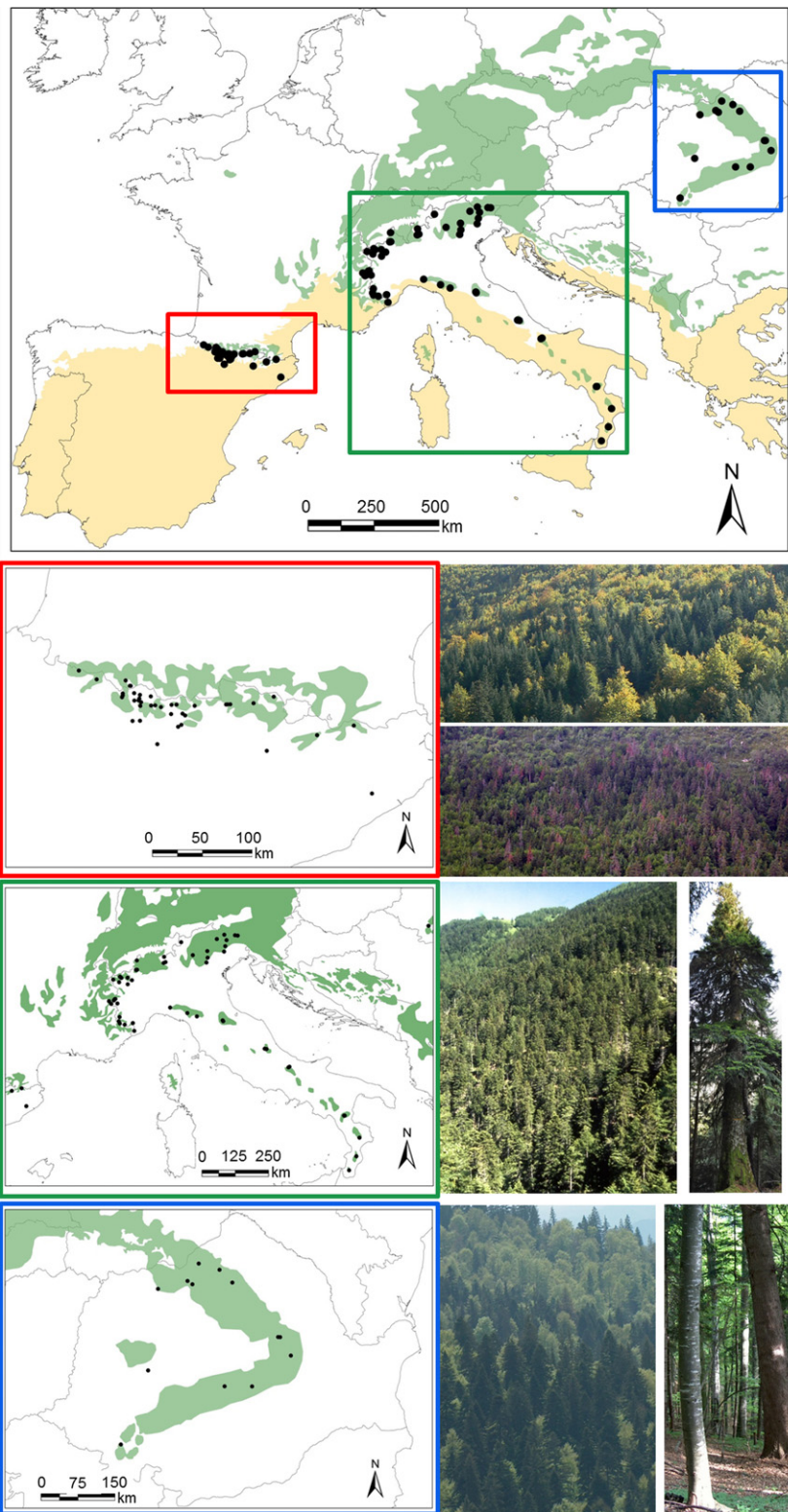


Figure 1 General map of the study sites in Europe (above) and maps and pictures of the silver fir (*Abies alba*) forests sampled in Spain (note the forest with severe dieback), Romania and Italy. The green polygons on the European map show the distribution of silver fir, the yellow area corresponds to the Mediterranean vegetation type, and the dots indicate the sampled sites.

Statistical methods

Long-term trends in silver fir growth

To analyse spatio-temporal patterns in silver fir growth we used generalized additive mixed models (GAMM; Wood,

2006). GAMM is a flexible semi-parametric method that characterizes nonlinear patterns observed between a ‘response’ variable and one or several ‘explanatory’ variables (Wood, 2006; Augustin *et al.*, 2009).

In the models, BAI trends in silver fir across Europe were considered the result of nonlinear interactions between

spatial location and the temporal trend. Latitudes and longitudes were used to define the spatial structure of BAI trends, while calendar years (hereafter termed 'year') were used to characterize temporal BAI trends. The variable year can reflect ontogeny, but can also contain information from changes in drivers such as rising atmospheric CO₂ concentrations, air temperatures and/or local disturbances (see Macias *et al.*, 2006). The final GAMM was in the form:

$$\log(\text{BAI}_i + 1) = tp(x_i, y_i, \text{year}_i) + s(\text{d.b.h.}_i) + s(\text{stand age}_i) + Z_i B_i + \varepsilon_i \quad (2)$$

In this model, BAI of site *i* is modelled as a function of a spatio-temporal additive model with a three-way interaction between year and the x_i (latitude) and y_i (longitude) coordinates, two variables reflecting site productivity (mean d.b.h._{*i*}, diameter at breast height) and ontogeny (stand age_{*i*}). A tensor product smoother (*tp*) is used to model the space × time interaction (Augustin *et al.*, 2009). Thin plate regression splines (*s*) are used to represent all the smooth terms. The degree of smoothing is determined by internal cross validation (Wood, 2006). In addition, as BAI represents multiple measurements performed on different trees from each site, site identity ($Z_i B_i$) was regarded as a random effect. An error term (ε_i) with an ARMA ($p = 1, q = 0$) correlation structure was also included in the model. In this study raw BAI_{*i*} data showed a skewed distribution, so we log-transformed this variable ($\log x + 1$). GAMM was fitted using the 'mgcv' library (Wood, 2006) in the R statistical environment (R Core Team, 2014).

Climatic drivers of silver fir growth

Residual tree-ring width site chronologies (RWI_{site}) were correlated with monthly climatic variables (temperature, precipitation and water balance) for the period 1902–1994. The temporal window for the correlation analyses spans from July of the previous year to October of the year of growth. To detect the effects of climate on growth extremes we calculated the percentage of narrow and wide ring-width indices at a country level for the same period by determining the relative frequency of sites in each country showing indices below and above the 5th and 95th percentiles, respectively. These extreme ring-width indices are assumed to be growth responses to extreme climate events such as droughts in the case of narrow rings (Fritts, 2001). Country-wide frequencies of narrow and wide rings indices were related to the climatic variables by using the Spearman correlation coefficient but extending the temporal window from the previous January up to the current December to detect extreme growth responses prior or subsequent to the beginning and end of the growing season. The Pearson product-moment correlation coefficient was used to test the strength and significance of the associations between growth indices and climate variables. To achieve a better understanding of the geographical differences in the growth–climate relationships we correlated

the Pearson correlation coefficients obtained by relating growth indices and climate variables (temperature, precipitation and water balance) with site latitude and longitude.

RESULTS

Spatio-temporal trends in basal area increment

Silver fir BAI for the period 1950–1994 varied widely across the study region, with decreases in growth in most Spanish sites and increases in most Romanian and Italian sites (Fig. 2). The model describing growth trends accounted for 69% of BAI variation (Table 1). Silver fir growth in sites at low latitude and longitude (i.e. Spain and southern Italy) increased from the 1950s to the late 1970s, and then decreased. In contrast, at high latitudes and longitudes (Alps, northern Apennines and Romania) silver fir growth decreased from the 1950s to early 1980s and then increased. During the 1990s, silver fir growth trends were markedly negative in most Spanish sites, but mainly positive in Romania and northern Italy (Fig. 2).

Structural and dendrochronological characteristics of the silver fir network

Several structural features and dendrochronological statistics of the silver fir chronologies differed among countries (Table 2). Spanish silver fir trees were younger, had lower diameter at breast height, and grew less than their Italian and Romanian counterparts. The mean sensitivity, the mean correlation between trees and the fraction of variance explained by the first principal component presented larger values in Spain than in Romania and Italy. Conversely, the first-order autocorrelation was larger in Romania than in the other two countries (Table 2). Lastly, the percentage of small rings (ring-width indices below the 5th percentile) was higher in Spain than elsewhere.

The results of the PCA represented the geographical variation of ring-width indexes (Fig. 3). The PC1 of the PCA accounted for 27.8% of variation (Fig. 3). PC1 loadings geographically separated the sites, locating Romanian and Spanish sites apart along the axis (Fig. 3). The PC2 explained a lower percentage of the variance (8.6%), and showed differences among sites in the same region.

Climatic drivers of silver fir growth

We found a common significant influence of previous year climate conditions on silver fir ring-width indices among sites (Figs 4 & 5). The percentage of wide rings was positively related to the July to September precipitation prior to the growth year (Fig. 4). However, we also found differences in the relationship between climate and extreme growth responses among countries. In Spain, the formation of wide rings was positively related to current June–July precipitation, and negatively to the temperatures of the previous

Figure 2 Long-term trends in basal area increment (BAI) of silver fir (*Abies alba*) based on fitted generalized additive mixed models. The left-side graphs show how basal area increment varies with latitude N (above) and longitude W–E (below). The right-side graphs show the predicted basal area increment data for the different populations. The upper and lower plots show populations located at latitudes above and below 43° N. Note that this corresponds to populations with increasing or decreasing trends, in that order. Solid circles correspond to the populations in Romania, triangles indicate populations from Italy, and squares show populations from Spain. Note that all Romanian and Spanish populations of silver fir are located above and below 43° N, respectively.

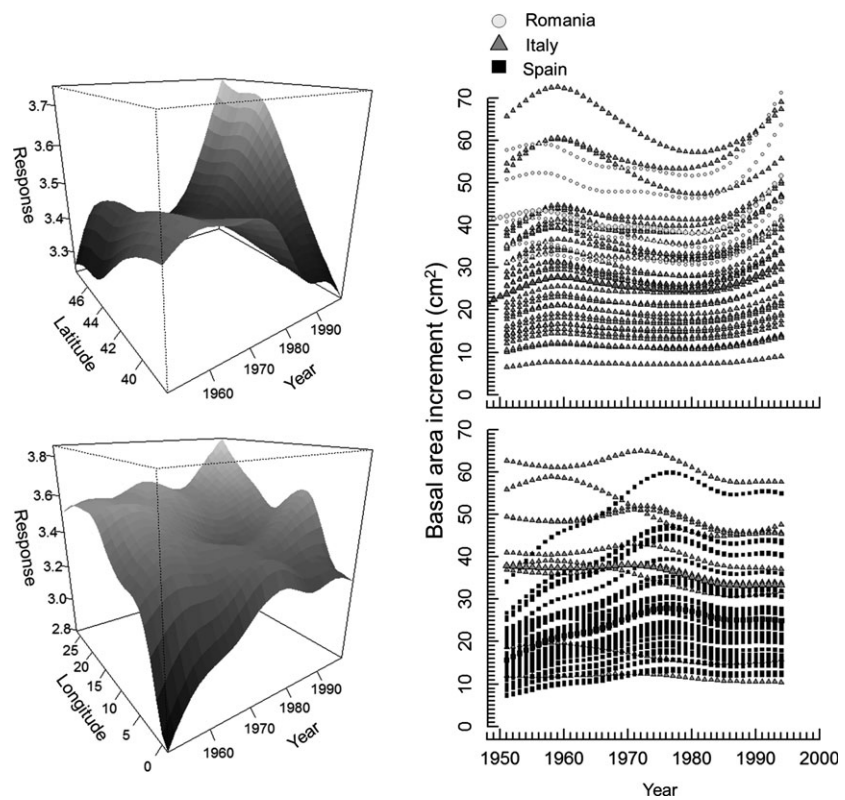


Table 1 Results of the generalized additive mixed models (GAMM) fitted to characterize trends in basal area increment (BAI) of silver fir (*Abies alba*) across the southern European limit of the species. The type of regression spline used for each variable, the estimated degrees of freedom (e.d.f.), *F*-statistic and its associated probability (*P*) are also shown. The model accounted for 69% of the variation in BAI.

Factor	Variable	Spline	e.d.f.	<i>F</i>	<i>P</i>
Spatio-temporal trend	Latitude, longitude and year	tensor product	45.1	5.92	< 0.01
Tree ontogeny	Age	thin plate	1	85.96	< 0.01
Tree size	Diameter at 1.3 m	thin plate	2.5	85.79	< 0.01

August up to October (Fig. 4). In addition, silver fir in Romania presented 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.

These general patterns were confirmed at the local scale using RWI_{site} (Fig. 5): precipitation and water balance ($P - PET$) from June to September during the year prior to growth were consistent drivers of silver fir growth across the whole study area. The strength of the relationship between growth and previous July water balance increased with latitude and longitude (Table 3, Figs 5 & 6). In addition, we found that growth of Spanish silver fir trees depended on sufficient precipitation and a positive water balance from June to July during the current year. Note that the relevance of water balance in the current spring for the growth of silver fir in Spain increased during the second half of the 20th

century (see Appendix S3). Consequently, the correlation between BAI and the June–July water balance decreased significantly with latitude and longitude, whereas it increased with June temperature (Table 3, Fig. 6). The higher sensitivity of the Mediterranean (Spain, southern Italy) populations of silver fir to water availability contrasted with the noticeable responsiveness of Romanian populations to temperature. A higher strength of the relationship between temperature and growth with latitude and longitude was observed mostly in cold months: a strong correlation with longitude was found for December, January and March (Table 3).

DISCUSSION

During the last three decades, the temperature in the growing season has increased considerably across the study region (IPCC, 2013). There has been a concurrent increase in potential evapotranspiration that has led to a decrease in

Table 2 Summary of the structural features (d.b.h., diameter at breast height; mean age) and dendrochronological statistics (calculated for the period 1900–1998) obtained for the studied silver fir (*Abies alba*) forests in each country. The mean (SD) and range (minimum – maximum) are shown. Abbreviations are as follows: MS, mean sensitivity; AC, first-order autocorrelation; rbt, mean correlation between trees; and PC1, fraction of variance explained by the first principal component; and the percentage of sites showing wide (indices above the 95th percentile) and narrow ring-width indices (indices below the 5th percentile). Superscript letters correspond to the comparison of country values using Dunnett's modified Tukey–Kramer pairwise multiple comparison test (Dunnett, 1980), where different letters indicate the presence of significant differences ($P < 0.05$) between countries.

	Spain		Italy		Romania	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
d.b.h. (cm)	56.0 (13.1) ^a	26.5–81.8	63.0 (17.3) ^{ab}	41.0–112.2	74.0 (10.3) ^b	65.0–90.2
Age (years)	112 (45) ^a	58–259	213 (85) ^b	117–533	260 (82) ^b	113–375
Tree-ring width (mm)	1.74 (0.56) ^a	0.89–3.67	2.39 (0.62) ^b	0.54–3.07	2.54 (0.69) ^b	1.90–4.25
MS	0.19 (0.05) ^c	0.10–0.30	0.14 (0.02) ^a	0.08–0.21	0.16 (0.02) ^b	0.12–0.19
AC	0.29 (0.15) ^a	0.12–0.61	0.29 (0.14) ^b	0.09–0.65	0.39 (0.10) ^b	0.23–0.57
rbt	0.40 (0.09) ^b	0.25–0.63	0.31 (0.06) ^a	0.20–0.47	0.31 (0.08) ^a	0.19–0.47
PC1 (%)	0.44 (0.08) ^b	0.31–0.66	0.36 (0.06) ^a	0.25–0.50	0.36 (0.07) ^a	0.26–0.50
Wide rings (%)	4.93 (3.9)	0.0–25.9	4.91 (3.4)	0.3–20.4	4.90 (4.5)	0.0–26.3
Narrow rings (5%)	4.94 (4.5) ^b	0.5–35.5	4.36 (3.0) ^a	0.2–14.0	4.41 (4.3) ^a	0.2–26.4

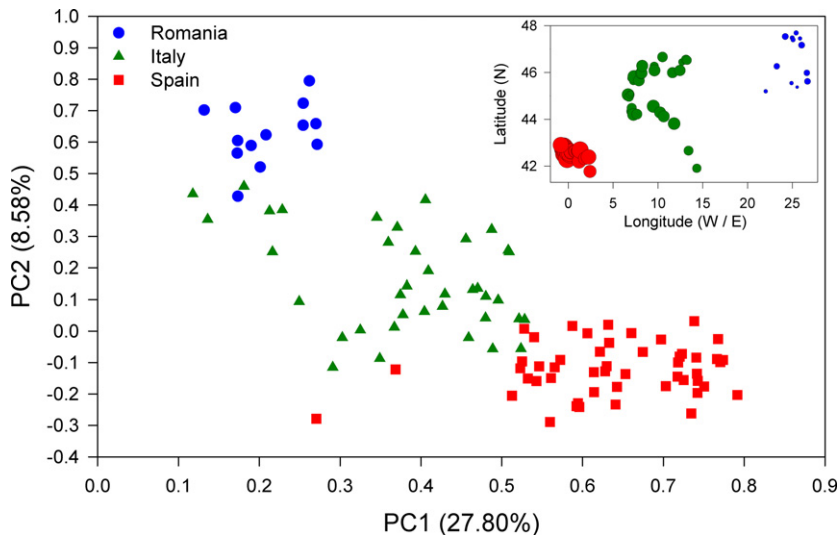


Figure 3 Scores of the two first principal components with their associated variance (PC1 and PC2, respectively) of a principal components analysis (PCA) calculated using all residual site chronologies (RWI_{site}) of silver fir (*Abies alba*). The PCA was created using the variance–covariance matrix of all residual ring-width chronologies, in which the columns are the sites and the rows are years. Thus, the PCA scores illustrate the variation in ring-width indices across space and time. The inset illustrates the geographical variability of the PC1 score in each country (the bigger the symbol, the higher the score). Different symbols and colours correspond to different countries.

water balance particularly in the Mediterranean region (Giorgi & Lionello, 2008). As hypothesized, the observed warming trend has contrasting effects on the performance of silver fir across its southern European distribution area. We found several pieces of evidence suggesting a growth decline in tree populations located at the lower latitudinal limit (warm and dry end of the distribution range) and a notable improvement in central and Eastern Europe, which is plausibly caused by recent warming trends (Macias *et al.*, 2006; Bošela *et al.*, 2014). Recent species distribution models and palaeoecological studies have demonstrated the intensity of the long-term influence of climate on European populations of silver fir (Tinner *et al.*, 2013; Di Pasquale *et al.*, 2014). Our combination of biogeographical and dendroecological approaches complement these previous findings by demonstrating the presence of different responses to recent climate trends between populations of silver fir located in southern

and northern sites of the species' southern distribution range.

The future responses of silver fir forests to climate warming are currently under discussion by the ecological community given that millennia of human impacts have greatly diminished the geographical distribution of the species (Tinner *et al.*, 2013). Regarding the climate responses, some discrepancies arise between the projections of different models: whereas Maiorano *et al.* (2013) predicted a reduction in the species' distribution range due to a moderate warming, others have suggested that this reduction will only occur if accompanied by a substantial decrease in precipitation (Di Pasquale *et al.*, 2014). Our findings contribute new information to this debate because they show that silver fir could become locally extinct in drought-prone regions near the southern limit of its distribution range, and this could lead to a contraction of the species distribution area. There are

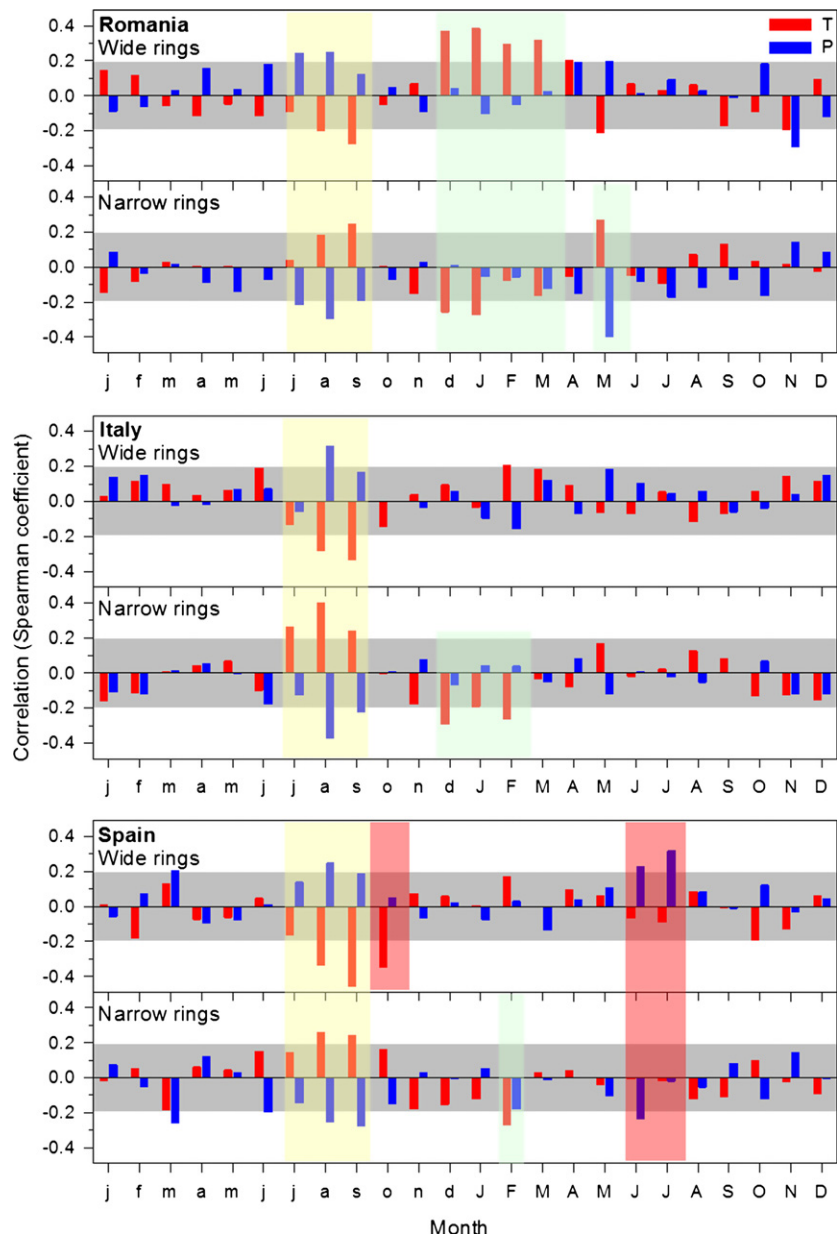


Figure 4 Correlations observed by comparing country series of narrow and wide ring-width indices of silver fir (*Abies alba*) with monthly climatic variables (T, mean temperature; P, total precipitation). Months abbreviated by lowercase and uppercase letters correspond to the previous and current years, respectively. The grey box indicates non-significant correlation values ($P > 0.05$). The coloured boxes indicate periods of high correlation between the climate variables and the ring-width indices.

two main reasons for the discrepancies between our results and those found by other palaeoecological studies. First, we use dendrochronological methods to track the performance of the species across a wide biogeographical range that allows us to understand the response to recent climate trends while accounting for local differences between populations. Second, our study is the only one that includes the south-western-most edge of the species' distribution range, which is one of the species' distribution limits where summer temperatures have risen most steeply. Indeed, it has been suggested that this warming edge could show very different responses to future climate warming depending on seasonal water availability and drought stress (Aussenac, 2002). For instance, no growth decline has been observed in wet upland areas of Italy, while growth decline and forest die-off have occurred

in the western Spanish Pyrenees (Camarero *et al.*, 2011). The growth trends and responses to climate presented in this study thus have important implications in advancing our understanding of the ecology of silver fir.

The growth of silver fir in Spain increased from the 1950s to the mid-1970s owing to favourable climatic conditions such as wet and cool summers (Macias *et al.*, 2006; Camarero *et al.*, 2011). This pattern has also been observed in other mountain conifer forests in the study region (Andreu *et al.*, 2007; Galván *et al.*, 2012). In the Mediterranean Basin, mild temperatures and high precipitation, which favour tree growth, also characterized this period (Sarris *et al.*, 2007). Almost synchronously, silver fir populations in central Europe experienced a pronounced growth decline potentially linked to increasing sulfur emissions (acid rain) and drought

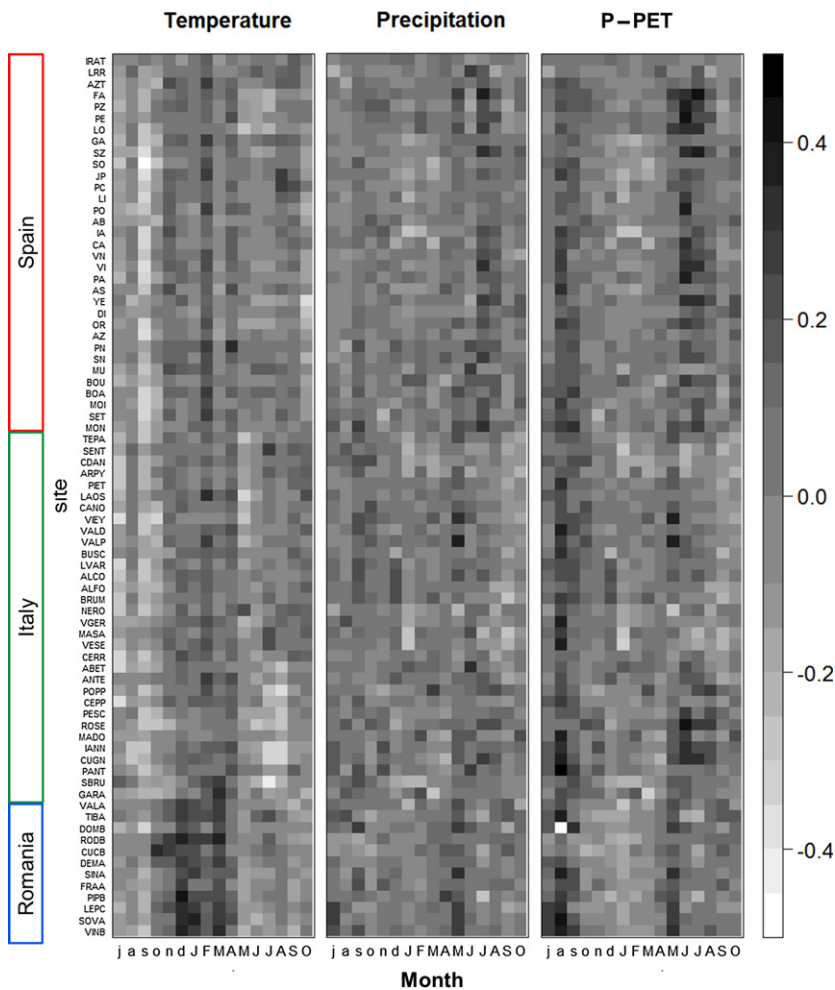


Figure 5 Site-specific growth–climate relationships for silver fir (*Abies alba*) based on the correlations calculated between residual tree-ring width indices and monthly climatic variables [mean temperature, total precipitation and water balance, i.e. the difference between precipitation and potential evapotranspiration ($P - PET$)] for the period 1902–1999. The temporal window includes months of the previous year starting from July up to October of the year of tree-ring formation (months abbreviated by lowercase and uppercase letters correspond to the previous and current years, respectively). The black and white scale shows the value of the Pearson product-moment correlation coefficient obtained by relating growth and climate.

(Büntgen *et al.*, 2014). The pollution reduction since the early 1980s, together with warmer springs and summers, led to a substantial recovery of silver fir growth in central Europe and in the Carpathians (Elling *et al.*, 2009; Bošela *et al.*, 2014). The spatio-temporal pattern of the growth of silver fir has therefore reversed during the last two decades with a marked growth decline in southern Europe and a notable improvement in central and Eastern Europe (Fig. 2). The growth decline is much more apparent in many Iberian sites than in the populations of southern Italy despite being at similar latitudes. These differences may be caused by the less intense water deficit in Italy (see Appendix S1) but also by the different evolutionary history and genetic differentiation of the populations in these two regions (Linares, 2011). Further research could compare growth trends and genetic information to derive predictions on future die-off events (Sancho-Knapik *et al.*, 2014).

Our results confirm previous studies indicating the high sensitivity of European silver fir to water balance at the end of the previous growing season (Rolland *et al.*, 1998; Tardif *et al.*, 2003; Lévesque *et al.*, 2013). However, we argue that temperature may be enhancing the growth and productivity of silver fir in mesic forests, whereas xeric forests are

becoming more sensitive to changes in water availability mediated by warming-triggered rising evaporative demand (Fig. 6). As we move eastwards, the importance of previous winter and early spring temperatures as drivers of growth increases. Conversely, south-western populations are more strongly linked to water availability and to late-spring and early-summer precipitation, confirming their sensitivity to drought. Similar biogeographical patterns were observed for Aleppo pine (*P. halepensis*), with growth positively affected by warming in cold regions and negatively by aridity in warm and dry regions (de Luis *et al.*, 2013). Given that most die-off episodes of silver fir have been detected in xeric sites near its southernmost European distribution limit, our findings corroborate that long-term growth declines portend drought-triggered die-off.

We speculate that the occurrence of severe drought events and increasingly warmer temperatures in northern Spain (1980s–1990s) may be the main factor triggering die-off in some Pyrenean populations of silver fir (Camarero *et al.*, 2011). Rainfall amounts, particularly in summer and autumn, are much higher and temperatures relatively milder in northern Italy and Romania than in Spain. This is probably the reason why the severe droughts starting in the 1980s

Table 3 Biogeographical variability of the climate–growth relationships based on site growth indices (RWI_{site}) observed across the silver fir (*Abies alba*) 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 product-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		Water balance	
		Latitude	Longitude	Latitude	Longitude	Latitude	Longitude
Year previous to growth (y_{-1})	July	-0.44	-0.12	0.21	0.49	0.25	0.48
	August	0.29	-0.17	0.09	0.41	-0.04	0.30
	September	0.14	0.10	-0.10	-0.10	-0.13	-0.07
	October	0.38	0.35	-0.12	-0.47	-0.18	-0.35
	November	0.61	0.17	-0.18	-0.02	-0.39	-0.25
	December	0.51	0.72	0.32	-0.04	0.02	-0.40
Year of growth (y)	January	0.44	0.73	-0.21	0.02	-0.44	-0.36
	February	0.10	-0.12	-0.14	-0.12	-0.24	-0.20
	March	0.36	0.86	0.45	0.34	0.10	-0.22
	April	-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
	June	-0.09	-0.23	-0.09	0.24	-0.44	-0.22
	July	0.61	0.01	-0.44	-0.49	-0.49	-0.44
	August	0.30	-0.33	-0.38	-0.15	-0.44	-0.07
	September	-0.09	-0.63	-0.07	0.18	-0.05	0.31
	October	0.47	0.17	-0.34	0.01	-0.36	-0.01

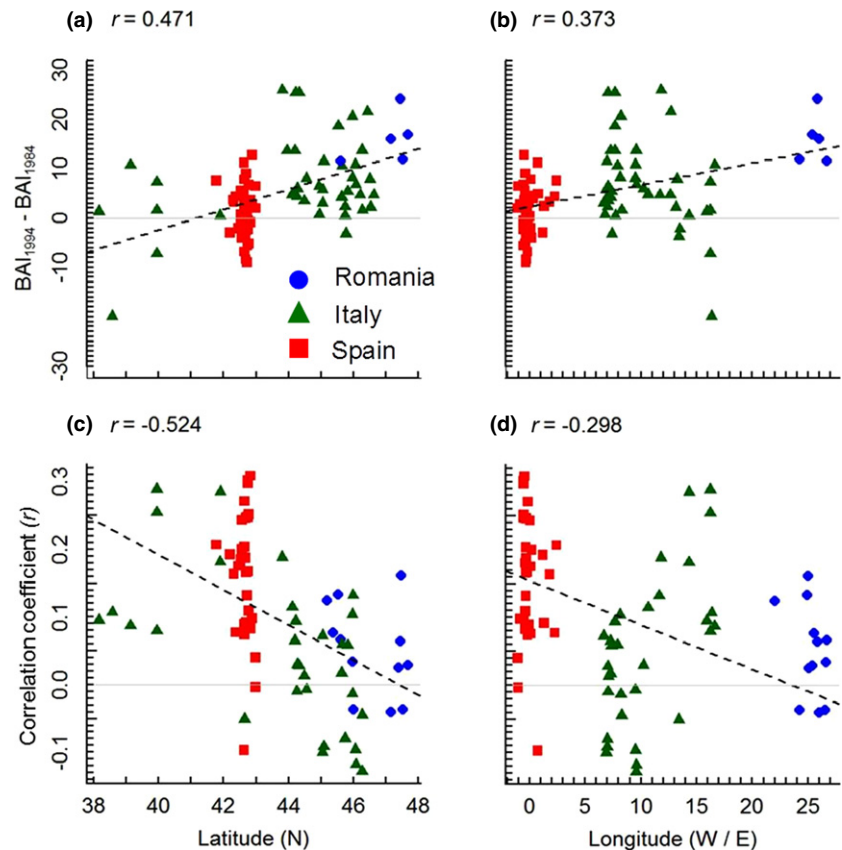


Figure 6 Biogeographical patterns in recent growth trends and responses to climate in silver fir (*Abies alba*). Differences in basal area increment (BAI; in cm^2) from 1994 to 1984 ($BAI_{1994} - BAI_{1984}$) in (a) latitude and (b) longitude; and responses of site growth indices (RWI_{site}) to June–July water balance ($P - PET$) during the period 1950–1999 in (c) latitude and (d) longitude. Negative longitude values correspond to western longitudes. Different colours and symbols are used for each country: Romania (blue circles); Italy (green triangles); Spain (red squares). Correlation coefficients describe the linear relationships (dashed lines) displayed on each map.

caused such negative consequences in those marginal sites at the driest limit of the species’ distribution range. Our analyses suggest that the growth of silver fir is very sensitive to

extreme drought events, as demonstrated by the influence of previous year precipitation and temperature on the frequency of extremely narrow rings. Two consecutive and severe

droughts during the 2000s also caused a decline in the growth of Scots pine in France (Thabeet *et al.*, 2009) and in dry Alpine valleys (Vacchiano *et al.*, 2012; Rigling *et al.*, 2013). Given that during low rainfall periods trees depend more strongly on cumulative precipitation and deep soil water reserves (Sarris *et al.*, 2007), prolonged dry and warm periods can have negative consequences on tree growth in drought-prone regions or in sites with low water retention capacity (Dorman *et al.*, 2013). To conclude, drier and warmer summer conditions will represent the major climatic constraints to the growth of silver fir.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Trends during the 20th century in summer air temperature and water balance in the three study countries.

Appendix S2 Site characteristics of each sampled stand.

Appendix S3 Site-specific correlations of tree-ring width indices to monthly climatic variables.

BIOSKETCH

Our research team aims to understand, from a multidisciplinary and global perspective, the effects of climate conditions on the performance of plant species, in order to improve our understanding of the consequences of climate warming and its implication for the conservation of populations and communities across wide biogeographical areas.

Author contributions: J.J.C., I.P. and M.C. conceived the ideas; J.J.C., E.G., I.P., L.A.-H., R.M., P.N., M.R., G.S.-B., C.U. and M.C. collected the data; A.G. and J.J.C. analysed the data; and A.G. led the writing. All the authors read and approved the final draft.

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