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Evidence that the Montseny Mountains are still a good climatic refugium for the southernmost silver fir forest on the Iberian Peninsula

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ABSTRACT

Many European temperate tree species reach their southern distribution limits in the Mediterranean region, and ongoing climate change will further restrict their climatic niche in this area. In this study, we investigated the effects of forest management and climate change on tree growth and the spatial extension of a silver fir forest (*Abies alba* Mill.) located at the species' southern distribution limit on the Iberian Peninsula (Montseny Mountains Natural Park, Spain). Different growth variables such as tree-ring width (RW), basal area increment (BAI), earlywood width (EwW) and latewood width (LwW) were assessed, and climate-growth relationships were established for the period 1914-2010.

Our results revealed that the main growth reductions and releases in the raw tree-ring width series were related to both volcanic activity and intensive logging. Since the establishment of the Natural Park in 1977, RW series have levelled off, and this has translated into an increase in BAI. This positive performance may have also facilitated the spatial expansion of the stand. Low precipitation during spring and summer was found to be the most limiting factor for tree growth during the period 1914-2010. Temperature had only a minor influence on tree growth. LwW was the growth variable most sensitive to climatic conditions. Such sensitivity explained the decreasing LwW trend since 1975.

In contrast, EwW mostly depended on the previous year's climatic conditions, and was not climatically limited during the growing season, resulting in an increasing trend over the study period. However, the temporal instability of most of these climate-growth relations indicated that climate change might have been beneficial for tree performance. Past logging events have fostered tree growth in the stand due to the increase in the availability of water, light, and nutrients, potentially alleviating the negative impacts of climate change. Furthermore, it is possible that the increase in the EwW improved water transport in the silver firs, which may also have helped them to endure ongoing climate change. Therefore, it is crucial to assess the role of forest management, as well as the potential acclimation of the tree species when considering the effects of climate change.

KEYWORDS

Abies alba, basal area increment, earlywood, forest management, latewood, rear-edge population.

1. Introduction

The Mediterranean region is one of the world's twenty-five global biodiversity hotspots. These are defined as areas that are biologically rich but highly threatened by climate change (Giorgi, 2006; Myers et al., 2000). This richness is explained in part by the fact that the Mediterranean region lies in a climatic transition zone between the arid climate of North Africa, and the temperate climate of central Europe (Giorgi and Lionello, 2008). These climatic conditions, together with a mountainous relief, generate a large diversity of habitats and facilitate the existence of both drought-adapted and temperate tree species in the region. However, climate projections for the area forecast a pronounced warming (an increase of ~7ºC in summer temperature) and a decrease in precipitation by the end of the 21st century, which will result in a substantial drying of the region (Bartolini et al., 2012; Brunet et al., 2007; IPCC, 2013). Thus, it is expected that the greatest changes in vegetation will occur in the transition zone between the Mediterranean and temperate regions (Thuiller et al., 2005). This will considerably affect the distribution areas of most of the European temperate and boreal tree species that reach their southern distribution limits in the Mediterranean region.

Tree populations at the southern margins of species distributions, the so-called 'rear-edge' populations (Hampe and Petit, 2005), are generally more vulnerable to climate change since they are already located at the limit of the species' climatic niche, and consequently, are likely to have a reduced tolerance to climatic shifts (Jump and Peñuelas, 2005). The high rates of warming experienced in the last few decades, combined with the reduced tolerance of rear-edge populations, have led to tree decline and mortality events in the Mediterranean region (see Allen et al., 2010). Such episodes are associated with substantial changes in forest structure and ecosystem function, and ultimately result in losses of biodiversity and ecosystem services (Anderegg et al., 2013). Therefore, understanding how these populations are adjusting to the novel climatic conditions is highly relevant for the long-term conservation of genetic diversity, phylogenetic history and the evolutionary potential of species (Hampe and Petit, 2005).

Plant strategies to cope with unfavourable climatic conditions involve a complex set of interacting traits such as changes in the structural properties of the xylem, among others. In the case of conifers, their wood is 95% comprised of tracheids, which have two key roles: transporting water and nutrients to the canopy, and providing mechanical and structural support (Hacke et al., 2015). The earlywood section of a tree ring has the highest level of conductivity, while the latewood confers the greatest wood stiffness as well as providing a location for water storage (Domec and Gartner, 2002). Although the age-related trend of tree-ring width series has been studied in depth since it is important for dendrochronological purposes e.g. detrending methods, less is known about the expected trends for the earlywood and latewood sections of the ring (Lachenbruch, 2011). However, an increase in the proportion of earlywood does necessitate a decrease in the latewood within a ring (Lachenbruch and McCulloh, 2014). The changes that occur as a result of this trade-off determine the hydraulic and mechanical properties of the wood, which play an important role in the tree's ability to respond to detrimental climatic conditions (Lachenbruch and McCulloh, 2014). It is therefore crucial to assess these changes in the xylem characteristics, since the persistence of tree species will depend on their ability to acclimatize to future climatic conditions (Nicotra et al., 2010).

Forest management is also an important strategy for mitigating the impacts of climate change, as well as for conserving endangered species (IPCC, 2014). Throughout history, anthropogenic activities have considerably altered natural landscapes, and nowadays, rural abandonment interacts with the impacts of climate change (Ruiz-Benito et al., 2013). For instance, species distribution models indicate that the actual distribution area of silver fir has been influenced by land-use changes over time, thus affecting the climate-related potential species distribution and obscuring the impacts of climate change (Tinner et al., 2013). Furthermore, thinning or reduction of stand density can enhance the growth of the remaining trees by increasing the availability of resources such as water, light, nutrients and space to grow (Aussenac, 2000; Bréda et al., 1995; Gómez-Aparicio et al., 2011). However, at sites where water availability is already scarce, thinning can also increase soil temperature, resulting in a higher level of soil evaporation (Covington et al., 1997). Therefore, in such environments, stand density reductions may even heighten the negative impact of droughts on tree growth and result in decline or even die-off events (Camarero et al., 2011).

In this study, we focus on a small relict population of silver firs, which represents the southernmost limit of the species on the Iberian Peninsula. Like other Circum-Mediterranean fir species, the spatial distribution of silver fir reached its peaked during the Pleistocene glacial cycles. Afterwards, the distribution area of the species suffered successive contractions due to climatic changes and anthropogenic activities during the Holocene. Consequently, silver fir forests were constrained to climate refugia in the Mediterranean region, a situation that persists to this day (Aussenac, 2002; Linares, 2011; Tinner et al., 2013). The study population is also surrounded by a dense European beech forest. Since both species, silver fir and European beech, are shade tolerant and have similar climatic niches, a high level of competition for the resources among different age classes in the transition zone between both stands is assumed (Klopcic and Boncina, 2011). The stand studied has also been under intense anthropogenic pressure for centuries, mostly due to logging activities: silver fir is a valuable wood, and the forest is located close to densely populated areas. After episodes of massive logging, legal protection measures were finally implemented in the 20th century in order to preserve the species in the area.

We hypothesize that climate change is currently limiting the trees' radial growth and thus, a reduction in growth rates is expected, particularly in recent decades as warming has increased at a faster rate. Furthermore, we also hypothesize that competition with *Fagus sylvatica* may have limited the expansion of this silver fir stand, since an upland shift of beech to higher altitudes has been reported in the area of study (Peñuelas and Boada, 2003). This would imply that the silver fir stand has not recovered from the previous periods of intense logging in spite of the legal protections implemented. As a consequence, we would also expect a retraction of the forest stand area regardless of whether an increase in tree density has occurred or not in the inner part of the forest. In order to assess the current state of this silver fir forest, our specific objectives were i) to identify and date the disturbance regime that has influenced the silver fir stand, ii) to assess whether the stand has spatially expanded or retracted since the mid-20th century, iii) to assess the impacts of the legal protection measures on tree growth and forest stand area, and iv) to analyse the responses to climatic changes of the different growth variables over time.

2. Methods

2.1. *Study species and site*

Silver fir (*Abies alba* Mill.) is one of the most economically valuable tree species in Europe. It is an evergreen conifer, and its distribution is mainly limited to mountainous regions in Europe, ranging from the Pyrenees to southern Poland. It grows in a wide variety of soil types with different nutrient contents and pH values, forming pure or mixed stands with other temperate tree species such as European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.) (Mauri et al., 2016). Silver fir is a shade-tolerant species and can maintain a “seedling bank” under the canopy of old dominant trees for decades (Dobrowolska et al., 2017). It is, however, sensitive to vapour pressure deficit and atmospheric drought (Aussenac, 2002), due to the relatively isohydric behaviour of the species under drought conditions (Martínez-Vilalta et al., 2004).

The Montseny Mountains are located 50 km north of Barcelona and 20 km west of the Mediterranean Sea (Fig. 1a). The area was declared a Natural Park in 1977 and a UNESCO Biosphere Reserve in 1978. It is characterized by an altitudinal gradient ranging from 100 to 1,706 m asl, and by a bioclimatic contrast due to its proximity to the Mediterranean Sea. At lower altitudes the Mediterranean climate has a considerable influence, and vegetation is typically Mediterranean; at higher altitudes (above 1,000 m asl), the climate becomes sub-Mediterranean without summer droughts on long-term average (Fig. 1c). This situation provides suitable conditions for Eurosiberian tree species such as European beech and silver fir. At high elevations, summer fog generated by clouds moving in from the Mediterranean Sea provides an extra source of water, reducing the incoming solar radiation and lowering evapotranspiration (Gutiérrez, 1988).

The Passavets silver fir forest (104608 m^2 in 2010) is one of the three small silver fir stands located within the Montseny Mountains Natural Park. This silver fir forest is located at an altitude of 1,200 – 1,500 m asl (41º46’36’’ N, 2º26’44’’ E) in shallow soils on the north-facing slope of the highest peak, Turó de l’Home (1,706 m asl). The stand is completely isolated from the main area of the species’ distribution in the Pyrenees, and it is surrounded by a dense beech forest (Fig. 1b).

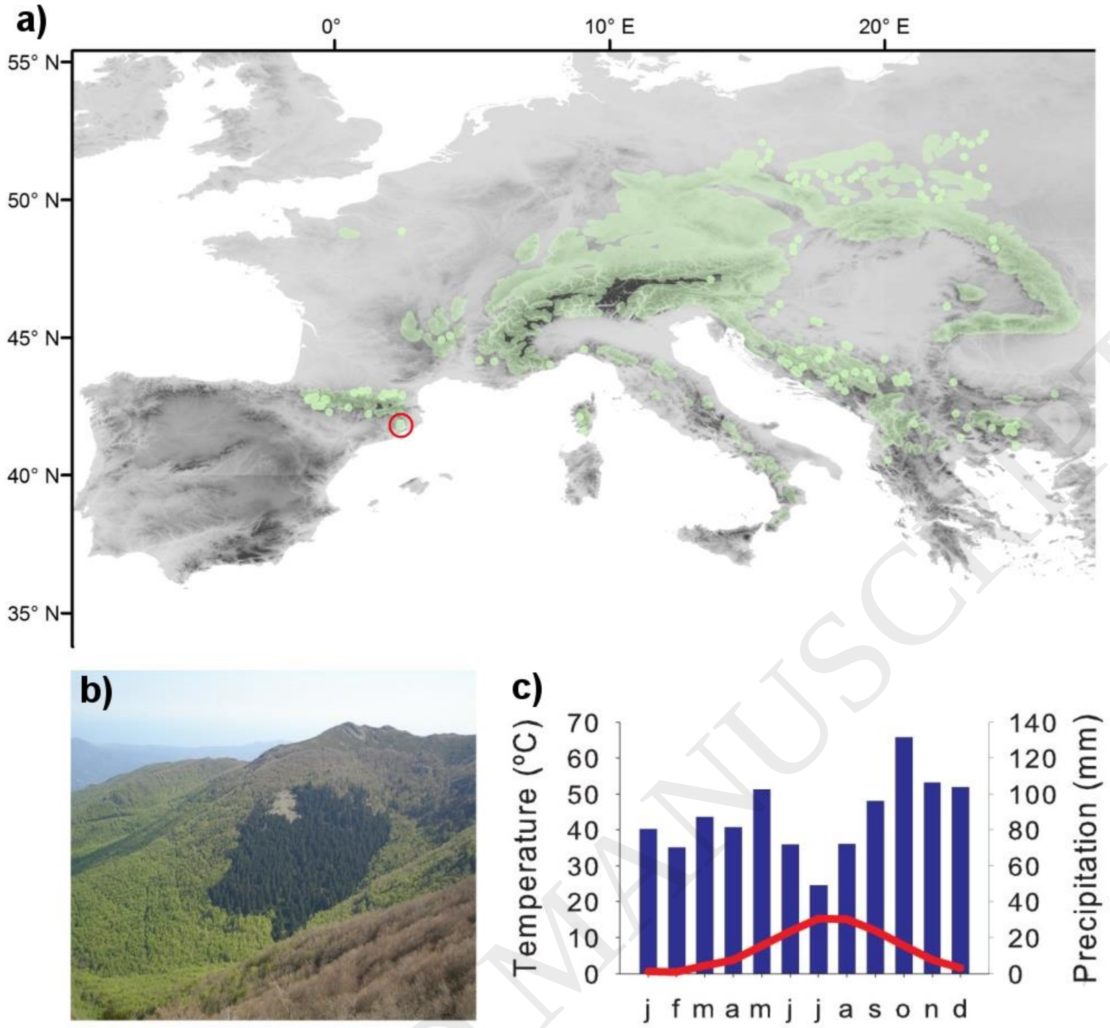

Figure 1. a) Natural distribution of *Abies alba* Mill. in Europe. Red circle indicates the location of the Passavets silver fir forest. b) Picture of the stand taken in spring 2011. c) Climate diagram of the study site (1914-2010).

2.2. *Sampling and construction of growth chronologies*

Wood samples were obtained from three different sampling campaigns in 1994, 1999 and 2011. In total, two or three increment cores were extracted from 24 silver fir dominant trees using 5-mm increment borers at breast height (1.26±0.18 m). Additionally, diameter at breast height, total height, sapwood and bark thickness were also measured (Table 1). Cores were air dried and sanded with progressively finer sanding paper until the rings were visible. Afterwards, cores were visually cross-dated under a binocular microscope and samples were scanned at 2400 dpi using a high-resolution scanner (Epson Expression 10000 XL, Seiko Epson Corporation, Suwa, Japan). Tree-ring width (RW), earlywood width (EwW) and latewood width (LwW) were measured for each tree ring using the ImageJ software (Schneider et al., 2012). EwW and LwW were defined using qualitative aspects (darkness) (Fig. S1). The quality and correct dating of the series were cross-checked using the COFECHA program (Holmes, 1983). Tree-ring width series were transformed into basal area increment as $\mathrm{BAI} = \pi(R^2_t - R^2_{t-1})$, where R is the tree radius and t is the year of the ring. BAI removes the ontogenic growth variation from the circumference stem increment, and is supposedly more sensitive to environmental factors than linear RW (Biondi and Quedan, 2008). Measurements of BAI, EwW and LwW obtained from a total of 40 cores from 19 trees were analysed.

Table 1. Characteristics of the sampled trees (N). DBH, Diameter at breast height.

	Mean	SD	N
DBH (cm)	55.78	19.41	24
Tree height (m)	13.90	3.50	24
Bark (cm)	2.30	0.47	19
Sapwood (cm)	42.28	34.90	5

2.3. Climatic data

The climatic data used in this study were provided by Jump et al. (2007), who previously carried out studies in the area. These data series consisted of mean monthly temperatures, and total precipitation for the period 1914-2004. Temperature (1961-2004) and precipitation records (1933-1938 and 1951-2004) were obtained from the meteorological station located at the summit of the “Turó de l’Home” peak (1,706 m asl) which was just 200 m up from our study site. The authors used the MET routine of the

Dendrochronology Program Library (Holmes, 2001) to interpolate data from nearby meteorological stations to fill in any gaps. We used climatic data from a recently constructed meteorological station located within the Montseny Mountains Natural Park, Tagamanent (1030 m asl), to extend these series until 2010 using the same methodology (Fig. 2). Further, total seasonal precipitation and mean seasonal temperature were calculated for winter (previous December, January, and February), spring (March, April and May), summer (June, July and August) and autumn (September, October and November). The 3-month August Standardized Precipitation Evapotranspiration Index (SPEI, Vicente- Serrano et al. 2010) was also calculated for the period studied.

2.4 *Growth trend and image analyses*

Linear trends during the period (1914 – 2010) were calculated using least-squares regressions for annual and seasonal climatic variables (temperature, precipitation and SPEI). To assess the occurrence and the periodicity of atmospheric summer droughts, years presenting summer droughts were visually identified using annual climate diagrams.

To assess abrupt changes in the annual growth rates over time, raw tree-ring width data were used to identify growth releases and reductions as $GC = 100 * [(M2 - M1)/M1]$ (Macias et al., 2006; Nowacki and Abrams, 1997), where GC is the percentage of growth, and M1 and M2 are the preceding and subsequent 10-year mean, respectively. An abrupt change along the chronology was defined as any |GC|>50%. We also aimed to relate the main growth releases and reductions to historical events. The effect of the legal protection of the silver fir stand on tree growth (RW, BAI, LwW and EwW) following the declaration of the Montseny Mountains as a Natural Park in 1977 was also evaluated. The trends of the four raw growth series were calculated using least-squares linear regressions for the period 1977-2010.

Changes in the stand area over time were assessed using orthophotos from the Institut Cartogràfic i Geològic de Catalunya (www.icgc.cat). We compared the difference in total area of the stand as measured in orthophotos from 1956 and 2010. This analysis was performed using ImageJ software.

2..5 *Standardization of the series*

Non-climatic signals from the growth series were removed in order to relate them to climate variables. The Friedman super smoother function was applied to detrend the series. This function is a nonparametric regression estimator based on local linear regression with adaptive bandwidths. First, a number of fixed bandwidth smooths are estimated using local linear regression. The leave-one-out cross-validated residuals from each of those initial estimates are then smoothed using a constant bandwidth (Friedman, 1984). In our detrending procedure, we used intermediate smooth values in both cases, which kept high frequency variations, and, at the same time, was flexible enough to track the effects of logging on tree growth (Fig. S2). The standardized and detrended series were then averaged for growth variables (RW, BAI, EwW and LwW). The Expressed Population Signal (EPS), a parameter that indicates how well the mean series represents the common variability of the entire population if it were infinitely replicated, was calculated for each growth chronology. EPS-values were > 0.85, this figure being a commonly used threshold for a well-replicated chronology (Wigley et al., 1984). These procedures were performed using the programme ARSTAN (Cook and Krusic, 2013).

The influence of monthly total precipitation and mean temperature on RW, BAI, EwW and LwW index chronologies for the study period (1914 – 2010) was assessed by means of bootstrapped correlation analyses using the software DendroClim2002 (Biondi and Waikul, 2004). The bootstrapped Pearson correlations were run from August of the previous year to December of the current year. Correlations displaying *P*-values<0.05 were considered statistically significant, and their temporal stabilities were further assessed by computing bootstrapped Pearson correlations using a 34-year moving window with a 1-year lag.

3. Results

3.1. Climatic changes

Mean annual temperature showed a significant positive trend ($r = 0.28$, $P<0.05$) (Table S1), whereas total annual precipitation did not show any significant change during the period 1914 – 2010 (Fig. 2, Table S1). Although all seasonal temperatures displayed positive trends during the period studied, only winter temperatures experienced a significant increase (r = 0.26, $P<0.05$) (Table S1). Seasonal precipitation did not show any significant trends.

Despite the fact that on long-term average there were no summer droughts during the period studied (Fig. 1), half of the years analysed showed atmospheric summer droughts (50.51%) (Fig. 2), indicating an increase in aridity over time: during the first third of the period studied, summer drought occurred every six years (51.6% of the years), and every three years during the last third (59.4% of summer drought occurrences). Additionally, the 3-month SPEI also showed a negative trend during the period studied (Fig. S3).

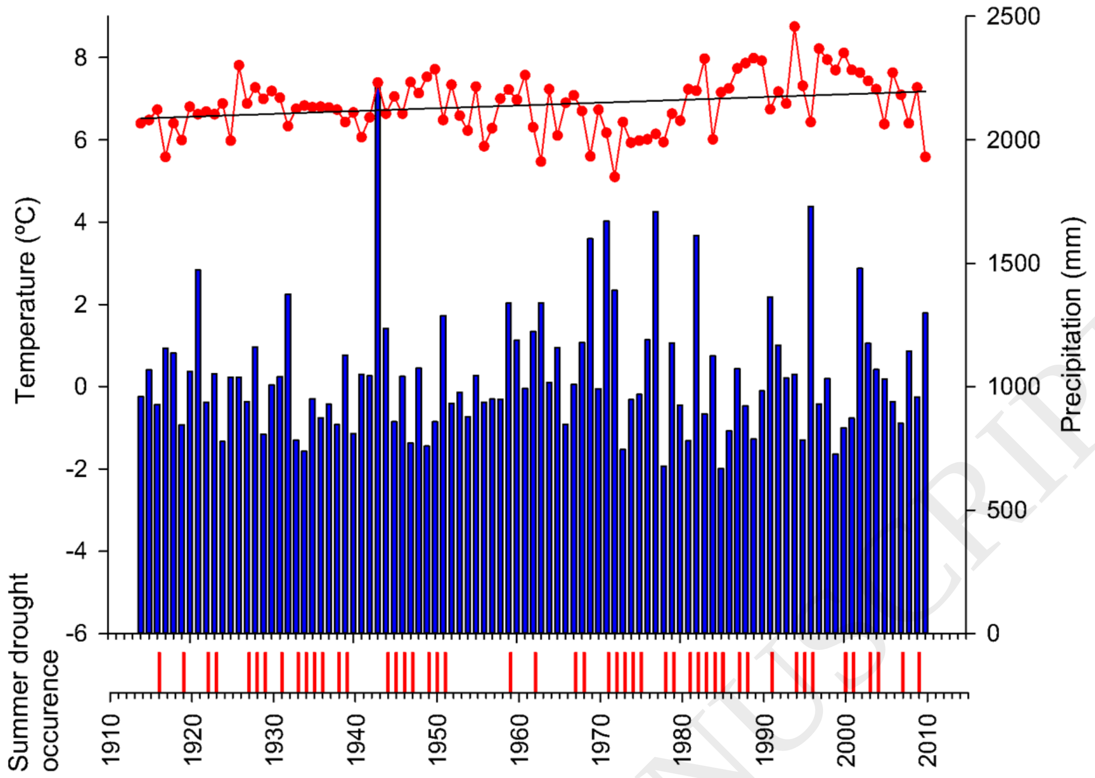

Figure 2. Mean annual temperature and total annual precipitation in Turó de l'Home for the period 1914-2010. Red points indicate mean annual temperature and the black line represents the linear trend of the mean annual temperature for the whole period. Blue bars show the total annual precipitation. Red bars bellow indicate years with summer drought.

3.2. Characteristics of the chronologies

A summary of the statistical characteristics of the chronologies is shown in Table 2. In general, all series displayed similar year-to-year variability and synchrony among series, as observed in the mean sensitivity values (MS) and the mean inter-series correlation (Cor), respectively. However, the LwW chronology showed a slightly higher MS and lower Cor in relation to the rest of the chronologies. Nevertheless, the reliable period for all chronologies was the same (1880-2010) as shown by an EPS> 0.85.

Table 2. Characteristics of the tree-ring width (RW), basal area increment (BAI), earlywood width (EwW) and latewood width (LwW) chronologies. NT/C, number of trees/cores; SP, span period; MS, Mean Sensitivity; Cor, mean inter-series correlation with master series; EPS, Expressed Population Signal.

Variable	NT/C	SP	Mean ± SD	MS	Cor	EPS>0.85 since
RW (mm)	24/50	1587-2010	1.23 ± 0.70	0.221	0.545	1710
BAI (cm^2)	19/40	1771-2010	11.04 ± 7.64	0.223	0.554	1880
EwW (mm)	19/40	1771-2010	0.83 ± 0.46	0.268	0.509	1880
LwW (mm)	19/40	1771-2010	0.51 ± 0.37	0.311	0.445	1880

3.3. Stand history and spatial analysis

Three major abrupt changes (|GC|>50%) were identified in the raw RW chronology during the period 1800-2010 (Fig. 3). A growth reduction was identified in the 1810s, when the series exhibited a significant drop in growth rates (80% of the trees sampled showed this growth reduction). The other two significant growth changes corresponded to growth releases observed in the 1860s and 1920s (seen in 100% and 84% of the trees, respectively). A minor drop in growth rates in 1946 was also identified, but this was not significant.

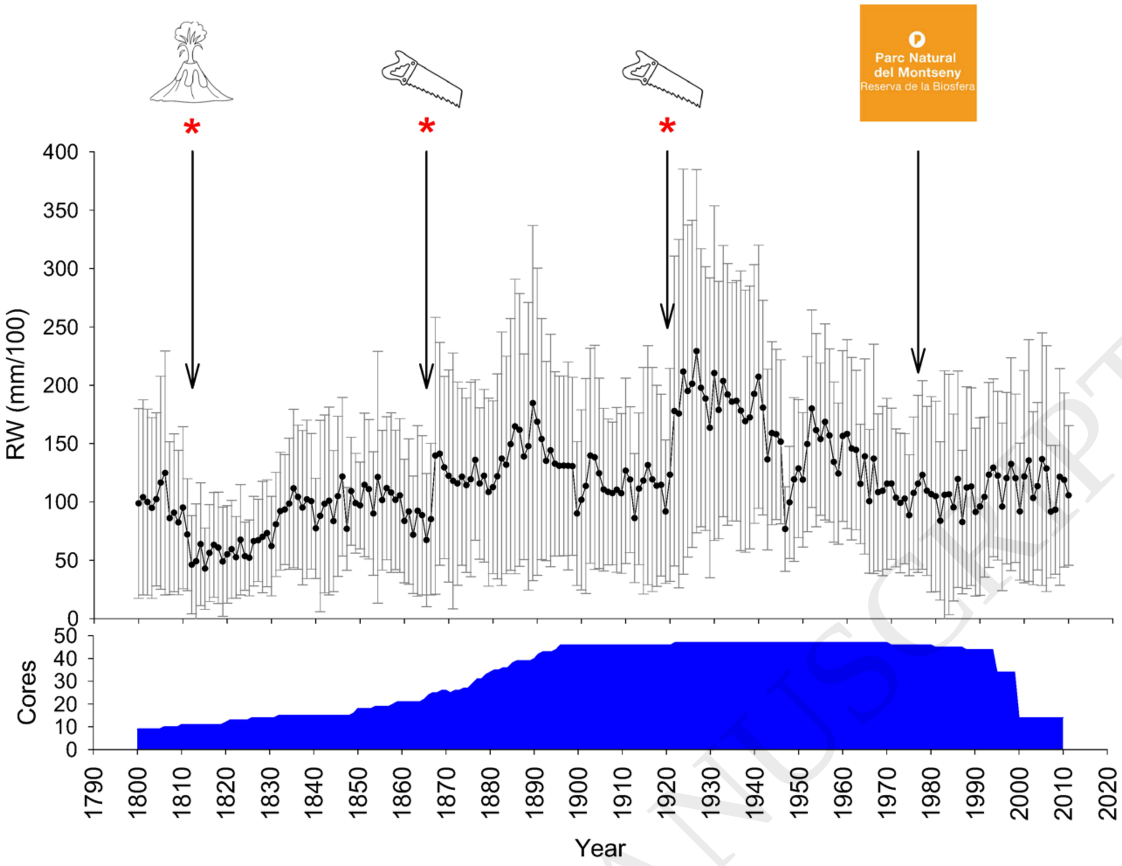

Figure 3. Evolution of the raw ring width series over the last two centuries (1800-2010). Full black dots represent the mean annual width and vertical bars indicate ±SD. The bottom panel shows sampled depth. Arrows point at major events in the history of the stand causing changes in the growth trend. Red asterisks indicate events with growth changes |GC|>50%.

Tree-ring width series levelled off after the declaration of the Montseny Mountains as a Natural Park in 1977 (Fig. 3). However, the trends of the growth variables (RW, BAI, EwW and LwW) differed from 1977-2010 (Fig. 4, Fig. S4). BAI presented a significant positive trend (r = 0.70, P<0.001). Although RW remained constant, its components differed in their trends. EwW showed a positive trend (r = 0.38, P<0.05) whereas LwW displayed a negative trend (r = -0.41, P<0.05) during the above-mentioned period.

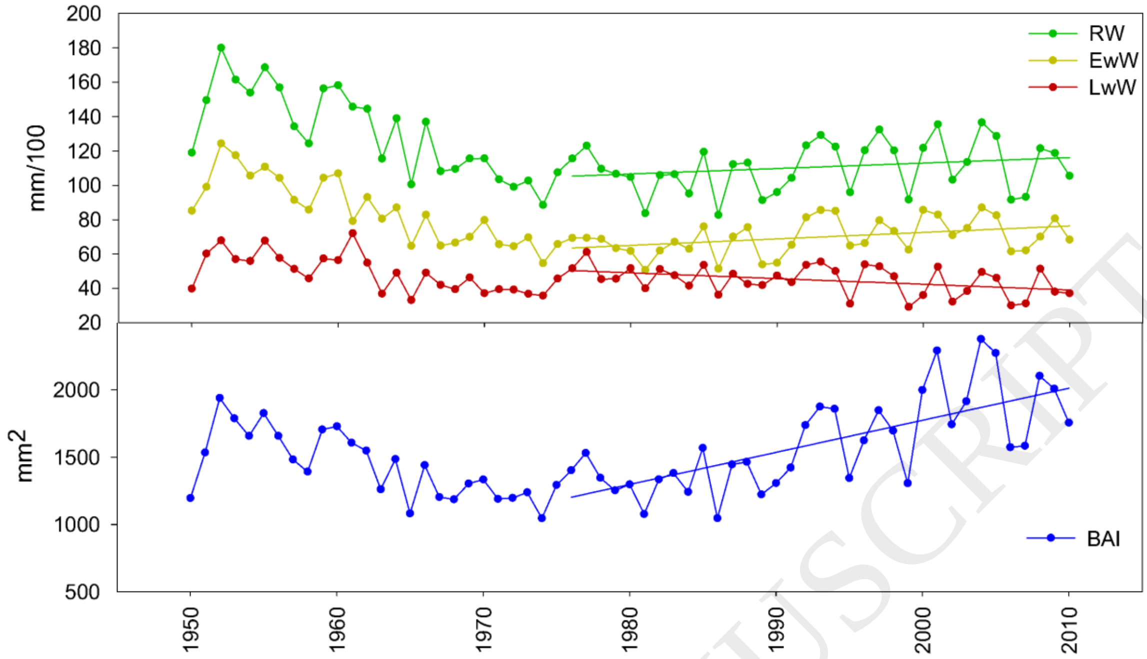

Figure 4. Evolution of the four growth variables during the period 1950-2010. Each variable shows its trend for the period (1977-2010). RW, mean tree-ring width; EwW, earlywood mean width; LwW, latewood mean width; BAI, basal area increment.

Stand area increased by 14,545 m^2 from 1956 to 2010, growing from 90,063 m^2 in 1956 to 104,608 m^2 in 2010 (Fig. 5). This forest expansion was mostly towards the east, but there was also expansion in the northeastern and southeastern parts of the stand. Moreover, the visual assessment of tree density using the orthopictures showed that this variable has also increased over time, although some dead trees were visible in the last orthopicture from 2010.

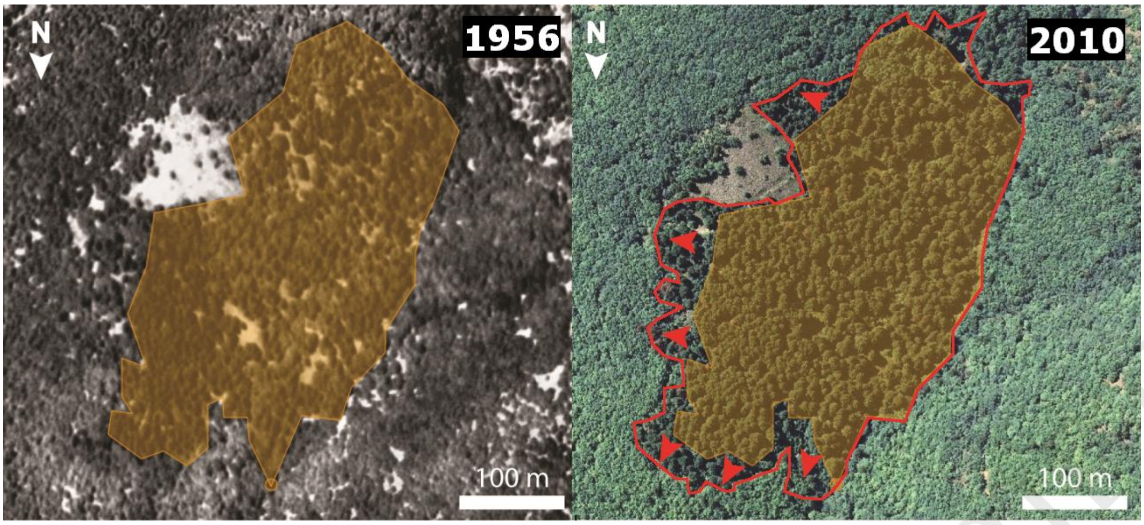

Figure 5. Aerial photographs of the silver fir stand. Left picture taken in 1956. Right picture in 2010. The perimeter of the stand in 1956 is marked in orange in both pictures and the perimeter of the stand in 2010 is marked in red in the picture of 2010. Red arrows indicate the net increased stand area (14545 m^2). (Orthophotographs from Institut Cartogràfic i Geològic de Catalunya, www.icgc.cat).

3.4. *Climate-growth relationships*

Pearson correlations were computed between the growth indices and the climatic data for each month over the period 1914 – 2010 to establish climate-growth relationships (Fig. 6). Contrary to our initial hypothesis, temperatures did not have any significant effect on tree growth during the growing period. However, the high temperatures from the October prior to the growing period (t-1) had a significant negative effect on all four growth variables (RW, BAI, EwW and LwW). RW also showed a significant positive correlation with warmer April (t) temperatures. Latewood width was the variable most sensitive to temperature, showing a significant positive correlation with spring temperatures (March and April) (t); and a significant negative relationship with autumn temperatures, October (t-1) and November (t).

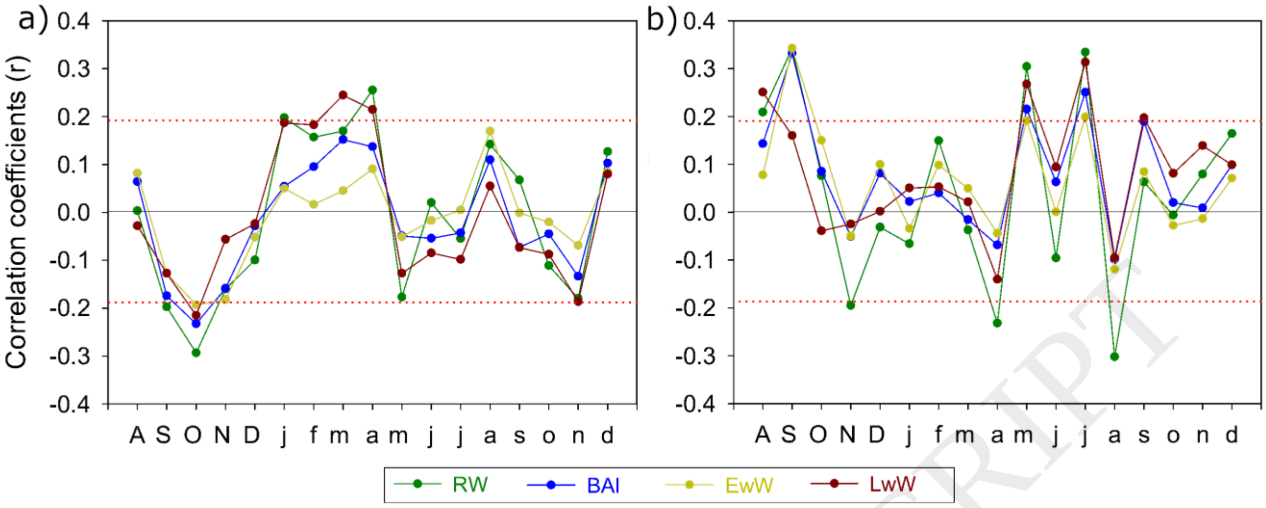

Figure 6. Bootstrapped Pearson correlation coefficients between mean monthly temperature (a) and total monthly precipitation (b) and ring width (RW), basal area increment (BAI), earlywood (EwW) and latewood (LwW) for the period 1914–2010. The window starts with August of previous year (t – 1) and ends with December of the current year of growth. Previous year is abbreviated by capital letters. Dashed red lines indicate significant coefficients (*P* <0.05).

Growth variables showed more significant correlation coefficients with precipitation than with temperature, as well as, a strong synchrony between growth response variability and water deficits (Fig. 6b). Previous summer - autumn precipitation had a positive and significant effect on all growth variables: September (t-1) for RW, BAI and EwW; and August (t-1) for LwW. Similarly, late spring, May (t) and summer precipitation July (t), exerted positive effects on all growth variables. Additionally, BAI and LwW displayed significant and positive correlations with September (t) precipitation. In sum, LwW was the growth variable that was most influenced by climatic factors.

However, these climate-growth relationships have not been stable over time (Fig. 7). Correlations with previous autumn temperatures became more negative for all growth variables, particularly for latewood. Conversely, April temperatures have always maintained positive growth correlations, or have become positive in the last century, depending on the growth variable analysed. Latewood width has maintained significant positive correlations with spring temperatures, and these correlations were even higher during the 1980s and 90s. Correlations between precipitation and growth variables have mainly been positive during the last century, but the strength of the relationships has diminished in recent years.

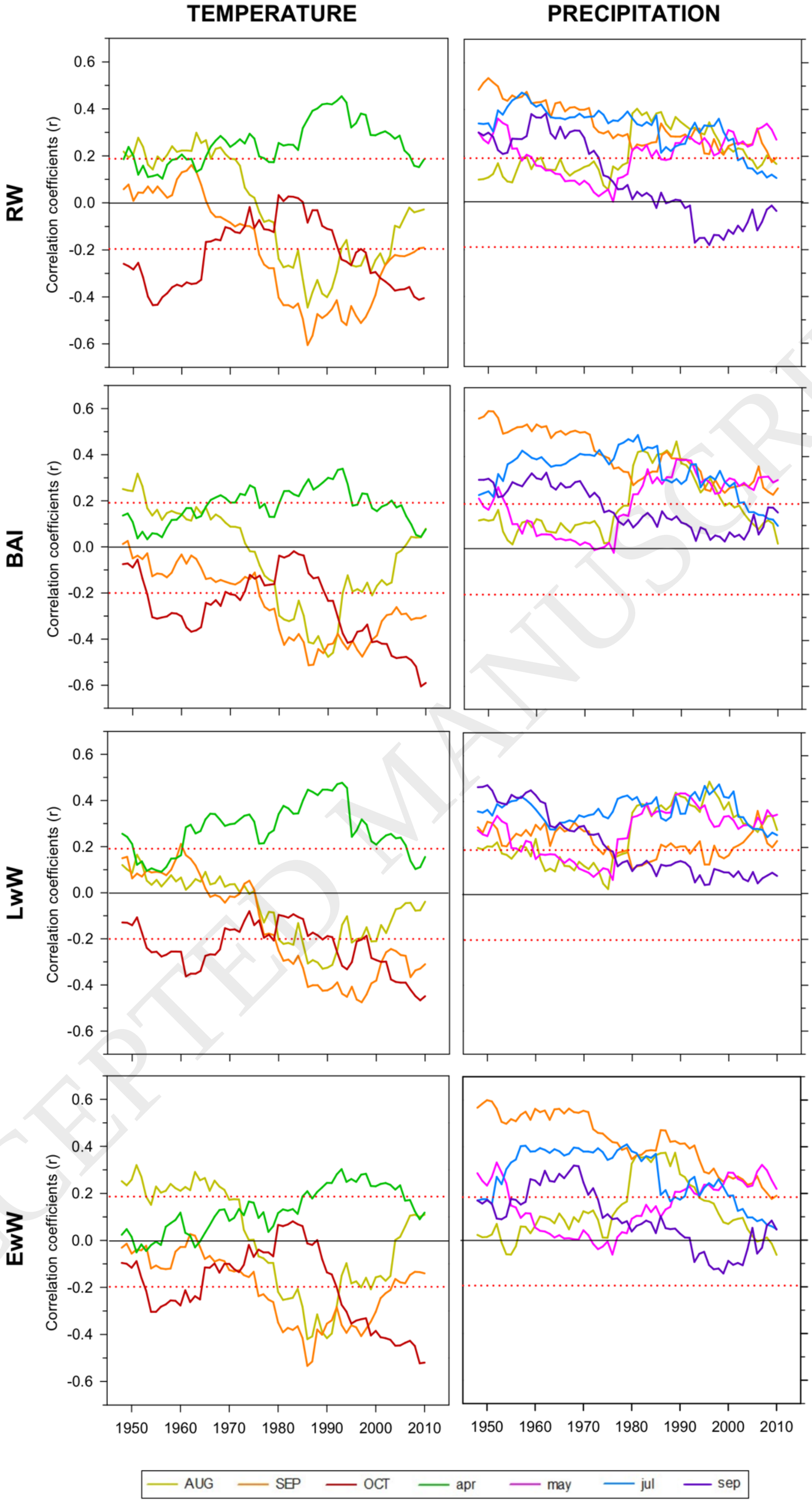
TEMPERATURE
PRECIPITATION
RW
BAI
LwW
EwW
Correlation coefficients (r)
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
1950
1960
1970
1980
1990
2000
2010
AUG
SEP
OCT
apr
may
jul
sep

Figure 7. Evolution of the bootstrapped Pearson correlation values between monthly climatic data and growth indices using 34-year windows lagged 1 year. Only variables that were significant for the whole period (see Fig. 6) are shown. Previous year is abbreviated by capital letters. Horizontal dashed red lines indicate significant coefficients ($P < 0.05$).

4. Discussion

4.1. History of the stand and its current situation

Our research revealed that the Passavets silver fir stand has been intensively managed and exploited throughout its history, and the growth changes identified in the tree-ring width raw series can be associated with historical documents (Fig. 3). The reduction in growth detected in the 1810s can be directly attributed to strong volcanic activity. This activity is an important climatic forcing factor as it creates a short-term global cooling effect (Sigl et al., 2015). *Abies alba* is a thermophilus species (Tinner et al., 2013), and the cooling effect therefore caused a significant reduction in growth. In fact, the decade of 1810-1820 is well-known as one of the coldest periods in recent history due to the eruption of a volcano in 1809, the 1814 eruption of Mayon in the Philippines and the Tambora eruption in 1815 (Briffa et al., 1998), the effects of which were widespread and lasted for several years. This association between tree rings and volcanic activity has been widely studied in the past (Génova, 2012). Growth reductions related to volcanic-induced cooling events are commonly observed and linked to cold-limited conifers located at high altitudes (LaMarche and Hirschboek, 1984), as was the case with our target population. Moreover, the Tambora eruption had an important impact on tree growth, even modifying the chemical composition in the tree rings of some forests, i.e.

populations from the Pyrenees experienced an increase in S, Fe, Cl, Zn and Ca tree-ring concentrations as result of the eruption (Hevia et al., 2018).

The two growth releases identified in the tree-ring width series were associated with the reduction in competition caused by intensive logging. A historic document, that dated back to 1879 (Vayreda, 1879), describes substantial silver fir logging activity in the stand, which coincides with the first growth release. However, logging activity actually peaked in 1915 when a sawmill and a road were built close to the stand to supplement the growing timber industry in the area (Sanchez, 2010). This sawmill was active until the beginning of the Spanish Civil war in 1936. Both abrupt radial growth increases are clearly related to logging due to the lessened competition for resources, indicating that the tree density was high (Fritts, 1976; Bosch et al., 1992; Bosch and Gutiérrez, 1999).

A variety of conservation measures were implemented during the last half of the 20th century, but it was not until 1977 that the Montseny Mountains were declared a Natural Park, and subsequently, a UNESCO Biosphere Reserve in 1978. Since logging was completely forbidden, there were no remarkable radial growth changes, which has since translated into the stabilization of the annual tree-ring width series. However, it is notable that the raw tree-ring width chronology showed an upward trend over the entire period studied, most likely due to the historical logging. Such a positive trend is contrary to the age-related negative trend common in tree-ring width series (Fritts, 1976).

Contrary to our initial hypothesis, the silver firs have shown a significant increase in basal area increment since the establishment of the Natural Park. Considering that radial tree growth is a proven proxy of tree performance, this indicates a good recovery and a good subsequent performance of the trees following the previous logging events. Although it is not common to find positive growth trends among rear-edge populations, there is some regional variability among populations in Italy (Carrer et al., 2010).

Differences in growth trends among western and eastern rear-edge silver fir populations across the Mediterranean Basin have also been reported by Gazol et al. (2015), and similar findings were also described for some broadleaf species (Dorado-Liñán et al., 2017; Martínez-Sancho et al., 2017; Tegel et al., 2014). Other studies analysing silver fir growth trends found a consistent growth decline among silver fir populations located on the Iberian Peninsula (Gazol et al., 2015), which have resulted in some die-off events in the central Pyrenees (Camarero et al., 2011). Furthermore, studies modelling tree growth under future climate scenarios also forecasted a dramatic growth decline in rear-edge silver fir populations (Sánchez-Salguero et al., 2017, 2016), but the authors of this study also highlighted that growth would increase in the case of moist refugia. In fact, the climatic conditions of our target silver fir stand lie almost in the central region of the bioclimatic niche according to Tinner et al. (2013), indicating reduced climatic limitations for the stand.

Since the establishment of the Natural Park, the stand under study has also increased in area and in tree density, as shown by the orthopictures. Although more detailed analyses are required to confirm the observed spatial extension of the Passavets silver fir stand, our findings are further supported by reports from the Natural Park, which observed i) a spatial extension of the stand and ii) two main cohorts of trees and a high rate of regeneration of silver fir seedlings and saplings both within and outside the stand (Andreu-Hayles et al., 2001; Nuet et al., 2014). In these reports, the authors highlighted the importance of thinning for silver fir seedlings and saplings since the density reduction increased the availability of water, light, space for growth and nutrients for both young age classes leading to a successful regeneration of the species, a process that is also taking place in the adjacent beech forest (Nuet et al., 2014).

We therefore hypothesize that logging led to a greater availability of resources and, consequently, less competition. This may have benefitted the remaining living trees in terms of growth, and might have helped them to withstand the negative impacts of climate change as well as facilitating the recruitment of new individuals, as previously suggested by other studies (Fernández-de-Uña et al., 2015; Gómez-Aparicio et al., 2011). Tree stand density reductions could have even modified carbon isotope discrimination due to heightened water availability, resulting in increased growth of individual trees via higher stomatal conductance (McDowell et al., 2003; Moreno-Gutiérrez et al., 2012), which is particularly important for relatively isohydric species (Giuggiola et al., 2016). Indeed, thinning could even induce a longer growing season, enhancing radial growth as has been reported for *Abies pinsapo* (Linares et al., 2009). In contrast, other studies analysing the interactions between silver fir growth and competition in the Pyrenees have suggested that past logging activities predisposed trees to drought-triggered tree mortality, particularly for small and slow-growing trees (Camarero et al., 2011). Thus, it seems that the response to global change can vary depending on the stand's structure, but, in any case, our results are concurrent with other studies that have reported tree growth enhancement due to the positive effects of warming (Gazol et al., 2015).

4.2. Differences in the climate response of the growth variables and the ecological consequences

Low levels of precipitation in May and July were the most limiting factors for tree growth, whereas temperatures did not show any significant effect on silver fir growth over these months. These results are in line with other studies analysing climate-growth relationships of silver fir populations located in Mediterranean regions (Gazol et al., 2015; Lebourgeois et al., 2010; Macias et al., 2006). Silver fir has a highly sensitive stomata regulation in response to water stress, typically avoiding drought with a relatively isohydric strategy (Aussenac, 2002; Martínez-Vilalta et al., 2004). In turn, evapotranspiration has been described as the key driver controlling growth and net primary production of silver firs in dry areas (Vicente-Serrano et al., 2015). However, the correlation between precipitation and tree growth shown in our results is not particularly significant, which may indicate that evapotranspiration and precipitation did not strongly inhibit radial tree growth.

The reduced influence of temperature on silver fir growth is also remarkably important. The region has experienced significant levels of warming over the last century, and consequently, the percentage of years with a summer drought has increased. Our results clearly show that silver fir growth was not limited by high summer temperatures during the current growing period, which is, at least, unexpected considering that the stand is the southernmost population of the species on the Iberian Peninsula. These results might be partly explained by the effects of persistent fog during the summer months that decreases solar radiation levels, as previously reported (Gutiérrez, 1988). However, the positive impact of spring temperatures on tree growth observed over the entire period studied may be directly related to growth resumption (Rossi et al., 2005). Growth resumption may occur earlier due to the lengthening of the growing season in the area as a result of the earlier phenological springtime events (Gordo and Sanz, 2010; Menzel and Fabian, 1999). This earlier growth resumption can benefit trees, as has been observed in high-elevation mountain pine populations (Sánchez-Salguero et al., 2016) and may simultaneously increase earlywood width.

The positive effects of precipitation and the negative effects of temperature from the previous late autumn period also influenced tree growth, as has been reported in other studies analysing conifer growth in the Mediterranean region (Andreu et al., 2007; Gazol et al., 2015; Lebourgeois, 2000; Lebourgeois et al., 2013; Macias et al., 2006). It has been shown that previous year drought can negatively impact the production and storage of metabolic reserves to be used in the following year (Barbaroux et al., 2003). However, the moving correlation analyses revealed that in recent years, autumn temperatures from the previous year have become more significant, pointing to the projected importance of temperatures in the near future. This increasing impact of temperatures on tree growth is most likely a consequence of both the heightened effect of climate change, and the intensifying competition following the cessation of logging activities.

Regarding the different ring components, earlywood and latewood displayed different sensitivities to climate. In our study, earlywood is mostly influenced by precipitation and, to a lesser degree, by temperature and its influence on previous year growth, which is concurrent with the results from Lebourgeois et al. (2010). Aside from the impact of the previous year's climatic conditions, earlywood formation was not curtailed during the growing season. A positive earlywood growth trend over the last 40 years suggests that warmer winters and a longer growing season may have been beneficial for the species. In contrast, latewood width is affected by the rise in atmospheric summer droughts, as suggested by the positive impact of July precipitation on this variable over the period studied. Indeed, latewood was the growth variable most impaired by climate, in line with other studies (Lebourgeois, 2000; Lebourgeois et al., 2010 but see Pasho et al., 2012), which has led to a declining latewood trend in recent years.

The varying climate sensitivity of the two tree-ring components has resulted in distinct trends for both variables. Changes in the proportion of earlywood and latewood within a ring are inter-related (Lachenbruch and Mcculloh, 2014). This negative trade-off modifies the hydraulic and mechanical wood properties of the trees. A higher proportion of earlywood implies a higher hydraulic conductivity. Earlywood tracheids transport water more efficiently than latewood ones since the former are less resistant to water flow due to their larger lumen areas (Hacke et al., 2015; Hacke and Sperry, 2001). In turn, a higher proportion of earlywood in the rings provides a larger conductive area for the sapwood, and this positive feedback may partly explain the positive growth trends found in our study. Yet, a larger conductive area may also mean that trees are more vulnerable to severe drought conditions (Choat et al., 2012; McDowell et al., 2008). This increase in earlywood also implies a reduced production of latewood that affects i) wood density and ii) the mechanical properties of the wood (Lachenbruch, 2011). In the current literature, low wood density is usually linked to higher conductivity rates typical of non-drought limited sites (Hacke and Sperry, 2001). However, the pattern found in our study (increasing EwW and decreasing LwW) does not match the typical radial pattern described by Lachenbruch (2011). Such a plastic response in tree-ring anatomy represents an adjustment to the new climatic conditions. Nevertheless, to better understand the implications of these changes on tree performance, further studies such as quantitative wood anatomical analyses are necessary to investigate whether the anatomical and functional characteristics of the tracheids such as cell wall thickness or cell lumen area have also been modified (Pellizari et al., 2016).

4.3. Future projections

Our results highlight the positive performance of the silver firs in the Passavets population located in the Montseny Mountains, the southernmost limit of the species on the Iberian Peninsula. Past logging events potentially helped these trees to withstand current climate change. A recent publication demonstrated that past forest management has directly impacted the distribution range of the species, since silver fir has historically been an important commercial wood, and remains one today. Thus, the intensive managing of silver fir forests led to the contraction of the species distribution area and masked the natural distribution range as shown in previous studies (Tinner et al., 2013; Ruosch et al., 2016). These authors of these studies also suggest that *Abies alba* is able to maintain its current distribution area and even expand under scenarios with moderate CO_2 emissions. Therefore, not all the populations located at the current rear-edge of the species range are as climatically constrained as the potential limit of the species, which may be located further south. This may be the case for the silver fir population studied here. Thus, the combination of the competition releases due to past logging, and the fact that this population might not be located at the extreme climatic limit of the species indicates that the Passavets population is currently geographically marginal but is not necessarily climatically limited.

In 2003, Peñuelas and Boada (2003) forecasted a generalised climate change-induced biome shift in the Montseny Mountains. Their study was based on a comparison of historical and current low- to medium-land vegetation distributions. The authors argued that these changes were a response to global warming and, consequently, that there would be an altitudinal retreatment of the species leading to a replacement of temperate ecosystems by Mediterranean ecosystems, which are better adapted to dry conditions. Species like *Fagus sylvatica* would shift upland to higher altitudes, which might indirectly displace the silver fir stand studied. A second study analysed the growth-climate relations of European beech along an altitudinal gradient in these mountains (Jump et al., 2007). The authors claimed that higher temperatures have promoted growth and seedling establishment at higher altitudes, and that an extension of the species at these altitudes is to be expected.

Our results suggest that the role of management and the potential acclimation of the silver fir stand studied need to be considered when assessing the potential upland expansion of the *Fagus* stand, since the silver fir stand is located at the upper limit of the

European beech forest. Our results provide the first piece of evidence demonstrating that the silver fir stand has expanded spatially during the last 55 years, and that the regeneration and the establishment of young individuals do not seem to be limited, as reported by other authors. These results are partially in agreement with those from Ruosch et al. (2016) which project a stable distribution of *A. alba* in southern Europe under the moderate warming scenario of RCP2.6, yet, we have demonstrated that the Passavets silver fir stand is actually expanding at present. Nevertheless, further studies assessing the recruitment of new trees and competition between silver fir and European beech are required to better understand the dynamics of both populations in the area of study.

5. Conclusions

Despite the growth limitations caused mainly by low levels of precipitation, the silver fir population studied has performed well overall. The historic logging events that almost caused the species' extinction in the region may have actually allowed the stand to later withstand the adverse climatic conditions caused by current global climatic change. Moreover, the intense historical logging that this species has suffered for centuries may have reduced its potential distribution area (Tinner et al., 2013). Thus, the Passavets silver fir population is the most geographically marginal population on the Iberian Peninsula, but this does not mean that it is currently climatically marginal. Furthermore, the different climatic sensitivities of the tree-ring components (early and latewood) resulted in a larger water-conducting tree-ring area, conferring a higher level of conductivity on the sapwood, which may also explain the increasing growth trend. Our results show a positive tree performance and an expansion of the stand area, in spite of some model predictions. Further studies are needed to assess the recruitment of new individuals, and the competition between silver fir and European beech at the limit of both forests in order to better predict the likelihood of a biome shift in the Montseny Mountains Natural Park.

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References

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684. doi:10.1016/j.foreco.2009.09.001

Anderegg, W.R.L., Kane, J.M., Anderegg, L.D.L., 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. Nat. Clim. Chang. 3, 30–36. doi: 10.1038/nclimate1635

Andreu-Hayles, L., Macias Fauria, M., Planells, O., 2001. Primera aproximació a l'estat ecològic de l'avetosa de Passavets. Barcelona.

Andreu, L., Gutiérrez, E., Macias, M., Ribas, M., Bosch, O., Camarero, J.J., 2007. Climate increases regional tree-growth variability in Iberian pine forests. Glob. Chang. Biol. 13, 804–815. doi:10.1111/j.1365-2486.2007.01322.x

Aussenac, G., 2002. Ecology and ecophysiology of circum-Mediterranean firs in the context of climate change. Ann. For. Sci. 59, 823–832. doi:10.1051/forest

Aussenac, G., 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. Ann. For. Sci. 57, 287–301. doi: 10.1051/forest:2000119

Barbaroux, C., Bréda, N., Dufrene, E., 2003. Distribution of above-ground and below-ground carbohydrate reserves in adult trees of two contrasting broad-leaved species (*Quercus petraea* and *Fagus sylvatica*). New Phytol. 157, 605–615. doi:10.1046/j.1469-8137.2003.00681.x

Bartolini, G., di Stefano, V., Maracchi, G., Orlandini, S., 2012. Mediterranean warming is especially due to summer season. Theor. Appl. Climatol. 107, 279–295. doi:10.1007/s00704-011-0481-1

Biondi, F., Quedan, F., 2008. A theory-driven approach to tree-ring standardization : defining the biological trend from expected basal area increment. Tree Ring Res. 64, 81–96. doi: 10.3959/2008-6.1

Biondi, F., Waikul, K., 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. Comput. Geosci. 30, 303–311. doi:10.1016/j.cageo.2003.11.004

Bosch, O., Giné, L., Ramadori, E. D., Bernat, A., Gutiérrez, E. 1992. Disturbance, age and size structure in stands of *Pinus uncinata* Ram. Pirineos, 140, 5-14.

Bosch, O., Gutiérrez, E. 1999. La sucesión en los bosques de *Pinus uncinata* del Pirineo: De los anillos de crecimiento a la historia del bosque. Ecología, 13, 133-172.

Bréda, N., Granier, A., Aussenac, G., 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). Tree Physiol. 15, 295–306. doi:10.1071/SR14309

Briffa, K.R., Jones, P.D., Osborn, T.J., 1998. Influence of volcanic eruptions on Northern Hemisphere summer temperature over the past 600 years. Nature 393, 450–455.

Brunet, M., Jones, P.D., Sigró, J., Saladié, O., Aguilar, E., Moberg, A., Della-Marta, P.M., Lister, D., Walther, A., López, D., 2007. Temporal and spatial temperature variability and change over Spain during 1850–2005. J. Geophys. Res. 112, D12117. doi:10.1029/2006JD008249

Camarero, J.J., Bigler, C., Linares, J.C., Gil-Pelegrín, E., 2011. Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests. For. Ecol. Manage. 262, 759–769. doi:10.1016/j.foreco.2011.05.009

Carrer, M., Nola, P., Motta, R., Urbinati, C., 2010. Contrasting tree-ring growth to climate responses of *Abies alba* toward the southern limit of its distribution area. Oikos 119, 1515–1525. doi:10.1111/j.1600-0706.2010.18293.x

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. Nature 491, 752–755. doi:10.1038/nature11688

Cook ER, Krusic PJ (2013) Program ARSTAN. A tree-ring standardization program based on detrending and autoregressive time series modeling, with interactive graphics. http://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software. Accessed June 2014

Covington, W.W., Fule, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Scakett, S.S., Wagner, M.R., 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. J. For. 95, 23–29.

Dobrowolska, D., Bončina, A., Klumpp, R., 2017. Ecology and silviculture of silver fir (*Abies alba* Mill.): a review. J. For. Res. 22, 1–10. doi:10.1080/13416979.2017.1386021

Domec, J.-C., Gartner, B.., 2002. How do water transport and water storage differ in coniferous earlywood and latewood? J. Exp. Bot. 53, 2369–2379. doi:10.1093/jxb/erf100

Dorado-Liñán, I., Zorita, E., Martínez-Sancho, E., Gea-Izquierdo, G., Di Filippo, A., Gutiérrez, E., Levanic, T., Piovesan, G., Vacchiano, G., Zang, C., Zlatanov, T., Menzel, A., 2017. Large-scale atmospheric circulation enhances the Mediterranean East-West tree growth contrast at rear-edge deciduous forests. Agric. For. Meteorol. 239, 86–95. doi:10.1016/j.agrformet.2017.02.029

Fernández-de-Uña, L., Cañellas, I., Gea-Izquierdo, G., 2015. Stand competition determines how different tree species will cope with a warming climate. PLoS One 10, 1–18. doi:10.1371/journal.pone.0122255

Friedman, J.H. 1984. A variable span smoother. Laboratory for Computational Statistics, Department of Statistics, Stanford University: Technical Report(5).

Fritts, H., 1976. Tree rings and climate. Academic Press Inc. (London) Ltd. 567 p.

Gazol, A., Camarero, J.J., Gutiérrez, E., Popa, I., Andreu-Hayles, L., Motta, R., Nola, P., Ribas, M., Sangüesa-Barreda, G., Urbinati, C., Carrer, M., 2015. Distinct effects of climate warming on populations of silver fir (*Abies alba*) across Europe. J. Biogeogr.

42, 1150–1162. doi:10.1111/jbi.12512

Génova, M., 2012. Extreme pointer years in tree-ring records of Central Spain as evidence of climatic events and the eruption of the Huaynaputina Volcano (Peru, 1600 AD). Clim. Past 8, 751–764. doi:10.5194/cp-8-751-2012

Giorgi, F., 2006. Climate change hot-spots. Geophys. Res. Lett. 33, 1–4. doi:10.1029/2006GL025734

Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region. Glob. Planet. Change 63, 90–104. doi:10.1016/j.gloplacha.2007.09.005

Giuggiola, A., Ogée, J., Rigling, A., Gessler, A., Bugmann, H., Treydte, K., 2016. Improvement of water and light availability after thinning at a xeric site: which matters more? A dual isotope approach. New Phytol. 210, 108–121. doi:10.1111/nph.13748

Gómez-Aparicio, L., García-Valdés, R., Ruíz-Benito, P., Zavala, M.A., 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: Implications for forest management under global change. Glob. Chang. Biol. 17, 2400–2414. doi:10.1111/j.1365-2486.2011.02421.x

Gordo, O., Sanz, J.J., 2010. Impact of climate change on plant phenology in Mediterranean ecosystems. Glob. Chang. Biol. 16, 1082–1106. doi:10.1111/j.1365-2486.2009.02084.x

Gutiérrez, E., 1988. Dendroecological study of *Fagus sylvatica* in the Montseny mountains (Spain). Acta Oecologica 9, 301–309.

Hacke, U.., Lachenbruch, B., Pittermann, J., Mayr, S., Domec, J.-C., Schulte, P.J., 2015. Hydraulic architecture of conifers, in: Hacke, U.G. (Ed.), Functional and ecologycal xylem anatomy. Springer International Publishing, pp. 39–76.

Hacke, U.G., Sperry, J.S., 2001. Functional and ecological xylem anatomy. Perspect. Plant Ecol. Evol. Syst. 4/2, 97–115. doi: 10.1078/1433-8319-00017

Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: The rear edge matters. Ecol. Lett. 8, 461–467. doi:10.1111/j.1461-0248.2005.00739.x

Hevia, A., Sánchez-salguero, R., Camarero, J.J., Buras, A., Sangüesa-barreda, G., Galván, J.D., Gutiérrez, E., 2018. Towards a better understanding of long-term wood-chemistry variations in old-growth forests : A case study on ancient *Pinus uncinata* trees from the Pyrenees. Sci. Total Environ. 625, 220–232. doi:10.1016/j.scitotenv.2017.12.229

Holmes, R.L., 2001. Dendrochronology Program Library.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43, 68–78.

IPCC, 2014. Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change. Cambridge, UK and New York, NY.

IPCC, 2013. Climate change 2013: The physical science basis. Contribution of working Group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge, UK and New York, NY.

Jump, A.S., Peñuelas, J., 2005. Running to stand still: Adaptation and the response of plants to rapid climate change. Ecol. Lett. 8, 1010–1020. doi:10.1111/j.1461-0248.2005.00796.x

Jump, a S., Hunt, J.M., Peñuelas, J., 2007. Climate relationships of growth and establishment across the altitudinal range of *Fagus sylvatica* in the Montseny Mountains, northeast Spain. Ecoscience 14, 507–518. doi:10.2980/1195-6860(2007)14

Klopcic, M., Boncina, A., 2011. Stand dynamics of silver fir (*Abies alba* Mill.) European beech (*Fagus sylvatica* L.) forests during the past century: A decline of silver fir? Forestry 84, 259–271. doi:10.1093/forestry/cpr011

Lachenbruch, B., 2011. Radial variation in wood structure and function in woody plants, and hypotheses for its occurence, in: Meinzer, F.C., Lachenbruch, B., Dawson, T.E. (Eds.), Size- and age-related changes in tree structure. Springer Netherlands, Dordrecht, pp. 121–164. doi:10.1007/978-94-007-1242-3

Lachenbruch, B., Mcculloh, K.A., 2014. Traits, properties, and performance: How woody plants combine hydraulic and mechanical functions in a cell, tissue, or whole plant. New Phytol. 204, 747–764. doi:10.1111/nph.13035

LaMarche, V.., Hirschboek, K.., 1984. Frost rings in trees as records of major volcanic eruptions. Nature 307, 121–126.

Lebourgeois, F., 2000. Climatic signals in earlywood, latewood and total ring width of Corsican pine fromwestern France. Ann. For. Sci. 57, 155–164. doi:10.1051/forest:2000166

Lebourgeois, F., Gomez, N., Pinto, P., Mérian, P., 2013. Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. For. Ecol. Manage. 303, 61–71. doi:10.1016/j.foreco.2013.04.003

Lebourgeois, F., Rathgeber, C.B.K., Ulrich, E., 2010. Sensitivity of French temperate coniferous forests to climate variability and extreme events (*Abies alba*, *Picea abies* and *Pinus sylvestris*). J. Veg. Sci. 21, 364–376. doi:10.1111/j.1654-1103.2009.01148.x

Linares, J.C., 2011. Biogeography and evolution of *Abies* (Pinaceae) in the Mediterranean Basin: The roles of long-term climatic change and glacial refugia. J. Biogeogr. 38, 619–630. doi:10.1111/j.1365-2699.2010.02458.x

Linares, J.C., Camarero, J.J., Carreira, J.A., 2009. Plastic responses of *Abies pinsapo* xylogenesis to drought and competition. Tree Physiol. 29, 1525–1536. doi:10.1093/treephys/tpp084

Macias, M., Andreu, L., Bosch, O., Camarero, J.J., Gutiérrez, E., 2006. Increasing aridity is enhancing silver fir (*Abies alba* Mill.) water stress in its south-western distribution limit. Clim. Change 79, 289–313. doi:10.1007/s10584-006-9071-0

Mauri, A., de Rigo, D., Caudullo, G., 2016. *Abies alba in Europe: distribution, habitat, usage and threats*. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, pp. e01493b+

Martínez-Sancho, E., Dorado-Liñán, I., Gutiérrez Merino, E., Matiu, M., Helle, G., Heinrich, I., Menzel, A., 2017. Increased water-use efficiency translates into contrasting growth patterns of Scots pine and sessile oak at their southern distribution limits. Glob. Chang. Biol. 1–17. doi:10.1111/gcb.13937

Martínez-Vilalta, J., Sala, A., Piñol, J., 2004. The hydraulic architecture of Pinaceae – a review. Plant Ecol. 171, 3–13. doi: 10.1023/B:VEGE.0000029378.87169.b1

McDowell, N., Brooks, J., Fitzgerald, S., Bond, B., 2003. Carbon isotope discrimination and growth response of old. Plant, Cell Environ. 26, 631–644. doi: 10.1046/j.1365-3040.2003.00999.x

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol. 178, 719–39. doi:10.1111/j.1469-8137.2008.02436.x

Menzel, A., Fabian, P., 1999. Growing season extended in Europe. Nature 397, 659. doi:10.1038/17709

Moreno-Gutiérrez, C., Battipaglia, G., Cherubini, P., Saurer, M., Nicolás, E., Contreras, S., Querejeta, J.I., 2012. Stand structure modulates the long-term vulnerability of *Pinus halepensis* to climatic drought in a semiarid Mediterranean ecosystem. Plant, Cell Environ. 35, 1026–1039. doi:10.1111/j.1365-3040.2011.02469.x

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. doi:10.1038/35002501

Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., Poot, P., Purugganan, M.D., Richards, C.L., Valladares, F., van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. Trends Plant Sci. 15, 684–692. doi:10.1016/j.tplants.2010.09.008

Nowacki, G.J., Abrams, M.D., 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecol. Monogr. 67, 225–249. doi:10.1890/0012-9615(1997)067[0225:RGACFR]2.0.CO;2

Nuet, J., González, V., Gasulla, M., 2014. L'aveteda de Passavets (Motnseny), caracterització i relació amb les avetoses dels Pirineus catalans, in: VIII Monografies del Montseny. p. 186-203. Diputació de Barcelona, Barcelona.

Pasho, E., Camarero, J.J., Vicente-Serrano, S.M., 2012. Climatic impacts and drought control of radial growth and seasonal wood formation in *Pinus halepensis*. Trees 26, 1875–1886. doi:10.1007/s00468-012-0756-x

Pellizzari, E., Camarero, J.J., Gazol, A., Sangüesa- Barreda, G., Carrer, M., 2016. Wood anatomy and carbon- isotope discrimination support long- term hydraulic deterioration as a major cause of drought- induced dieback. Glob. Chang. Biol. 22, 2125-2137. doi: 10.1111/gcb.13227

Peñuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). Glob. Chang. Biol. 9, 131–140. doi: 10.1046/j.1365-2486.2003.00566.x

Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R., Borghetti, M., 2005. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. New Phytol. 170, 301–310. doi: 10.1111/j.1469-8137.2006.01660.x

Ruiz-Benito, P., Lines, E.R., Gómez-Aparicio, L., Zavala, M.A., Coomes, D.A., 2013. Patterns and drivers of tree mortality in iberian forests: climatic effects are modified by competition. PLoS One 8, e56843. doi:10.1371/journal.pone.0056843

Ruosch, M., Spahni, R., Joos, F., Henne, P. D., Van der Knaap, W. O., & Tinner, W. (2016). Past and future evolution of *Abies alba* forests in Europe–comparison of a dynamic vegetation model with palaeo data and observations. Glob. Chang. Biol., 22(2), 727-740. doi: 10.1111/gcb.13075

Sánchez-Salguero, R., Camarero, J.J., Carrer, M., Gutiérrez, E., Alla, A.Q., Andreu-Hayles, L., Hevia, A., Koutavas, A., Martínez-Sancho, E., Nola, P., Papadopoulos, A., Pasho, E., Toromani, E., Carreira, J.A., Linares, J.C., 2017. Climate extremes and predicted warming threaten Mediterranean Holocene firs forests refugia. Proc. Natl. Acad. Sci. 114, 201708109. doi:10.1073/pnas.1708109114

Sánchez-Salguero, R., Camarero, J.J., Gutiérrez, E., González Rouco, F., Gazol, A., Sangüesa-Barreda, G., Andreu-Hayles, L., Linares, J.C., Seftigen, K., 2016. Assessing forest vulnerability to climate warming using a process-based model of tree growth: bad prospects for rear-edges. Glob. Chang. Biol. 1–15. doi:10.1111/gcb.13541

Sanchez, S., 2010. Anàlisi socioeconòmica a la vall de Santa Fe (Massís del Montseny). Universitat Autònoma de Barcelona.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ : 25 years of image analysis. Nat. Methods 9, 671–675. doi:10.1038/nmeth.2089

Sigl, M., Winstrup, M., McConnell, J.R., Welten, K.C., Plunkett, G., Ludlow, F., Büntgen, U., Caffee, M., Chellmann, N., Dahl-Jensen, D., Fischer, H., Kipfstuhl, S., Kostick, C., Maselli, O.J., Mekhaldi, F., Mulvaney, R., Muscheler, R., Pasteris, D.R., Pilcher, J.R., Salzer, M., Schüpbach, S., Stteffensen, J.P., Vinther, B.M., Woodruff, T.E., 2015. Timing and climate forcing of volcanic eruptions for the past 2,500 years. Nature 523, 543–549. doi:10.1038/nature14565

Tegel, W., Seim, A., Hakelberg, D., Hoffmann, S., Panev, M., Westphal, T., Büntgen, U., 2014. A recent growth increase of European beech (*Fagus sylvatica* L.) at its Mediterranean distribution limit contradicts drought stress. Eur. J. For. Res. doi:10.1007/s10342-013-0737-7

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proc. Natl. Acad. Sci. 102, 8245–8250. doi:10.1073/pnas.0409902102

Tinner, W., Colombaroli, D., Heiri, O., Henne, P.D., Steinacher, M., Untenecker, J., Vescovi, E., Allen, J.R.M., Carraro, G., Conedera, M., Joos, F., Lotter, A.F., Luterbacher, J., Samartin, S., Valsecchi, V., 2013. The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. Ecol. Monogr. 83, 419–439. doi:10.1890/12-2231.1

Vayreda, E., 1879. Plantas notables por su utilidad ó rareza que crecen espontáneamente en Cataluña, ó sea apuntes para la flora catalana. Imprenta Fortanet, Madrid.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multi-scalar drought index sensitive to global warming: The Standardized Precipitation Evapotranspiration Index – SPEI. J. Clim. 23, 1696–1718. doi: 10.1175/2009JCLI2909.1

Vicente-Serrano, S.M., Camarero, J.J., Zabalza, J., Sangüesa-Barreda, G., López-Moreno, J.I., Tague, C.L., 2015. Evapotranspiration deficit controls net primary production and growth of silver fir: Implications for Circum-Mediterranean forests under forecasted warmer and drier conditions. Agric. For. Meteorol. 206, 45–54. doi:10.1016/j.agrformet.2015.02.017

Wigley, T.M.., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometereology. J. Clim. Appl. metereology 23, 201–213. doi: 10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2