Relict deciduous oaks show high resilience to drought despite the effect of land-use legacies along a climatic gradient in the rear-edge

A.J. Perez-Luque1,2; G. Gea-Izquierdo3 and Zamora, R.1,2

## **Short Title**: Resilience of relict oaks in the rear-edge (máximo 45 caracteres)

1 Instituto Interuniversitario de Investigación del Sistema Tierra en Andalucía (CEAMA), Universidad de Granada. Avda. del Mediterráneo s/n, E-18006 Granada, Spain

2 Grupo de Ecología Terrestre, Departamento de Ecología, Facultad de Ciencias, Universidad de Granada, Avda. Fuentenueva s/n, E-18071 Granada, Spain

3 INIA-CIFOR. Ctra. La Coruña km 7.5. E-28040 Madrid, Spain

## **Author Contributions**

AJPL conceived and desing the study. AJPL and GGI conducted lab work and led article preparation. AJPL, GGI and RZ conducted field work, collect the data and contribute to writing and editing the manuscript. All authors contribute to the drafts and gave final approval for publication.

# Abstract (369)

* Global change challenges forest ecosystems particularly in species-specific dry locations where land-use legacies have modified species composition and the forest structure as a result of intensive human pressure in the past. We analyzed forest resilience of adult trees to drought and climate change of relict Mediterranean *Quercus pyrenaica* Willd. populations in the Southern Iberian Peninsula. Forest resilience was analyzed using both dendroecological growth estimates and MODIS satellite images as proxies for secondary and primary growth respectively.
* Past intense land-use in the studied populations were likey expressed by disturbance chronologiess, hence partly reflecting the origin of the current forest structure and land-use legacies. Trees expressed a high sensitivity to drought. Both resilience indices of primary and secondary growth expressed that trees showed high resilience both to recent drought events and also to long-term climatic changes (*i.e.* warming). This would contradict the *a priori* vulnerability that we expected in respone to climate change of the studied relict stands at the species current rear-edge. Yet, there was variation in the response to climate and resilience following a water-stress gradiente along our three studied forests. We found a positive growth trend that was strongest in the high elevation stand and non-significant in the most xeric site (or the most transformed???) since the end of the 1970s matching the simultaneous increase in temperature observed.
* Resilience to drought followed a dryness gradient among the three populations studied: Northern populations thriving under a drier climate were less resilient to drought both in primary and secondary growth than Southern populations where lower altitudes were also less resilient than those at high-altitudes.
* Despite being considered relict stands at the dry rear-edge for the species, the trees showed high resilience in response to drought. Yet, there were a divergent response to a changing climate along very short climatic gradients. The oaks were more sensitive to water availability expressed at the most xeric sites whereas they exhibited positive growth trends only in the coldest and more humid stands. These results suggest that stand dynamics, particularly at the lowest elevations (*i.e.* the altitudinal rear-edge), need to be monitored under future expected drier and warmer climatic scenarios bearing in mind that management legacies likely play a key role in current stand dynamics.

## keywords

extreme drought, resilience, rear-edge, *Quercus pyrenaica*, tree-growth, dendrocronology, remote-sensing

## Manuscript highlights

* H1
* H2 %>% %>%
* H3

Provide three bullets (up to 85 characters for each, including spaces) that highlight the important contributions of your study for a general reader.

# Introduction

Intense drought is one of the most frequent and widespread climatic extremes affecting ecological systems worldwide and is considered a key feature of Mediterranean climate (Dai 2011). There has been an increase in the frequency and severity of drought events in the last decades, along with a trend towards drier summers particularly for southern Europe (Vicente-Serrano and others 2014b; Stagge and others 2017). This is especially critical, since the climate change projections for the Mediterranean area forecast that climate extreme events, like droughts, will become more frequent and severe (Spinoni and others 2017).

Drought causes significant changes in ecosystem productivity and water dynamics that can severely affect forests through changes in plant physiology, phenology and carbon allocation. The assessment of the drought impacts on ecosystems has gained attention in the last decades (Allen and others 2010; Clark and others 2016), and the functional response of vegetation to drought has been analyzed at global and local scales (*e.g.*, Vicente-Serrano and others 2013; see Martínez-Vilalta and Lloret 2016 for a revision).

Ecosystem responses to drought are influenced by other drivers of environmental changes (Peñuelas and others 2017). In a global-change context, the impacts of drought on vegetation need to be evaluated considering the interactions with other drivers of change (Doblas-Miranda and others 2017). This is especially relevant for areas with a long history of landscape modification, such us the Mediterranean region, where land-use change plays a significant role in current ecosystem ecology (Navarro-González and others 2013), considering also that the interactions of these two factors, namely drought and land-use change, are crucial for Mediterranean forests (Doblas-Miranda and others 2017).

The impacts of drought are also especially relevant for populations located in the rear edge (either latitudinal or altitudinal along climatic gradients) of their distribution, where climatic conditions often corresponds to the species-limits and the populations are likely to be more sensitive to small variations on climate (Hampe and Petit 2005). The response of rear-edge populations to variations on climate could be useful to estimate the adaptation of the species to predicted climatic changes (Jump and others 2010). It becomes even more important for relict populations driven by historical land-uses, which can harbour high levels of intraspecific genetic diversity (Valbuena-Carabaña and Gil 2013).

Many studies have analyzed the effects of drought on Mediterranean tree species representing the southernmost limit of their distribution (*e.g.*, Sánchez-Salguero and others 2012; Dorado-Liñán and others 2017b; Caminero and others 2018). Some of these studies focused on the resilience to drought of rear-edge populations (*e.g.*, Herrero and Zamora 2014). Resilience is the capacity of an ecosystem, community or individual to recover pre-disturbance structure and function after a disturbance (Holling 1973). The assessment of resilience to climate disturbances like droughts provides critical information about the capacity of the forests to maintain their structure and to continue providing valuable ecosystem services. This is particularly relevant for populations located in the rear-edge of their current distribution, especially when they are located in Mediterranean mountains.

The resilience to drought of species is better assessed when several aproacches like remote sensing and dendrocronology are combined simultaneously. Dendroecological estimates of growth (*i.e.* tree-ring width) are a widely used proxy to study tree vitality (Fritts 1976; Bhuyan and others 2017) and the analysis of annual-tree ring widths can be used to study changes in growth as response to drought at the individiual tree-scale (Fritts 1976). The combination of both approaches (remote sensing and dendroecology), has been used to assess the effects of droughts on vegetation along ecological or elevational gradients (*e.g.* Vicente-Serrano and others 2013; Coulthard and others 2017), and also for the analysis of growth resilience to drought on several tree species (Gazol and others 2018). Remote sensing can be used for studying droughts impacts on ecosystems (*e.g.* Zhang and others 2013). Vegetation indices obtained from satellite are used as a proxy for assessing vegetation functioning and aboveground net primary production (Alcaraz-Segura and others 2009), and changes in the patterns of these indices are considered as an indicator of the forest response to external environmental factors, such us droughts (*e.g.* Vicente-Serrano and others 2013). Drought impacts on vegetation using remote sensing have been analyzed at different scales. For instance, a global-scale study showed a stronger influence of drought for drier biomes (Vicente-Serrano and others 2013) whereas for Mediterranean area, studies at regional and local scales found a large spatial and seasonal variability of the effects of drought on vegetation (Gouveia and others 2017).

Vegetation responses to drought requires of integrative and multidisciplinary strategies for assessing the impacts of disturbances on forest at several scales (Hartmann and others 2018). Several works assessed vegetation responses in term of resistance and resilience to drought events highlithg a stronger reponse of tree-ring (tree-level) to drought variability compared to the greenness (ecosystem-level) (*e.g.* Peña-Gallardo and others 2018; Gazol and others 2018). Nonetheless, is crucial to know if the responses at the tree level differ from responses at the ecosystem level, particularly in rear edge populations.

In this work we used remote sensing information and dendroecological methods to evaluate the drought impacts in both canopy greenness (as a proxy to primary growth) and tree-radial growth of a Mediterranean tree species (*Quercus pyrenaica* Willd.) on southern relict forests at the rear-edge of species distribution and where species performance is considered to be threatened by climate change. We also assessed the resilience of these forests both to several extreme drought episodes and to climate change in the long-term in the last decades. Our main hypothesis is that these relict populations driven by historical land-use at their present climatic (either altitudinal or latitudinal) rear-edge are particularly vulnerable to climate change, and hence they will show lower-values of resilience after several extreme drought only at the dry edge of climatic gradients. To address this hyphotesis our specifics aims were: (*i*) To quantify how two recent extreme drought events influenced primary and secondary growth of *Q. pyrenaica* forests in their rear edge; (*ii*) to analyze the long-term resilience of these forests to extreme drought events using time-series of radial growth; (*iii*) and to explore differences in the resilience metrics between populations located in contrasting ecological conditions within the rear edge of the distribution of this species to detect vulnerability to climate change along climatic gradients. To achieve goal (*iii*) within the region of study we assessed whether the effect of aspect and microclimatic conditions expressed in northern and southern populations of Pyrenean oak forests differ in their resistance, resilience and recovery to extreme drought events.

# Materials and methods

## Tree species and study site

Pyrenean oak (*Quercus pyrenaica* Willd.) forests extend through south-western France and the Iberian Peninsula reaching its southern limit in mountains areas of northern Morocco (Franco 1990). In the Iberian Peninsula these forests live on siliceous soils under meso-supramediterranean and mesotemperate areas and subhumid, humid and hyperhumid ombroclimate. *Q. pyrenaica* requires over 650 mm of annual precipitation and a summer minimal precipitation between 100 and 200 mm. Summer rainfall is a key factor for the species, which is considered to have low drought tolerance compared to genuine evergreen Mediterranean taxa (Río and others 2007).

The forests of this species reaches one of their southernmost European limit in Sierra Nevada, a high-mountain range located in southern Spain (37°N, 3°W) with elevations between 860 m and 3482 m *a.s.l.*. The climate is Mediterranean, characterized by cold winters and hot summers, with pronounced summer drought (July-August). There are eight Pyrenean oak patches (2400 Has) identified in this mountain range (Figure 1), ranging between 1100 and 2000 m *a.s.l.* and often associated to major river valleys. Sierra Nevada mountain is considered a glacial refugia for deciduous *Quercus* species (Brewer and others 2002; Olalde and others 2002). In this mountain region, *Q.* *pyrenaica* woodlands represent a rear edge of their habitat distribution, which is important for determining habitat responses to expected climate change (Hampe and Petit 2005). They are the richest vascular-plant forest formation of Sierra Nevada, sheltering several endemic and endangered plant species (Lorite and others 2008). These relictic forests undergone intensive anthropic use in history (Camacho-Olmedo and others 2002; Valbuena-Carabaña and Gil 2017). Furthermore, conservation status of this species for southern Spain is considered “Vulnerable” (Vivero and others 2000) and they are expected to suffer the impact of climate change, reducting its suitable habitats in the rear-edge (Gea-Izquierdo and others 2013).

## Drought episodes

During the second half of the twentieth century the Iberian Peninsula suffered several extreme drought episodes (*e.g*. 1994-1995, 1999, 2005, 2012) (Vicente-Serrano and others 2014b).The 2005 and 2012 drought events have been documented among the worst droughts in the last decades for the southern Iberian Peninsula (García-Herrera and others 2007; Páscoa and others 2017) and they were characterized as extreme drought in our climatic data (Figures S1-S2; Table S3). We focused on these two drought events because they were included in the period where there is availability of high-spatial resolution remote sensing information (MODIS started on 2000; see below). Nevertheless, for radial growth-time series, a greater number of older drought events were also analyzed to contextualize results obtained in 2005 and 2012 drought events and analyze forest resilience to drought in a longer term (see Table S3). The identification of a drought event were done using the Standardized Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano and others 2010) following similar procedure as proposed by Spinoni and others (2015). We used SPEI-12 months scale for all 0.5º grid cells covering Sierra Nevada obtained from Global SPEI Database (<http://spei.csic.es/database.html>). A severe drought event starts in the month when SPEI falls below the threshold of -1.28 (Páscoa and others 2017; Spinoni and others 2017). A drought event is considered only when SPEI values are below the threshold for at least two consecutive months. Several indicators were computed for each drought event: ***duration*** as the number of consecutive months with the SPEI lower than a certain threshold; ***severity*** of a drought event is the sum of the SPEI values (absolute values) during the duration of the drought event; the ***intensity*** and the ***Lowest SPEI*** refer to the mean and lowest value of SPEI respectively during the drought event.

## Greenness data

Vegetation greenness of *Q. pyrenaica* was characterized by means of the *Enhanced Vegetation Index* (EVI), derived from MOD13Q1 product of the MODIS (*Moderate Resolution Imaging Spectroradiometer*) sensor. MODIS EVI Data (Collection 6) were obtanied for the period 2000 - 2016. EVI data consits of 16-day maximum value composite images (23 per year) of the EVI value with a spatial resolution of 250 m x 250 m. We selected the pixels covering the distribution of *Q. pyrenaica* forests in Sierra Nevada (*n* = 928 pixels). Values affected by high content of aerosols, clouds, snow and shadows, were filtered out following recommendations for mountain regions (Reyes-Díez and others 2015).

As a surrogate of mean annual primary production, annual mean EVI () value was computed for each pixel for the period 2000 - 2016. To explore the effect of drought on greenness, the EVI standardized anomaly () was computed pixel-by-pixel, since it minimizes biases in the evaluation of anomalies, providing more information about the magnitude of the anomalies (Samanta and others 2012). For each pixel, an annual EVI value was obtained by averaging EVI valid values. Then, the standardized anomaly was computed as:

where is the EVI standardized anomaly for year ; the annual mean value of EVI for year ; the average of the annual EVI values for the period of reference 2000-2016 (all except year); and the standard deviation for the reference period. Each pixel was categorized according the EVI standardized anomalies as “greening” (), “browning” () or “no changes” ()(Samanta and others 2012).

Rather than other vegetation indices like the NDVI, was chosen since it is highly stable under the use of any filter (Reyes-Díez and others 2015) and because it showed high significant correlations with annual ( = 0.81) and seasonal EVI values ( = 0.76 and = 0.88). For exploratory purposes, temporal trends of were explored at a pixel scale, using Mann–Kendall nonparametric test.

## Field sampling and dendrochronological methods

Tree sampling was carried out during autumn 2016. Trees were sampled at two locations in contrasting N-S slopes of Sierra Nevada: San Juan (SJ), a xeric site located at northern aspect; and Cáñar (CA), a humid but warmer site located at the southern aspect (Figure 1; Table 1). For the southern site two elevations were sampled: CA-Low and CA-High, which constitutes the current altitudinal rear-edge (CA-Low) and tree-line (CA-High), respectively in the sampled slope. Sampling sites follow a moisture gradient: SJ < CA-Low < Ca-High (Table 1). All the sites were oak monospecific and representatives of the population clusters identified for the species in this mountain range (Pérez-Luque and others 2015a). In each site between 15 and 20 trees from either the single dominant-codominant layer (CA) or the open canopy (SJ) were randomly selected. Two cores of 5 mm of diameter were taken from each tree at breast heigth (1.3 m) using an increment borer. Diameter at breast height (DBH) and total height were measured for each tree. In addition, stand competition of target trees was assessed by recording distance, azimuth, DBH, species and total height of all neighboring living trees with DBH > 7.5 cm within a circular plot of 10 m radius. Several competition indices were calculated: the distance independent indices *density* (), and *basal area* (BA, ); and the distance dependent index size ratio proportional to distance (*srd*) as . Differences between sites for height, DBH and competition indices were analysed using non-parametric Kruskal-Wallis rank sum tests. When significant differences were observed, we run multiple comparisons using the Dunn’s-test with Bonferroni adjustment to correct significance values.

Tree cores were air dried, glued onto wooden mounts and sanded. Annual radial growth (ring width, RW) was measured with a measuring device coupled to a stereomicroscope, with an accuracy of 0.001 mm. Individual ring series were first visually and statistically cross-dated with TSAP software (Rinntech, Heidelberg, Germany), using the statistics Gleichläufigkeit (GLK), t-value and the crossdating index (CDI). Cross-dating validation was finally done using COFECHA software (Holmes 1983).

The growth trends were analyzed at different time scales. To study the response of growth to the inter-annual variability of climate (short-term response), pre-whitened residual chronologies (RWI) were used. They were calculated from ratios between raw growth measurements and individual cubic splines with a 50 % frequency cutoff at 30 years (Fritts 1976). Tree-ring width series were standardized and detrended using dplR (Bunn 2010). Mean residual site chronologies were obtained computing the biweight robust mean of all prewhitened growth indices for the trees of the same site (Cook and Kairukstis 1990). The statistical quality of each chronology was checked via the expressed population signal. A threshold value of EPS > 0.85 was used to determine the cutoff year of the time span that could be considered reliable.

The long-term growth response was analyzed using basal area increment (hereafter BAI, ). Theoretically, BAI represents a more accurate indicator of growth than ring-width, since it removes variation in growth attributable to increasing stem circumference after 30-40 years of juvenile increasing growth (Biondi and Qeadan 2008). Raw ring-widths and measured DBH were used to compute BAI by subtracting twice the annual ring width from the annual diameter, starting from the measured diameter outside the bark (Piovesan and others 2008). We used the following equation:

where is the radius of the tree and is the year of tree-ring formation. For each individual tree, a mean BAI serie was calculated. Then, mean site BAI chronologies were obtained by averaging individual tree BAI time series.

Both RWI and BAI chronologies were compared to different climatic indices to analyse the low and the high-frequency response to climate of trees.

### Climate and growth

Climate data were obtained from the European Daily High-Resolution Observational Gridded Dataset (E-OBS v16) (Haylock and others 2008). Monthly precipitation and minimum and maximum temperatures were obtained at a 0.25 x 0.25 º resolution for the 1950-2016 period. We selected grid cells covering each sampled sites. The Standardized Precipitation-Evapotranspiration Index (SPEI) with a temporal scale of 6 months was used to characterize the drought conditions for the period 1961-2014.

Relationships between residual site chronologies and climatic variables were assessed ussing bootstrapped Pearson’s correlations estimated using treeclim package (Zang and Biondi 2015).

### Disturbance analyses

Disturbance chronologies were built using tree-ring width to identify abrupt and sustained increases (release events from competition) or decreases (supressions) in radial growth (Nowacki and Abrams 1997) as indirect estimates of possible disturbance events (e.g. logging, neighbor mortality) in the past. By using a temporal window of reasonable length this method is intended to filter out the response to short-term changes in temperature and precipitation and minimizes the long-term growth trends (Nowacki and Abrams 1997). Growth changes (GC) were calculated for the individual tree-ring series using a 10-year running window as either positive (PGC) or negative (NGC) growth changes:

where is preceding 10-year median and is subsequent 10-year median. Medians were used since they are more robust estimator of central tendency than means (Rubino and McCarthy 2004). Site disturbance chronologies were constructed by averaging the individual disturbances series annually. To separate growth peaks produced by disturbance events and expressing stand-wise disturbances from those by climate, we considered a threshold of 50 % of GC and more than 50% of the individual trees displaying the same growth changes was considered a stand-wise disturbance.

In addition, the forest and managment history of our sampling sites was inferred from a detailed analysis of historical land-use changes. For this purpose, an exhaustive review of historical documents was done to compile information about socio-economical activities affecting forest (Table S4).

## Assessing ecosystem and tree individual resilience to drought

To evaluate the effects of drougth events on ecosystem resilience (using greeennes data) and tree individual resilience (using BAI growth data) we used resilience indices proposed by Lloret and others (2011): resilience (*Rs*), resistance (*Rt*), and recovery (*Rc*). The Resistance index, estimated as the ratio between the performance during and before the disturbance (), quantifies the severity of the impact of the disturbance in the year it occurred. The Recovery index, computes as the ratio between performance after and during disturbance (), represents the ability to recover from disturbance relative to its severity. Finally, the Resilience index () is the capacity to reach pre-disturbance performance levels. The values of these indices were computed for tree growth (BAI) and greenness (EVI mean) during each drought event. 2005 and 2012 were considered as single drought events. The predrought and postdrought values of each target variable (*i.e.* BAI or EVI) were computed as the mean value during a period of three years before and after the drought event respectively. A period of three years was chosen because we found similar results comparing periods of two, three and four years (Figure S6) and this length was used in other studies (*e.g.* Gazol and others 2018). To put in context in a longer-term the resilience observed for 2005 and 2012 drought events, as well as to test whether the resilience indices were ecologically meaningful, resilience metrics for BAI data were additionally computed for the most severe drought events since 1950 and compared them with drought severity (Figure 6, Table S3).

## Statistical analysis

For each of the three resilience indices studied, robust two-way ANOVAs were used to test for differences between drought events (2005 and 2012) and the studied oak populations (northern and southern aspects). These tests were used because original and log-transformed data did not follow the assumptions of normality and homogeneity of variance (Wilcox 2012). Robust measures of central tendency (M-estimator based on Huber’s Psi) were used since they were close to the mean value in all cases (Wilcox 2012). When running the robust ANOVA test, data were boostrapped 3000 times and trimmed automatically to control the potential influence of outliers. Post-hoc differences were assessed pairwise using a similar boostrap test. All the robust ANOVA and post-hoc tests were carried out using the WRS2 package. The level of significance was set to 0.05 and adjusted for multiple comparisons.

# Results

## Time trends in vegetation greenness

The analysis of greenness time trends showed that EVI in 78.9 % of the pixels of *Quercus pyrenaica* forests experienced a positive trend for the 2000-2016 period. The lowest values of EVI standardized anomalies for the studied period were recorded during the 2005 drought, and the minimum EVI values were expressed in northern (dry) populations (Figure 2). In fact, a “browning” episode () was observed for *Q. pyrenaica* forests during this drought event, whereas no changes in greenness were observed in response to the 2012 drought (Figure 3).

## Analysis of radial growth trends and disturbances

The trees of the southern population were older than those from the northern one. In addition trees from the southern population at high altitude were taller and their growth was significantly faster than that of trees from the other two sites (Table 1, Figure 4). Both growth and height of trees from the northern and the low-elevation southern population were similar (Figures 4 and S6). Competition was similar among all sites. Yet plot basal area was greatest in CA-High (Table 1), despite the highest individual BAI growth at that site (Figure 4). Only trees from the southern sites showed significant positive growth trends since the late 1970s (Figure 4), being more pronunced for the highest site (CA-High).

Drought events produced reduction of RWI for all sites (Figure S3), being particularly evident the negative effect of the 1995 drought, when the greatest reduction of tree-growth were recorded for all chronologies. The southern sites (CA-High and CA-Low) showed weaker reductions of tree-growth than the northern site (SJ), especially for 2005 and 2012 (Figure S3). Tree-growth reduction followed a moisture-gradient, being weaker for the wetter site (CA-High). Trees from northern site also suffered a great reduction during 1945-1946 drought event (Figure 5).

The northern site (SJ) showed two major release events (GC > 50 % occurring in more than 50 % of sampled trees): the first during the 1940 decade (the most evindent) and the second in the period 1995-2000. These periods alternate with periods of supression for over 40 years. The two southern sites showed no release events except for CA-High at the beginning of the 1830s and no suppression events in the last 50 years.

## Resilience to drought events at the ecosystem and individual tree levels

The exploration of the resilience metrics of tree-growth for severe drought events since 1950 (*i.e.* for the share period among the three chronologies, excluding juvenile years, Table S3) revealed a positive relation between drought severity and Recovery (*Rc*), significant for all oak populations (Figure 6). A similar pattern was obtained for Resilience (*Rs*) but only significant for SJ site (Figure 6). Non-significant patterns were obtained if we exclude 1995 from the analysis (Figure S8). Trees showed the highest value of tree-growth resilience for 1995, the worst drought event in our study area (Table S3), and particularly SJ, where our results suggest a major release event after 1995 (Figure 5).

During the last two drought events, resilience metrics for greenness and tree-growth were significantly different bewteen drought events (Table 3). The 2005 drought event reduced greennes and growth more than that of 2012 (Tables S1 and S2) but the two metrics of resilience generally covaried in the same direction. We obtained significantly higher Resilience (*Rs*) and Resistance (*Rt*) values for the 2012, the most severe event, than for 2005 in both variables (Tables S1-S2; Figure 7). Recovery (*Rc*) showed contrasting pattern for EVI and tree-growth. Recovery values for greenness was higher for 2005 than for 2012 drought event (Table S1, Figure 7).

Resilience metrics significantly varied between sites, except for Resilience (*Rs*) of tree-growth (p = 0.534; Table 3). The two southern populations showed lower values for Recovery (*Rc*) than the northern site both for greenness and tree-growth (Tables S1 and S2). In contrast, Resistance and Resilience values were significantly higher for southern sites than for northern ones (Tables S1 and S2).

## Tree-growth response to climate

Tree-growth exhibited a significant greater response to water availability than to temperatures, as it can be expected for a Mediterranean site and a species located closer to its xeric/dry distribution limit (rear-edge). Cumulative precipitation of the hydrological year was the climatic variable with the highest relationship with growth and influenced similarly and positively the tree-growth for both northern and southern populations (Figure 8a). Precipitation of previous december was also positively correlated with tree growth in the northern population and in the highest location of the southern population. Hydrological, Spring and Summer SPEI showed a strong positive correlation with tree-growth (Figure 8a), being this relationship higher in the northern population (r > 0.6 *vs.* r < 0.5). Relationships with temperatures were lower than those with moisture variables. Yet there were differences between northern and southern populations: spring maximum temperature was the most significant limitation for the tree-growth of the southern population at both elevations while no significant limitations were recorded for northen site regarding the temperatures (Figure 8b and 8c). Remarkably minimum and maximum temperatures of current September positively influenced the tree-growth only in the northern population. No positive relationship with temperature was found for southern trees.

# Discussion

## Rear-edge oaks show high resilience in response both to recent drought events and long-term climatic variability.

Severe drought events negatively affected to primary and secondary growth of *Q. pyrenaica* forests in the rear edge of their distribution. Our findings show that 2005 and 2012 drought events, provoked reductions in greenness and tree-growth of these forests. These results are consistent with previous studies that reported significant reductions of tree-growth for this oak species during extreme drought events (Corcuera and others 2006; Gea-Izquierdo and Cañellas 2014). In fact, when we explore the effects of drought at a longer-term scale, we observed the greatest reduction of tree-growth during the 1995 drought, a characteristic pointer-year that caused severe and extensive damage to the Mediterranean vegetation across the Iberian Peninsula (Peñuelas and others 2001; Gazol and others 2018). Although the south of Iberian Peninsula suffered severe drought events in the last decades (*e.g* 2005 and 2012 were considered two of the worst recorded drought; García-Herrera and others 2007; Trigo and others 2013; Vicente-Serrano and others 2014b) (Table S3), we found a positive trend for vegetation greenness of *Q. pyrenaica* (78.9 % of the pixels showed a positive trend during the 2000 to 2016 period). This confirms previous findings that pointed out an increase in primary productivity for these forests (Pérez-Luque and others 2015b), being the most productive ecosystems in this mountain region during that period (Alcaraz-Segura and others 2016). For tree-growth, we also observed positive trends in the last decades, particularly for the southern high-elevation site (CA-High, Figure 4). Similar long-term trends were described for this species along its distribution range (Gea-Izquierdo and Cañellas 2014) and could be related to the rising of the temperatures in the last decades (Gea-Izquierdo and Cañellas 2014) particularly after 1970. Howewer, the observed pattern for our sites (a rear-edge) differs from the decline trends observed for several Mediterranean and temperate tree-species located in their rear-edges (*e.g.*, *Pinus nigra*; *P. sylvestris*; Sánchez-Salguero and others 2012; Camarero and others 2015b; *Fagus sylvatica*; Dorado-Liñán and others 2017a).

Resilience (*Rs*) values observed in our study sites for the latest drought events in both tree-growth and greenness were close to 1, except for the tree-growth during 2005 event (Tables S1 and S2). Despite the 2012 drought event was more severe and intense than 2005, according with our analysis with SPEI data (Table S3), resilience values for greenness and tree-growth were greater for 2012 than for 2005. These results could be explained by the different timing of the two droughts, *i.e.* the 2012 drought was a winter drought (Trigo and others 2013) that occurred earlier than the 2005 drought. The latter lasted less than 2012 drought, but matched the period of maximum growth for *Q. pyrenaica* forests (Figure S7). Our results are in line with recently studies that indicate the timing of the drought as a key factor determining tree recovery after drought (Huang and others 2018), that also has been observed for other Mediterranean oak species (*e.g.* Holm oak; Camarero and others 2015a).

As we mentioned previously, we found strong declines of tree-growth during the most severe drought events occurred (1995 and 1999) (Table S3; Figure S3), matching similar declining patterns observed for other species in their rear edge (Sánchez-Salguero and others 2012; Camarero and others 2015b). But, interestingly, we obtained the highest values of resilience for tree-growth for these two drought events (Figure 6). In addition, the analysis from a long-term perspective of the severe droughts suggests a positive relation between the tree-growth resilience and drought severity (Figures 6). Surprisingly this result seems contradict our initial hypothesis in which we predict low resilience values for this oak species in their rear-edge after extreme drought events.

Rear-edge populations live in environmental narrow margins, and small variations in environmental conditions can increase the vulnerability of the species (Hampe and Petit 2005). A high vulnerability to drought is often assumed for populatios located at their rear-edge (Martínez-Vilalta 2018). However we obtained positive trends in greenness and tree-growth for the rear-edge of *Q. pyrenaica* and high values of resilience to severe droughts were also reported. Our findings are in agreenment with those studies that have shown that the assumed higher vulnerability of dry edges does not necessarily hold (Cavin and Jump 2017). Martínez-Vilalta (2018) pointed out the importance of the local adaptation and plasticity, and also of the local environmental factors on the vulnerability showed by rear-edge populations. The high values of resilience to drought reported here together with previously works showing high values of genetic resilience for those forests at Sierra Nevada, seem to be indicative of high local adaptation of this oak to this mountain range. In addition the local environmental conditions of the sites where this species inhabit at Sierra Nevada would explain the low vulnerability to drought showed by this oak. A key consideration for rear-edge populations is the different ways in which marginality can be defined, *i.e.* if it is defined according to geographic, climatic criteria, or according to other ecological factors (Martínez-Vilalta 2018). In this sense, the high values of resilience to the drought events that we have observed, could suggest that the populations of *Q. pyrenaica* in Sierra Nevada are located in a geographical but not climatic rear-edge.

A remarkably result is the higher values of resilience for tree-growth obtained during the worst and more severe drought events in our study area (1995 and 1999) (Table S3; Figure 6). A plausible explanation could be the water availability previously and after the drought event. For instance, cumulative precipitation of the 1992-1994 years (pre-1995 drought) had precipitation values below the mean of the whole period (Figure S1), while 1996-1998 years (post-1995 drought) showed a wet opposite pattern (*e.g.* first months of 1996 recorded the highest cumulative rainfall of the past century for our southern sites). This could explain the higher values of recovery found for 1995 (Figure 6). The high resilience values obtanied for the 1995 drought in the most xeric site (SJ) could be related with drought-induced mortality occurred in this area (*personal communications*).

Greenness and tree-growth of *Q. pyrenaica* showed different sensitivity to severe droughts. During the last drought events EVI was reduced to 90.25 % (Table 1), whereas BAI was reduced to 70.83 % (Table S2), suggesting a lower sensitivity of the greenness than tree-growth to drought, particularly for sites under drier climate. For our driest site (SJ, the northern one), BAI were reduced to 44.5 % respect to that of the preceding period during 2005 drought event, whereas the EVI was reduced to 81.9 % (Tables S1 and S2). These findings are in accordance with previously works which showed that tree-growth are more sensitive metrics of forest resilience than net primary productivty (*e.g.* Babst and others 2013; Coulthard and others 2017; Gazol and others 2018). Besides the different scales of both approaches, *i.e.* tree-based *versus* pixel-based; the growth reduction seems to be more mediated by sink that by source limitations (Gazol and others 2018). Response of greenness to drought not only reflects response of tree, because remote sensing indices (EVI) captures signals from all vegetation covered by the pixel (not only tree but also understory vegetation) (see Dionisio and others 2012). On the other hand, tree-ring width data provide an accurate measure of growth responses to droughts (Bhuyan and others 2017; Gazol and others 2018).

## Microenvironment shapes differential sensitivity to climate and drought of rear-edge oaks

Our results showed differences for greenness and tree-growth between northern and southern oak populations (Table 3). The former, which have drier conditions (Table 1), were more impacted by the drought events than the latter. For instance, the northern site showed more negative EVI standardized anomalies (higher browning intensity) than the southern sites during the 2005 drought event (Figure 2). In addition, the stronger correlations of tree-growth with SPEI (Hydrological and summer) observed for northern site (Figure 8), can be interpreted as higher sensitivity to drought of a drier site (Gea-Izquierdo and Cañellas 2014).

Moisture availability has been reported as the most limiting factor driving radial growth of *Q. pyrenaica* along their distribution range in Iberian Peninsula (Gea-Izquierdo and Cañellas 2014). We found a singnificant positive relation between precipitacion (hydrological year and previous December) and tree-growth (Figure 8a). Our results are consistent with previous studies highlighting the influence of precipitation on tree-ring growth in oaks (*e.g.* Gea-Izquierdo and Cañellas 2014; González-González and others 2014; García-González and Souto-Herrero 2017)

A striking result is the difference for tree growth between sites (Figure 4). The trees of CA-High site, which are located around 1900 m. *a.s.l.* and representing the upper limit of the treeline of the species in this southernmost location, showed higher BAI than those located at low-elevations sites (CA-Low and SJ) (Figure 4). This is especially interesting for southern sites, which are very close to each other. Our findings are in line with previous works that pointed out that tree growth and tree responses to drought are site-dependent (*e.g.* soil features, tree competence, etc.) (Babst and others 2013; Vicente-Serrano and others 2014a), particularly for rear-edge populations (Cavin and Jump 2017; Dorado-Liñán and others 2017b). The higher values of tree growth that we observed in CA-High site could be related with lower water stress at high-elevation sites, since moisture availability is a key factor limiting tree growth for *Q. pyrenaica* (Gea-Izquierdo and Cañellas 2014). In fact, soil analyses along an elevational gradient in this location revealed higher content of available water for forest soils located on high elevation (Cobo-Díaz and others 2017). Recent works have found a clearly effect of elevation on the resistance to drought of several tree-species, where stands located at higher elevations were less drought sensitive. (Bhuyan and others 2017).

In addition to the lower water stress, it is likely that the sites at higher elevation had a lower anthropic impact and the abandonment of traditional uses was earlier, due to their farthest location from human settlements and therefore less access to forest resources (Table S4).

## Land-use legacies shape distribution and sensitivity to climate change at the read-edge

The Mediterranean mountains, even at high elevations, have suffered strongly transformation of the landscapes driven by human activities throughout history. Multiple evidence from palaeoecological studies indicated an intense human impact on vegetation of Sierra Nevada since 3000 cal year BP (García-Alix and others 2017). From that moment onwards, increases on fire occurrence and both grazing and mining activities, were recorded for this mountain region, with an sharp intensification of the human activities in the last 150 years (García-Alix and others 2017). Mining, forest clearings, fuelwood and charcoal exploitations, pastoralism and also wars, have strongly impacted on the forest resources in Sierra Nevada, and on Pyrenean oak forest, as can be derived from the results of the review of historical documents (Table S4). As a consequence of all those activities a loss of about 90% of broadleaf *Quercus* species cover from medium and low elevation occurred in this mountain region (Jiménez-Olivencia and others 2015).

Our study sites have been subjected to an intense exploitation of forest resources in history and landscape transformation. Although the estimated age for our sampled trees was not more than 180 years (Tables 1, 2), several documents reported the presence of oaks before that date. For instance, the inventories of trees made by the Spanish Navy during the second half of 18th century, reported for Cáñar and SJ sites more than two millions and 700 000 trees respectivley, most of them juveniles, suggesting recent wood fellings (Cruz 1991). These numbers are a reflect of the intense exploitation of the forest resources occurring up to the end of nineteenth century (Calatrava and Sayadi 2019) and also concur with the regeneration peaks observed for several Iberian oak woodlands (e.g. Gea-Izquierdo and Cañellas 2014; Gea-Izquierdo and others 2015; Dorado-Liñán and others 2017a).

We found similar tree competence levels in our sampled sites (Table 1), but differences in tree size and age suggest different management origin (*i.e.* land-use legacy). Our study sites had different land-use trajectories driven mainly by the differential pattern of the natural resource use (Jiménez-Olivencia and others 2015) (Table S4). On the one hand, the northern sites (*e.g.* San Juan), show a sequentially distribution of the land uses along the elevational gradient (Jiménez-Olivencia and others 2015): grasslands and shrublands for cattle farming are located at high elevations; then forests formation with some croplands; and at lowlands, irrigated terraces with tree crops. Other activities (*e.g.* mining) could also determine the use of natural resources, and therefore the forest structure. For instance, the SJ oak woodland is located in an area with a high concentration of mines and quarries that have been exploited intermitently throughout history (Table S4). On the other hand, woodland areas of the southern slopes (Cáñar) are mixed with a greater percentage of croplands, even reached high elevation (Calatrava and Sayadi 2019). Forest resources, like firewood, charcoal and acorns, have been continuously exploited in southern sites through history (Valbuena-Carabaña and Gil 2013). In Cáñar site, there were an arraigated tradition of charcoal extraction since fifteenth century (Jiménez-Serrano and Serrano-Gutiérrez 2004) up to middle of the 20th century. From this moment to the present, there were a sharp decrease of the wood extraction, mainly due to rural abandonment. Acorn resources have been tradiotionally exploited in this location up to 1950s (Tabla S4).

Those different patterns of resource uses can help to understand the tree-growth changes recorded in our chronologies (Figure 5). We observed a tree-growth release event at 1940s in the SJ oak woodland (Figures 5, S4) which concurs with one period of maximum mining activity for this area (1925 to 1957) (Table S4). During this period there were an increase on the use of timbers for the tunnels of the mines and several furnaces that required great quantities of fuelwood to melt the mineral were active in this area (Titos 1990). This heavily exploitation of the forest resources could affect to a major part of this oak woodland, since percentage of trees affected by GC > 50 % reaches values above 50 % (Figure S4). Our results also coincide with a concurrent but less intense tree-growth release event reported for a closed oak woodland (Gea-Izquierdo and Cañellas 2014). In addition, paleoecological studies carried out in nearby alpine bogs have recorded increases in the heavy metals concentration since the end of 18th century until mid-20th, which coincides with the maximum activity of the mining in this area (García-Alix and others 2017). The other release event observed for SJ site during 1995-2000 was lower than the occurred at 1940, but affecting more trees (Figures 5, S4). We revised the forest practices carried out in this area in the last 30 years (Bonet and others 2016), but we did not find any clearing or cutting event during 1995 - 2000 period. Two non-mutually exclusive ways could explain the tree-growth release observed. Firstly it could be related with a natural drought-induced mortality event after 1995 (*personal communications*) as was reported for Mediterranean tree species (*e.g.* Peñuelas and others 2000; Lloret and others 2004). On the other hand, we obtained strong positive correlations of SPEI with tree-growth for this site (Figure 8), which suggests a high sensitivity to water availability of this slightly more xeric site (Table 1) (Gea-Izquierdo and Cañellas 2014). Previous works reported a sharp decline (or non-production) in latewood production during extreme drought events (Corcuera and others 2006). Since latewood are less vulnerable to embolism than earlywood vessels (Corcuera and others 2006), the reduction or even the non-production of former could negatively affect to tree-growth and also enhanced the mortality, particularly for drier sites (Corcuera and others 2006; Gea-Izquierdo and Cañellas 2014).

For southern sites, the only positive release events showed for CA-High site could be related with conversion from closed forest to an open silvopastoral system, a common management applied in the past (Cañellas and others 2004; Gea-Izquierdo and Cañellas 2014) documented in this site (Valbuena-Carabaña and Gil 2013).

Climatic drivers are key factors determining the growth of tree species, especially at the rear edge of their distribution but in Mediterranean forests we must also considered the management history, *i.e* *land-use legacies* (Navarro-González and others 2013; Doblas-Miranda and others 2017; Peñuelas and others 2017) since, as we inferred from our results, the land-use legacy can conditioned tree-growth and resilience of tree species. Although the abandonment of the traditional activities have provoked a stagnation for this species (Cañellas and others 2004), we have observed an increase in the growth, especially in the high elevation sites, where the water is less-limiting resource. This pattern concurs with a forest expansion into marginal abandonded croplands and an increase in the tree-cover (Camacho-Olmedo and others 2002).

# Conclussions

Severe drought events have provoked important reductions in primary and secondary growth of *Q. pyrenaica* forests at Sierra Nevada mountain range. However, despite the expected vulnerability for those relict stands, we observed positive trends of both primary (*i.e.* greenness) at ecosystem scale and secondary growth at tree level in our study site, particularly at the most humid site along the climatic gradient analyzed. Surprisingly we observed high resilience values to drought, particularly at long-term scales. These results are consistent with research showing high genetic resilience values and overall suggest this mountain region still acting as refuge for deciduous *Quercus*. The differences observed in tree-growth and resilience to drought between very close sites show that responses to drought were site-dependent. This is particularly relevant for rear-edge populations where topographic and biophysical variablity facilitates the existence of microrefugia, as reflected along the climatic gradient analysed (Vilà-Cabrera and others 2019). The analysis of tree-growth dynamics revealed suppression and release events that are consistent with legacies left by land-use in local forest dynamics, as inferred from an exhaustive review of historical documents. In this sense our results highlight the importance of land-use legacies for highly transformed Mediterranean systems. This is relevant for tree species with higher sensitivity to climate change, such us *Q. pyrenaica*, not only for conservation per se of this species, but for all ecosystem services that these singular forests offer at Mediterranean mountain. Following our study it is necessary to disentangle how ecosystem services and stand dynamics are affected by the combination of climate change and land-use legacies in highly transformed landscapes like the one studied here.

# Acknowledgments

We would like to thank Sammy Lucy Behle, M. Suarez-Muñoz and F.J. Bonet-García for their assistence in the field monitoring. A. Reyes and J. Blanco helped in the filtering of satellite data. F.J. Cano-Manuel and F.J. Navarro provided worthwhile information about oak management projects in Sierra Nevada. We also are very thankful to F.J. Bonet-García for his valuable comments in an earlier version of the manuscript. Environment Department of Andalusian Regional Government and Director of Sierra Nevada National and Natural Park provided permission for field work. This research work was conducted in the collaborative framework of the “Sierra Nevada Global Change Observatory” Project from the Environment Department of Andalusian Regional Government (with the support of European Union FEDER Project). We also thank to LIFE-ADAPTAMED (LIFE14 CCA/ES/000612): *Protection of key ecosystem services by adaptive management of Climate Change endangered Mediterranean socioecosystems* and H2020 project *ECOPOTENTIAL: Improving future ecosystem benefits through earth observations* (<http://www.ecopotential-project.eu/>) (No 641762), for their funding support.

# References

Alcaraz-Segura D, Cabello J, Paruelo JM, Delibes M. 2009. Use of descriptors of ecosystem functioning for monitoring a national park network: A remote sensing approach. Environmental Management 43:38–48.

Alcaraz-Segura D, Reyes A, Cabello J. 2016. Changes in vegetation productivity according to teledetection. In: Zamora R, Pérez-Luque A, Bonet F, Barea-Azcón J, Aspizua R, editors. Global change impacts in Sierra Nevada: Challenges for conservation. Consejería de Medio Ambiente y Ordenación del Territorio. Junta de Andalucía. pp 142–5.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg E (Ted), Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J-H, Allard G, Running SW, Semerci A, Cobb N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–84.

Babst F, Poulter B, Trouet V, Tan K, Neuwirth B, Wilson R, Carrer M, Grabner M, Tegel W, Levanic T, Panayotov M, Urbinati C, Bouriaud O, Ciais P, Frank D. 2013. Site‐ and species‐specific responses of forest growth to climate across the European continent. Global Ecology and Biogeography 22:706–17.

Bhuyan U, Zang C, Menzel A. 2017. Different responses of multispecies tree ring growth to various drought indices across Europe. Dendrochronologia 44:1–8.

Biondi F, Qeadan F. 2008. A theory-driven approach to tree-ring standardization: Defining the biological trend from expected basal area increment. Tree-Ring Research 64:81–96. <https://doi.org/10.3959/2008-6.1>

Bonet F, Aspizua R, Navarro J. 2016. History of Sierra Nevada forest management: Implications for adaptation to global change. In: Zamora R, Pérez-Luque A, Bonet F, Barea-Azcón J, Aspizua R, editors. Global change impacts in Sierra Nevada: Challenges for conservation. Consejería de Medio Ambiente y Ordenación del Territorio. Junta de Andalucía. pp 153–6.

Brewer S, Cheddadi R, Beaulieu J de, Reille M. 2002. The spread of deciduous Quercus throughout Europe since the last glacial period. Forest Ecology and Management 156:27–48.

Bunn AG. 2010. Statistical and visual crossdating in r using the dplR library. Dendrochronologia 28:251–8.

Calatrava J, Sayadi S. 2019. Evolution of farming systems in the mediterranean high mountain: The case of the Alpujarra Alta (Spain). Sustainability 11:704. <https://doi.org/10.3390/su11030704>

Camacho-Olmedo M, García-Martínez P, Jiménez-Olivencia Y, Menor-Toribio J, Paniza-Cabrera A. 2002. Dinámica evolutiva del paisaje vegetal de la Alta Alpujarra granadina en la segunda mitad del s. XX. Cuadernos Geográficos 32:25–42.

Camarero J, Franquesa M, Sangüesa-Barreda G. 2015a. Timing of drought triggers distinct growth responses in holm oak: Implications to predict warming-induced forest defoliation and growth decline. Forests 6:1576–97.

Camarero JJ, Gazol A, Sangüesa-Barreda G, Oliva J, Vicente-Serrano SM. 2015b. To die or not to die: Early warnings of tree dieback in response to a severe drought. Journal of Ecology 103:44–57.

Caminero L, Génova M, Camarero JJ, Sánchez-Salguero R. 2018. Growth responses to climate and drought at the southernmost European limit of Mediterranean *Pinus pinaster* forests. Dendrochronologia 48:20–9.

Cañellas I, Del Río M, Roig S, Montero G. 2004. Growth response to thinning in quercus pyrenaica willd. Coppice stands in spanish central mountain. Annals of Forest Sciences 61:243–50. <https://doi.org/10.1051/forest:2004017>

Cavin L, Jump AS. 2017. Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree Fagus sylvatica l. Not the equatorial range edge. Global Change Biology 23:362–79. <http://dx.doi.org/10.1111/gcb.13366>

Clark JS, Iverson L, Woodall CW, Allen CD, Bell DM, Bragg DC, D’Amato AW, Davis FW, Hersh MH, Ibanez I, Jackson ST, Matthews S, Pederson N, Peters M, Schwartz MW, Waring KM, Zimmermann NE. 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Global Change Biology 22:2329–52.

Cobo-Díaz JF, Fernández-González AJ, Villadas PJ, Toro N, Tringe SG, Fernández-López M. 2017. Taxonomic and functional diversity of a *Quercus pyrenaica* Willd. rhizospheric microbiome in the Mediterranean mountains. Forests 8:390. <http://www.mdpi.com/1999-4907/8/10/390>

Cook E, Kairukstis L. 1990. Methods of dendrochronology: Applications in the environmental sciences. Doredrecht: Springer

Corcuera L, Camarero JJ, Sisó S, Gil-Pelegrín E. 2006. Radial-growth and wood-anatomical changes in overaged quercus pyrenaica coppice stands: Functional responses in a new mediterranean landscape. Trees 20:91–8.

Coulthard BL, Touchan R, Anchukaitis KJ, Meko DM, Sivrikaya F. 2017. Tree growth and vegetation activity at the ecosystem-scale in the eastern Mediterranean. Environmental Research Letters 12:084008.

Cruz M. 1991. Atlas historico-forestal de Andalucia: siglo XVIII. Granada: Universidad de Granada

Dai A. 2011. Drought under global warming: A review. Wiley Interdisciplinary Reviews: Climate Change 2:45–65.

Dionisio MA, Alcaraz-Segura D, Cabello J. 2012. Satellite-based monitoring of ecosystem functioning in protected areas: Recent trends in the oak forests (quercus pyrenaica willd.) of sierra nevada (spain). In: Young SS, Silvern SE, editors. International perspectives on global environmental change. pp 355–74.

Doblas-Miranda E, Alonso R, Arnan X, Bermejo V, Brotons L, Heras J de las, Estiarte M, Hódar J, Llorens P, Lloret F, López-Serrano F, Martínez-Vilalta J, Moya D, Penuelas J, Pino J, Rodrigo A, Roura-Pascual N, Valladares F, Vilà M, Zamora R, Retana J. 2017. A review of the combination among global change factors in forests, shrublands and pastures of the Mediterranean region: Beyond drought effects. Global and Planetary Change 148:42–54.

Dorado-Liñán I, Cañellas I, Valbuena-Carabaña M, Gil L, Gea-Izquierdo G. 2017a. Coexistence in the Mediterranean-temperate transitional border: Multi-century dynamics of a mixed old-growth forest under global change. Dendrochronologia 44:48–57.

Dorado-Liñán I, Zorita E, Martínez-Sancho E, Gea-Izquierdo G, Filippo AD, Gutiérrez E, Levanic T, Piovesan G, Vacchiano G, Zang C, Zlatanov T, Menzel A. 2017b. Large-scale atmospheric circulation enhances the Mediterranean east-west tree growth contrast at rear-edge deciduous forests. Agricultural and Forest Meteorology 239:86–95.

Franco A. 1990. *Quercus* L. In: Castroviejo A, Laínz M, López-González G, Montserrat P, Muñoz-Garmendia F, Paiva J, Villar L, editors. Flora Ibérica. Vol. 2. Madrid: Real Jardín Botánico, CSIC. pp 15–36.

Fritts HC. 1976. Tree rings and climate. London: Academic Press

García-Alix A, Jiménez-Espejo FJ, Toney JL, Jiménez-Moreno G, Ramos-Román MJ, Anderson RS, Ruano P, Queralt I, Delgado Huertas A, Kuroda J. 2017. Alpine bogs of southern spain show human-induced environmental change superimposed on long-term natural variations. Scientific Reports 7:7439.

García-González I, Souto-Herrero M. 2017. Earlywood vessel area of *Quercus pyrenaica* Willd. is a powerful indicator of soil water excess at growth resumption. European Journal of Forest Research 136:329–44.

García-Herrera R, Hernández E, Barriopedro D, Paredes D, Trigo RM, Trigo IF, Mendes MA. 2007. The outstanding 2004/05 drought in the Iberian Peninsula: Associated atmospheric circulation. Journal of Hydrometeorology 8:483–98.

Gazol A, Camarero JJ, Vicente-Serrano SM, Sánchez-Salguero R, Gutiérrez E, Luis M de, Sangüesa-Barreda G, Novak K, Rozas V, Tíscar PA, Linares JC, Martín-Hernández N, Martínez del Castillo E, Ribas M, García-González I, Silla F, Camisón A, Génova M, Olano JM, Longares LA, Hevia A, Tomás-Burguera M, Galván JD. 2018. Forest resilience to drought varies across biomes. Global Change Biology:1–16.

Gea-Izquierdo G, Cañellas I. 2014. Local climate forces instability in long-term productivity of a Mediterranean oak along climatic gradients. Ecosystems 17:228–41. <http://dx.doi.org/10.1007/s10021-013-9719-3>

Gea-Izquierdo G, Fernández-de-Uña L, Cañellas I. 2013. Growth projections reveal local vulnerability of Mediterranean oaks with rising temperatures. Forest Ecology and Management 305:282–93. <http://www.sciencedirect.com/science/article/pii/S0378112713003678>

Gea-Izquierdo G, Montes F, Gavilán RG, Cañellas I, Rubio A. 2015. Is this the end? Dynamics of a relict stand from pervasively deforested ancient Iberian pine forests. European Journal of Forest Research 134:525–36.

González-González BD, Rozas V, García-González I. 2014. Earlywood vessels of the sub-Mediterranean oak *Quercus pyrenaica* have greater plasticity and sensitivity than those of the temperate *Q. Petraea* at the Atlantic–Mediterranean boundary. Trees 28:237–52.

Gouveia C, Trigo R, Beguería S, Vicente-Serrano S. 2017. Drought impacts on vegetation activity in the Mediterranean region: An assessment using remote sensing data and multi-scale drought indicators. Global and Planetary Change 151:15–27.

Hampe A, Petit RJ. 2005. Conserving biodiversity under climate change: The rear edge matters. Ecology Letters 8:461–7.

Hartmann H, Moura CF, Anderegg WRL, Ruehr NK, Salmon Y, Allen CD, Arndt SK, Breshears DD, Davi H, Galbraith D, Ruthrof KX, Wunder J, Adams HD, Bloemen J, Cailleret M, Cobb R, Gessler A, Grams TEE, Jansen S, Kautz M, Lloret F, O’Brien M. 2018. Research frontiers for improving our understanding of drought-induced tree and forest mortality. New Phytologist 218:15–28.

Haylock MR, Hofstra N, Klein Tank AMG, Klok EJ, Jones PD, New M. 2008. A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. Journal of Geophysical Research 113:D20119. <http://dx.doi.org/10.1029/2008JD010201>

Herrero A, Zamora R. 2014. Plant responses to extreme climatic events: A field test of resilience capacity at the southern range edge. PLOS ONE 9:e87842.

Holling CS. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Holmes RL. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43:69–78.

Huang M, Wang X, Keenan TF, Piao S. 2018. Drought timing influences the legacy of tree growth recovery. Global Change Biology 24:3546–59.

Jiménez-Olivencia Y, Porcel L, Caballero A. 2015. Medio siglo en la evolución de los paisajes naturales y agrarios de Sierra Nevada (España). Boletín de la Asociación de Geógrafos Españoles 68:205–32.

Jiménez-Serrano B, Serrano-Gutiérrez J. 2004. El Catastro del Marqués de la Ensenada en el antiguo Reino de Granada.

Jump AS, Cavin L, Hunter PD. 2010. Monitoring and managing responses to climate change at the retreating range edge of forest trees. Journal of Environmental Monitoring 12:1791–8.

Lloret F, Keeling EG, Sala A. 2011. Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120:1909–20. <http://dx.doi.org/10.1111/j.1600-0706.2011.19372.x>

Lloret F, Siscart D, Dalmases C. 2004. Canopy recovery after drought dieback in holm-oak mediterranean forests of catalonia (NE spain). Global Change Biology 10:2092–9. <https://doi.org/10.1111/j.1365-2486.2004.00870.x>

Lorite J, Salazar C, Peñas J, Valle F. 2008. Phytosociological review on the forests of quercus pyrenaica willd. Acta Botanica Gallica 155:219–33.

Martínez-Vilalta J. 2018. The rear window: Structural and functional plasticity in tree responses to climate change inferred from growth rings. Tree Physiology.

Martínez-Vilalta J, Lloret F. 2016. Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics. Global and Planetary Change 144:94–108.

Navarro-González I, Pérez-Luque AJ, Bonet FJ, Zamora R. 2013. The weight of the past: Land-use legacies and recolonization of pine plantations by oak trees. Ecological Applications 23:1267–76.

Nowacki GJ, Abrams MD. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origing oaks. Ecological Monographs 67:225–49. <http://dx.doi.org/10.1890/0012-9615(1997)067[0225:RGACFR]2.0.CO;2>

Olalde M, Herrán A, Espinel S, Goicoechea PG. 2002. White oaks phylogeography in the Iberian Peninsula. Forest Ecology and Management 156:89–102.

Páscoa P, Gouveia C, Russo A, Trigo R. 2017. Drought trends in the Iberian Peninsula over the last 112 years. Advances in Meteorology:ID4653126.

Peña-Gallardo M, Vicente-Serrano SM, Camarero JJ, Gazol A, Sánchez-Salguero R, Domínguez-Castro F, El Kenawy A, Beguería-Portugés S, Gutiérrez E, De Luis M, Sangüesa-Barreda G, Novak K, Rozas V, Tíscar PA, Linares JC, Martínez del Castillo E, Ribas Matamoros M, García-González I, Silla F, Camisón Á, Génova M, Olano JM, Longares LA, Hevia A, Galván JD. 2018. Drought sensitiveness on forest growth in peninsular spain and the balearic islands. Forests. <https://www.mdpi.com/1999-4907/9/9/524>

Peñuelas J, Filella I, Lloret F, Piñol J, Siscart D. 2000. Effects of a severe drought on water and nitrogen use by quercus ilex and phyllyrea latifolia. Biologia Plantarum 43:47–53.

Peñuelas J, Lloret F, Montoya R. 2001. Severe drought effects on mediterranean woody flora in spain. Forest Science 47:214–8.

Peñuelas J, Sardans J, Filella I, Estiarte M, Llusià J, Ogaya R, Carnicer J, Bartrons M, Rivas-Ubach A, Grau O, Peguero G, Margalef O, Pla-Rabés S, Stefanescu C, Asensio D, Preece C, Liu L, Verger A, Barbeta A, Achotegui-Castells A, Gargallo-Garriga A, Sperlich D, Farré-Armengol G, Fernández-Martínez M, Liu D, Zhang C, Urbina I, Camino-Serrano M, Vives-Ingla M, Stocker DB, Balzarolo M, Guerrieri R, Peaucelle M, Marañón-Jiménez S, Bórnez-Mejías K, Mu Z, Descals A, Castellanos A, Terradas J. 2017. Impacts of global change on Mediterranean forests and their services. Forests 8.

Pérez-Luque AJ, Zamora R, Bonet FJ, Pérez-Pérez R. 2015a. Dataset of migrame project (global change, altitudinal range shift and colonization of degraded habitats in Mediterranean mountains). PhytoKeys 56:61–81.

Pérez-Luque A, Pérez-Pérez R, Bonet-García F, Magaña P. 2015b. An ontological system based on modis images to assess ecosystem functioning of natura 2000 habitats: A case study for *Quercus pyrenaica* forests. International Journal of Applied Earth Observation and Geoinformation 37:142–51.

Piovesan G, Biondi F, Filippo AD, Alessandrini A, Maugeri M. 2008. Drought-driven growth reduction in old beech (Fagus sylvatica l.) forests of the central apennines, italy. Global Change Biology 14:1265–81. <http://dx.doi.org/10.1111/j.1365-2486.2008.01570.x>

Reyes-Díez A, Alcaraz-Segura D, Cabello-Piñar J. 2015. Implicaciones del filtrado de calidad del índice de vegetación evi para el seguimiento funcional de ecosistemas. Revista de Teledeteccion 2015:11–29.

Río S del, Herrero L, Penas Á. 2007. Bioclimatic analysis of the *Quercus pyrenaica* forests in Spain. Phytocoenologia 37:541–60.

Rubino D, McCarthy B. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. Dendrochronologia 21:97–115.

Samanta A, Ganguly S, Vermote E, Nemani RR, Myneni RB. 2012. Interpretation of variations in MODIS-measured greenness levels of amazon forests during 2000 to 2009. Environmental Research Letters 7:024018.

Sánchez-Salguero R, Navarro-Cerrillo RM, Swetnam TW, Zavala MA. 2012. Is drought the main decline factor at the rear edge of Europe? The case of southern Iberian pine plantations. Forest Ecology and Management 271:158–69.

Spinoni J, Naumann G, Vogt J, Barbosa P. 2015. European drought climatologies and trends based on a multi-indicator approach. Global and Planetary Change 127:50–7.

Spinoni J, Vogt JV, Naumann G, Barbosa P, Dosio A. 2017. Will drought events become more frequent and severe in Europe? International Journal of Climatology.

Stagge JH, Kingston DG, Tallaksen LM, Hannah DM. 2017. Observed drought indices show increasing divergence across Europe. Scientific Reports 7:14045. <https://doi.org/10.1038/s41598-017-14283-2>

Titos M. 1990. Las minas de la Estrella. In: Titos M, editor. La aventura de Sierra-Nevada 1717-1915. Editorial Universidad de Granada. pp 226–36.

Trigo RM, Añel JA, Barriopedro D, García-Herrera R, Gimeno L, Castillo R, Allen MR, Massey A. 2013. The record Winter drought of 2011-12 in the Iberian Peninsula. In: Peterson MPH T. C., Herring S, editors. Explaining extreme events of 2012 from a climate perspective. Vol. 94. pp S41–5.

Valbuena-Carabaña M, Gil L. 2013. Genetic resilience in a historically profited root sprouting oak (*Quercus pyrenaica* Willd.) at its southern boundary. Tree Genetics & Genomes 9:1129–42.

Valbuena-Carabaña M, Gil L. 2017. Centenary coppicing maintains high levels of genetic diversity in a root resprouting oak (*Quercus pyrenaica* Willd.). Tree Genetics & Genomes 13:28.

Vicente-Serrano SM, Beguería S, López-Moreno JI. 2010. A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. Journal of Climate 23:1696–718.

Vicente-Serrano SM, Camarero JJ, Azorin‐Molina C. 2014a. Diverse responses of forest growth to drought time‐scales in the northern hemisphere. Global Ecology and Biogeography 23:1019–30.

Vicente-Serrano SM, Gouveia C, Camarero JJ, Beguería S, Trigo R, López-Moreno JI, Azorín-Molina C, Pasho E, Lorenzo-Lacruz J, Revuelto J, Morán-Tejeda E, Sanchez-Lorenzo A. 2013. Response of vegetation to drought time-scales across global land biomes. Proc Natl Acad Sci U S A 110:52–7.

Vicente-Serrano SM, López-Moreno JI, Beguería S, Lorenzo-Lacruz J, Sanchez-Lorenzo A, García-Ruiz JM, Azorín-Molina C, Morán-Tejeda E, Revuelto J, Trigo R, Coelho F, Espejo F. 2014b. Evidence of increasing drought severity caused by temperature rise in southern Europe. Environmental Research Letters 9:044001.

Vilà-Cabrera A, Premoli AC, Jump AS. 2019. Refining predictions of population decline at species’ rear edges. Global Change Biology 25:1549–60.

Vivero J, Prados J, Hernández-Bermejo J. 2000. *Quercus pyrenaica* Willd. In: Blanca G, Cabezudo B, Hernández-Bermejo J, Herrera C, Muñoz J, Valdés B, editors. Libro rojo de la flora silvestre amenzada de andalucía. II. Especies vulnerables. Sevilla: Consejería de Medio Ambiente, Junta de Andalucía. pp 303–6.

Wilcox R. 2012. Introduction to robust estimation and hypothesis testing (third edition). Third Edition. Academic Press

Zang C, Biondi F. 2015. Treeclim: An r package for the numerical calibration of proxy-climate relationships. Ecography 38:431–6.

Zhang Y, Peng C, Li W, Fang X, Zhang T, Zhu Q, Chen H, Zhao P. 2013. Monitoring and estimating drought-induced impacts on forest structure, growth, function, and ecosystem services using remote-sensing data: Recent progress and future challenges. Environmental Reviews 21:103–15.