Oak resilience to drought and land-use show how the ecological and geographical rear-edges do not necessarily meet today

### Short title: *Relict oak resilience at the rear-edge*

### Authors[[1]](#footnote-21)

A.J. Pérez-Luque1,2,a; G. Gea-Izquierdo3,b and Zamora, R.1,2,c

1Instituto Interuniversitario de Investigación del Sistema Tierra en Andalucía (CEAMA), Universidad de Granada. Avda. del Mediterráneo s/n, E-18006 Granada, Spain. 2Grupo de Ecología Terrestre, Departamento de Ecología, Facultad de Ciencias, Universidad de Granada, Avda. Fuentenueva s/n, E-18071 Granada, Spain. 3INIA-CIFOR. Ctra. La Coruña km 7.5. E-28040 Madrid, Spain

a [ajperez@ugr.es](mailto:ajperez@ugr.es) b [gea.guillermo@inia.es](mailto:gea.guillermo@inia.es) c [rzamora@ugr.es](mailto:rzamora@ugr.es)

### Manuscript highlights

* *Quercus pyrenaica* rear-edge forests showed high resilience at tree and stand-levels
* The responses to climate and resilience followed a water-stress gradient
* Trees and stand expressed high sensitivity to drought and land-use legacies

## Abstract

* Global change challenges ecosystems in dry locations transformed by intensive human use. Forest resilience to drought of relict Mediterranean *Quercus pyrenaica* Willd. populations in the Southern Iberian Peninsula was analyzed in relation to historical records of land-use using dendroecological growth of adult trees and greenness (EVI) as proxies for secondary and primary growth.
* The growth trends reflected a strong influence of land-use legacies (*e.g.* firewood extraction) in the current forest structure. Trees were highly sensitive to moisture availability and both primary and secondary growth expressed high resilience to drought events in the short- and the long-term. The response to climate and resilience followed a water-stress gradient. Primary and secondary growth were generally less resilient to drought in xeric than in mesic sites, whereas a positive growth trend matching the warming climate since the late 1970s was particularly evident in mesic (*i.e.* colder and more humid) high-elevation stands, but absent in the most xeric site.
* Adult trees of the studied species showed high resilience to drought despite being considered relict and at its rear-edge. Yet, the trees exhibited a variable response to the changing climate along a very short climatic gradient and showed that the ecological and geographical rear-edges do not need to meet today in forests with strong land-uses legacies. Forest resilience including that of regeneration needs to be monitored at xeric locations (*i.e.* the low altitudinal rear-edge) under future expected climatic scenarios bearing in mind that land-use legacies play a key role in stand dynamics.

### Keywords

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

## Introduction

The response of species to changing environments is likely to be determined largely by population responses at range margins (Hampe and Petit 2005). Peripheral populations are usually considered more vulnerable compared with populations occurring at the center of a species’ range (*i.e.* centre-periphery hypothesis) (Sagarin and Gaines 2002; Pironon and others 2016). It has been assumed that rear-edge populations have a concordance between geographical and ecological marginality, with lower performance and thus higher risk of extinction than those populations at the core of the species’ range (Pironon and others 2016; Vilà-Cabrera and others 2019). Nonetheless, recent reviews found species- and population- specific responses highlight that this hypothesis not always fulfill (Sexton and others 2009; Abeli and others 2014). In this respect, to fully understand changes in distribution and abundance of species as a consequence of global change we need to know in which environmental conditions geographical marginallity does not correspond with ecological marginallity (Vilà-Cabrera and Jump 2019).

Climate change is expected to cause important changes in the distribution and abundance of plant communities, and there are already obvious signs of processes associated with increased intensity and duration of droughts (Allen and others 2010). In this respect, several studies have warned on the rapid extinction of plant species in the near future, especially in mountain areas of southern Europe (*e.g.* Engler and others 2011). Under this climatic change context, it is reasonable to expect that population loss and range retractions should be seen in the most low-latitude, drought-prone areas of a species’ distribution, *i.e.* the rear edge (Hampe and Petit 2005).

Assessment of drought impacts on forest ecosystems has gained much attention in last decades (Allen and others 2010), and the functional response of vegetation to drought has been analyzed at global and local scales (*e.g.*, Vicente-Serrano and others 2013; Martínez-Vilalta and Lloret 2016). 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 2014; Stagge and others 2017). This is especially critical, since climate change projections for the Mediterranean area forecast that climate extreme events will become more frequent and severe (Spinoni 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 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 considered to be located in the rear-edge (either latitudinal or altitudinal along climatic gradients) of their distribution, where climatic conditions mark the species-limits and the populations are likely to be more sensitive to small variations on climate and the microtopography (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). Yet it is crucial to accurately characterize the rear-edge of species. This can be particularly misleading in ecosystems with strong land-use legacies because it is established from current species distribution (Vilà-Cabrera and others 2019). Furthermore, it becomes even more important for relict populations driven by historical land-uses if they harbour high levels of intraspecific genetic diversity (Valbuena-Carabaña and Gil 2013).

Many studies have analyzed the effects of drought on tree species which southernmost limit of their distribution is encountered in the Mediterranean (Sánchez-Salguero and others 2012; Dorado-Liñán and others 2017b), and some focused on the resilience to drought of rear-edge populations (Herrero and Zamora 2014). Resilience is the capacity of an ecosystem, community or individual to recover its 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 provide valuable ecosystem services.

Understanding the vegetation response to drought requires of integrative and multidisciplinary strategies to assess the impacts of disturbances on forest at several scales (Hartmann and others 2018). The resilience to drought of species is better assessed when several approaches like dendrocronology and remote sensing are combined simultaneously. Dendroecological estimates of growth (*i.e.* tree-ring width) are a widely used proxy to study tree vitality 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). Remote sensing can be used for studying droughts impacts on ecosystems, hence the stand level (*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 as drought. The combination of both approaches (remote sensing and dendroecology), has been used to assess the effects of droughts on vegetation along ecological 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). Several works assessed vegetation responses in term of resistance and resilience to drought events highlighting a stronger response 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, it is crucial to know if the responses at the tree level differ from responses at the ecosystem level and characterize the spatial variability of this response in rear-edge populations.

We used remote sensing information and dendroecological methods to evaluate the impact of drought in both canopy greenness (as a proxy to primary growth) and tree-radial growth (as a proxy to secondary growth) of *Quercus pyrenaica* Willd. (*melojo oak*) on southern relict forests at the rear-edge of the species distribution and where species performance is considered to be severely threatened by climate change. We also assessed the resilience of these forests both to several extreme drought episodes and to climate change (*i.e.* warming) in the long-term in the last decades. Our main hypothesis is that these relict populations driven by historical land-use are particularly vulnerable to climate change at their present climatic (either altitudinal or latitudinal) rear-edge, and will show low resilience after extreme drought particularly at the dry edge along climatic gradients at the small scale within the rear-edge. To address this hypothesis our specific aims were: (*i*) To quantify how recent extreme drought events influenced primary and secondary growth of *Q. pyrenaica* forests in its 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 (*i.e.* xeric *vs.* mesic) within the rear edge to detect vulnerability to climate change along climatic gradients at the small spatial scale. To achieve goal (*iii*) and characterize variability in the forest response to drought within the rear-edge we assessed whether the effect of aspect and environmental conditions expressed in northern and southern populations of *melojo* oak forests differ in their resistance, resilience and recovery to extreme drought events.

## Materials and methods

### Tree species and study site

*Quercus pyrenaica* Willd. (*melojo* oak) 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* is a deciduous species that requires over 650 mm of annual precipitation and some summer precipitation. It is a submediterranean species, hence with lower drought tolerance than genuine evergreen Mediterranean taxa (Río and others 2007).

The forests of this species reach their southernmost European limit in mountains from Southern Andalusia like Sierra Nevada (37°N, 3°W), a high-mountain range with elevations between 860 and 3482 m *a.s.l.*. The climate is Mediterranean, characterized by cold winters and hot summers, with pronounced summer drought but with marked variability set by altitude. Sierra Nevada is considered a glacial refugia for deciduous *Quercus* species (Olalde and others 2002). There are eight melojo 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. Today, *Q. pyrenaica* woodlands in this mountain region represent a rear edge of their habitat distribution (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 relict forests undergone intensive anthropic use in history (Camacho-Olmedo and others 2002). Furthermore, conservation status of this species for southern Spain is considered “Vulnerable” and it is expected to suffer the impact of climate change, reducing its suitable habitats in the rear-edge (Gea-Izquierdo and others 2013).

### Drought episodes

The Iberian Peninsula suffered several extreme drought episodes in the last three decades (*e.g*. 1994-1995, 1999, 2005, 2012) (Vicente-Serrano and others 2014). The 2005 and 2012 drought events have been documented among the worst droughts in the last decades for the southern Iberian Peninsula (Páscoa and others 2017) and they were characterized as extreme drought in our climatic data (Figure S1; Table S3). We focused on these two drought events because they were included in the period where there is availability of high-spatial resolution of 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 to 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 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 that threshold for at least two consecutive months. For each drought event we computed: the *duration*, *i.e.* number of consecutive months with the SPEI lower than a certain threshold; the *severity* as 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 to assess ecosystem resilience

Vegetation greenness of *Q. pyrenaica* was characterized by means of the *Enhanced Vegetation Index* (EVI), derived from MOD13Q1 product of the MODIS sensor. EVI data consists of 16-day maximum value composite images (23 per year) of the EVI value with a spatial resolution of 250 m x 250 m. MODIS EVI data were obtained for the period 2000 - 2016. 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).

Annual mean EVI () as a surrogate of mean annual primary production was computed for each pixel for the period 2000 - 2016. The EVI standardized anomaly () was computed pixel-by-pixel, to minimize bias in the evaluation of anomalies and provide more information about the magnitude of 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 to assess tree individual resilience

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 the northern aspect; and Cáñar (CA), a more humid site located at the southern aspect (Figure 1; Table 1). For the southern site two elevations were sampled: CA-Low and CA-High, which constitute the current altitudinal rear-edge (CA-Low) and tree-line (CA-High), respectively in the sampled aspect. Sampling sites followed a moisture gradient: SJ < CA-Low < Ca-High (Table 1). All the sites were oak monospecific and representative of the population clusters identified for the species in this mountain range (Pérez-Luque and others 2015b). 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 affecting 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 as (see Gea-Izquierdo and Cañellas 2009 for more details). 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 for significance.

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 verified using COFECHA (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 (Fritts 1976). 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 (Piovesan and others 2008) using 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 series was calculated. Then, mean site BAI chronologies were obtained by averaging individual tree BAI time series.

### 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. SPEI index with a temporal scale of 6 months was used to characterize the drought conditions for the period 1961-2014. Relationships between RWI and BAI site chronologies and climatic variables were assessed using bootstrapped Pearson’s correlations estimated using treeclim (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, drought induced neighbor mortality) in the past. 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 the preceding 10-year median and is the subsequent 10-year median.

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 (*e.g.* Gea-Izquierdo and Cañellas 2014). In addition, the forest and management history of our sampling sites was inferred from a detailed analysis of historical land-use changes. For this purpose, an exhaustive review of existing abundant historical documents was done to compile information about socio-economical activities affecting the studied forests (Table S4).

### Assessing ecosystem and tree individual resilience to drought

To evaluate the effects of drought events on ecosystem resilience (using greenness data) and tree individual resilience (using BAI data) we used resilience indices proposed by Lloret and others (2011). The Resistance index estimated as the ratio between 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. 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 S3b) 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 with drought severity (Table S3).

### Statistical analysis

For each of the three resilience indices studied we used robust two-way ANOVAs 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 bootstrapped 3000 times and trimmed automatically to control the potential influence of outliers. Post-hoc differences were assessed pairwise using a similar bootstrap 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 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 the northern (dry) population (Figure 2a). A “browning” episode () was observed during this drought event, whereas no changes in greenness were observed in response to the 2012 drought (Figure 2b).

### 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 and despite competition measured as plot basal area was greatest in CA-High (Table 1, Figure 3). Growth and height of trees from the northern and the low-elevation southern population were similar (Figures 3 and S3a). Only trees from the southern sites showed significant positive growth trends since the late 1970s (Figure 3), being much more pronounced for the high-elevation, hence more humid, site (CA-High).

Drought events reduced radial growth for all sites (Figure S2a), being particularly evident the negative effect of the 1995 drought (the worst drought spell in our climatic record, Table S3), when the greatest growth reduction was recorded for all chronologies. Tree-growth reduction followed a moisture-gradient. 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 S2a), being the weakest for the wettest site (Figure 3).

The northern site (SJ) showed two major release events (GC > 50 % occurring in more than 50 % of sampled trees): the first during the 1940s (the most evident) and the second in 1995-2000 (Figure 4). These periods alternated with periods of suppression. In contrast, 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

*Rs* and *Rt* varied in the same direction whereas *Rc* varied inversely to *Rs* and *Rt*. Resilience metrics of tree-growth for drought events since 1950 (*i.e.* shared period among the three chronologies excluding the juvenile years, Table S3) revealed a positive relationship between drought severity and *Rc*, significant for all oak populations (Figure 5). A similar pattern was obtained for *Rs* but only significant for SJ site. Importantly, non-significant patterns were obtained if we excluded 1995, except for *Rc* in SJ (Figure S5). The trees showed the highest value of tree-growth resilience for 1995, the worst drought event in our study area, particularly SJ where our results suggest a major release event also after 1995 (Figure 4).

During the last two drought events, resilience metrics for greenness and tree-growth were significantly different between drought events (Table 3). The 2005 drought event reduced greenness and growth more than that of 2012 (Tables S1-S2) but the metrics of resilience generally covaried in the same direction those two years. We obtained significantly higher resilience and resistance values for 2012, the most severe event, than for 2005 in both variables (Tables S1-S2; Figure 6). Thus, recovery values for greenness were higher for 2005 than for the 2012 drought event (Table S1, Figure 6). Recovery showed a contrasting pattern for EVI and tree-growth.

The resilience metrics calculated significantly varied between sites, except for resilience of tree-growth (p = 0.534; Table 3), which was similar among the three sites. The two southern populations showed lower values for recovery than the northern site both for greenness and tree-growth but resistance and resilience values were significantly higher for the southern site (Tables S1-S2).

### Tree-growth response to climate

The response of tree-growth to water availability was greater than that to temperatures, as it can be expected for a Mediterranean site and particularly a species located closer to its xeric/dry distribution limit (rear-edge). Cumulative precipitation of the hydrological year and seasonal SPEI values (*i.e.* for the Hydrological year, Spring and Summer) were the climatic variables exhibiting the highest (positive) relationship with growth for all populations (Figure 7a). Yet there were some differences between northern and southern populations: the positive relationship with SPEI was highest in the northern population (r > 0.6 *vs.* r < 0.5; Figure 7a). In addition, spring maximum temperature was the most significant limitation for tree-growth only for the southern populations (Figure 7b and 7c), whereas minimum and maximum temperatures of current September positively influenced tree-growth only in the northern population.

## Discussion

### Land-use legacies shape sensitivity to climate change of forests and the present rear-edge

The Mediterranean landscapes have suffered a strong transformation driven by human activities throughout history even at high elevations (García-Alix and others 2017). The review of historical documents shows how forest clearings, firewood extraction, charcoal exploitations and mining have strongly impacted the forests at Sierra Nevada (Table S4) where in addition it has been estimated a historical loss of about 90% of broadleaf *Quercus* species cover from medium and low elevations (Jiménez-Olivencia and others 2015). Therefore, it seems logic to think that the geographical limit of the current rear-edge and relict stands of the deciduous oak studied does not necessarily match the potential distribution limit related to edaphoclimatic constraints (*i.e.* the ecological rear-edge). Together with the analysis of the disturbance chronologies, the observed strong differences in stand structures, tree size and age suggest different forest history and a different management origin (*i.e.* land-use legacy) between northern (coppice) and southern populations (high forest, open woodland). It has been described a sequential distribution of historical land uses along the elevational gradient in the northern slopes of Sierra Nevada (*e.g.* SJ site): grasslands and shrublands for cattle farming were located at the highest elevations; then forest stands with some croplands; and at the lowest elevations, irrigated terraces with tree crops (Jiménez-Olivencia and others 2015). In addition, other activities like mining should have modified the forest structure at that northern location where there is with a high concentration of mines and quarries that were exploited intermittently throughout history. On the other hand, woodlands in the southern slopes (*e.g.* CA site) were mixed with a greater percentage of croplands along the elevational gradient where oaks occur (Jiménez-Olivencia and others 2015). Firewood, charcoal extraction and acorns have been resources intensively exploited in southern sites, until at least the middle of the 20th century when these activities sharply decreased mainly due to rural abandonment and use of gas and fossil fuels (Valbuena-Carabaña and Gil 2013).

Some of the previous historical records of land-use were likely expressed by the growth chronologies. The release event in 1940s in the northern site concurs with one period of maximum mining activity in this area (1925 to 1957) (Table S4), with an increase on the use of timbers for the mine tunnels and furnaces that additionally required great quantities of fuelwood to melt the mineral. This heavily exploitation of the neighbouring forest resources should have affected a major part of this oak woodland as shown by growth of the remnant trees included in the northern site (Figure S2b). The other release event observed for SJ site during 1995-2000 was lower than that occurred at 1940, but also affected most trees (Figures 4, S2b). There are no records of forest practices carried out in this area in the last 30 years (Bonet and others 2016) and no record for any logging during 1995 - 2000 period (F.J. Cano-Manuel *personal communications*). Therefore this release might be related with a natural drought-induced mortality event after 1995 as has been reported for other Mediterranean tree species after severe drought (*e.g.* Peñuelas and others 2001; Lloret and others 2004). On the other hand, the strong positive correlations of SPEI with tree-growth for this site show a high sensitivity to water availability (Gea-Izquierdo and Cañellas 2014). For southern sites, the only positive release event showed at the earliest years for CA-High site could be related with conversion from closed forest to an open silvopastoral system, a common management applied in the past in Iberian oak woodlands (Cañellas and others 2004; Gea-Izquierdo and others 2011) and which has been documented for this site (Valbuena-Carabaña and Gil 2013). In this site we observed an increase in growth especially in high elevation trees, where moisture is less limiting, a pattern which concurs with a forest expansion into marginal abandonded croplads and an increase in tree-cover (Camacho-Olmedo and others 2002).

### Relict oaks show high resilience to recent drought events and long-term climatic variability

Severe drought negatively affects both primary and secondary growth of *Q. pyrenaica* forests. This was expressed by the observed reduction in greenness and tree-growth in response to the 2005 and 2012 drought events, and the consistent radial growth suppression for this oak species during extreme drought events (Corcuera and others 2006; Gea-Izquierdo and Cañellas 2014). Furthermore, the greatest reduction of tree-growth was observed during the 1995 drought, a characteristic precipitation negative anomaly that caused severe and extensive damage to the Mediterranean vegetation across the Iberian Peninsula (Peñuelas and others 2001; Gazol and others 2018). Despite the severe drought events suffered in the last decades (Table S3), we found a positive trend for vegetation greenness of *Q. pyrenaica* for the last 16 years, which is consistent with previous findings stressing a recent short-term increase in primary productivity for these forests coinciding with a rather humid decade in the 2000s after a dry decade in the 1990s (Pérez-Luque and others 2015a). For tree-growth, we also observed positive trends in the last decade, particularly for the southern high-elevation site (CA-High, Figure 4). Similar long-term trends were described for this species along its distribution range only at high elevation sites (Gea-Izquierdo and Cañellas 2014), which could be related to a non-linear positive effect of warming at species-wise cold limited high elevation sites (Salzer and others 2009; Gea-Izquierdo and Cañellas 2014). Importantly, for rear-edges where climate change is a threat we would have expected negative growth trends as shown for temperate and Mediterranean species (Sánchez-Salguero and others 2012; Camarero and others 2015b; Dorado-Liñán and others 2017a). Therefore there is much small-scale variability in the response to climate within the rear-edge we had “a priori” considered in our study, where we even observed positive effects of climate change in certain stands. This suggests that the rear-edge needs to be redefined in consequence (Vilà-Cabrera and others 2019), partly because of land-use legacies and their effect on the possible mismatch between the current distribution of species (*i.e.* determining the “available” geographical rear-edge) and the potential ecological (limiting) rear-edge of species.

Despite that 2012 drought event was more severe and intense than that in 2005 (Table S3), resilience values for greenness and tree-growth were greater for 2012. This could be explained by the different timing of the two droughts. The 2012 drought was a winter drought (Trigo and others 2013) occurring earlier than the shorter 2005 drought. The latter matched the period of maximum growth for oak forests in late spring (Figure S4). This highlights the importance of the timing of drought as a key factor determining the tree recovery after drought (Camarero and others 2015a; Huang and others 2018). For tree-growth, the highest values of resilience were obtained for the two most severe events (1995 and 1999)(Table S3) and we observed a positive relationship between the tree-growth resilience and drought severity (Figure 5). This result seems to contradict our initial hypothesis in which we predicted low resilience values for this oak species in their rear-edge after extreme drought events. Yet, the high resilience values obtained for the 1995 drought in the most xeric site (SJ) could be related with drought-induced mortality (F.J. Navarro *personal communications*), which would show the influence of stand dynamics partly shadowing interpretation of tree resilience estimated from individual growth series.

Rear-edge populations live in environmental narrow margins, and small variations in environmental conditions can increase the vulnerability of species (Hampe and Petit 2005). A high vulnerability to drought is often assumed for populations 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. Our findings are in agreement 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 local adaptation and plasticity, and also of local environmental factors on the vulnerability showed by rear-edge populations. Our results would highlight the ample small-scale variability at the ecological boundary and need to better confine the rear-edge limit in our studied forest. 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 (Valbuena-Carabaña and Gil 2013, 2017) seem to be indicative of high local adaptation of this oak. In addition the local environmental conditions of the sites where this species inhabits at Sierra Nevada would explain the low vulnerability to drought showed by this oak. All this, together with the characteristic resprouting ability of the species from its stoloniferous root system, would suggest a long-term persistence of those populations. It needs to be mentioned that we only studied adult individuals established decades or centuries ago, meaning that it needs to be assessed if the species expresses resilience or to the contrary vulnerability if we analyzed seedling regeneration, likewise many other Mediterranean species at their xeric limit (2-3 CITAS). 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; Vilà-Cabrera and others 2019). In this sense, the high values of resilience observed, could suggest that the populations of *Q. pyrenaica* in Sierra Nevada are located in a geographical but not a climatic rear-edge. And the current niche is a result of land-use changes, which further complicates the definition of potential rear-edges. Similarly, high values of resilience showed by other Mediterranean species located in their rear-edge (*e.g.* *Pinus sylvestris*, Herrero and Zamora 2014) seem to be related with stabilizing mechanisms promoting community resilience that can buffer the impacts of extreme events.

### Small-scale environmental variability shapes sensitivity to climate of trees within the rear-edge

Since spatio temporal patterns of tree-ring measurement and earth observations (*i.e.* EVI) reflects processes at different spatio-temporal scales (Gea-Izquierdo and others 2015; Babst and others 2018) a combined analysis as in our study allows to better disentangle the small and large-scale variability in growth induced by climate from that driven by community-level ecological processes (Babst and others 2017). Greenness exhibited a lower sensitivity to drought than tree-growth, particularly for drier sites. These findings are in accordance with previously works showing that tree-growth is a more sensitive metric of forest resilience than net primary productivity (*e.g.* Babst and others 2013; Coulthard and others 2017; Gazol and others 2018) and would suggest that the growth reduction could more mediated by sink that by source limitations (Körner 2013; Fatichi and others 2014). On the other hand, tree-ring records allow to complement remote sensing data in a longer time scale, by reflecting climate or disturbance induced tree-growth anomalies over decades to centuries (Babst and others 2017) and provide an accurate measure of growth responses to droughts (Bhuyan and others 2017; Gazol and others 2018).

Greenness and tree-growth were more affected by drought events in drier northern populations than in more humid southern oak populations, *e.g.* the northern site showed higher browning intensity than the southern sites during the 2005 drought event and the stronger correlations of tree-growth with SPEI (Hydrological and summer) in the northern site can be interpreted as higher sensitivity to drought in drier sites (Gea-Izquierdo and Cañellas 2014). Similar to many other forest species under Mediterranean climates, moisture availability is generally the most limiting factor driving radial growth of *Q. pyrenaica* along their distribution range in the Iberian Peninsula (Gea-Izquierdo and Cañellas 2014). Thus, our results are consistent with previous studies highlighting the influence of precipitation on tree-ring growth in different oak species (*e.g.* Di Filippo and others 2010; Gea-Izquierdo and others 2011; García-González and Souto-Herrero 2017).

Higher elevations within warm and dry ecosystems can help species alleviate climatic stress and increase resistance to drought and stands of several tree-species located at higher elevations were less drought sensitive. Thus high-elevations are generally considered as potential local refuge for species in response to climate change (Bhuyan and others 2017). It is well known that tree growth and tree responses to drought are site-dependent (*e.g.* soil features, tree competence, etc.) (Babst and others 2013), particularly for rear-edge populations (Cavin and Jump 2017; Dorado-Liñán and others 2017b). Trees at CA-High sowhed higher BAI than those located at lower-elevations (CA-Low and SJ) (Figure 4). This shows the high variability in the response to climate exhibited in a small gradient, which is especially interesting for southern sites, which are very close to each other, and overall both constitute the rear-edge for the species. The higher values of tree growth in taller trees that we observed in CA-High site strongly suggests lower water stress at high-elevation sites (as shown by soil analyses along an elevational gradient in this location Cobo-Díaz and others 2017). Furthermore, as mentioned, the recent growth increase only at the most humid locations a likely concomitant positive effect of a warming climate (Gea-Izquierdo and Cañellas 2014). Finally and in a context of global change, in addition to withstanding lower water stress, it is likely that the less accessible sites at higher elevations would suffer 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). Overall, our results show how management history conditions tree-growth and resilience to climate change of tree species, highlighting the importance of land-use legacies in Mediterranean forests (Navarro-González and others 2013; Doblas-Miranda and others 2017) which, hence, will also strongly determine the current geographical distribution of marginal stands, regardless of the potential extent of ecological marginality of species.

## Conclusions

The ecological and geographical read-edges did not seem to fully match in our study. Severe drought events provoke important reductions in primary and secondary growth of *Q. pyrenaica* forests in the studied relict, rear-edge forest. However, we observed no negative growth trends despite we had expected vulnerability to climate change for these relict stands. Furthermore, we observed positive trends for primary growth (*i.e.* greenness) at the ecosystem scale and a positive steep trend of secondary growth at the tree level at the most humid site along the climatic gradient analyzed. The trees exhibited high resilience values in response to drought, particularly in the long-term scale, and resilience was directly related to drought severity. These results would be consistent with other research showing that this mountain region is still acting as a refuge for deciduous species, including *Quercus*. The differences observed in tree-growth and resilience to drought between very close sites show that responses to drought were site-dependent and can vary in very small gradients (*i.e.* following ecological thresholds). This is particularly relevant for rear-edge populations where topographic and biophysical variability facilitates the existence of microrefugia. The analysis of tree-growth dynamics revealed suppression and release events that were 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 a high sensitivity to climate change, such us *Q. pyrenaica*, not only for conservation per se of the species, but for all ecosystem services that these singular forests offer at Mediterranean mountain. Following our study it is necessary to further 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. Since we only studied resilience of already established adult trees, monitoring should be enlarged to analyze overall species resilience including that of seedling regeneration. Our results show how management history conditions tree-growth and resilience to climate of tree species. They highlight the importance of land-use legacies and how they affect the current geographical distribution of marginal stands, which therefore can be partly disconnected from actual ecologically marginal conditions.

## Acknowledgements

We would like to thank to Sammy L. Behle, F.J. Bonet and M. Suárez-Muñoz for field assistance. 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 are grateful for the comments made by F.J. Bonet in an earlier version of the manuscript. AJPL wants to thank the invaluable support received from his family over the years. This research work was conducted in the collaborative framework of the “Sierra Nevada Global Change Observatory” 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* (No 641762), for their funding support.

## References

Abeli T, Gentili R, Mondoni A, Orsenigo S, Rossi G. 2014. Effects of marginality on plant population performance. Burns KC, editor. Journal of Biogeography 41:239–49. <https://doi.org/10.1111/jbi.12215>

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.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH (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, Bodesheim P, Charney N, Friend AD, Girardin MP, Klesse S, Moore DJP, Seftigen K, Björklund J, Bouriaud O, Dawson A, DeRose RJ, Dietze MC, Eckes AH, Enquist B, Frank DC, Mahecha MD, Poulter B, Record S, Trouet V, Turton RH, Zhang Z, Evans MEK. 2018. When tree rings go global: Challenges and opportunities for retro- and prospective insight. Quaternary Science Reviews 197:1–20.

Babst F, Poulter B, Bodesheim P, Mahecha M, C Frank D. 2017. Improved tree-ring archives will support earth-system science. Nature Ecology and Evolution 1:1–2.

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.

Bonet FJ, Aspizua R, Navarro J. 2016. History of Sierra Nevada forest management: Implications for adaptation to global change. In: Zamora R, Pérez-Luque AJ, Bonet FJ, Barea-Azcón JM, 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.

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

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.

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.

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.

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.

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.

Di Filippo A, Alessandrini A, Biondi F, Blasi S, Portoghesi L, Piovesan G. 2010. Climate change and oak growth decline: Dendroecology and stand productivity of a Turkey oak (Quercus cerris L.) Old stored coppice in Central Italy. Annals of Forest Science 67:706–6. <https://doi.org/10.1051/forest/2010031>

Doblas-Miranda E, Alonso R, Arnan X, Bermejo V, Brotons L, Heras J de las, Estiarte M, Hódar JA, Llorens P, Lloret F, López-Serrano FR, 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.

Engler R, Randin CF, Thuiller W, Dullinger S, Zimmermann NE, Araújo MB, Pearman PB, Lay GL, Piedallu C, Albert CH, Choler P, Coldea G, Lamo XD, Dirnböck T, Gégout J-C, Gómez-García D, Grytnes J-A, Heegaard E, Høistad F, Nogués-Bravo D, Normand S, PuşcaŞ M, Sebastià M-T, Stanisci A, Theurillat J-P, Trivedi MR, Vittoz P, Guisan A. 2011. 21st century climate change threatens mountain flora unequally across europe. Global Change Biology 17:2330–41. <https://doi.org/10.1111/j.1365-2486.2010.02393.x>

Fatichi S, Leuzinger S, Körner C. 2014. Moving beyond photosynthesis: From carbon source to sink-driven vegetation modeling. New Phytologist 201:1086–95.

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.

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. 2009. Analysis of Holm Oak Intraspecific Competition Using Gamma Regression. Forest science 55:310–22.

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.

Gea-Izquierdo G, Cherubini P, Cañellas I. 2011. Tree-rings reflect the impact of climate change on quercus ilex l. Along a temperature gradient in spain over the last 100 years. Forest Ecology and Management 262:1807–16. <https://doi.org/10.1016/j.foreco.2011.07.025>

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.

Gea-Izquierdo G, Guibal F, Joffre R, Ourcival JM, Simioni G, Guiot J. 2015. Modelling the climatic drivers determining photosynthesis and carbon allocation in evergreen mediterranean forests using multiproxy long time series. Biogeosciences 12:3695–712.

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.

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.

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.

Körner C. 2013. Growth controls photosynthesis Mostly. Nova Acta Leopoldina 114:273–83.

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.

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.

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 38:155–8.

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.

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.

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

Pérez-Luque AJ, Pérez-Pérez R, Bonet-García FJ, Magaña PJ. 2015a. 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.

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

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.

Pironon S, Papuga G, Villellas J, Angert AL, Garcı́a MB, Thompson JD. 2016. Geographic variation in genetic and demographic performance: New insights from an old biogeographical paradigm. Biological Reviews 92:1877–909. <https://doi.org/10.1111/brv.12313>

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.

Sagarin RD, Gaines SD. 2002. The abundant centre distribution: To what extent is it a biogeographical rule? Ecology Letters 5:137–47. <https://doi.org/10.1046/j.1461-0248.2002.00297.x>

Salzer MW, Hughes MK, Bunn AG, Kipfmueller KF. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. Proceedings of the National Academy of Sciences 106:20348–53.

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.

Sexton JP, McIntyre PJ, Angert AL, Rice KJ. 2009. Evolution and ecology of species range limits. Annual Review of Ecology, Evolution, and Systematics 40:415–36.

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.

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, 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. 2014. Evidence of increasing drought severity caused by temperature rise in southern Europe. Environmental Research Letters 9:044001.

Vilà-Cabrera A, Jump AS. 2019. Greater growth stability of trees in marginal habitats suggests a patchy pattern of population loss and retention in response to increased drought at the rear edge: Tree growth responses at the rear edge. Ecology Letters 22:1439–48.

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

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.

1. Author Contributions. AJPL, GGI and RZ conceived the study, conducted field work and collected the data. AJPL and GGI conducted lab work. AJPL analyzed data and led the writing of the paper. GGI and RZ contributed in the writing process. All authors contributed to the drafts and gave final approval for publication. [↑](#footnote-ref-21)