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*

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### Manuscript highlights

* *Quercus pyrenaica* rear-edge forests showed high resilience at tree and stand-levels
* The growth response 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 but 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 mesic than in xeric 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 oak trees showed high resilience to drought despite being considered relict and at its rear-edge. 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 of the species under future expected climatic scenarios bearing in mind that ecological boundaries for species distribution can be narrow and that land-use legacies can 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 largely determined 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 marginality does not correspond with ecological marginality (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 fact, 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). Under this climatic change context, it is reasonable to expect that population loss and range retractions in boreal, temperate and Mediterranean species should be seen in the lowest latitudes, altitudes and drought-prone areas of a species’ distribution, *i.e.* the rear edge (Hampe and Petit 2005). 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 species to predicted climatic changes (Jump and others 2010). Yet it is crucial to accurately characterize the ecological 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).

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 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. 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). 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 (*e.g.* Gazol and others 2018; Peña-Gallardo 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.

In this study 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 current geographical 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* 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 up to 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 ha) 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 near future (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 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 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 their magnitude (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 (around 1700 m) and CA-High (around 1860 m), which constitute the current low altitudinal limit (CA-Low) and the tree-line (CA-High), respectively in the sampled aspect. Despite the proximity of these two elevations (less than 200 m difference in altitude) the stands greatly differ in their structure and characteristics (Table 1). The three 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 in CA or the open canopy in 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 (EPS). 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 (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 (*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 historical documents was done to compile information about socio-economical activities affecting the studied forests (Table S4). We reviewd several documentary sources: historical documents and maps; detailed mining reports; official information about recent wildfires events and forest management practices; livestock farming; traditional irrigation ditches and other studies concerning the socioeconomic dynamics of forest of Sierra Nevada at different scales (see Table S4 for references).

### 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). Resilience metrics for BAI data were additionally computed for the most severe drought events since 1940 (*n* = 8; Table S3) and compared with drought severity.

### 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 (*i.e.* the more humid aspect) showed significant positive growth trends since the late 1970s (Figure 3), being much more pronounced for the high-elevation, hence more humid and colder, 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 growth reductions in trees from 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. 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. 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 more xeric 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

By using a combined approach of remote sensing information and dendrocronology we have quantified the drought impacts on melojo oak forests on Sierra Nevada and its resilience to several severe drought events in the last decades. Our results clearly indicated that these relict oak populations driven by historical land-use are resilient to climate change at their present (either altitudinal or latitudinal) rear-edge. However, resistance, resilience and forest recovery to extreme drought events are strongly influenced by mountain aspect, local environmental conditions, and management legacies.

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

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). 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). In the northern slopes of Sierra Nevada (*e.g.* SJ site), land uses have been historically distributed along an altitudinal gradient: grasslands and shrublands for cattle farming at the highest elevations; then forest stands with some croplands; and irrigated terraces with tree crops at the lowest elevations (Jiménez-Olivencia and others 2015). In addition, other activities like mining should have modified the forest structure, *e.g.* SJ site contains a high concentration of small mines an quarries that were exploited intermittently throughout history. The release growth event observed in 1940s concurs with a period of maximum mining activity in this area (1925 to 1957) (Table S4), during wich there was an increase in the use of timbers for mine tunnels and furnaces, that also required large amounts of fuelwood to melt the mineral. This heavily exploitation of the neighbouring forest resources should have affected a significant part of this oak woodland as shown by growth of the remnant trees included in the northern site (Figure S2b). 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). For CA-High site, the only positive release event showed at the earliest years 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).

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). No records of forest practices carried out in this area in the last 30 years were found (Bonet and others 2016), and no logging was recorded during 1995 - 2000 (F.J. Cano-Manuel *personal communications*). Therefore this release might be related to natural drought-induced mortality 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).

### Relict oaks sensitivity (resistance) to recent drought events

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). 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.* Tessier and others 1994; Di Filippo and others 2010; Gea-Izquierdo and others 2011; García-González and Souto-Herrero 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; Peña-Gallardo 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). The use of 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).

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

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). It is well known that tree growth and tree responses to drought are site-dependent (*e.g.* soil features, tree competition, 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 are considered to constitute the rear-edge for the species.

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

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 humid and cold 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 some temperate and Mediterranean species (Sánchez-Salguero and others 2012; Camarero and others 2015b; Dorado-Liñán and others 2017a).

Albeit 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).

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. Our findings are in agreement with those studies that have shown that the assumed higher vulnerability of dry edges does not necessarily hold (*e.g.* 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 shown 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. All this, together with the characteristic high resprouting ability of the species, would suggest a long-term persistence of those populations (Bellingham and Sparrow 2000). 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 trees express resilience at the species level or to there is vulnerability if we analyzed seedling regeneration, likewise other Mediterranean species at their xeric limit (Castro and others 2004; Vilà-Cabrera and others 2011; Gea-Izquierdo and others 2015).

Summarizing, two mains results stand out from this research. First, the high values of resilience observed in our study suggest that the populations of *Q. pyrenaica* in Sierra Nevada are located in a geographical but not a climatic, ecological rear-edge (*sensu* Martínez-Vilalta 2018; Vilà-Cabrera and others 2019). The current niche is a result of land-use changes, which further complicates the definition of potential rear-edges. The high resilience values observed could be also related with stabilizing mechanisms promoting community resilience that can buffer the impacts of extreme events, as it has been described for other species (*e.g.* *Pinus sylvestris*, Herrero and Zamora 2014).

Second, these resilience responses of oak forest to drought events are not spatially homogeneous around all mountain range, due to differences in ecological conditions and/or past management legacies. In fact, there was much small-scale variability in the response to climate within the rear-edge that we had “a priori” considered in our study. Furthermore we even observed positive effects of climate change in certain stands, as discussed, and which would be in disagreement with our hypothesis expecting oak vulnerability in the studied geographical rear-edge. 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 ecological (limiting) rear-edge of species.

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 spatial 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. Following our study it is necessary to disentangle how forest resistance and resilience are affected by the combination of climate change and land-use legacies in highly transformed landscapes such us Mediterranean mountain ecosystems.

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