



**Land-use legacies and high oak resilience to drought show
how the ecological and geographical rear edges do not
necessarily meet today**

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Land-use legacies and high oak resilience to drought 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
- Resilience and growth response to climate 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 employing

1 Author Contributions. AJPL, GGI and RZ conceived of the study, conducted field work, and collected the data. AJPL and GGI performed the 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.

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 removal) in the current forest structure. Trees were highly sensitive to moisture availability but both primary and secondary growth expressed high resilience to drought events over the short and the long term. Resilience and response to climate 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 wetter) high-elevation stands, but absent in the most xeric (*i.e.* warmer and drier) site.
- Adult oak trees showed high resilience to drought despite being considered relict and at its rear edge. The trees varied in response to the changing climate along a narrow climatic gradient and showed that the ecological and geographical rear edges do not need to meet today in forests with strong land use legacies. Forest resilience including that of regeneration needs to be monitored at xeric of the species under future expected climatic scenarios given 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, dendrochronology, 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.* center-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, higher vulnerability, and thus higher risk of extinction than do populations at the core of the species' range (Pironon and others 2016; Vilà-Cabrera and others 2019). Nonetheless, recent reviews report that species- and population-specific responses do not always support this hypothesis (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 determine under what environmental conditions geographical marginality does not correspond with ecological marginality (Vilà-Cabrera and Jump 2019).

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3 50 Climate change is expected to cause major shifts in the distribution and abundance of plant communities,
4 51 and there are already signs of processes associated with increased intensity and duration of droughts
5 52 (Allen and others 2010). In fact, the frequency and severity of drought events have increased in recent
6 53 decades, along with a trend towards drier summers, particularly for Southern Europe (Vicente-Serrano
7 54 and others 2014; Stagge and others 2017). This is especially critical, since climate-change projections for
8 55 the Mediterranean area forecast more frequent and severe extreme climate events (Spinoni and others
9 56 2017). In this climatic-change context, population loss and range retractions are expected in boreal,
10 57 temperate, and Mediterranean species at the lowest latitudes, elevations, and drought-prone areas of a
11 58 species' distribution, *i.e.* the rear edge (Hampe and Petit 2005). In a global-change context, the impact of
12 59 drought on vegetation needs to be evaluated regarding the interactions with other drivers of change
13 60 (Doblas-Miranda and others 2017). This is especially relevant for areas with a long history of landscape
14 61 alteration, such as the Mediterranean region, where land-use change plays a major role in current
15 62 ecosystem ecology (Navarro-González and others 2013), given that the interactions of drought and land-
16 63 use change are crucial for Mediterranean forests (Doblas-Miranda and others 2017).

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19 64 The effects of drought are also especially relevant for populations considered to be located along the rear
20 65 edge (either latitudinal or altitudinal along climatic gradients) of their distribution, where climatic conditions
21 66 mark the species limits, and the populations are likely to be more sensitive to minor climatic and
22 67 microtopographic variations (Hampe and Petit 2005). The response of rear-edge populations to climate
23 68 variations could be useful in estimating the adaptation of species to predicted climatic changes (Jump and
24 69 others 2010). Yet it is crucial to accurately characterize the ecological rear-edge of species. This can be
25 70 particularly misleading in ecosystems with strong land-use legacies because it is established from current
26 71 species distribution (Vilà-Cabrera and others 2019). Furthermore, this characterization becomes even
27 72 more critical for relict populations driven by historical land uses when they harbor high levels of
28 73 intraspecific genetic diversity (Valbuena-Carabaña and Gil 2013).

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31 74 Understanding the vegetation response to drought requires integrative and multidisciplinary strategies to
32 75 assess the disturbances of forest at several scales (Hartmann and others 2018). The assessment of
33 76 resilience to climate disturbances such as droughts provides critical information concerning the capacity
34 77 of the forests to maintain their structure and render valuable ecosystem services. The drought resilience
35 78 of species is better assessed when several approaches, such as dendrochronology and remote sensing,
36 79 are combined. Dendroecological estimates of growth (*i.e.* tree-ring width) are commonly used proxies to
37 80 characterize tree vitality, and annual tree-ring widths can be used to study changes in growth as a
38 81 response to drought at the individual-tree scale (Fritts 1976). Remote sensing can be used to study the
39 82 impact of drought on ecosystems and hence the stand level (*e.g.* Zhang and others 2013). The
40 83 combination of both approaches (remote sensing and dendroecology) has been used to assess the
41 84 effects of droughts on vegetation along ecological gradients (*e.g.* Vicente-Serrano and others 2013;
42 85 Coulthard and others 2017), and also to evaluate growth resilience to drought in several tree species (*e.g.*

Gazol and others 2018; Peña-Gallardo and others 2018). Nonetheless, it is crucial to ascertain whether the responses at the tree level differ from those at the ecosystem level and characterize the spatial variability of this response in rear-edge populations.

In the present 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 radial tree growth (as a proxy for secondary growth) of *Quercus pyrenaica* Willd. (Pyrenean oak, *melojo*) in 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) over the long term (in the last few decades). Our main hypothesis is that these relict populations driven by historical land use are vulnerable to climate change at their present climatic (either elevational or latitudinal) rear edge, and hence will show low resilience to extreme drought along climatic gradients at a small scale within the rear edge. To test this hypothesis, we: (i) quantified how recent extreme drought events influenced primary and secondary growth of *Q. pyrenaica* forests at their present geographical rear edge; (ii) analyzed the long-term resilience of these forests to extreme drought events, using time-series of radial growth; (iii) and examined differences in the resilience metrics between populations located in contrasting ecological conditions (*i.e.* xeric vs. mesic) along environmental gradients within the rear edge in order to detect vulnerability to climate change at the small spatial scale. For the latter task, we characterized the variability in the forest response to drought within the current geographical rear edge and 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 throughout south-western France and the Iberian Peninsula reaching their southern limit in mountain areas of northern Morocco (Franco 1990). In the Iberian Peninsula, these forests occupy 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. As a submediterranean species, it has lower drought tolerance than evergreen Mediterranean taxa (Río and others 2007).

The forests of this species reach their southernmost European limit in Andalusian mountains such as Sierra Nevada (37°N, 3°W), a high-mountain range with elevations of 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 according to elevation. Sierra Nevada is considered a glacial refuge for deciduous *Quercus* species (Olalde and others 2002). Eight melojo oak patches (2400 ha) have been identified in this mountain range (Figure 1), from 1100 to 2000 m a.s.l. and often associated with 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 forest formation of Sierra Nevada, sheltering several endemic and endangered plant species (Lorite and others 2008). These relict forests have undergone intensive human use throughout history (Camacho-Olmedo and others 2002). Furthermore, the conservation status of this species for southern Spain is considered “Vulnerable” and it is expected to suffer from climate change, reducing its suitable habitats in the near future (Gea-Izquierdo and others 2013).

Climatic data and drought episodes

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 had a 0.25 x 0.25 ° resolution for the 1950-2016 period. Grid cells were select to cover each sampled site. The SPEI (Standardized Precipitation-Evapotranspiration Index) (Vicente-Serrano and others 2010) index with a temporal scale of 6 months was used to characterize the drought conditions for the period 1961-2014.

The Iberian Peninsula underwent several extreme drought episodes in the last three decades (e.g. 1995, 1999, 2005, 2012) (Vicente-Serrano and others 2014). The 2005 and 2012 drought events have been documented as being among the worst in recent 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 having remote-sensing information of high spatial resolution (MODIS started on 2000; see below). Nevertheless, for radial growth-time series, a greater number of older drought events were also analyzed to contextualize the results for 2005 and 2012 and to evaluate forest resilience to drought over a longer term (see Table S3). A drought event was identified using the SPEI 12-months scale, following a procedure similar to the one proposed by Spinoni and others (2015). We used 0.5° grid cells covering Sierra Nevada taken from the 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 fall below that threshold for at least two consecutive months. For each drought event, we computed: the *duration* as the number of consecutive months with the SPEI lower than a certain threshold; the *severity* as the sum of the absolute SPEI values during the drought event; the *intensity* and the *Lowest SPEI* refer to the mean and lowest value of SPEI respectively during the drought event.

153 Greenness data to assess ecosystem resilience

154 Vegetation greenness of *Q. pyrenaica* was characterized by means of the *Enhanced Vegetation Index*
 155 (EVI), derived from MOD13Q1 product of the MODIS sensor. EVI data consists of 16-day maximum value
 156 composite images (23 per year) of the EVI value with a spatial resolution of 250 m x 250 m. MODIS EVI
 157 data were compiled for the period 2000 - 2016. We selected the pixels covering the distribution of *Q.*
 158 *pyrenaica* forests in Sierra Nevada ($n = 928$ pixels). Any values affected by clouds, snow, shadows or
 159 high content of aerosols, were filtered out following recommendations for mountain regions (Reyes-Díez
 160 and others 2015).

161 The mean Annual EVI (EVI_{mean}) as a surrogate of mean annual primary production was computed for
 162 each pixel for the period 2000 - 2016. The EVI standardized anomaly (EVI_{sa}) was computed pixel-by-
 163 pixel, in order to minimize bias in the evaluation of anomalies and to provide more information concerning
 164 their magnitude (Samanta and others 2012). For each pixel, an annual EVI value was calculated by
 165 averaging EVI valid values. Then, the standardized anomaly was computed as: $EVI_{sa,i} = (EVI_{mean,i} - EV$
 166 $I_{mean,ref})/\sigma_{ref}$, where $EVI_{sa,i}$ is the EVI standardized anomaly for year i ; $EVI_{mean,i}$ the annual mean value of
 167 EVI for year i ; $EVI_{mean,ref}$ the average of the annual EVI values for the period of reference 2000-2016 (all
 168 except year i); and σ_{ref} the standard deviation for the reference period. Each pixel was categorized
 169 according the EVI standardized anomalies as “greening” ($EVI_{sa} > 1$), “browning” ($EVI_{sa} < -1$) or “no-
 170 changes” ($-1 > EVI_{sa} > 1$)(Samanta and others 2012).

171 Rather than other vegetation indices such as the NDVI, EVI_{mean} was chosen because it is highly stable
 172 under the use of any filter (Reyes-Díez and others 2015) and because it showed highly significant
 173 correlations with annual ($r = 0.81$) and seasonal EVI values ($r_{spring} = 0.76$ and $r_{summer} = 0.88$). For
 174 exploratory purposes, temporal trends of EVI_{mean} were examined at the pixel scale, using the Mann–
 175 Kendall nonparametric test.

176 Field sampling and dendrochronological methods to assess individual tree resilience

177 Trees were sampled during autumn 2016 at two locations in contrasting N-S slopes of Sierra Nevada:
 178 San Juan (SJ), a xeric site located at the northern aspect; and Cáñar (CA), a wetter site located at the
 179 southern aspect (Figure 1; Table 1). For the southern site, two elevations were sampled: CA-Low (around
 180 1700 m) and CA-High (around 1860 m), constituting the current low-elevational limit (CA-Low) and the
 181 tree-line (CA-High), respectively, in the sampled aspect. Despite the proximity of these two elevations
 182 (less than a 200-m difference) the stands differ markedly in their structure and characteristics (Table 1).
 183 The three sampling sites followed a moisture gradient: $SJ < CA-Low < Ca-High$ (Table 1). All the sites
 184 were oak monospecific and representative of the population clusters identified for the species in this
 185 mountain range (Pérez-Luque and others 2015b). At each site, between 15 and 20 trees from either the

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3 186 single dominant-codominant layer in CA or the open canopy in SJ were randomly sampled. Two cores of
4 187 5 mm of diameter were taken from each tree at breast height (1.3 m) using an increment borer. Diameter
5 188 at breast height (DBH) and total height were measured for each tree. In addition, stand competition
6 189 affecting target trees was assessed by recording distance, azimuth, DBH, species, and total height of all
7 190 neighboring living trees with DBH > 7.5 cm within a circular plot with a 10-m radius. Several competition
8 191 indices were calculated: the distance independent indices *density* (trees · ha⁻¹), and *basal area* (BA, m² ·
9 192 ha⁻¹); and the distance dependent index size ratio proportional to distance as $srd = \sum_{i=1}^n (dbh_j/dbh_i) \cdot$
10 193 $[1/(dist_{ij} + 1)]$ (see Gea-Izquierdo and Cañellas 2009 for more details). Differences between sites for
11 194 height, DBH and competition indices were analyzed using non-parametric Kruskal-Wallis rank sum tests.
12 195 When significant differences were detected, multiple comparisons were run using the Dunn's-test with
13 196 Bonferroni adjustment to correct for significance.
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15 197 Tree cores were air dried, glued onto wooden mounts, and sanded. Annual radial growth (ring width, RW)
16 198 was determined with a measuring device coupled to a stereomicroscope, for an accuracy of 0.001 mm.
17 199 Individual ring series were first visually and statistically cross-dated with TSAP software (Rinntech,
18 200 Heidelberg, Germany), using the statistics Gleichläufigkeit (GLK), t-value and the crossdating index (CDI).
19 201 Cross-dating validation was finally verified using COFECHA (Holmes 1983).
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21 202 The growth trends were analyzed at different time scales. To study the growth response to the inter-
22 203 annual variability of climate (short-term response), pre-whitened residual chronologies (RWI) were used.
23 204 These were calculated from ratios between raw growth measurements and individual cubic splines with a
24 205 50% frequency cutoff at 30 years (Fritts 1976). Tree-ring width series were standardized and detrended
25 206 using dp1R (Bunn 2010). Mean residual site chronologies were established by computing the biweight
26 207 robust mean of all prewhitened growth indices for the trees of the same site (Fritts 1976). The statistical
27 208 quality of each chronology was checked via the expressed population signal (EPS). A threshold value of
28 209 EPS > 0.85 was used to determine the cutoff year of the time span that could be considered reliable.
29
30 210 The long-term growth response was analyzed using basal area increment (hereafter BAI, cm² · year⁻¹). In
31 211 theory, BAI represents a more accurate indicator of growth than ring width, since it removes variation in
32 212 growth attributable to increasing stem circumference after 30-40 years of juvenile growth (Biondi and
33 213 Qeadan 2008). Raw ring widths and measured DBH were used to compute BAI (Piovesan and others
34 214 2008) with the following equation: $BAI = \pi(r_t^2 - r_{t-1}^2)$ where r is the radius of the tree and t is the year of
35 215 tree-ring formation. For each individual tree, a mean BAI series was calculated. Then, mean site BAI
36 216 chronologies were determined by averaging individual tree BAI time series.

217 Disturbance analyses

218 Disturbance chronologies were built using tree-ring width to identify abrupt and sustained increases
 219 (release events from competition) or decreases (suppressions) in radial growth (Nowacki and Abrams
 220 1997) as indirect estimates of possible disturbance events (e.g. logging, drought-induced neighbor
 221 mortality) in the past. Growth changes (GC) were calculated for the individual tree-ring series using a 10-
 222 year running window as either positive (PGC) or negative (NGC) growth changes: %GC =
 223 $[(M1 - M2)/M2] \times 100$, where $M1$ is the preceding 10-year median and $M2$ is the subsequent 10-year
 224 median (Rubino and McCarthy 2004).

225 Site-disturbance chronologies were constructed by annually averaging the individual disturbance series.
 226 To separate growth peaks caused by disturbance events and expressing stand-wise disturbances from
 227 those by climate, we considered a threshold of 50% of GC and more than 50% of the individual trees
 228 displaying the same growth changes (e.g. Gea-Izquierdo and Cañellas 2014). In addition, the history of
 229 the forest and management of our sampling sites was inferred from a detailed analysis of historical land-
 230 use changes. For this, existing historical documents were exhaustively reviewed to compile information
 231 on socio-economical activities affecting the forests being studied (Table S4). We reviewed several
 232 documentary sources: historical documents and maps; detailed mining reports; official information on
 233 recent wildfires events and forest-management practices; livestock farming; traditional irrigation channels;
 234 and studies concerning the socioeconomic dynamics of forests on Sierra Nevada at different scales (see
 235 Table S4 for references).

236 Assessing ecosystem and tree individual resilience to drought

237 To evaluate the effects of drought events on ecosystem resilience (using greenness data) and individual
 238 tree resilience (using BAI data), we used resilience indices proposed by Lloret and others (2011). The
 239 Resistance index estimated as the ratio between performance during and before the disturbance ($R_t =$
 240 $Drought/PreDrought$) quantifies the severity of the impact of the disturbance in the year it occurred. The
 241 Recovery index, computed as the ratio between performance after and during disturbance ($R_c = Pos$
 242 $tDrought/Drought$), represents the ability to recover from disturbance relative to its severity. Finally, the
 243 Resilience index ($R_s = PostDrought/PreDrought$) is the capacity to reach pre-disturbance performance
 244 levels. The values of these indices were computed for tree growth (BAI) and greenness (EVI mean)
 245 during each drought event. The predrought and postdrought values of each target variable (i.e. BAI or
 246 EVI) were computed as the mean value over a period of three years before and after the drought event,
 247 respectively. A period of three years was chosen because we found similar results on comparing periods
 248 of two, three, and four years (Figure S3b), and this time period has been used in other studies (e.g. Gazol
 249 and others 2018). Resilience metrics for BAI data were additionally computed for the most severe drought
 250 events since 1940 ($n = 8$; Table S3) and compared with drought severity.

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Statistical analysis

Relationships between RWI and BAI site chronologies and climatic variables were assessed using bootstrapped Pearson’s correlations estimated using `treeclim` (Zang and Biondi 2015). 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 oak populations studied (northern and southern aspects). These tests were used because original and log-transformed data did not follow the assumptions of normality or homogeneity of variance (Wilcox 2012). Robust measures of central tendency (M-estimator based on Huber’s Psi) were used because they were close to the mean value in all cases (Wilcox 2012). When the robust ANOVA test was run, 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 time trends in greenness showed that 78.9% of the EVI pixels followed a positive trend for the 2000-2016 period. The lowest values of EVI standardized anomalies for the study period were recorded during the 2005 drought, and the minimum EVI values were expressed in the northern (dry) population (Figure 2a). A “browning” episode ($EVI_{sa} < -1$) was found during this drought event, whereas no changes in greenness in response to the 2012 drought were detected (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 elevation were taller and their growth was significantly faster than that of trees from the other two sites, despite the competition measured as plot basal area was greatest in CA-High (Table 1, Figure 3). The growth and height of trees from the northern and the low-elevation southern population proved similar (Figures 3 and S3a). Only trees from the southern sites (*i.e.* the wetter aspect) showed significant positive growth trends since the late 1970s (Figure 3), this trend being far more pronounced for the high elevation, the wetter, colder site (CA-High).

Drought events reduced radial growth for all sites (Figure S2a), this negative effect being particularly evident for 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 less tree-growth reductions than did the northern site

(SJ), especially for 2005 and 2012 (Figure S2a), with the weakest growth reductions being 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 trees sampled): the first during the 1940s (the most evident) and the second in 1995-2000 (Figure 4). These periods alternated with periods of suppression. By 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

R_s and R_t varied in the same direction whereas R_c varied inversely to R_s and R_t . 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 R_c , significant for all oak populations (Figure 5). A similar pattern was found for R_s but proved significant only for SJ.

Importantly, non-significant patterns resulted when we excluded 1995, except for R_c 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 S1). The 2005 drought event reduced greenness and growth more than that of 2012 (Table S2) but the metrics of resilience generally covaried in the same direction during those two years. Resilience and resistance values were significantly higher for 2012, the most severe event, than for 2005 in both variables (Table S2; Figure 6). Thus, recovery values for greenness were higher for 2005 than for the 2012 drought event. Recovery showed a contrasting pattern for EVI and tree growth.

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

Tree-growth response to climate

The response of tree growth to water availability was greater than 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). Nevertheless, differences appeared 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, the spring maximum temperature was the most significant limitation for

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treemgrowth only for the southern populations (Figure 7b and 7c), whereas minimum and maximum temperatures of the current September positively influenced tree growth only in the northern population.

Discussion

By using a combined approach of remote-sensing information and dendrochronology, we have quantified the drought impact on the melojo oak forests of Sierra Nevada and their resilience to several severe drought events in the recent decades. Our results indicated that these relict oak populations driven by historical land use are resilient to climate change at their present rear edge. However, resistance, resilience, and forest recovery to extreme drought events are strongly influenced by mountain aspect, local environmental conditions, and management legacies. This means that the geographical and the ecological rear edges do not necessarily match and, at a small spatial scale, tree performance varies markedly along the rear edge under climate change.

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

The review of historical documents revealed that forest clearings, firewood removal, charcoal making, and mining have strongly affected the forests on Sierra Nevada (Table S4), where an estimated historical loss of broadleaf *Quercus* species approaches 90% of the cover at medium and low elevations (Jiménez-Olivencia and others 2015). Together with the analysis of the disturbance chronologies, the observed notable differences in stand structure, tree size, and age suggest different forest histories and a different management origin (*i.e.* land-use legacy) between northern (coppice) and southern populations (high forest, open woodland). On the northern slopes of Sierra Nevada (*e.g.* SJ site), land uses have been historically distributed along an elevational 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 such as mining must have altered the forest structure, *e.g.* the SJ site has many small mines and quarries that were exploited intermittently throughout history. The release growth event discerned for the 1940s concurs with a period of maximum mining activity in this area (1925 to 1957) (Table S4), during wich timbers use increased for mine tunnels and furnaces, these also requiring large amounts of firewood to melt the mineral. This heavy exploitation of the neighboring forest resources must 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 on the southern slopes (*e.g.* CA site) were mixed with a greater percentage of croplands along the elevational gradient where oaks grow (Jiménez-Olivencia and others 2015). Firewood, charcoal, and acorns have been resources intensively exploited at 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). At the CA-High site, the only positive release event found for the earliest years could be related with conversion from closed forest to an open silvopastoral system,

a common management type which has been 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 the SJ site during 1995-2000 was lower than during 1940, but also affected most trees (Figures 4, S2b). No records of forest practices in this area over the last 30 years have been found (Bonet and others 2016), and no logging has been recorded during the period 1995 - 2000 (F.J. Cano-Manuel *personal communication*). 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 high sensitivity to water availability (Gea-Izquierdo and Cañellas 2014).

Sensitivity (resistance) of relict oaks 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 as well as by 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 detected during the 1995 drought, a characteristic negative precipitation 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 the situation with many other forest species under Mediterranean climates, moisture availability is generally the most limiting factor driving radial growth of *Q. pyrenaica* along its 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 proved less sensitive to drought than did tree growth, particularly for drier sites. These findings agree with previous works showing tree growth to be a more sensitive metric of forest resilience than is net primary productivity (e.g. Babst and others 2013; Coulthard and others 2017; Gazol and others 2018; Peña-Gallardo and others 2018), suggesting that the growth reduction could be mediated by sink more than by source limitations (Körner 2013; Fatichi and others 2014). Tree-ring records complement remote-sensing data in longer time scales by reflecting tree-growth anomalies induced by climate or disturbance 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 wetter southern oak populations. For example, the northern site showed higher browning intensity than

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382 did the southern sites during the 2005 drought event, and the stronger correlations of tree-growth with
383 SPEI (hydrological year and summer) in the northern site can be interpreted as higher sensitivity to
384 drought at drier sites (Gea-Izquierdo and Cañellas 2014). It is well known that tree growth and tree
385 responses to drought are site-dependent (e.g. soil features, tree competition, etc.; Babst and others
386 2013), particularly for rear-edge populations (Cavin and Jump 2017; Dorado-Liñán and others 2017b).
387 Trees at CA-High registered higher BAI than those located at lower elevations (CA-Low and SJ; Figure
388 4). This shows the high variability in the response to climate exhibited along a narrow gradient, which is
389 especially noteworthy for southern sites, as these lie very close to each other and overall both are
390 considered to constitute the rear edge for the species.

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

392 Despite the severe drought events in recent decades (Table S3), we found a positive trend for vegetation
393 greenness of *Q. pyrenaica* for the last 16 years, which is consistent with previous findings stressing a
394 recent short-term increase in primary productivity for these forests coinciding with a rather wet decade in
395 the 2000s after a dry decade in the 1990s (Pérez-Luque and others 2015a). For tree growth, positive
396 trends also appeared in the last decade, particularly for the southern high-elevation site (CA-High, Figure
397 4). Similar long-term trends have been described for this species along its distribution range only at high-
398 elevation wet and cold sites (Gea-Izquierdo and Cañellas 2014), which could be related to a non-linear
399 positive effect of warming for the species at cold-limited high-elevation sites (Salzer and others 2009;
400 Gea-Izquierdo and Cañellas 2014). Importantly, for rear edges threatened by climate change, negative
401 growth trends would have been expected, as shown for some temperate and Mediterranean species
402 (Sánchez-Salguero and others 2012; Camarero and others 2015b; Dorado-Liñán and others 2017a).

403 Although the 2012 drought event was more severe and intense than that of 2005 (Table S3), resilience
404 values for greenness and tree-growth were greater for 2012. This could be due to the different timing of
405 the two droughts. The 2012 event was a winter drought (Trigo and others 2013) occurring earlier than the
406 shorter 2005 drought. The latter matched the period of maximum growth for oak forests in late spring
407 (Figure S4). This highlights the importance of the timing of the drought as a key factor determining tree
408 recovery after drought (Camarero and others 2015a; Huang and others 2018). For tree growth, the
409 highest values of resilience were found for the two most severe events (1995 and 1999; Table S3) and
410 tree-growth resilience was positively related to drought severity (Figure 5).

411 The high drought-resilience values reported here, coinciding with high values of genetic resilience for
412 those forests at Sierra Nevada reported elsewhere (Valbuena-Carabaña and Gil 2013, 2017) appear to
413 indicate the strong local adaptation of this oak. Our findings agree with those of studies showing that the
414 assumed higher vulnerability of dry edges does not necessarily hold (e.g. Cavin and Jump 2017).
415 Martínez-Vilalta (2018) pointed out the importance of local adaptation and plasticity, and also of local
416 environmental factors on the vulnerability shown by rear-edge populations. Our results highlight the

ample small-scale variability at the ecological boundary and need to better confine the rear-edge limit in our 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 should be mentioned that we studied only adult individuals established decades or centuries ago, meaning that it needs to be assessed whether the trees express resilience at the species level or whether we would find 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).

In summary, two main results stand out from this research. First, the high values of resilience observed in our study suggest that *Q. pyrenaica* populations 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 complicate the definition of potential rear edges. The high resilience values observed could also be related to stabilizing mechanisms promoting community resilience that can buffer the impact of extreme events, as 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 throughout the 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 found positive effects of climate change in certain stands, as discussed, in disagreement with our hypothesis of expecting oak vulnerability in the geographical rear edge studied. This suggests that the rear edge therefore needs to be redefined (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 that management history influences 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 rear edges did not appear to fully match in our study. Severe drought events provoke major reductions in primary and secondary growth of *Q. pyrenaica* forests in the relict, rear-edge forest studied. However, we found no negative growth trends despite our expectation of vulnerability to climate change for these relict stands. Furthermore, we detected positive trends for primary growth (*i.e.* greenness) at the ecosystem scale and a steep positive trend of secondary growth at

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3 451 the tree level at the wettest site along the climatic gradient analyzed. The trees exhibited high resilience
4 452 values in response to drought, particularly in the long-term scale, and resilience was directly related to
5 453 drought severity. These findings are consistent with other results showing that this mountain region is still
6 454 acting as a refuge for deciduous species, including *Quercus*. The differences found in tree growth and
7 455 resilience to drought between sites close together show that responses to drought were site dependent
8 456 and can drastically vary even in very narrow spatial gradients (*i.e.* following ecological thresholds). This is
9 457 particularly relevant for rear-edge populations where topographic and biophysical variability facilitates the
10 458 existence of microrefugia. The analysis of tree-growth dynamics revealed suppression and release events
11 459 that were consistent with legacies left by land use in local forest dynamics, as inferred from an exhaustive
12 460 review of historical documents. In this sense, our results highlight the importance of land-use legacies for
13 461 highly transformed Mediterranean systems. This is relevant for tree species with a high sensitivity to
14 462 climate change, such as *Q. pyrenaica*, not only for conservation *per se* of the species, but for all
15 463 ecosystem services that these singular forests offer. As a follow-up to our study, research would be
16 464 informative to disentangle how forest resistance and resilience might be affected by the combination of
17 465 climate change and land-use legacies in highly transformed landscapes such as Mediterranean mountain
18 466 ecosystems.

26
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1 **Table 1.** Characteristics of sampled plot. Lat = latitude; Long = longitude. Dbh and height of all trees, Basal Area
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3 **Table 2.** Characteristics of the mean tree-ring chronologies. Length values in parentheses indicate the number of
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5 trees (see Materials and methods). Temp.: annual average of mean monthly minimum and maximum
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7 temperatures. Values shown here correspond to site averages. Standard deviations are shown in parentheses.
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9 Different letters indicate statistically significant differences between sites (Kruskal-Wallis test followed by Dunn’s
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11 test, $p<0.05$). Stands were monospecific, hence all results correspond to oak data.

12 **Table 2.** Characteristics of the mean tree-ring chronologies. Length values in parentheses indicate the number of
13
14 years replicated with more than five series. RW = mean annual ring width (standard deviation in parenthesis). MS
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16 = mean sensitivity. AR(1) = mean autocorrelation of raw series. Rbt = mean correlation between series. EPS =
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18 mean expressed population signal. EPS and Rbt were calculated for the mean residual chronologies of growth
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20 indices.

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Table 1

							Cored trees				Stand competition				
Site	Lat (°)	Long (°)	Elevation (m)	Slope (°)	Prec. (mm)	Temp. (° C)	# trees (# cores)	Dbh (cm)	Height (m)	Age (years)	Dbh all (cm)	Height all (m)	BA (m² ha⁻¹)	Density (trees ha⁻¹)	SRD
CA-High	36.97	-3.42	1846 - 1884	12.11 (3.28)	731	3.4-13.8	15 (30)	69.8 (20.5) a	15.4 (1.8) a	161.0 (32.2) a	34.1 (24.3) a	10.8 (4.4) a	39.13 (24.31) a	348.0 (147.1) a	0.91 (0.63) a
CA-Low	36.96	-3.42	1691 - 1751	12.86 (2.98)	658	4.7-15.6	15 (30)	45.9 (8.6) a	12.6 (1.6) b	148.5 (16.5) a	21.7 (14.4) b	9.0 (2.8) b	18.02 (7.11) ab	409.6 (226.0) a	0.89 (0.44) a
SJ	37.13	-3.37	1322 - 1474	27.33 (5.59)	555	4.9-16.35	20 (48)	31.9 (3.7) b	11.8 (2.3) b	72.6 (11.1) b	20.6 (8.1) b	9.7 (3.6) ab	11.64 (5.47) b	339.0 (130.3) a	1.11 (0.52) a

15 **Table 2**

Site	First year	Last year	Length (years)	# trees	# cores	RW (mm)	MS	AR(1)	Rbt	EPS
CA-Low	1836	2016	181 (164)	15	30	1.253 (0.781)	0.208	0.799	0.520	0.897
CA-High	1819	2016	198 (188)	15	30	1.500 (0.879)	0.203	0.827	0.522	0.907
SJ	1921	2016	96 (90)	20	48	1.725 (1.207)	0.319	0.692	0.637	0.959

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Figure 1. Distribution of *Quercus pyrenaica* forests in the Iberian Peninsula (a) and in Sierra Nevada mountain range (b). Different colors indicate oak-population clusters identified in Sierra Nevada (Pérez-Luque et al. 2015). For each population, a grid with the MODIS pixels is shown (see Material and methods). Detailed location of the dendroecological sampling sites: northern (San Juan, SJ) (c), and southern ones (Cáñar: CA-Low and CA-High) (d). Color orthophotography of 2009 from Regional Ministry of the Environment.

Figure 2. a) EVI standardized anomaly during the period 2000-2016 for northern and southern populations. Error bars show standard error. See main text for details on EVI calculation. **b)** Percentage of pixels showing browning, greening or no changes during the 2005 and 2012 drought events according to EVI standardized anomalies. See main text for an explanation of greening and browning.

Figure 3. Basal Area Increment (BAI) chronologies of *Q. pyrenaica* for northern population (SJ; *red*) and southern ones: low-elevation (CA-Low; *green*) and high-elevation (CA-High, *blue*) sites. Shading areas correspond to standard error of the mean. Number of series is displayed in the upper plot. Only years replicated with # series > 5 are shown. Linear trends since 1975 are indicated for all sites (numbers indicate r^2 values; asterisks indicate significant linear trend, $p < 0.001$).

Figure 4. Comparison of median growth change (*GC*) following Nowacki and Abrams (1997) for *Q. pyrenaica* sites. Dashed black lines indicate a threshold of 50% of *GC* (see Material and methods). Note that y-axes do not correspond in all of the three panels for the sake of clarity. Error bars indicate standard error.

Figure 5. Resilience metrics of tree-growth for eight severe drought events since 1950 (see main text for details) as a function of drought severity. *Left:* Resistance (*Rt*); *Center:* Recovery (*Rc*); *Right:* Resilience (*Rs*). Points indicate resilience metrics for oak populations: SJ (*red*), CA-High (*blue*) and CA-Low (*green*). Resilience metrics were computed for each population (sample depth > 10) and drought event. Gray lines represent overall relationships for each Resilience metrics.

Figure 6. Comparison of the response of *Q. pyrenaica* forests to drought in terms of resistance, recovery, and resilience of greenness (a) and tree growth (b). For EVI, northern populations (*red circle*) were compared with southern ones (*green circle*). For BAI, the more xeric northern population (San Juan, SJ; *red circle*) was compared with the two southern populations, Cáñar-High (CA-High; *blue circle*) and Cáñar-Low (CA-Low; *green circle*). Different letters indicate significant *post hoc* differences between groups (see Material and methods for details).

Figure 7. Correlation coefficients found by relating tree-ring residual chronologies (RWI) of *Q. pyrenaica* and monthly climatic data: precipitation and 6-month SPEI (a), minimum (b) and maximum (c) temperatures. *green* bars: northern site (SJ); *light blue* bars: low-elevation southern site (CA-Low); and *dark blue* bars: high-elevation southern site (CA-High). Asterisks indicate significant ($P < 0.05$) correlation coefficients.

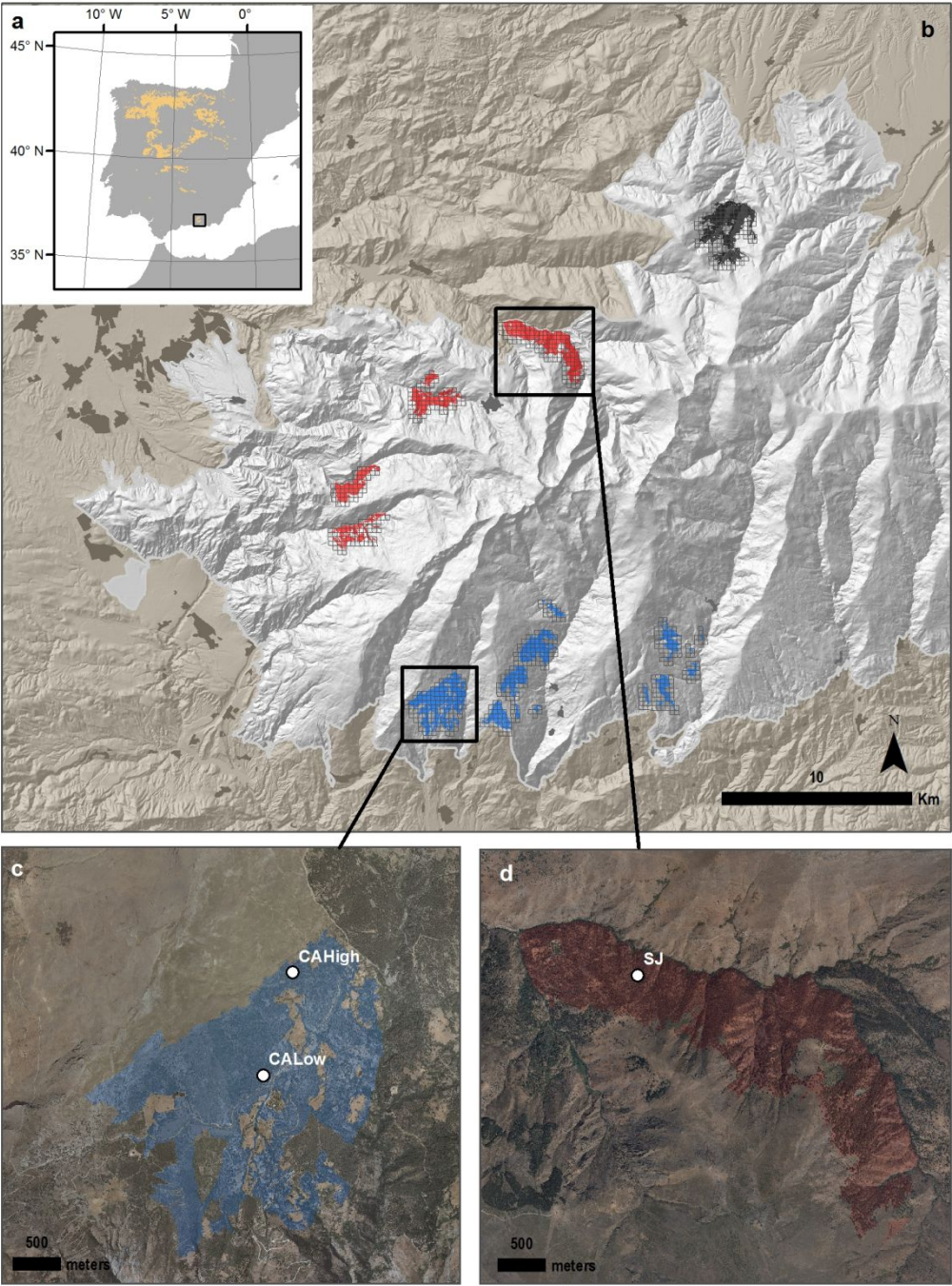
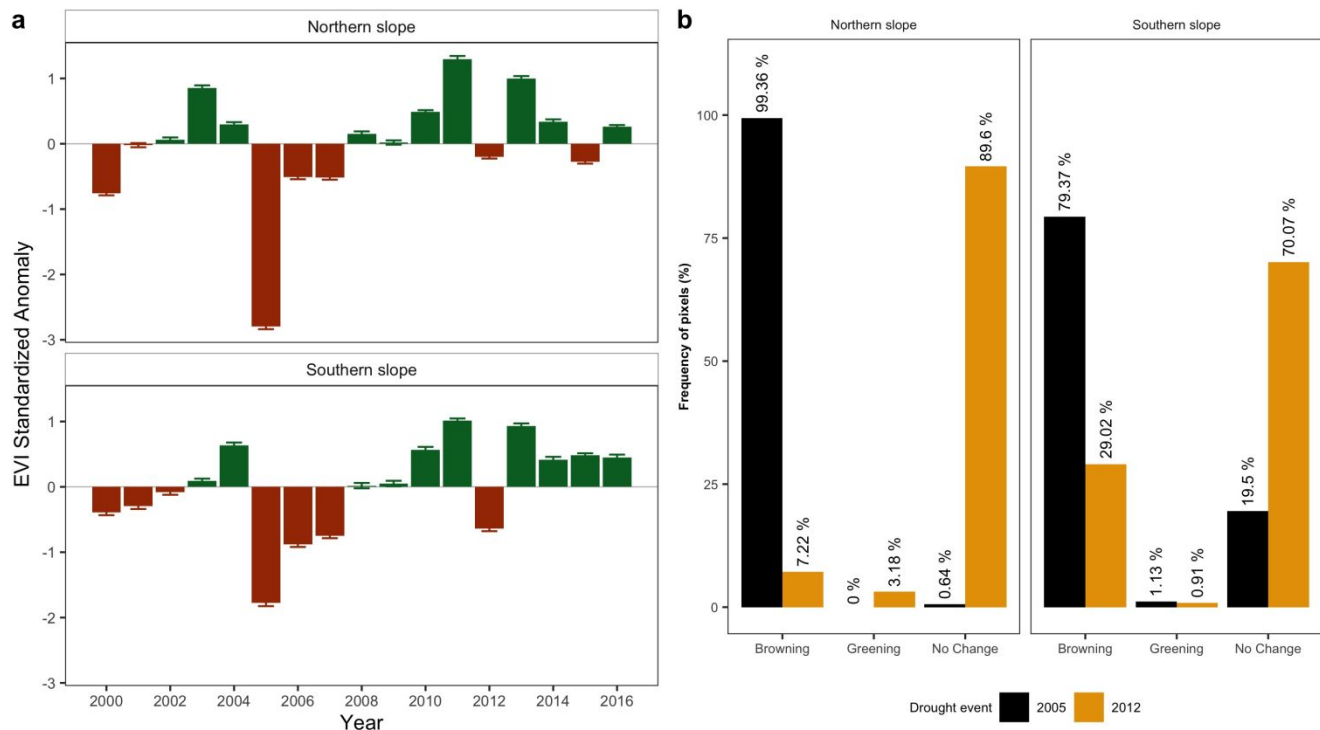


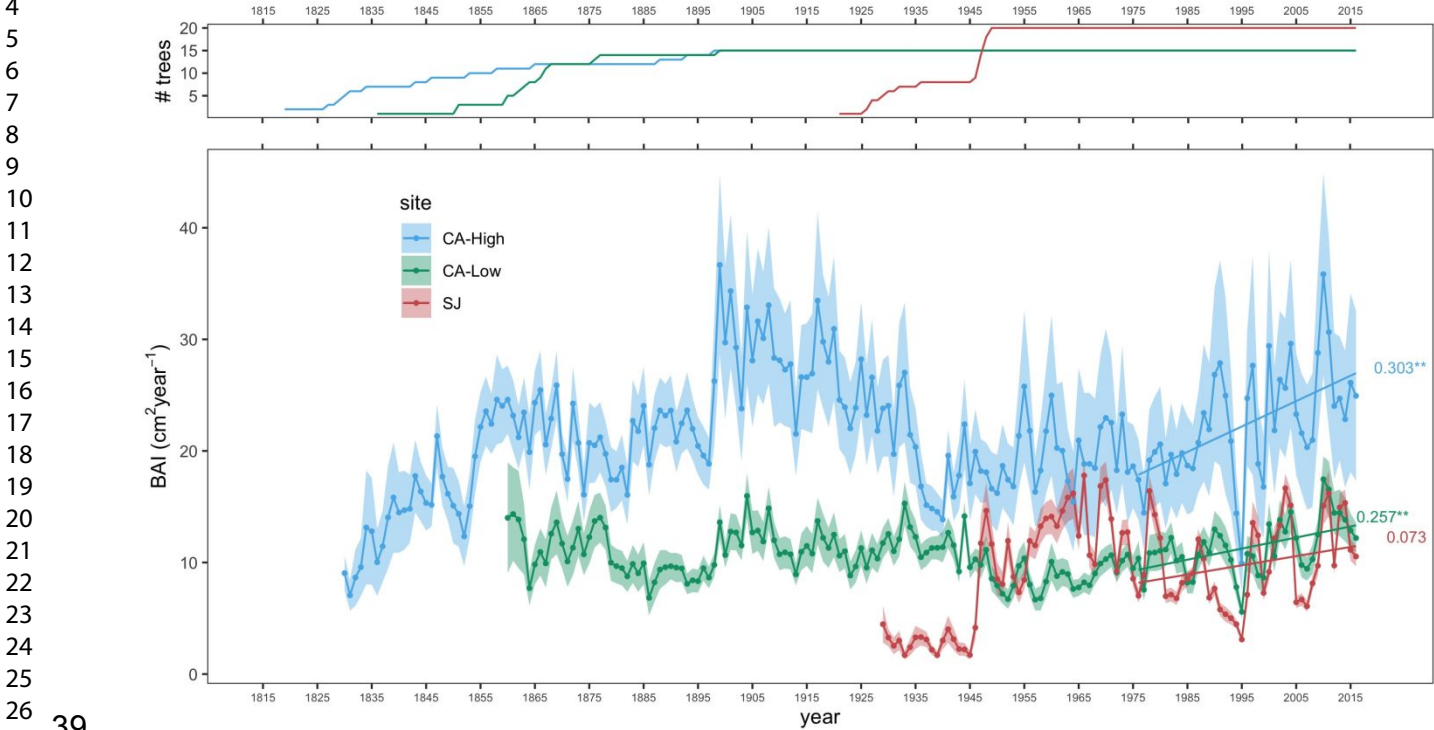
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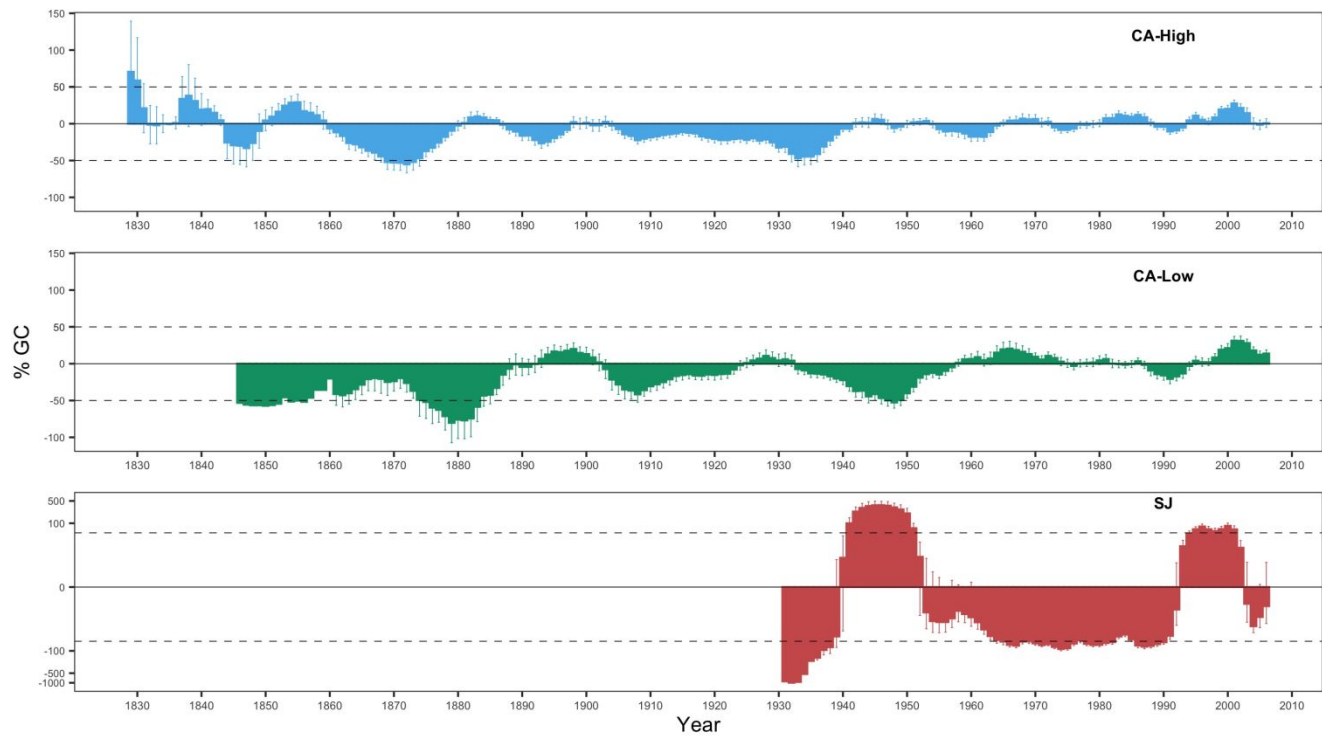


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2 38 **Figure 3**

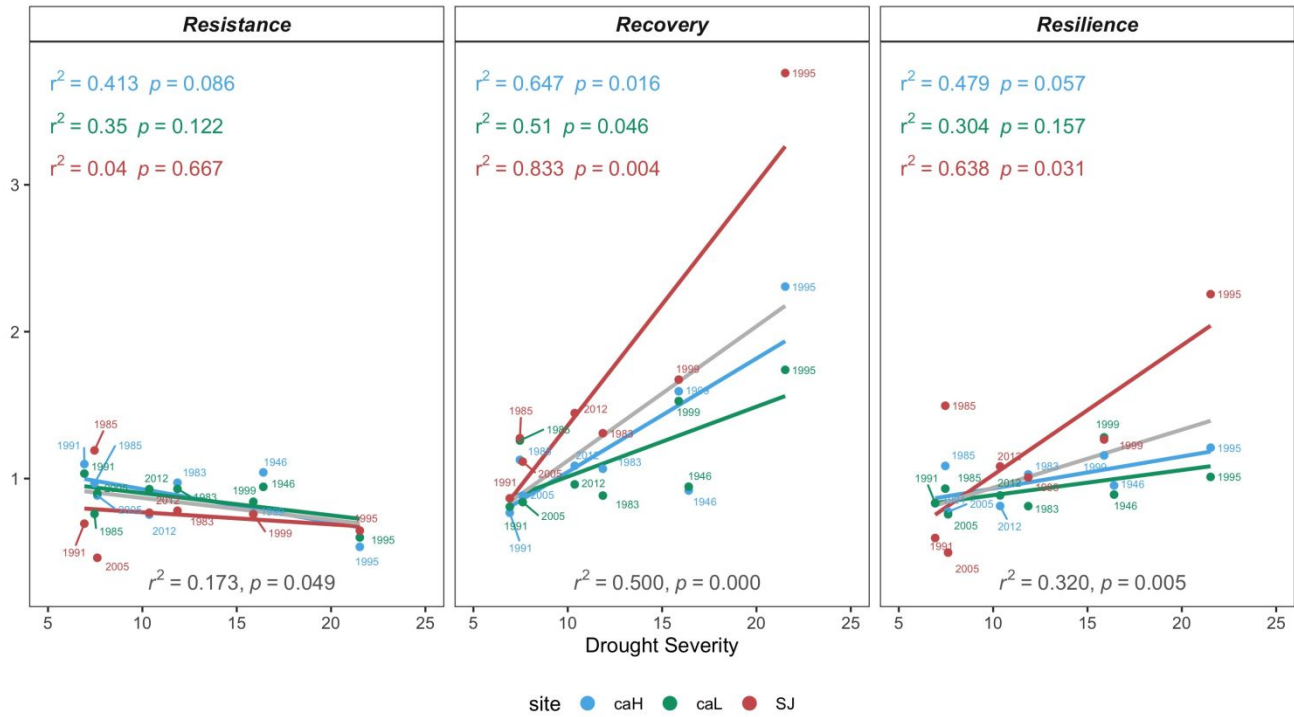
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40 **Figure 4**

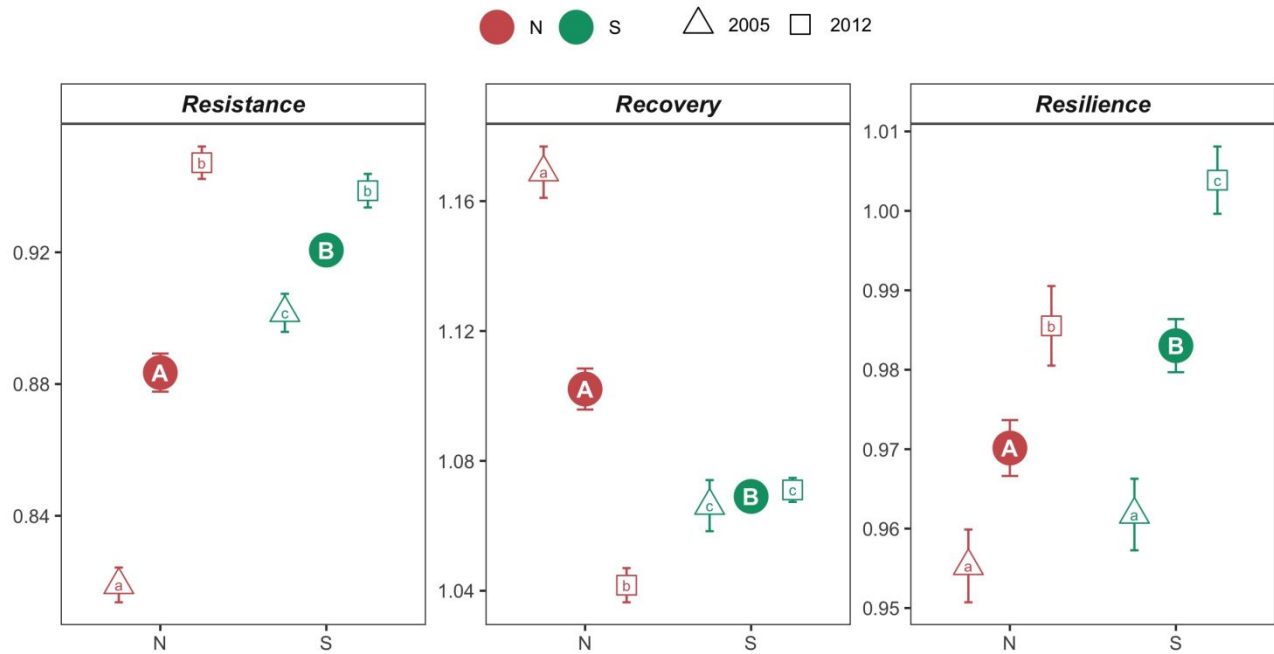
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Figure 5

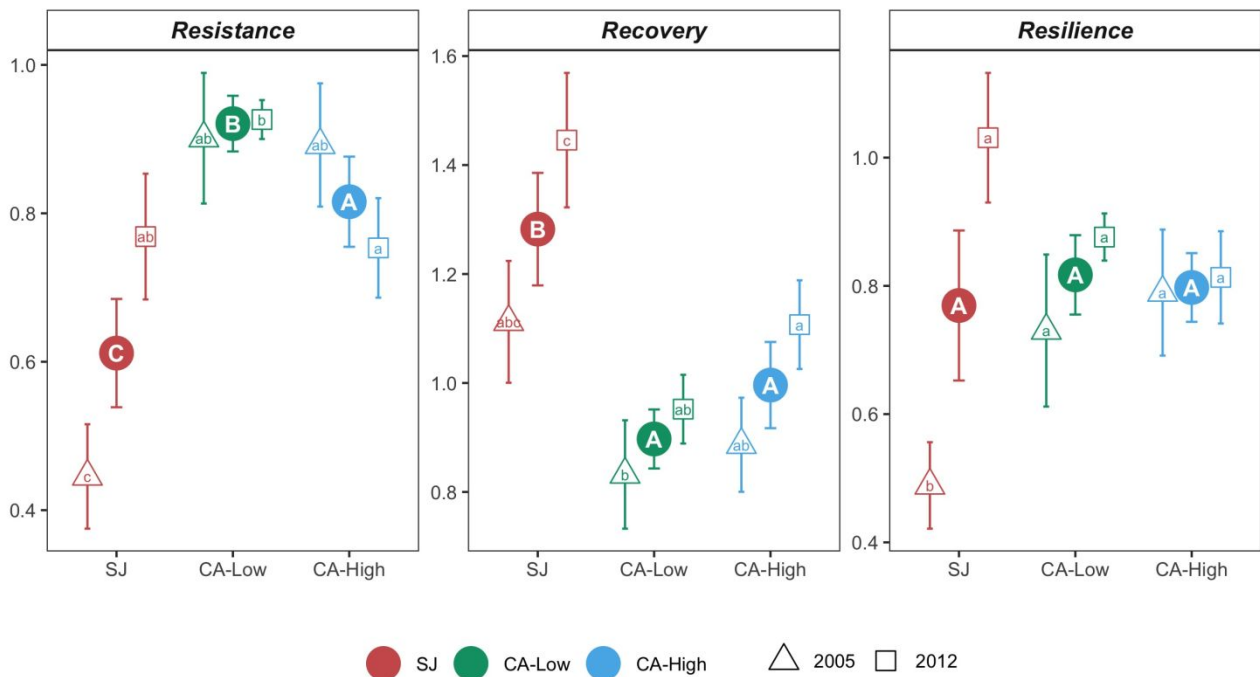


44 **Figure 6**

a

EVI

b

BAI

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Figure 7

