



**Land-use legacies and climate change as a double challenge
to oak forest resilience: mismatches of geographical and
ecological rear edges**

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Land-use legacies and climate change as a double challenge to oak forest resilience: mismatches of geographical and ecological rear edges

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. 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 the tree growth response to climate followed a water-stress gradient. A positive growth trend 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.
- The high values of resilience observed in our study suggest that *Quercus pyrenaica* populations in Sierra Nevada are located in a geographical but not a climatic, ecological rear edge. 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. This is particularly relevant for rear-edge populations where topographic and biophysical variability can facilitate the existence of refugia

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 geographical and ecological rear-edge populations match. This means lower performance, higher vulnerability, and thus higher risk of extinction than for 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 the geographical rear edge does not correspond with the ecological one (Vilà-Cabrera and Jump 2019).

Climate change is expected to cause major shifts in the distribution and abundance of plant communities, and there are already signs of more intense and longer droughts (Allen and others 2010). In fact, drought frequency and severity have increased in recent decades, with a trend towards drier summers,

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3 52 particularly for Southern Europe (Vicente-Serrano and others 2014; Stagge and others 2017). This is
4 53 especially critical, since climate-change projections for the Mediterranean area forecast more frequent
5 54 and severe extreme climate events (Spinoni and others 2017). In this climatic-change context, population
6 55 loss and range retractions are expected in boreal, temperate, and Mediterranean species at the lowest
7 56 latitudes, elevations, and drought-prone areas of a species' distribution, *i.e.* the rear edge (Hampe and
8 57 Petit 2005). In a global-change context, the impact of drought on vegetation needs to be evaluated
9 58 regarding the interactions with other drivers of change (Doblas-Miranda and others 2017). This is
10 59 especially relevant for areas with a long history of landscape alteration, such as the Mediterranean
11 60 region, where land-use change plays a major role in current ecosystem ecology (Navarro-González and
12 61 others 2013), given that the interactions of drought and land-use change are crucial for Mediterranean
13 62 forests (Doblas-Miranda and others 2017).

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16 63 The effects of drought are also especially relevant for populations considered to be located along the rear
17 64 edge (either latitudinal or altitudinal along climatic gradients) of their distribution. In these cases, climatic
18 65 conditions mark the species limits, and the populations are likely to be more sensitive to minor climatic
19 66 and microtopographic variations (Hampe and Petit 2005). The response of rear-edge populations to
20 67 climate variations could be useful in estimating the adaptation of species to predicted climatic changes
21 68 (Jump and others 2010). Also, it is crucial to accurately characterize the ecological rear-edge of species.
22 69 This can be particularly misleading in ecosystems where land-use legacies have strongly modified
23 70 species distribution (Vilà-Cabrera and others 2019). Furthermore, this characterization becomes even
24 71 more critical for relict populations driven by historical land uses when they harbor high levels of
25 72 intraspecific genetic diversity (Valbuena-Carabaña and Gil 2013).

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28 73 The assessment of resilience to climate disturbances such as droughts provides critical information
29 74 concerning the capacity of the forests to maintain their structure and render valuable ecosystem services.
30 75 The drought resilience of species is better assessed by a combination of several approaches, such as
31 76 dendrochronology and remote sensing. Dendroecological estimates of growth (*i.e.* tree-ring width) are
32 77 commonly used proxies to characterize tree vitality, and annual tree-ring widths can be used to study
33 78 growth changes in response to drought among individual trees (Fritts 1976). Remote sensing can be
34 79 used to analyze the impact of drought on ecosystems and hence on the stand (*e.g.* Zhang and others
35 80 2013). The combination of both approaches (remote sensing and dendroecology) has been used to
36 81 assess the effects of droughts on vegetation along ecological gradients (*e.g.* Vicente-Serrano and others
37 82 2013; Coulthard and others 2017), and also to evaluate growth resilience to drought in several tree
38 83 species (*e.g.* Gazol and others 2018; Peña-Gallardo and others 2018). Nonetheless, it is crucial to
39 84 ascertain whether the responses at the tree level differ from those at the ecosystem level and
40 85 characterize the spatial variability of this response in rear-edge populations.

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43 86 In the present study, we used remote-sensing information and dendroecological methods to evaluate the
44 87 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) 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). In the study area, the rear edge of relict populations is imposed by historical land use. Our main hypothesis is that, limited by their land-use legacy, these stands will show low resilience to extreme drought from climate change a small-scale gradient. To test this hypothesis, we: (*i*) quantified how recent extreme drought events influenced primary and secondary growth of *Quercus 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 Pyrenean 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. Pyrenean oak 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 Pyrenean 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, *Quercus 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, containing 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 selected 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), appearing 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.

Greenness data to assess ecosystem resilience

Vegetation greenness of *Quercus 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 compiled for the period 2000 - 2016. We selected the pixels covering the distribution of *Quercus pyrenaica* forests in Sierra Nevada ($n = 928$ pixels). Any values affected by clouds, snow,

shadows or high content aerosols, were filtered out following recommendations for mountain regions (Reyes-Díez and others 2015).

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

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

Field sampling and dendrochronological methods to assess individual tree resilience

Trees were sampled during the autumn of 2016 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 wetter 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), constituting the current low-elevational limit (CA-Low) and the tree-line (CA-High), respectively, in the site sampled. Despite the proximity of these two elevations (less than a 200-m difference) the stands differ markedly 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). At each site, between 15 and 20 trees from either the single dominant-codominant layer in CA or the open canopy in SJ were randomly sampled. Two cores of 5 mm in diameter were taken from each tree at breast height (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 with a 10-m radius. Several competition indices were calculated: the distance independent indices *density* ($trees \cdot ha^{-1}$), and *basal*

area ($BA, m^2 \cdot ha^{-1}$); and the distance dependent index size ratio proportional to distance as $srd = \sum_{i=1}^n (d_{bh_i/dbh_i}) \cdot [1/(dist_{ij} + 1)]$ (see Gea-Izquierdo and Cañellas 2009 for more details). Differences between sites for height, DBH, and competition indices were analyzed using non-parametric Kruskal-Wallis rank sum tests. When significant differences were detected, multiple comparisons were run 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 determined with a measuring device coupled to a stereomicroscope, for 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 growth response to the inter-annual variability of climate (short-term response), pre-whitened residual chronologies (RWI) were used. These 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 dp1R (Bunn 2010). Mean residual site chronologies were established by 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, $cm^2 \cdot year^{-1}$). In theory, 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 growth (Biondi and Qeadan 2008). Raw ring widths and measured DBH were used to compute BAI (Piovesan and others 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 tree-ring formation. For each individual tree, a mean BAI series was calculated. Then, mean site BAI chronologies were determined by averaging individual tree BAI time series.

Disturbance analyses

Disturbance chronologies were built using tree-ring width to identify abrupt and sustained increases (release events from competition) or decreases (suppressions) 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: $\%GC = [(M1 - M2)/M2] \times 100$, where M1 is the preceding 10-year median and M2 is the subsequent 10-year median (Rubino and McCarthy 2004).

Site-disturbance chronologies were constructed by annually averaging the individual disturbance series. To separate growth peaks caused by disturbance events and expressing stand-wise disturbances from those caused 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 history of the forest and management of our sampling sites was inferred from a detailed analysis of historical land-use changes. For this, existing historical documents were exhaustively reviewed to compile information on socio-economical activities affecting the forests being studied (Table S4). We reviewed several documentary sources: historical documents and maps; detailed mining reports; official information on recent wildfires events and forest-management practices; livestock farming; traditional irrigation channels; and studies concerning the socioeconomic dynamics of forests on 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 individual tree 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 ($R_t = \text{Drought} : \text{PreDrought}$) quantifies the severity of the impact of the disturbance in the year it occurred. The Recovery index, computed as the ratio between performance after and during disturbance ($R_c = \text{PostDrought} : \text{Drought}$), represents the ability to recover from disturbance relative to its severity. Finally, the Resilience index ($R_s = \text{PostDrought} : \text{PreDrought}$) 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 over a period of three years before and after the drought event, respectively. A period of three years was chosen because we found similar results on comparing periods of two, three, and four years (Figure S3b), and this time period has been 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

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 exposures). 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 exposure) 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). The strongest reduction in radial growth occurred in the 1995 drought (the worst drought spell in our climatic record, Table S3) for all sites. Tree-growth reduction followed a moisture gradient. The southern sites (CA-High and CA-Low) showed less tree-growth reduction 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 (CA-High).

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.

282 Resilience to drought events at the ecosystem and individual-tree levels

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

290 During the last two drought events, resilience metrics for greenness and tree growth significantly differed
 291 between drought events (Table S1). The 2005 drought event reduced greenness and growth more than
 292 that of 2012 (Table S2) but the metrics of resilience generally covaried in the same direction during those
 293 two years. Resilience and resistance values were significantly higher for 2012, the most severe event,
 294 than for 2005 in both variables (Table S2; Figure 6). Thus, recovery values for greenness were higher for
 295 2005 than for the 2012 drought event. Recovery showed a contrasting pattern for EVI and tree growth.

296 The resilience metrics calculated varied significantly between sites, except for resilience of tree growth (p
 297 = 0.534; Table S1), which was similar among the three sites. The two southern populations showed lower
 298 recovery values than did the northern site both for greenness and tree growth, but resistance and
 299 resilience values were significantly higher for the southern site (Table S2).

300 Tree-growth response to climate

301 The response of tree growth to water availability was greater than to temperatures. Cumulative
 302 precipitation of the hydrological year and seasonal SPEI values (*i.e.* for the Hydrological year, Spring and
 303 Summer) were the climatic variables exhibiting the highest (positive) relationship with growth for all
 304 populations (Figure 7a). Nevertheless, differences appeared between northern and southern populations:
 305 the positive relationship with SPEI was highest in the more xeric northern population ($r > 0.6$ vs. $r < 0.5$;
 306 Figure 7a). In addition, the spring maximum temperature was the most significant limitation for tree growth
 307 only for the southern populations (Figure 7b and 7c), whereas minimum and maximum temperatures of
 308 the current September positively influenced tree growth only in the northern population.

309 Discussion

310 By using a combined approach of remote-sensing information and dendrochronology, we have quantified
 311 the drought impact on the *Quercus pyrenaica* forests of Sierra Nevada and their resilience to several
 312 severe drought events in the recent decades. Our results indicated that these relict oak populations
 313 driven by historical land use are resilient to climate change at their present rear edge. However,

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3 314 resistance, resilience, and forest recovery to extreme drought events are strongly influenced by mountain
4 315 exposure, local environmental conditions, and management legacies. This means that the geographical
5 316 and the ecological rear edges do not necessarily match and, at a small spatial scale, tree performance
6 317 varies markedly along the rear edge under climate change.
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10 318 **Land-use legacies shape sensitivity to climate change of forests and the present rear edge**
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13 319 The review of historical documents revealed that forest clearings, firewood removal, charcoal making, and
14 320 mining have strongly affected the forests on Sierra Nevada (Table S4), where an estimated historical loss
15 321 of broadleaf *Quercus* species approaches 90% of the cover at medium and low elevations (Jiménez-
16 322 Olivencia and others 2015). Together with the analysis of the disturbance chronologies, the observed
17 323 notable differences in stand structure, tree size, and age suggest different forest histories and a different
18 324 management origin (*i.e.* land-use legacy) between northern (coppice) and southern populations (high
19 325 forest, open woodland). On the northern slopes of Sierra Nevada (*e.g.* SJ site), land uses have been
20 326 historically distributed along an elevational gradient: grasslands and shrublands for cattle farming at the
21 327 highest elevations; then forest stands with some croplands; and irrigated terraces with tree crops at the
22 328 lowest elevations (Jiménez-Olivencia and others 2015). In addition, other activities such as mining must
23 329 have altered the forest structure, *e.g.* the SJ site has many small mines and quarries that were exploited
24 330 intermittently throughout history. The release growth event discerned for the 1940s concurs with a period
25 331 of maximum mining activity in this area (1925 to 1957), during which timber use increased for mine
26 332 tunnels and furnaces, these also requiring large amounts of firewood to melt the mineral (Table S4). This
27 333 heavy exploitation of the neighboring forest resources must have affected a significant part of this oak
28 334 woodland, as shown by growth of the remnant trees at the northern site (Figure S2b).
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36 335 On the other hand, woodlands on the southern slopes (*e.g.* CA site) were mixed with a greater
37 336 percentage of croplands along the elevational gradient where oaks grow (Jiménez-Olivencia and others
38 337 2015). Firewood, charcoal, and acorns have been intensively exploited at the southern sites, until at least
39 338 the mid-20th century, when these activities sharply declined due mainly to rural abandonment and the
40 339 use of gas and fossil fuels (Valbuena-Carabaña and Gil 2013). At the CA-High site, the only positive
41 340 release event found for the earliest years could be related with conversion from closed forest to an open
42 341 silvopastoral system, a common management type which has been applied in the past in Iberian oak
43 342 woodlands (Cañellas and others 2004; Gea-Izquierdo and others 2011) and which has been documented
44 343 for this site (Valbuena-Carabaña and Gil 2013).
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50 344 The other release event observed for the SJ site during the period 1995-2000 was lower than during
51 345 1940, but also affected most trees (Figures 4, S2b). No records of forest practices in this area over the
52 346 last 30 years have been found (Bonet and others 2016), and no logging has been recorded during the
53 347 period 1995 - 2000 (F.J. Cano-Manuel *personal communication*). Therefore this release might be related
54 348 to natural drought-induced mortality after 1995, as has been reported for other Mediterranean tree
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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 *Quercus 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). As with many other forest species under Mediterranean climates, moisture availability is generally the most limiting factor driving radial growth of *Quercus pyrenaica* along its distribution range in the Iberian Peninsula (Gea-Izquierdo and Cañellas 2014). Thus, our results are consistent with those of 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 did the southern sites during the 2005 drought event, and the stronger correlations of tree-growth with SPEI (hydrological year and summer) in the northern site can be interpreted as higher sensitivity to drought at 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; Babst and others 2013), particularly for rear-edge populations (Cavin and Jump 2017; Dorado-Liñán and others 2017b). Trees at CA-High registered 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 along a narrow gradient, which is especially noteworthy for southern sites, as these lie close to each other and overall both are considered to constitute the rear edge for the species.

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

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

Although the 2012 drought event was more severe and intense than that of 2005 (Table S3), resilience values for greenness and tree growth were greater for 2012. This could be due to the different timing of the two droughts. The 2012 event 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 the drought as a key factor determining tree recovery after drought (Camarero and others 2015a; Huang and others 2018). For tree growth, the highest values of resilience were found for the two most severe events (1995 and 1999; Table S3) and tree-growth resilience was positively related to drought severity (Figure 5).

The high drought-resilience values reported here, coinciding with high values of genetic resilience for those forests on Sierra Nevada reported elsewhere (Valbuena-Carabaña and Gil 2013, 2017) appear to indicate the strong local adaptation of this oak. Our findings agree with those of studies showing 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 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, as in 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 *Quercus 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.

Concluding comments

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 *Quercus 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 the tree level at the wettest site along the climatic gradient analyzed. The trees exhibited high resilience values in response to drought, particularly in the long-term scale. These findings are consistent with other results showing that this mountain region is still acting as a refuge for deciduous species, including *Quercus*. The differences found in tree growth and resilience to drought between sites close together show that responses to drought were site dependent and can drastically vary even in very narrow 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 as *Quercus pyrenaica*, not only for conservation *per se* of the species, but for all ecosystem services that these singular forests offer.

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Table 1. Characteristics of sampled plot. Lat = latitude; Long = longitude. Dbh and height of all trees, Basal Area (BA), Density and SRD (size ratio proportional to distance) are computed for all trees within a 10-m radius of focal trees (see Materials and methods). Temp.: annual average of mean monthly minimum and maximum temperatures. Values shown here correspond to site averages. Standard deviations are shown in parentheses. Different letters indicate statistically significant differences between sites (Kruskal-Wallis test followed by Dunn's test, $p < 0.05$). Stands were monospecific, hence all results correspond to oak data.

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

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 (m ² 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

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.

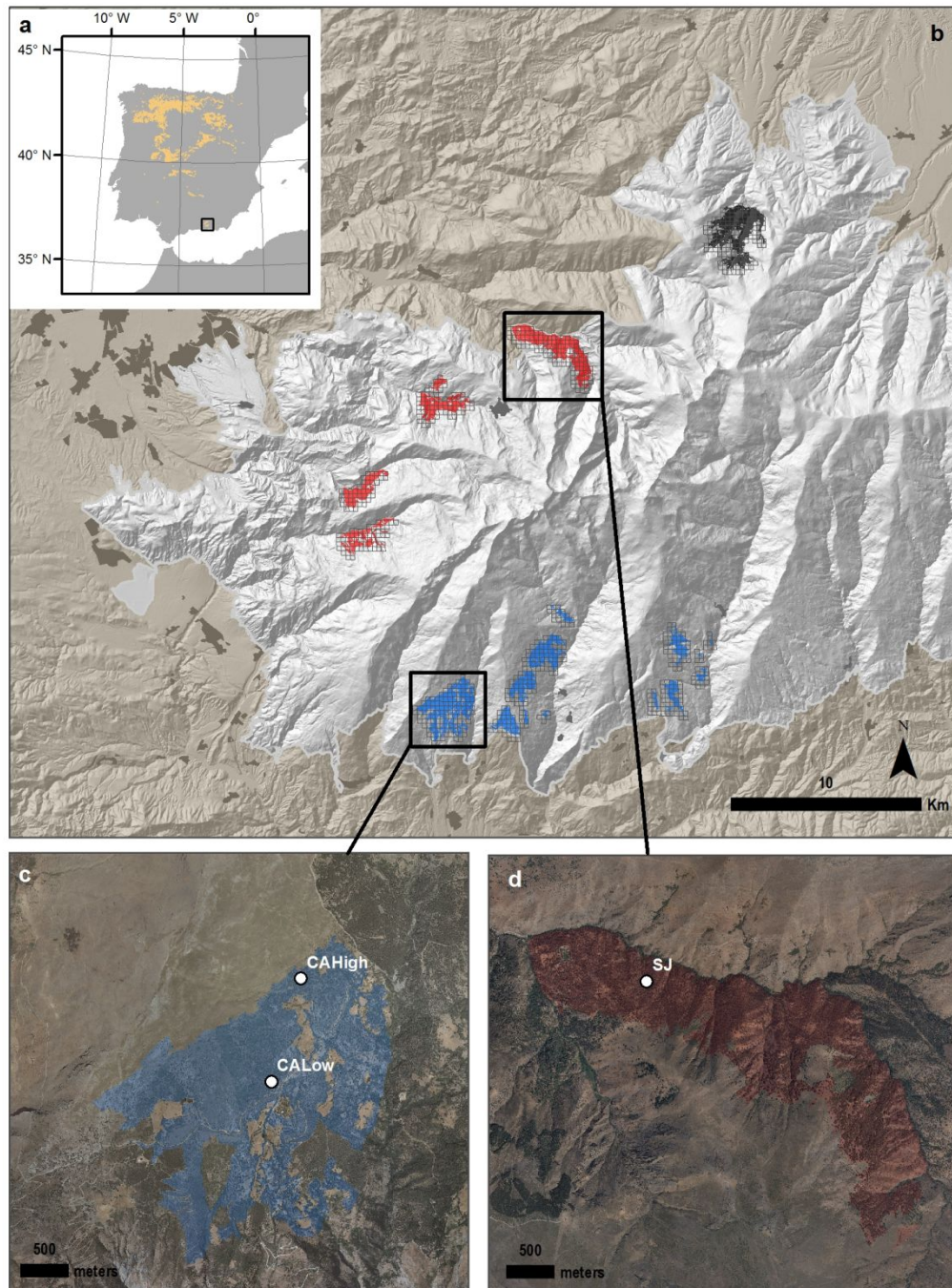
Figure 3. Basal Area Increment (BAI) chronologies of *Q. pyrenaica* for northern population (SJ; *red*) and southern ones: low-elevation (CA-Low; *green*) and high-elevation (CA-High, *blue*) sites. Shading areas correspond to standard error of the mean. Number of series is displayed in the upper plot. 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.

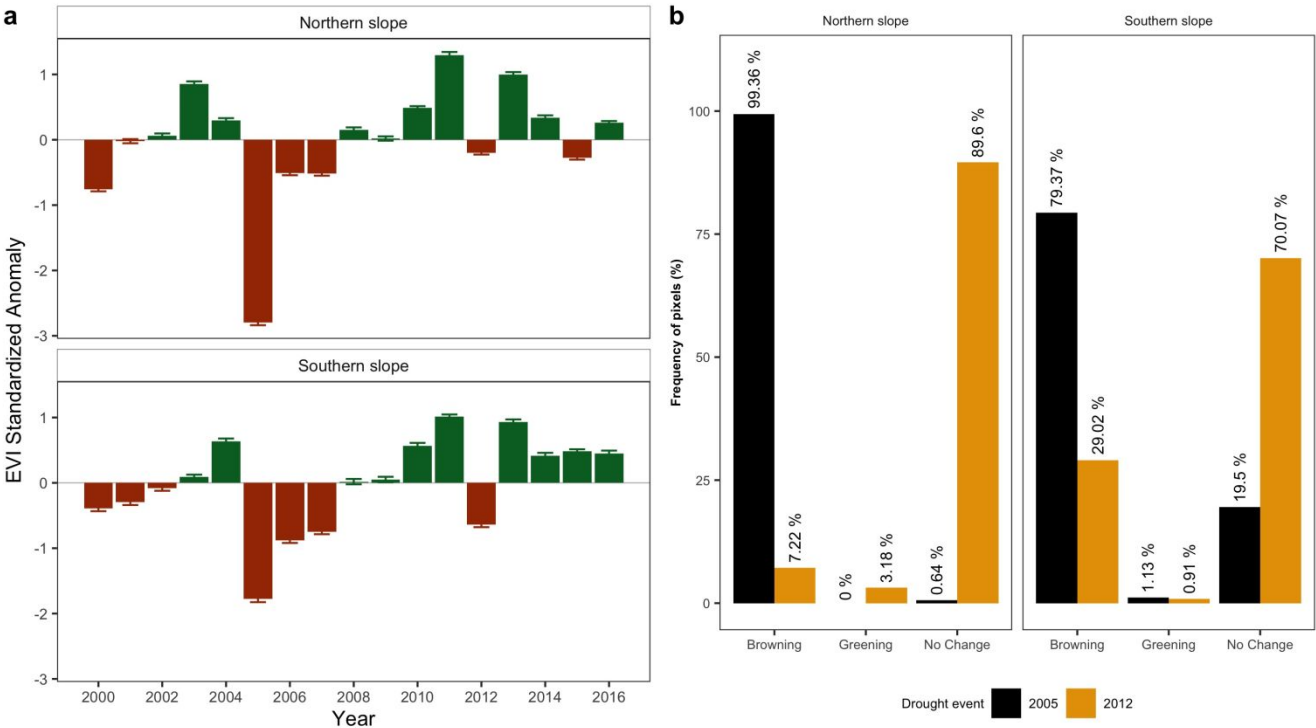
Figure 6. Comparison of the response of *Q. pyrenaica* forests to drought in terms of resistance, recovery, and resilience of greenness (a) and tree growth (b). For EVI, northern populations (*red circle*) were compared with southern ones (*green circle*). For BAI, the more xeric northern population (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).

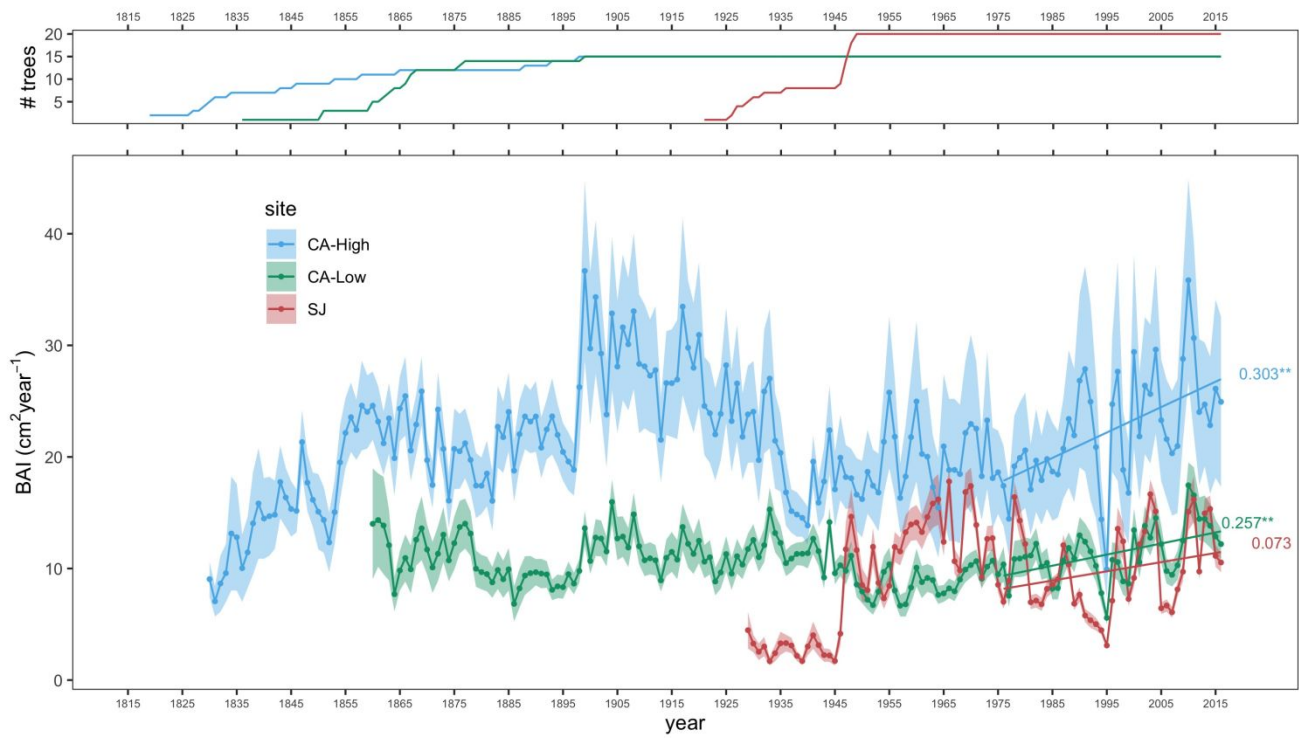
Figure 7. Correlation coefficients found by relating tree-ring residual chronologies (RWI) of *Q. pyrenaica* and monthly climatic data: precipitation and 6-month SPEI (a), minimum (b) and maximum (c) temperatures. *green* bars: northern site (SJ); *light blue* bars: low-elevation southern site (CA-Low);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

34 **Figure 1**

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36 **Figure 2**



38 **Figure 3**

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Figure 4

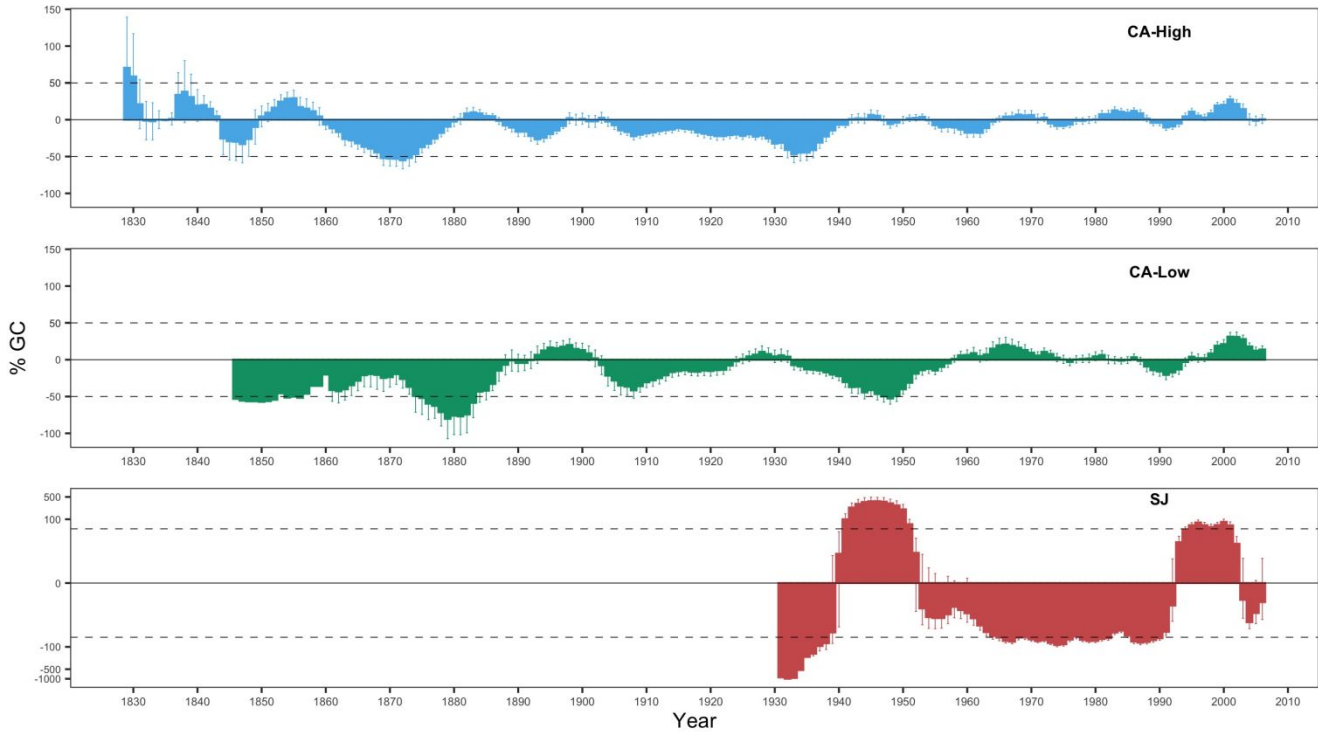


Figure 5

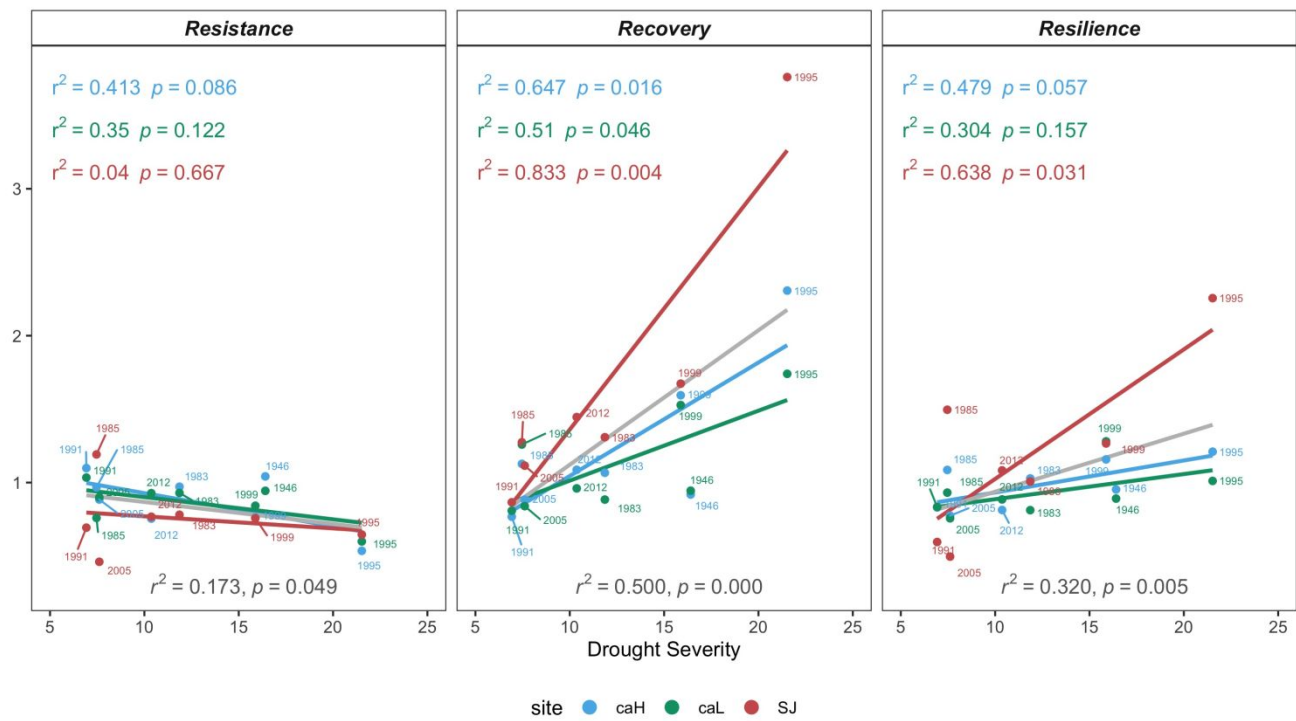
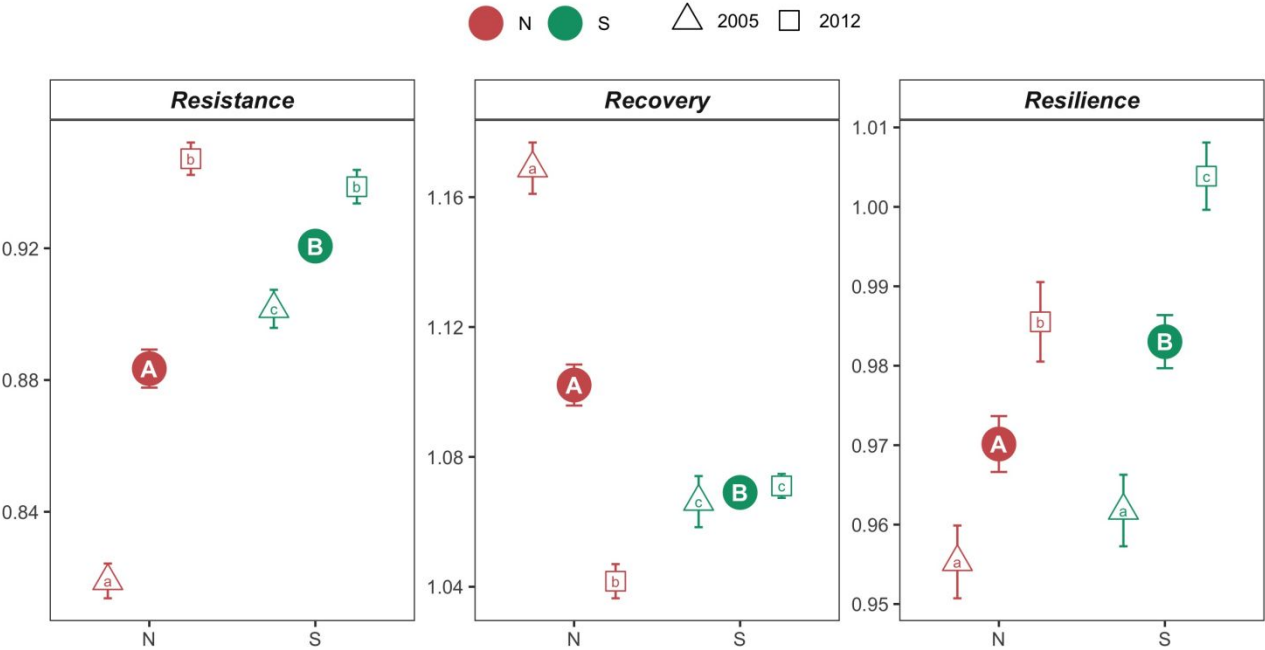


Figure 6

a

EVI



b

BAI

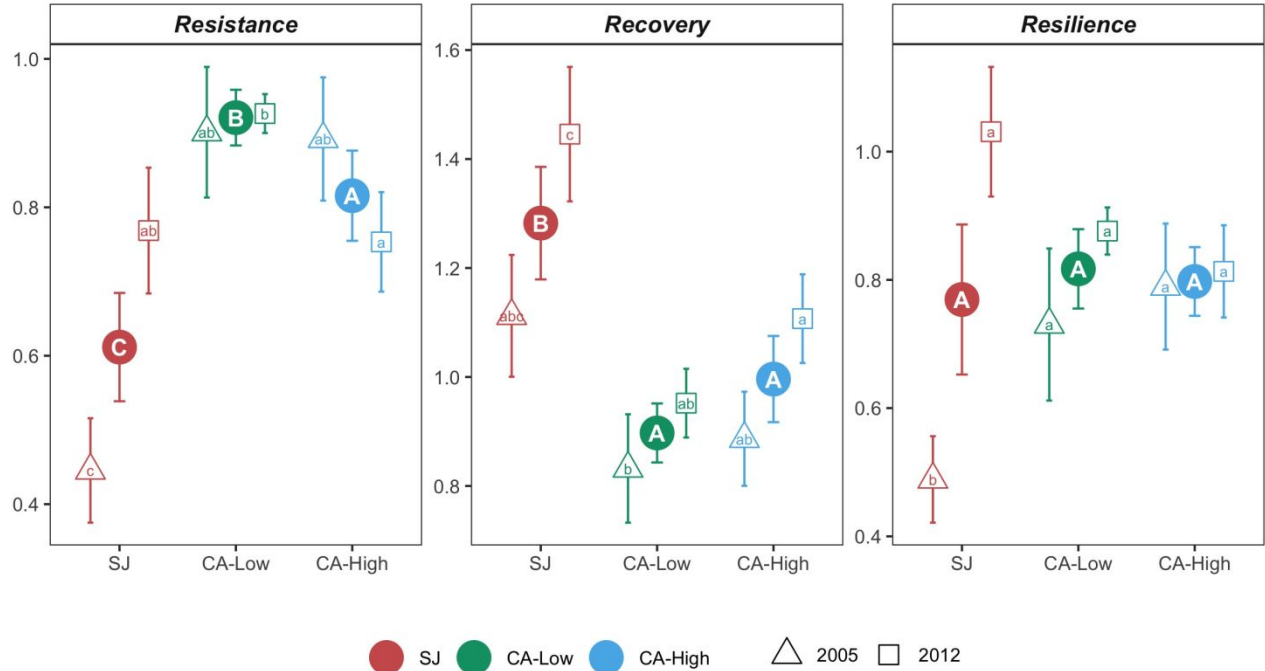
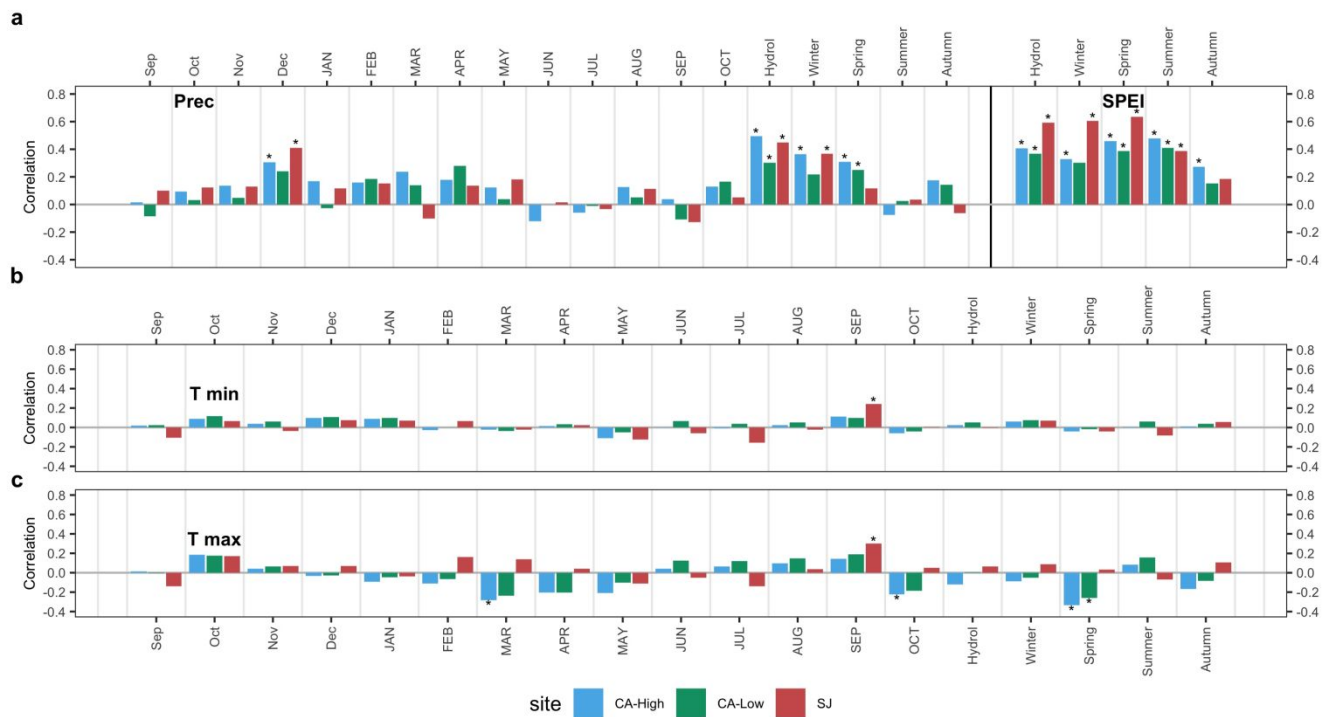


Figure 7



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2 1 **Supplemental Material**
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5 2 **Table S1.** Robust two-way ANOVAs of the resilience metrics of greenness (EVI) and tree growth (BAI)
6 3 for the two drought events (in 2005 and 2012) and site.
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9 4 **Table S2.** Robust measures of central tendency of resilience indices for greenness (EVI) and tree growth
10 5 (BAI), grouped by drought events, site, and interaction. Measures of central tendency are M-estimators
11 based on Huber’s Psi (see Materials and methods). In parentheses are the 95% confidence intervals
126 based on 3000 bootstraps. *Total* corresponds to the average of 2005 and 2012.
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16 8 **Table S3.** Drought events for the 1901-2016 period for Sierra Nevada ranked according to drought
17 9 severity calculated from the SPEI index (12 months scale). See Materials and methods for details.
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20 10 **Table S4.** Review of the forest and management history of the sampling sites. Historical documents were
21 11 exhaustively reviewed to compile information on socio-economical activities affecting forests: historical
22 documents and maps (e.g. Titos 1990); detailed mining reports (e.g. Maestre 1858); official information
23 on recent wildfire events and forest-management practices (e.g. Bonet and others 2016); livestock
24 farming (e.g. Moreno-Llorca and others 2016); traditional irrigation ditches (e.g. Ruiz-Ruiz 2017) and
25 other studies reviewing the socioeconomic dynamics of forest of Sierra Nevada at different scales (e.g.
26 Jiménez-Olivencia and others 2015).
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Table S1

Variable	Factor	Resistance		Recovery		Resilience	
		F	p	F	p	F	p
EVI	Drought event	799.9	< 0.001	312.0	< 0.001	207.2	< 0.001
	Site	153.2	< 0.001	105.4	< 0.001	29.8	< 0.001
	Drought event:Site	234.7	< 0.001	364.3	< 0.001	6.1	0.014
BAI	Drought event	6.0	0.019	29.5	< 0.001	44.3	< 0.001
	Site	59.3	< 0.001	53.1	< 0.001	1.3	0.534
	Drought event*Site	32.2	< 0.001	4.4	0.134	30.0	< 0.001

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Table S2

		2005			2012			Total		
Variable	Sites	Resistance	Recovery	Resilience	Resistance	Recovery	Resilience	Resistance	Recovery	Resilience
EVI	Northern slope	0.819 (0.814 - 0.824)	1.169 (1.161 - 1.177)	0.955 (0.951 - 0.960)	0.947 (0.942 - 0.952)	1.042 (1.036 - 1.047)	0.986 (0.980 - 0.990)	0.884 (0.878 - 0.889)	1.102 (1.096 - 1.108)	0.970 (0.967 - 0.974)
	Southern slope	0.902 (0.896 - 0.907)	1.066 (1.058 - 1.074)	0.962 (0.957 - 0.966)	0.939 (0.934 - 0.944)	1.071 (1.067 - 1.075)	1.004 (1.000 - 1.008)	0.921 (0.917 - 0.925)	1.069 (1.065 - 1.073)	0.983 (0.980 - 0.986)
	All	0.858 (0.854 - 0.863)	1.120 (1.113 - 1.126)	0.958 (0.955 - 0.962)	0.943 (0.940 - 0.947)	1.057 (1.054 - 1.060)	0.995 (0.991 - 0.998)			
BAI	CA-High	0.892 (0.809 - 0.975)	0.887 (0.800 - 0.973)	0.790 (0.691 - 0.888)	0.753 (0.686 - 0.820)	1.107 (1.026 - 1.188)	0.813 (0.741 - 0.885)	0.816 (0.755 - 0.876)	0.996 (0.917 - 1.075)	0.798 (0.744 - 0.851)
	CA-Low	0.901 (0.813 - 0.989)	0.832 (0.733 - 0.932)	0.730 (0.612 - 0.849)	0.926 (0.900 - 0.953)	0.952 (0.889 - 1.015)	0.876 (0.839 - 0.913)	0.921 (0.883 - 0.958)	0.897 (0.843 - 0.951)	0.817 (0.755 - 0.879)
	SJ	0.445 (0.375 - 0.516)	1.112 (1.000 - 1.224)	0.489 (0.421 - 0.556)	0.769 (0.684 - 0.853)	1.446 (1.322 - 1.569)	1.031 (0.930 - 1.132)	0.612 (0.539 - 0.685)	1.282 (1.179 - 1.386)	0.769 (0.652 - 0.886)
	All	0.721 (0.644 - 0.798)	0.946 (0.879 - 1.013)	0.653 (0.585 - 0.721)	0.819 (0.776 - 0.863)	1.161 (1.081 - 1.240)	0.911 (0.865 - 0.957)			

Table S3

Duration	Intensity	Severity	Lowest	Months	Year
11	-1.957	21.524	-2.585	Jan - Nov	1995
11	-1.581	17.391	-2.024	Nov - Sep	1913-1914
9	-1.823	16.409	-2.42	May - Jan	1945-1946
9	-1.764	15.880	-2.056	Dec - Aug	1998-1999
8	-1.482	11.859	-1.654	Feb - Sep	1983
6	-1.728	10.367	-1.906	Mar - Aug	2012
5	-1.905	9.527	-2.300	Jan - May	1925
5	-1.522	7.611	-1.571	May - Sep	2005
5	-1.493	7.463	-1.537	May - Sep	1985
5	-1.385	6.926	-1.444	Apr - Aug	1991
4	-1.714	6.855	-1.833	May - Aug	1931
4	-1.363	5.453	-1.441	May - Aug	1927

24 **Table S4**

Use	Cáñar (CA sites)	Güejar-Sierra (SJ site)	References
Land use	Oak Woodlands mixed with a high percentage of croplands even reached high elevations (mainly barley, rye, and potatoes). Irrigated crops near the village (" <i>regadío de vega</i> ")	Grasslands and shrublands for cattle raising located at high elevations. Then forest formations (oak woodlands) with some croplands (mainly herbaceous and potatoes). Irrigated terraces with tree crops (chestnut trees, cherry trees)	Jiménez-Olivencia and others (2015); Zoido and Jiménez Olivencia (2015); Moreno-Llorca and others (2016); Calatrava and Sayadi (2019)
Forest Management Practices	Nearby areas were afforested (pine plantations) to avoid soil erosion in 1925, 1928, 1950, and 1970 Selective thinning during 2007 in a small area near " <i>Casa Forestal</i> " Tree cleaning near trails/paths (2009-2010)	Afforestation of the upper areas of the Genil River basin (1942) Tree cleaning (2006 - 2007) near our study site (<i>La Hortichuela</i>) Scattered afforestation (creation of small, scattered islands of oaks) (2008)	Bonet and others (2016); Moreno-Llorca and others (2016); J. Navarro and F.J. Cano-Manuel <i>personal communications</i> ; Romero-Zurbano (1909)
Forest structure	Inventories of trees made by the Spanish Navy during the second half of 18th century: 2,010,200 new trees; 10,791 growing trees . For the Cáñar site, more than 2,000,000 trees were reported, most of them new, and no old trees were counted, suggesting recent tree felling.	Inventories of trees made by the Spanish Navy during the second half of 18th century: 639 550 new trees; 56 700 growing trees; 220 old trees	Cruz (1991); Wing (2015)
Fires	Several small fires. 1979: 44 Has of Pyrenean oak forests (near " <i>Casa Forestal</i> ") 1984: 189 Has of Pine plantations and Holm oak forests (" <i>El Jara</i> ") 1994: 65 Has of Pine plantation (" <i>Puente Palo</i> ")	Not recorded in the area since 1975	Bonet and others (2014); Moreno-Llorca and others (2016); CMA (2018)
Fruit production (acorns)	Old references have indicated traditional acorn gathering. Auctions of public forests to collect acorns (1927; 1954)		Catastro (1752); Mesa-Torres (2009); Bonet and others (2014)
Wood	Traditional charcoal (" <i>carboneo</i> ") making and firewood cutting throughout history. Several references have indicated firewood collection at this site at least since 1572. At the beginning of the last century (1900s), 3 - 4 woodcutters collected firewood from Pyrenean forests daily.	Some references of wood removal for subsistence (1826; 1847). Massive logging during the first decades of 20th century. As a result, several old photos show areas without trees where oak forests stand today (1925; 1932)	Catastro (1752); López (1776); Madoz (1846); Titos Martínez (1997); Ferrer (1999); Jiménez-Serrano and Serrano-Gutiérrez (2004); Mesa-Torres (2009); Bonet and others (2014)
Mining activities	No mining in the area, only scattered private excavations	Intermittent exploitation throughout history. Historical documents indicated two periods of intense mining: the second half of the 19th century after the publication of detailed mineralogical reports and during the first decades of the 20th century until 1960, which is the last year with evidence of mining. Evidence of several furnaces to melt minerals (Cooper)	Maestre (1852); Maestre (1858); Titos (1990); Arnedo (2007); Mesa-Torres (2009)
Quarries		Exploitation of serpentine quarries from the 16th to 19th century (<i>Jaspe Verde</i>)	Navarro and others (2014)
Traditional irrigation channel	An irrigation channel (" <i>Acequia de la Era Alta</i> ") is located uphill of the CA-High site (<i>i.e.</i> >2000 m), which functioned from March to June	Several historical irrigation channels, known as <i>acequias de careo</i> , were used since the Middle Ages to cultivate these valleys. Most are abandoned and deteriorated, probably at least since the 1960s.	Martín-Civantos (2014); Martín-Montañés and others (2015); Ruiz-Ruiz (2017)

Figure S1. a) Temporal evolution of cumulative precipitation (hydrological year) during the period 1950-2017. Points represent the mean, and error bars the standard error. The black line indicates mean for the entire period (585 mm). The red lines represent -1 and -2 standard deviation (dotted and dashed lines, respectively). The blue lines represent +1 and +2 standard deviation (dotted and dashed lines, respectively). Years with average values below -1SD are labeled. Data from 28 meteorological stations distributed around the Sierra Nevada area (from the National Spanish Meteorological Services, AEMET). **Inset plot:** cumulative precipitation during the hydrological years 2004-2005 (blue line) and 2011-2012 (red line). The boxplot representing the average from 1950-2015 period. Data from meteorological station Granada, Base Aérea. **b)** Drought severity in Sierra Nevada for the 1901-2016 period based on the Standardized Precipitation-Evapotranspiration Index (SPEI). Data from Global SPEI database (<http://spei.csic.es/database.html>). We took the SPEI data for a 12-month scale and for all 0.5° grid cells covering Sierra Nevada. Horizontal gray bars indicate the years 2005 and 2012.

Figure S2. a) Residual tree-ring chronologies determined for the *Q. pyrenaica* sites. Dashed red lines indicate the start of the reliable period ($EPS > 0.85$). Dotted black lines show the severe drought years identified in our climatic data (Table S3 and Figure S1). **b)** Percentage of *Q. pyrenaica* trees affected by GC > 50 % by site. **Black** line shows number of trees (right-axis). Data for number of trees > 2 is shown.

Figure S3. a) Correlation among site chronologies (CA-High, CA-Low and SJ) in different time domains after pre-filtering the time series with increasing size of the moving-average window (1 to 40 years). Each site chronology was smoothed using centered moving averages with different window sizes (1 to 40 years), and then Pearson's correlation coefficient between the each pair of chronologies was calculated. Significance was tested using 1000 bootstrap replicates and with 95% confidence intervals built using the R package boot. **b)** Correlation between indices of resilience (R_t , resistance; R_c , recovery; R_s , Resilience) using periods of several lengths (2, 3 and 4 years after a drought).

Figure S4. EVI annual profile (average of the period 2000-2016) for *Q. pyrenaica* forests in Sierra Nevada and drought events. Horizontal bars correspond to the most severe droughts for Sierra Nevada since 1900 (computed as in Table S3). Their position indicates the start and end months of each drought event. Bars lengths show the duration of the drought event (number of consecutive months with SPEI lower than -1.28, see (Páscoa et al. 2017)).

Figure S5. Resilience metrics of the tree growth for severe drought events since 1950 (excluding 1995 drought event). **Left:** Resistance (R_t); **Center:** Recovery (R_c); **Right:** Resilience (R_s). Points indicate resilience metrics for oak populations: SJ (*blue*), CA-High (*red*) and CA-Low (*green*). Resilience metrics were computed for each population (sample depth > 10) and drought event. The gray line represents overall relationship for each Resilience metrics.

Figure S1

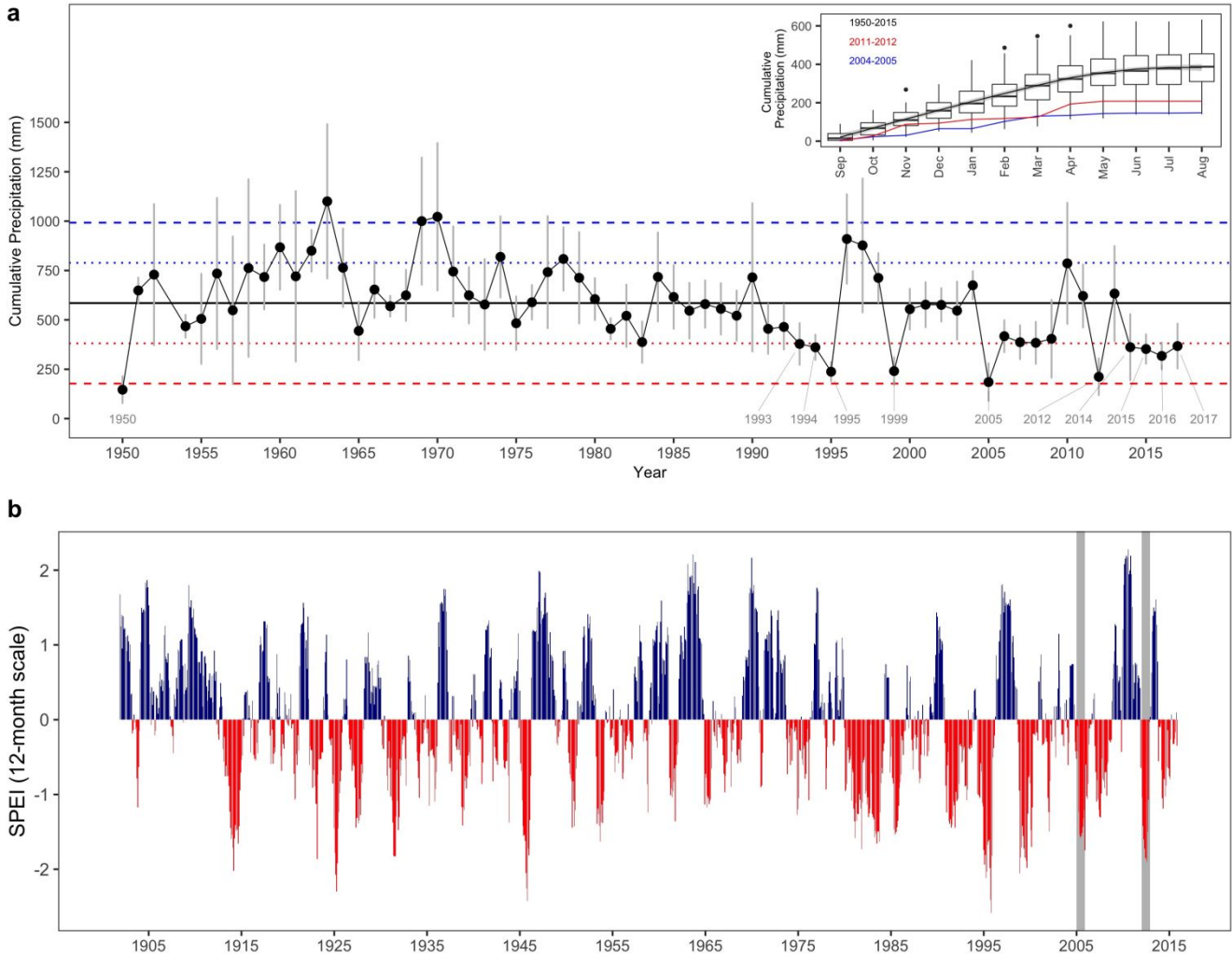
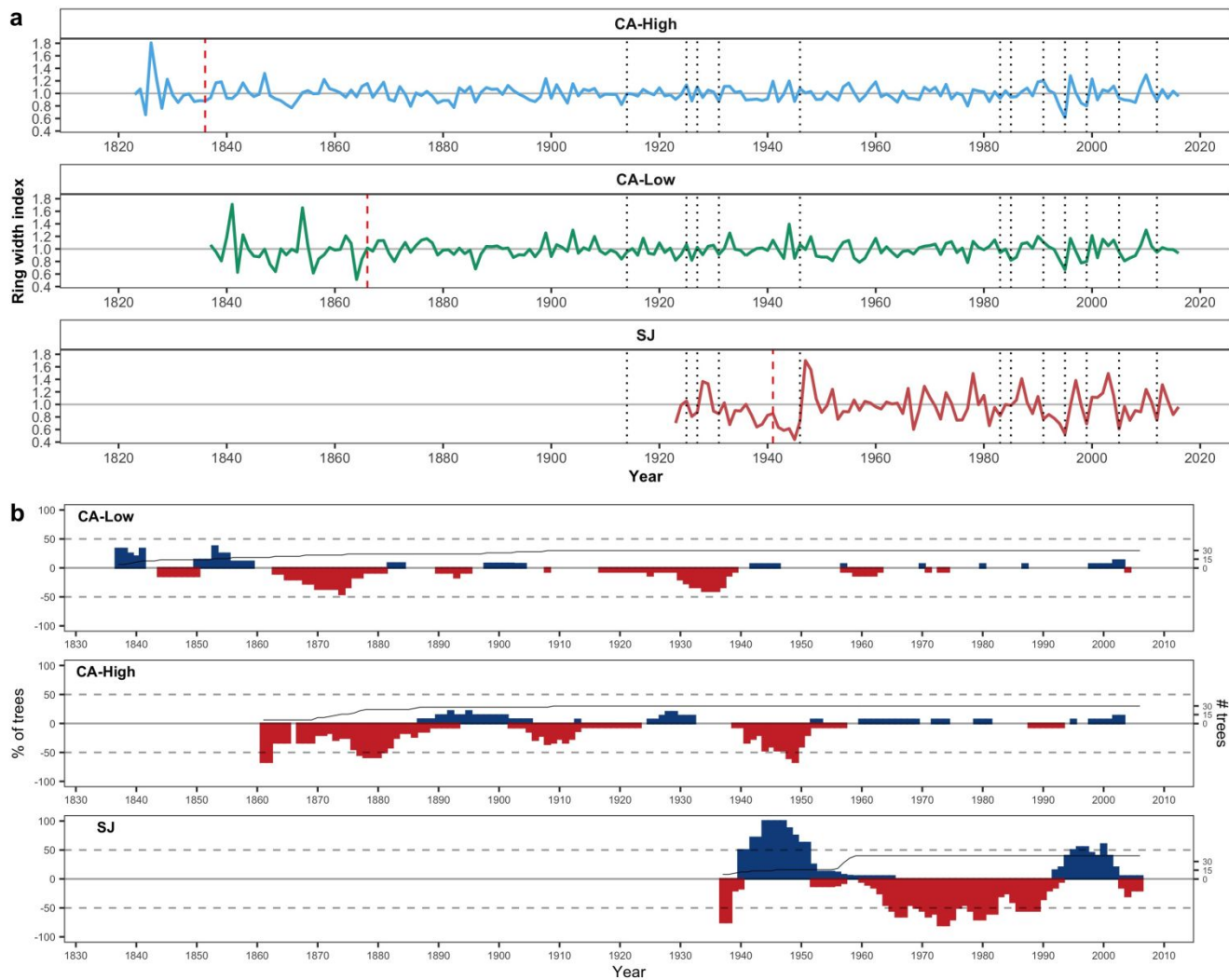


Figure S2



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Figure S3

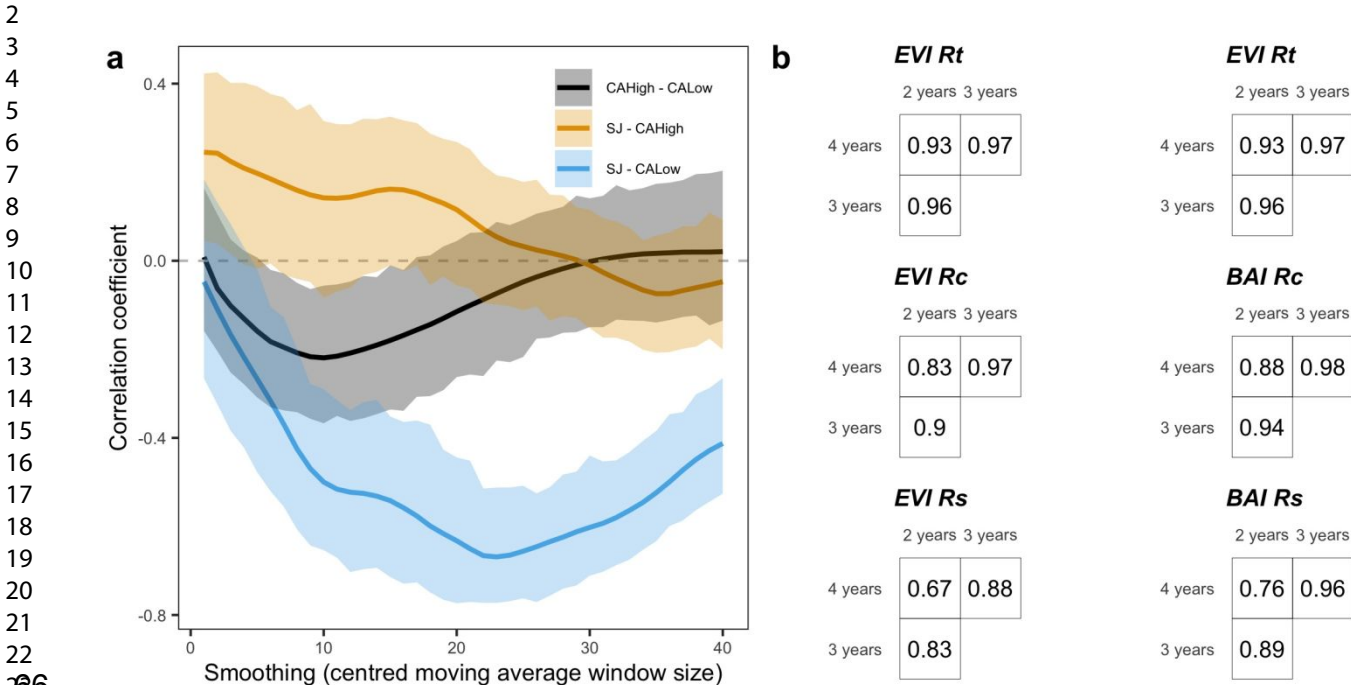


Figure S4

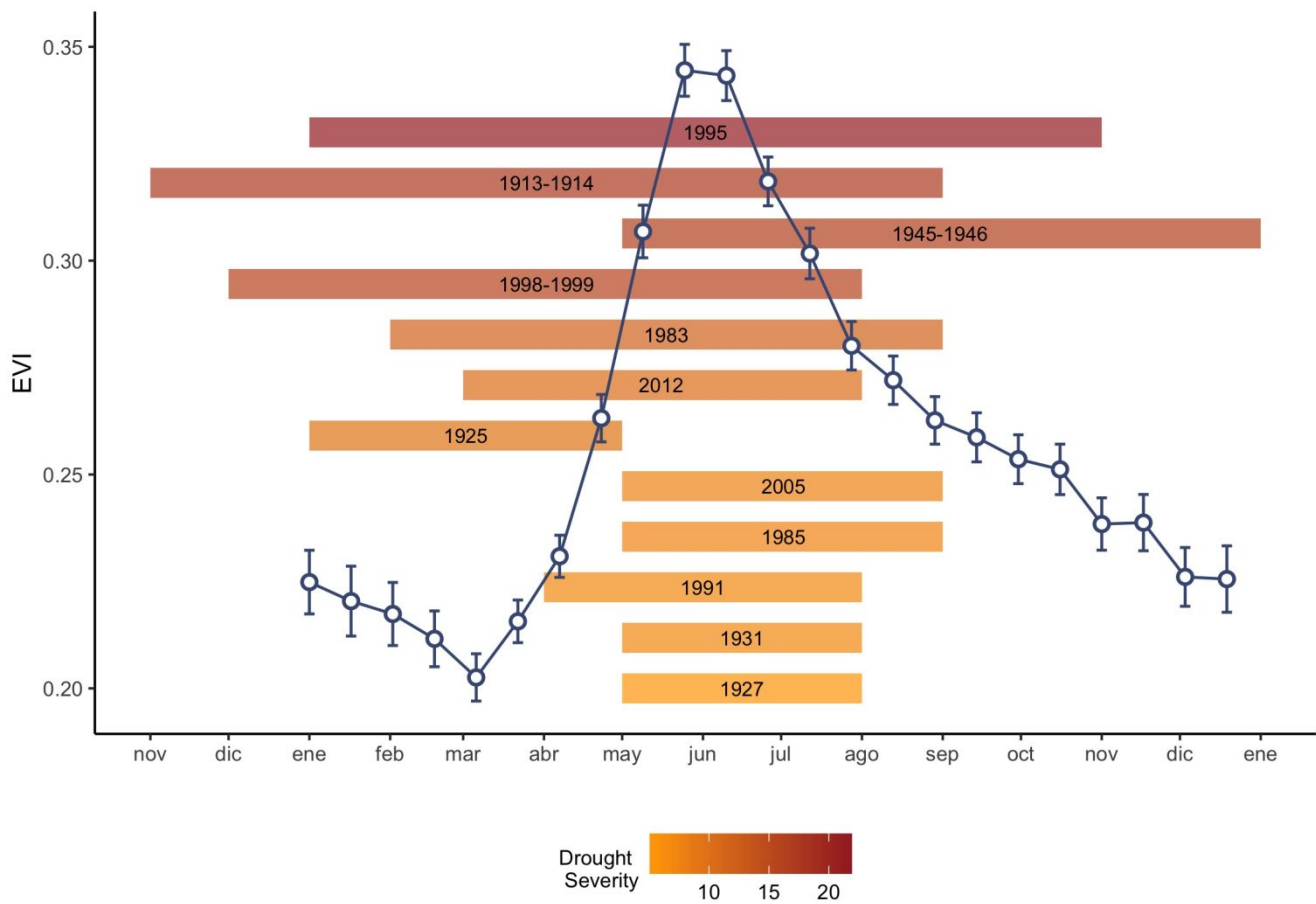
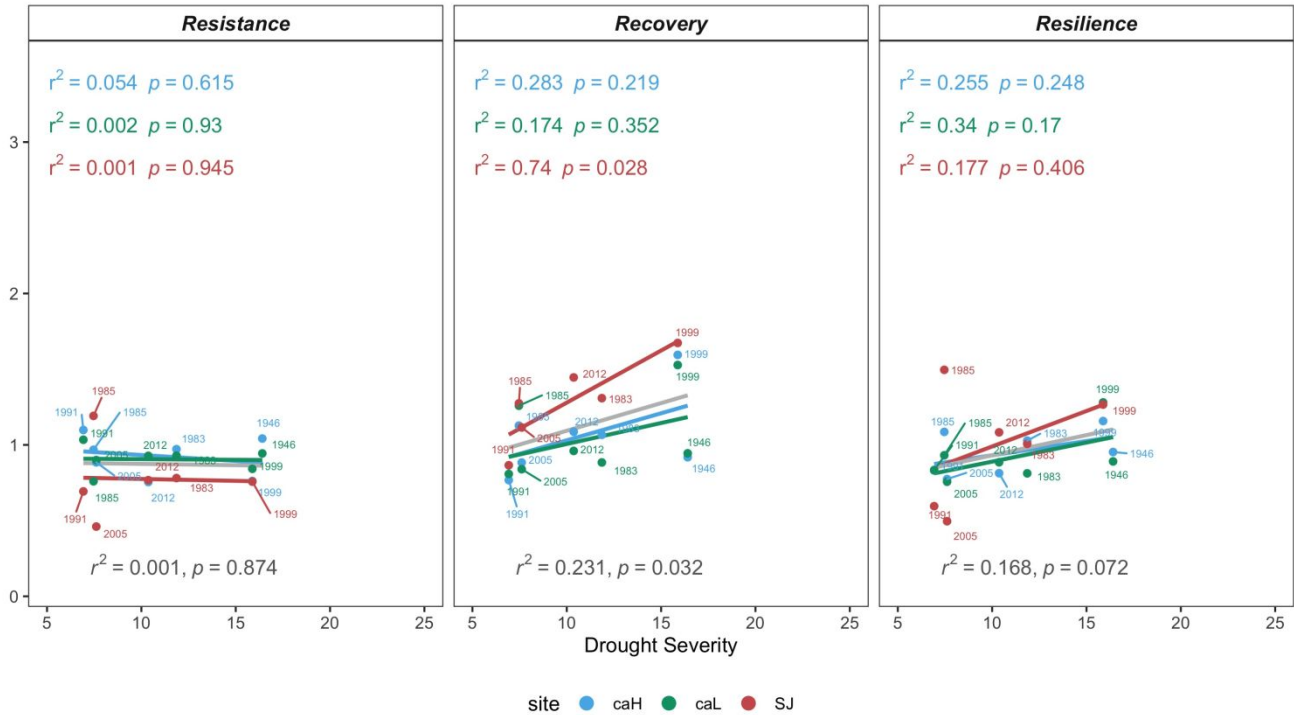


Figure S5



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