RESPUESTA DE LOS BOSQUES MIXTOS DE QUECINEAS A LOS CAMBIOS EN EL CLIMA

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Abstract:

Recent changes in climate have induced mortality episodes affecting many oak forests worldwide. However, and despite the ecological importance of these ecosystems, there is scarce information regarding the current health status of oak forests and their response to extreme climate events over time. *Quercus canariensis* is a deciduous oak, sensitive to summer drought characteristic of Mediterranean climate, currently showing growth decline and defoliation or mortality episodes. Here, we investigated how radial growth respond to climate and the changes in resilience to extreme drought events over time in five sites in "Los Alcornocales" Natural Park (Spain) using a dendrochronological approach. This study shows how the microclimate and latitudinal gradient affect to growth and determine the health status of the different populations using the resilience index. Our results show that although the temperature is steadily increasing since 1950, the growth in *Q. canariensis* is mainly limited by low temperatures and, surprisingly, there is only a weak effect of precipitation at some sites. *Q.canariensis* resilience to extreme droughts is overall decreasing since 1970, resulting in a reduced capacity to recover pre-drought growth. These conditions preceded growth declines in some populations, indicating that trees are vulnerable to the observed aridification trend. By the use of growth analyses, we have detected early-warning signals of decline for this Mediterranean oak highlighting the most sensitive populations to further changes in climate.

Introduction

The changes registered in climate over the last decades have the potential to modify the phenology, growth, and the biotic interactions of plant species across the Earth (Parmesan, 2006). The Mediterranean region has been considered as a climate-change hot spot, since it is affected by the interaction between climate processes in mid-latitudes and tropical latitudes (Giorgi & Lionello, 2008). The reconstruction of the last 500 years' climate indicates a negative winter rainfall trend since 1960s in the Mediterranean region (Luterbacher & Xoplaki, 2003). In addition, precipitation during the wet season in this area (October-March) is in a steady decline since 1950 (Esteban-Parra et al., 2022; Zittis et al., 2021) and the climate change models predict an increase in temperatures, a further decrease in precipitation (mainly during spring and summer), together with an increase in the frequency of extreme climate events (IPCC, 2021; Lindner et al., 2010; Moemken & Pinto, 2022). This increased drought stress and higher precipitation variability has been considered the main abiotic cause of forest dieback in the Mediterranean region (Camarero, 2015a; Sánchez-Salguero et al., 2012).

Climate warming can influence performance of tree species by modifying the carbon balance, since drought induce stomatal closure and reduce the photosynthesis, therefore limiting the growth process, modifying the duration of growing season and amplifying the evaporation rates (Colangelo et al., 2018; Muller et al., 2011; Palacio et al., 2014). Consequently, trees under heat stress commonly experience growth reductions and/or defoliations, increasing the mortality risk (Sánchez-Salguero et al., 2012, 2020). Accordingly, understanding the susceptibility of tree populations to increased drought and warming is therefore urgently needed in order to increase our ability to predict and mitigate the negative impacts of changes in climate on forest ecosystems.

Extreme climatic events have the capacity to disrupt existing dynamics of tree species across different scales, ranging from the community level down to individual species. Extreme drought events have the potential to induce a decline in biodiversity (Matías et al., 2011; Thuiller et al., 2005), lead to extensive forest decline (Allen et al., 2012; Breshears et al., 2005), or reduce net growth (Cavin et al., 2013; Matías et al., 2017; Thabeet et al., 2009). Consequently, these extreme events are capable of significantly alter diversity and dominance patterns within plant communities (Matías et al., 2018). Given the escalating frequency of such extreme drought occurrences, particularly in regions like the Mediterranean (Spinoni et al., 2018), studying their consequences has become increasingly vital.

The acclimatation to drought events depends on a multitude of factors including drought history of the growth (Vicente-Serrano et al., 2013), life history strategies (Anderegg et al., 2016), tree size, age and microclimatic conditions related to the topography, among other factors (Anderegg et al., 2016; Bose et al., 2020). In consequence, determining the capacity of tree species to resist and to recover from extreme climate is essential to determine the vulnerability of current forest under a changing climate scenario.

Oak species are among the most important species in terms of economic, cultural, and ecological values in the Mediterranean Region (Nixon, 2006). However, oak species are suffering an alarming mortality increase across the northern hemisphere (Gentilesca et

al., 2017). The oak decline is a process that has been known since the 18th Century in Germany (González Alonso & Johansson, 2008). In Spain, this phenomenon is commonly known as "*la seca*" since the 90s (Brasier, 1992; Tuset et al., 1997). *La seca* affect different *Quercus* species such as *Q.ilex, Q. suber* and *Q. canariensis* with increased defoliation and subsequent mortality (Camarero et al., 2016). Among these, *Q.canariensis* is an isohydric ring-porous tree and winter-deciduous species (Sánchez-Salguero et al., 2020), with a high ecological relevance in Mediterranean forests. However, little is known about the ecological conditions triggering dieback process or about the resilience of deciduous oak species to extreme climatic events in the Mediterranean region.

The geographical region of the north of the Gibraltar Strait is an area of high interest given its high diversity in plant and animal species (Díaz-Villa et al., 2003), geology (limestones and sandstones), elevation (ranging from the sea level to 1654 m a.s.l.) and the key position between Africa and Eurasia (Arroyo & Marañón, 1990). Moreover, dominant warm winds arrive from northern Africa, giving the humidity from the Mediterranean Sea and creating a characteristic fog mainly in the southern mountains, which receive an extra rainfall that is not recorded by the meteorological stations (Jurado-Doña et al., 2022). These local conditions can often result in microclimates that differ from the regional macroclimate, being necessary to explore the influence of topography and local characteristic on vegetation (Kovács et al., 2020). Therefore, understanding how forest can resist drought and recover after these events in different regions is crucial for understanding how drier climate will impact tree functioning and forest productivity (Anderegg et al., 2015). Differences in growth resilience are associated to the loss of adaptive plasticity in drought events, which can be quantified by comparing the growth before and after the drought event (Lloret et al., 2011), and the trade-off between resistance and recovery in some tree species show a strong growth resistance and low growth recovery and vice versa (eg. Camarero et al., 2015b; Sánchez-Salguero et al., 2018).

In this study we follow dendroecological approach using *Quercus canariensis* Willd., as focal species, which is showing an increasing dieback process at Los Alcornocales Natural Park (southern Spain), one of the largest and best-preserved natural forests for this species. We used dendrochronological methods to characterize long-term growth responses to climate and extreme drought event across a geographical gradient varying in distance to sea. The study species is very sensitive to increasing aridity, although has been scarcely studied using dendroecological approaches (Colangelo et al., 2017, 2018; Sánchez-Salguero et al., 2020). Gaining knowledge about the growth behaviour of this species will advance our understanding of drought vulnerability thresholds, as well the current the health status of an important forest area as Los Alcornocales Natural Park.

In this study, we hypothesize that *Q. canariensis* has a differential sensitivity to climate following a latitudinal gradient across Los Alcornocales Natural Park. To prove this, we analysed the growth-climate relations in five *Q. canariensis* populations distributed across a latitudinal gradient within the Natural Park, and evaluated the resistance, recovery capacity and resilience to different drought events occurred during the last decades in the area. This information will allow us to determine the health status of the

different populations sampled and the resilience of these populations to future extreme events.

Materials and methods

Field site

The study was performed at Los Alcornocales Natural Park (Cádiz province, South Spain; 36° 20′N, 5° 36′W; Fig. 1). The area is mainly dominated by a mixed *Quercus suber-Q. canariensis* forest, one of the most important Mediterranean oak woodlands, currently affected by a severe dieback process (Gómez-Aparicio et al., 2012). This area is part of the protected areas of Andalusia since 1989 under the figure of Natural Park and has a north-south orientation between Tarifa coastline and the municipalities of Ubrique, Cortes de la Frontera and El Bosque, occupying an area of 167,767 ha.

Dominant bedrock is made up of Oligo-Miocene siliceous sandstone soils, giving acid and sandy soils (Jurado-Doña et al., 2022; Paneque & Bellinfante, 1999), with basic materials such limestones, calcarenites and malstones in some valleys (Paneque et al., 2000). The mountains follow a north-south orientation at the southern end of the Natural Park, while in the north part they follow a south-east or north-west orientation, being the highest point the Aljibe mountain (1092 m).

Focal species

The Algerian oak (*Quercus canariensis* Willd.) is native to southern Portugal, Spain, Tunisia, Algeria and Morocco (Sánchez-Salguero et al., 2020). It habits in acid soils in the most humid and warm parts of the Mediterranean coastal region in the South of the Iberian Peninsula and Northern Africa (Costa et al., 1998). This species supports a wide range of temperature conditions (0-24ºC; Costa et al., 1998), although it is very sensitive to dry and warm springs (Gea-Izquierdo et al., 2012), distributing across a long altitudinal distribution (100-1.000 m a.s.l.).

At the study area, *Q. canariensis* is associated with the streams and valley bottoms, where the micro-climate conditions are more humid (Urbieta et al., 2008). There are many plant species associated with this tree, such as the epiphytes *Polypodium cambricum* or *Davallia canariensis*, and some vine-like species as *Smilax aspera, Hedera helix, Lonicera periclymenum o Tamus communis* (Pérez-Ramos & Marañón, 2009), usually forming mixed stands together with *Quercus suber* L.

Field sampling

Five different mixed-forest stands dominated by *Q. canariensis* and *Q. suber* were selected during 2022 along a latitudinal gradient within Los Alcornocales Natural Park. To minimize human management impact as far as practicable, populations (Hurones, Sauceda, Picacho, Tala and Comares) were selected within the protected area, trying to maintain differences in tree density, orientation and slope as minimum as possible. In every population, 15 adult trees were randomly selected, covering the natural size distribution of the population.

Each tree was geo-referenced by GPS (GPSMAP 66st, Garmin Ltd., USA) also recording height of the tree, the diameter at breast height (DBH, measured at 1,3 m) and the tree health using the semi-quantitative scale proposed by the ICP Forest Network (Fischer & Lorenz, 2011): no defoliation (0%), light defoliation (1%-25%), moderated defoliation (26-60%), severe defoliation (61-99%) and dead (100%). To characterize any possible competition effects, the position, DBH and species identity of every tree in the population were recorded using a LiDAR sensor and the app ForestScanner (Tatsumi et al., 2022).

Table 1 Location and climate data (mean ±SE) values of maximum mean temperature (MMT), minimum mean temperature (mmt), and mean annual precipitation of the study sites. Dendrocronology section describes tree characteristics: mean values of density, number of trees and cores, recorded period, diameter at breast height (DBH), tree height, tree age at 1.3 m and mean basal area increment for the 1900-2021 period (BAI). Different letters indicate significantly (p < 0.05) different mean values across sites based on Tukey tests.

| Site	Hurones	Sauceda	Picacho	Tala	Comares
Climate					
Latitude	36.66	36.53	36.51	36.47	36.10
Longitude	-5.49	-5.58	-5.64	-5.59	-5.51
Altitude (m)	217	417	445	670	451
MMT (ºC)	21.43 ± 5.34c	19.54 ± 5. 33a	20.15 ± 5.61b	19.85 ± 5.31ab	18.69 ± 4.67d
mmt (ºC)	12.09 ± 4.21c	10.84 ± 4. 25a	10.92 ± 4.25ab	11.21 ± 4.22b	11.83 ± 4.00c
Precipitation (mm)	524 ± 172a	600 ± 202a	615 ± 210a	612 ± 210a	630 ± 225a
Dendrocronology					
Tree density (ind/ha)	169,8 ± 57,4	340,8 ± 33,6	121,3 ± 7,6	301,0 ± 36,3	562,8 ± 74,4
No. Trees (cores)	12 (22)	12(12)	8 (16)	15 (30)	15 (29)
Time spam	1842-2021	1889-2021	1844-2021	1835-2021	1958-2021
Defoliation	0.46 ± 0.64 ab	0 a	1 ± 1 b	0.15 ± 0.36 a	0 a
DBH (cm)	41.08 ± 14.57a	67.31 ± 22. 42b	38.97 ± 14. 57a	42.53 ± 13. 38a	34.00 ± 3.00a
Height (m)	8.7 ± 1.1b	14.5 ± 1. 0a	8.1 ± 1.2b	12.7 ± 1. 5a	11.4 ± 1. 1a
Age (yr)	78 ± 39a	68 ± 37a	65 ± 21ab	80 ± 37a	52 ± 9b
BAI (cm^{2}year^{-1})	5.77 ± 2.27a	8.35 ± 4.00d	0.05 ± 0.04c	5.55 ± 2.88b	7.79 ± 3.93b
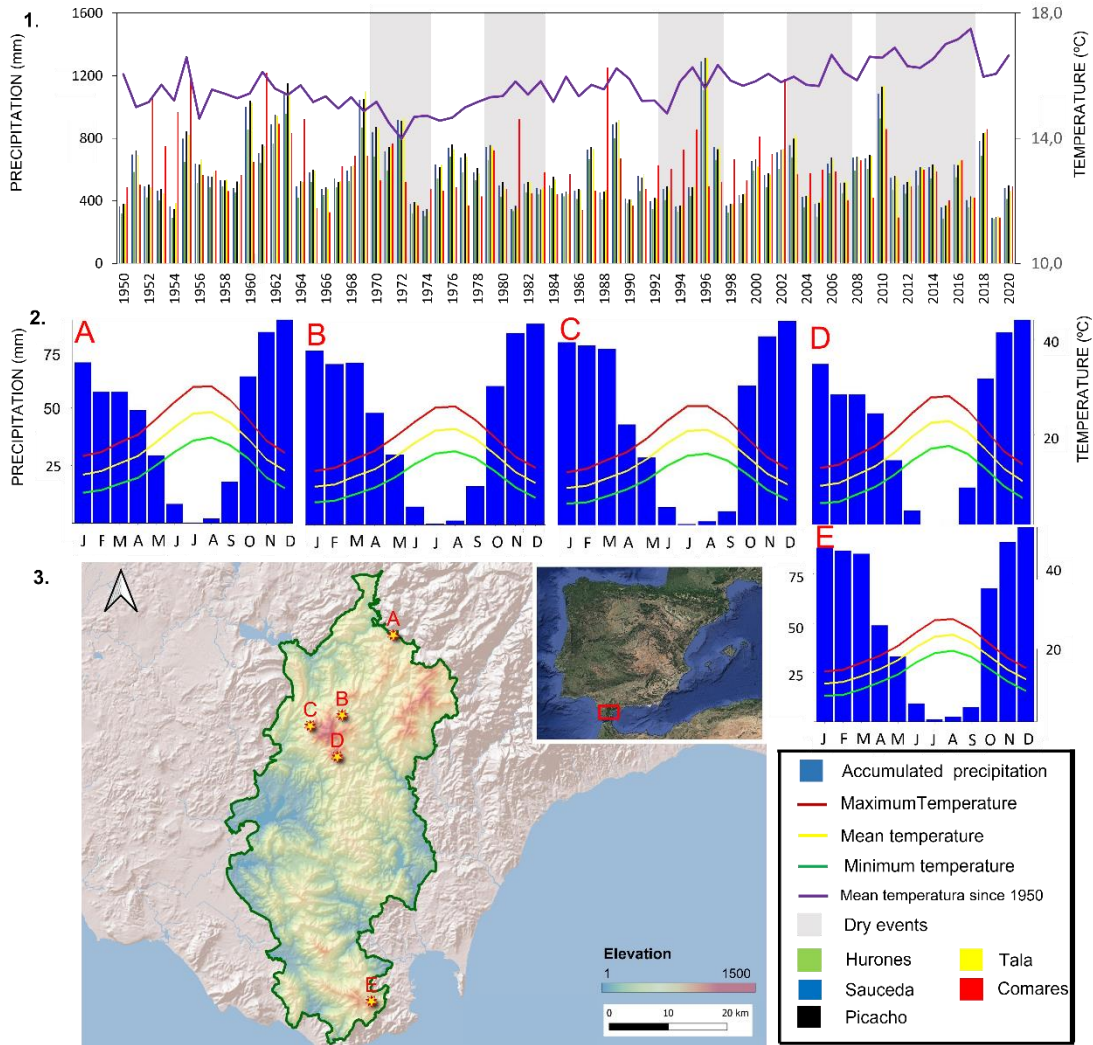
Figure 1 (1) Annual precipitation (bars) at Hurones (green), Sauceda (blue), Picacho (black), Tala (yellow), Comares (red), with the mean annual temperature since 1950 (purple line) and diferent pre/pos drought event (grey areas) . (2) Climatic diagrams for each study site A(Hurones), B (Sauceda), C (Picacho), D (Tala), E (Comares). (3) Localitation of the study sites at "Los Alcornocales" Natural Park.

Tree coring and width measurements

A standard dendrochronological method (Fritts, 1976) was followed for the selected trees. For each tree, two cores were taken using a 5 mm increment borer at 1.3 m above ground level. Wood Samples were air-dried, mounted, polished with successively finer grit sandpaper until rings were visible. Tree rings were visually cross-dated, and tree-ring widths were measured to the nearest 0.01 mm using a binocular microscope coupled to a computer with the LINTAB[TM] package (Rinntech, Heidelberg, Germany). Then, tree-ring width series were evaluated and cross-dated per population using COFECHA software (Holmes, 1983). The number of annual rings at 1.3 m was counted to estimate age. To evaluate climate-growth relationships, we first removed age and size-related long-term trends of the tree-ring width (TRW, mm year^{-1}) series converting raw tree-ring width series to Basal Area Increment (BAI, cm^2 year^{-1}), using the formula:

$$\mathbf{BAI} = \frac{\pi\left(r_t^2 - r_{t-1}^2\right)}{100}$$

where *r* is the tree radius increment and *t* is the year of the ring formation. The chronology included 62 trees for the period 1835- 2022.

Climate data

Climate at the study areas is Mediterranean with wet and mild winters, and dry and warm summers (Fig.1, Table 1). Daily climate data series since 1950 were obtained from the interpolation of the three nearest meteorological stations using the r package *easyclimate* (Cruz-Alonso et al., 2023). For modelling we used the monthly mean temperature and the total monthly precipitation, and we converted to a seasonal value (December, January and February, winter—WI; March, April and May, spring—SP; June, July and August, summer—SU; September, October and November, autumn—AU) either by averaging (temperature) and summing (precipitation).

To evaluate the droughts since 1950 we downloaded the Standardized Precipitation Evapotranspiration Index (SPEI) for the 0.5° grid where the study sites are located using the World Meteorological Organization (WMO) database webpage. This is a multiscale drought index and expresses monthly cumulative drought at different scales. This index considers the effects of the temperature and evapotranspiration on drought severity and indicate wet (SPEI positive) and dry (SPEI negative) conditions (Fig. A1) (Vicente-Serrano et al., 2010).

Resistance, recovery and resilience indices

We followed Lloret et al., 2011, to define resilience, resistance and recovery, based on BAI during the drought period and growth during the previous and subsequent year. We chose 3 characteristic droughts for the 1950-2000 period and other three for 2000-2020 period. these droughts were chosen when occurs the lowest SPEI values in 10 years period, except the 2012/2015 drought, where are two peaks appeared very close (Fig. A1). We used 2000 as a separator since, it changes the BAI trends in the different study populations. Resistance, recovery and resilience were calculated using the formulas:

$$\textbf{Resistance } (R_t) = \frac{BAI_D}{BAI_{BAIpreD}}$$

$$\textbf{Recovery } (R_c) = \frac{BAI_{BAIposD}}{BAI_D}$$

$$\textbf{Resilience } (R_s) = \frac{BAI_{BAIpostD}}{BAI_{BAIpreD}}$$

where BAI_D is the BAI during the corresponding drought period, BAI_{preD} is the average BAI for the 3 years preceding the drought event and BAI_{postD} is the average BAI for the 3 years following the drought event. BAI_D was calculated as annual BAI for years 1974, 1981, 1995, 2005, 2012 and 2015. All these indices were calculated at the individual tree level for each of the drought periods studied.

Data analysis

We checked the normality of the variables by using Shapiro-Wilk tests. To compare variables between different populations, we used Mann-Whitney *U* test for non-parametric analyses and linear models for variables following normality.

We quantified the climate-growth association for the common and best-replicated period 1950-2022 using Pearson correlations. Correlations were calculated considering monthly and seasonal climate variables (mean temperature, accumulated precipitation; Sánchez-Salguero et al., 2020). The window of analyses included from August of the previous year to ring formation until October of the year when ring was formed based on previous studies on this species (Colangelo et al., 2017; Sánchez-Salguero et al., 2020; Voltas et al., 2013), considering the significance level at p < 0.05. Correlations were calculated on mean, pre-whitened BAI series. We calculated 72 years moving correlations overlapping by one year, between BAI series and climate variables. We used linear models to test the differences between pre and post 2000 resilience values and Pearson correlations to show the changes in trends of resistance, recovery and resilience indices among the periods 1950-2000, 2000-2020 and 1950-2020.

Results

Climate trends

According to our data, the warmest and coldest months are July (22.2 ± 1.1 ℃) and January (9.00 ± 1.00), respectively. The wettest month is December (94.8 ± 87 mm), and the driest July (0.4 ± 2 mm). In this site, the most intensive drought occurs from June to August (Fig. 1). Moreover, temperatures have been rising steadily since 1950 at the study area (slope 0.02 ℃ yr^{-1}, p <0.01) with some peaks in 1955, 1961, 1974, 1981,1983, 1995, 1998, 2005, 2012, 2015, 2017 (Fig. 1). Some of these warm episodes are associated with severe drought events: 1981, 1995, 2005, 2012 and 2015. Seasonal precipitation shows no tends since 1950, even though the driest years occurred in the last decade (e.g the driest year was 2015 in Hurones with 289 mm) and the frequency of extreme dry events is increasing (Fig. 1).

The precipitation is similar throughout the study area (Table 1). However, the minimum and maximum temperature changes across the north-south gradient, with the warmer temperatures found in the north part of the gradient (Hurones) and Comares (south) showing the coldest temperatures (Table 1).

Size and growth patterns

We found marked differences in tree size, age and defoliation across populations (Table 1). The tallest and shortest trees appeared at Sauceda and Picacho sites, respectively. Trees at Sauceda site had significantly higher DBH than any other of the study sites. The crown defoliation was overall very low in all the selected sites with the exception of Picacho site, where trees suffered a light defoliation (1-25%).

Mean Area Basal Increment (BAI) for the common period 1950-2021 was higher in Sauceda, while Picacho site present the lowest BAI values. *Q. canariensis* growth

showed different trends depending on the site: northernmost and southernmost populations show positive trends, while central populations (Tala and Picacho) present a negative trend, with the lowest BAI since 1950 in Picacho (Fig. 2).
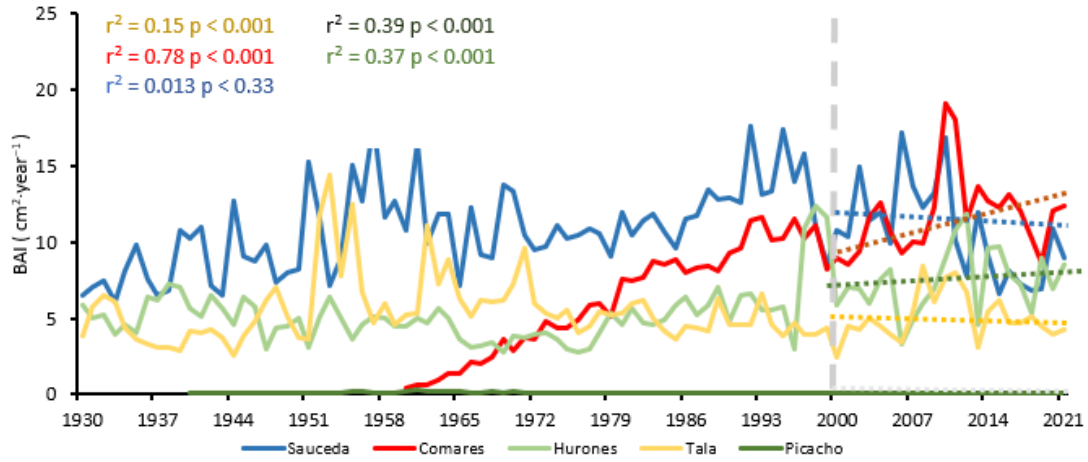

Figure 2: Basal Area Increment (BAI) growth series of the different study areas (Sauceda-blue; Comares-red;Hurones-green; Tala-yellow;Picacho-black). The vertical dashed line indicate the year 2000. The statistics show growth trends (r^2 ,correlation of determination, p, probability level).

Climate-growth associations

Growth was controlled by different factors across the distribution of *Q. canariensis* in the Natural Park, depending on their micro-climate environment although, overall, temperature exerted an important role in the control of tree growth. Surprisingly, we found lack of evidence supporting a relationship between *Q. canariensis* growth and precipitation except at one site. At Hurones, temperature is the most important variable throughout the year, with warmer summer and spring of the same year enhancing growth (Fig 3).

Q. canariensis growth at Sauceda site increases with wet summer (July) and winter (December-January) (Fig.3 , Table 2). In contrast higher temperature in the previous September is associated with slower growth. Growth at Picacho site responded negatively to warm December (Fig. 3). Although geographically close to Picacho population, trees growing at Tala, site strongly differed in the climate sensitivity. At Tala growth is related with a warm winter (November-December). Finally, at the south of the gradient (Comares), *Q. canariensis* growth shows the highest positive correlation with temperature (previous August, December, March-April, June August).
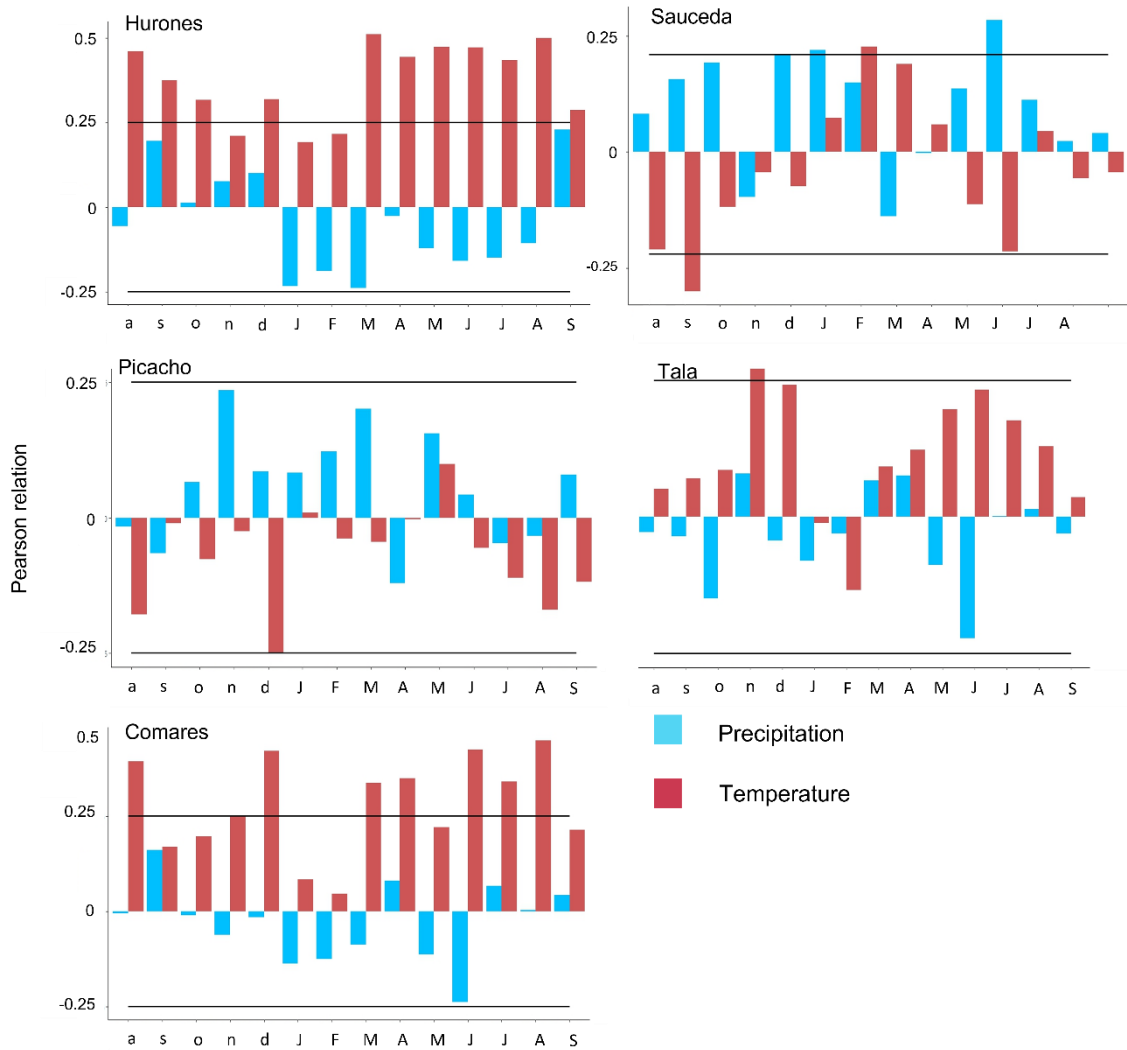
Figure 3 Climate-growth relationships at the different study sites. Bars are Pearson correlations obtained by relating population mean BAI and monthly mean temperature (red) and total precipitation (blue). Black horizontal lines show the significance at P< 0,05 levels. Lower case letters indicate the months of the year preceding the ring formation, while, capital letters indicate the months of the same year.

Table 2 Seasonal and annual temperature and precipitation with BAI at the different study sites. Colour scale (green, positive; red, negative) represent the Pearson correlation. White asterisks indicate the significance at p< 0.05.

	Site/season	Hurones	Sauceda	Tala	Picacho	Comares
Temperature	Year	*				*
	summer	*				*
	autumn	*				*
	Winter	*				*
	Spring	*				*
	Summer	*		*		*
	Autumn	*				*
Precipitation	Year	*	*		*	
	summer					
	autumn					
	Winter		*			
	Spring	*			*	
	Summer	*	*			
	Autumn				*	

1 to 0,2	
0,19 to 0,1	
0,09 to 0,01	
0	
-0,01 to -0,09	
-0,1 to -0,19	
-0,2 to -1	

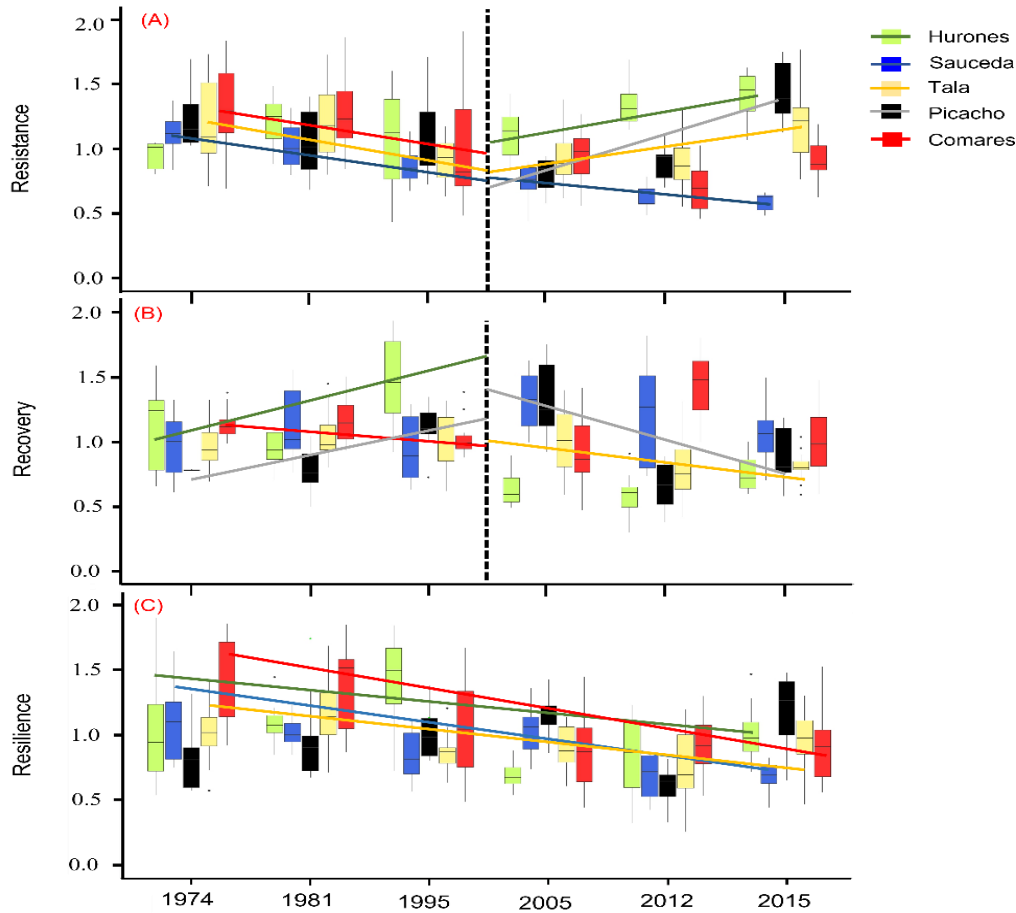*Resilience, resistance and recovery indices*

Figure 4 Resilience components, a) Resistance, b) Recovery, c) Resilience, calculated for individual tree BAI series to extreme drought during 1974-2015. These extreme droughts correspond to temperature and precipitation anomalies in 1974,1981,1995, 2005,2012,2015. The results are presented separated in two blocks before 2000 and after 2000. The indexes are estimated for 3-year windows pre- and post-droughts. The lines represent the trends of the index, in resistance and recovery pre- and post-2000 and in resilience shows the trend from 1974 to 2020.

The impact of extreme drought events on growth varied among study sites. The resistance is decreasing across the last decades in Sauceda with a steepest decline since the year 2000, currently showing the lowest values of the resistance index (F = 64.67; p<0.0001). Other sites as Tala present a different pattern, with a declining trend in resistance for the 1974-1995 period that changes to positive since the year 2000. A positive trend of increased resistance appeared at Hurones site during the 21st century (F = 7.69; p<0.0001) (Fig. 4.a.), while at Comares resistance decreased during the last part of the 20th century (F = 64.67 p<0.0001), but no trend appears since then.

As in the case of resistance, post-drought recovery also varied geographically across sites. Hurones and Picacho (northern distribution), present increasing values for the pre-2000 period, while negative trends appear at Picacho and Tala during the post-200 period (Fig 4.b). No trends in the temporal variation in recovery were detected at the other study sites.

Growth resilience is consistently decreasing in all study sites since 1950 except at Picacho, being Comares the site with the steepest decline. Resilience index was higher during the 1950-2000 period at Hurones (F= 27, p<0.0001), Sauceda (F=7.246, p<0.0001), Tala (F=8.84, p<0.0001) and Comares (F=57.19, p<0. 0.0001) than for the post-200 period.

Discussion

Climate variability and growth trends

The study area presents a gradient of temperature from north to south, determined by the Atlantic influence (García-Mas et al., 2008). Moreover, our results reveal a steady increase in temperature since 1950, which triggered more severe drought and dieback episodes (Sánchez-Salguero et al., 2020). The study sites have different microclimatic conditions, associated to the topography and water availability (Urbieta et al., 2008). Although Tala, Picacho and Sauceda sites are geographically very close, local differences in topography impose strong climatic differences. For example, Sauceda site is located in a "Canuto", a local structure formed by narrow valleys following a stream course with gallery forest and particularly wet and cold conditions (Rodríguez-Sánchez & Arroyo, 2009). In an opposite way, Picacho site is located in a flat open area with lower tree density, which increase solar radiation rising temperature and water evaporation (Makarieva & Gorshkov, 2007) and Tala which is located on the south face of the mountain, where the Atlantic influence attract more moisture and the high tree density determines a more humid microclimate.

These climatic differences induce different BAI values across the selected study sites. The cooler microclimates at Sauceda and Comares sites result in an overall higher growth, followed by Hurones and Tala with intermediate values and Picacho with an extremely low BAI (Fig. 2). It has been proven that aridity alters *Q. canariensis* responses in term of growth and phenology (Camarero et al., 2016), as it is the case of the studied sites and other populations in the Mediterranean region (Sarris et al., 2007). At Hurones site (northern edge), the proximity to the artificial water reservoir (less than 50 m) exert a strong influence on the surrounding area (Sun et al., 2021). This reservoir was built in 1953 (Rodríguez-Barroso et al., 2002) and the water availability and relative humidity have increased since then, resulting in a BAI growth increase since the 1960s decade, as highlighted in other works (Besson et al., 2014; Tumajer & Treml, 2016). Finally, Comares site (Southern edge) has a strong influence from the ocean, resulting in colder temperature and higher humidity and high growth.

These results confirm *Q.canariensis* as a sensitive species to changes in climate, suggesting that drier and warmer conditions could induce growth reductions, as occurs in others deciduous oaks in drought-prone Mediterranean areas (Sánchez-Salguero et al., 2020). Our data have also detected a general change in growth trends since the year 2000 in all sites except in Comares, probably because of the younger age of this stand and the higher growth rate characteristic of young trees (Johnson & Abrams, 2009). This general growth reduction is common for other oak species in the Mediterranean region (Camarero et al., 2015; Gentilesca et al., 2017; Sánchez-Salguero et al., 2020) and has been previously associated to changes in climate. These results confirm the

declining trends of European oaks and rise alarm about the urgent need of specific management plant aimed to assure the conservation of these important ecosystems.

Spatial patterns of climate-growth responses
Our results indicate that different climatic variable drive growth in *Q. canariensis* even at relatively low spatial scales as the study area, with all the selected sites located within the same Natural Park. Overall, temperature exert a stronger control of growth than precipitation in this species. This is especially evident at sites with more water availability (Hurones and Comares), where growth is mainly regulated by the temperature (Fig. 3). Higher temperatures in autumn and winter extend the period of physiological activity, when the water availability is higher, and allows more time to complete the relocation of transportable assimilates from leaves to perennial part of the tree (Drobyshev et al., 2008). At the same time, easy access to groundwater and higher air relative humidity can buffer the negative effects of summer drought on tree growth (Skiadaresis et al., 2019). This effect is especially evident at Comares site, where the humidity-laden Atlantic winds buffer the effect of the summer drought, Hurones by the higher evaporation for the water reservoir and Tala, where the geographical position and the closed canopy increase the moisture retention (Kovács et al., 2020), resulting in mild microclimate conditions enhancing growth. However, high temperature can also constrain growth in some cases, as is the case of Sauceda site, where high temperature in September is significantly associated to reduced BAI. This result confirm that previous autumn condition play an important role on the generation of carbohydrate reserves for earlywood formation (García-González & Souto-Herrero, 2023; Lebourgeois et al., 2004).

Precipitation has an overall low effect on *Q. canariensis* growth, although in the driest sites (Picacho and Sauceda) seasonal precipitation is the main environmental control of growth (Table 2). In these sites with high evaporation rates, *Q. canariensis* can modify its xylem hydraulic system increasing the vessel density and reducing their size (Gea-Izquierdo et al., 2012). Larger vessels are more sensitive to be embolism under drought conditions (Corcuera et al., 2004a, 2004b), so a higher density promotes a safer but lower whole-plant hydraulic conductance, with consequences for tree growth. In addition, previous studies have demonstrated that long-term drought leads to different morphological and physiological changes, such as modifications of the photosynthesis timing and capacity, changes in the root system or reductions of the leaf area (Bréda et al., 2006; Fichot et al., 2009; Gea-Izquierdo et al., 2012; Limousin et al., 2010; Matías, et al., 2019a; Morillas et al., 2023), all of this with strong implications on radial growth.

Changes in resistance, recovery and resilience to extreme drought events
The resilience of *Q.canariensis* to extreme drought events has been progressively decreasing since 1950, in agreement with previous studies in Mediterranean region (Gentilesca et al., 2017; Serra-Maluquer et al., 2018). These results show that most populations are not able to recover pre-drought growth values (Fig. 4.b), especially since year 2000. This reduction can be partially explained by the higher frequency and intensity of the drought periods recorded during the 21st century (Fig. A1). Drought

events do not follow a clear temporal pattern over the last decades, suggesting that the observed declines in recovery capacity and resilience are not related to drought intensities, but probably, might be linked to the frequency of these.

These variations in resistance indices are also influenced by forest structure, with sites with high DBH as Sauceda showing a consistent negative trend since in resilience and resistance since 1950, while the site with lower tree density (Picacho) has a positive trend in resistance since 2000s. The relationship between stand density and defoliation or mortality has been previously described in other oak species (Matías, et al., 2019b) and overall, these results suggest that the consecutive drought events might have a cumulative effect in the resilience values, as previous studies indicating high mortality with consecutive droughts (Camarero et al., 2016; Serra-Maluquer et al., 2018). The mechanisms driving this loss of resilience might be the long-term hydraulic loss caused by the successive cavitations during the drought period (Serra-Maluquer et al., 2018), which can lead to massive tree death (Anderegg et al., 2013). Moreover, the consumption of carbohydrates stocks during the drought period limits the reserves for the post-drought recovery and consequently, tree ring width is frequently smaller during several years following a severe drought (Bréda et al., 2006).

Sauceda and Comares where the sites with the highest decline in resilience. It is known from previous studies across the Iberian Peninsula that wetter sites are more impacted by drought (Martínez-Vilalta & Piñol, 2002). The inter-population variability of the growth resistance and recovery suggests the presence of different strategies to cope the drought depending on local environment (Fig. 4B). Humid sites present a higher recovery capacity and could significantly buffer the dry events (Sánchez-Salguero et al., 2018). However, we can even observe a change in the strategy of response to drought even within sites. At Hurones site, trees presented a high recovery previous 2000s, but this capacity sharply declined after this date currently showing increased resistance values. All these results highlight the importance of taking into account wide spatial and temporal scales for the determination of forest responses to environmental alterations, since multiple factors can determine the long-term variation in the functionality of forests.

Conclusions

Los Alcornocales Natural Park present a heterogeneous pattern of microclimate conditions that induced differential Q. *canariensis* growth trends across the protected area. Increasing temperature could enhance *Q. canariensis* growth, since it is the main factor controlling basal area increment, although drier conditions could trigger dieback episodes. The resilience capacity to extreme drought events of this species is consistently decreasing since 1950, showing a declining health status in all of the populations that could lead to changes in tree physiology and in the future response to the drought events. Our approach allowed us to identify the vulnerability of tree species to climate change by calculating the resilience to extreme dry events, showing early-warning signals of decline in this Mediterranean winter-deciduous oak under an aridity increase scenario.

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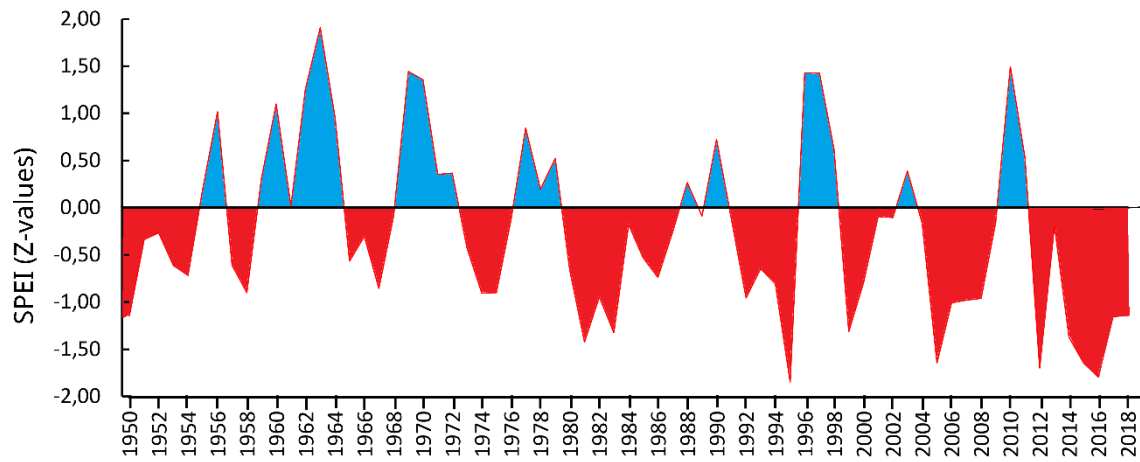
APENDIX I

Figure A1 Standardised precipitation-evaporation index (SPEI) indicating drought severity values calculated at 10-month long scale for the 1950-2018 period. Blue areas show the wet periods, while red areas indicate the drought events.