# The role of climate change in the widespread mortality of Holm oak in open woodlands of Southwestern Spain

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## Highlights

- We obtained robust dendroclimatic signal in *Quercus ilex* from low latitudes in Iberia.
- We report massive die-off of *Quercus ilex* trees in SW Iberia.
- Tree growth was strongly controlled by climatic shifts in recent decades.
- Warmer climate with longer droughts had a key-role determining the mortality process.

## Abstract

Forest decline and increasing tree mortality are of global concern and the identification of the causes is necessary to develop preventive measures. Global warming is an emerging factor responsible for the increasing tree mortality in drought-prone ecosystems. In the southwestern Iberian Peninsula, Mediterranean holm oak open woodlands currently undergo large-scale population-level tree die-off. In this region, temperature and aridity have increased during recent decades, but the possible role of climate change in the current oak mortality has not been investigated.

To assess the role of climate change in oak die-off in managed open woodlands in southwestern Spain, we analyzed climate change-related signals in century-long tree ring chronologies of dead holm oaks. We examined the high/low-frequency variability in growth and the relationship between growth and climate.

Similar to other Mediterranean forests, growth was favored by precipitation from autumn of the year prior to ring formation to spring of the year of ring formation, whereas high temperatures during spring limited growth. Since the 1970s, the intensity of the high-frequency response to water availability increased simultaneously with temperature and aridity. The growth trends matched those of climatic changes. Growth suppressions occurred during droughts in the 1970s, 1980s and 1990s. Widespread stand-level, age-independent mortality occurred since 2005 and affected trees that can not be considered old for the species standards.

The close relationship between growth and climate indicate that climate change strongly controlled the growth patterns. This suggests that harsher climatic conditions, especially increased aridity, affected the tree performance and could have played a significant role in the mortality process. Climate change may have exacerbated or predisposed trees to the impact of other factors (e.g. intense management and pathogens). These observations could suggest a similar future increase in oak mortality which may occur in more northern oak open woodlands if aridity further increases.

**Keywords.** Dendroecology; Quercus ilex; Tree mortality; Drought; Growth trends

## Introduction

Increases in tree mortality have been recently observed in forest ecosystems worldwide (Allen et al.,2010; Choat et al., 2012). However, it is necessary to further understand the actual causes of tree mortality to assess the vulnerability of forest ecosystems and to evaluate potential preventive measures (McDowell et al., 2008; Allen et al., 2010). In the Western Mediterranean, different species show signs of decline, e.g. sustained growth reduction and defoliation (see Fig. 6 and Table 4 in Allen et al. 2010; Carnicer et al., 2011), which may indicate an increasing risk of tree mortality (Bigler and Bugmann, 2004; Gea-Izquierdo et al., 2014). In the southwest of the Iberian Peninsula, there is an alarming increase of oak mortality in managed oak open-woodlands over large areas (Carrasco, 2009). These ecosystems, dominated by evergreen holm oaks (*Quercus ilex* L.) and cork oaks (*Q. suber* L.), are among the most representative Iberian Mediterranean landscapes and have considerable socio-economic value (Carevic et al., 2010; Alejano et al. 2011). In recent decades, certain oak stands have undergone a decline characterized by nonspecific symptoms, including wilting of leaves, twigs, and branches, bark necrosis, and production of epicormic shoots (Brasier, 1996; Navarro, 2011). In Southwestern Spain, this decline has extended to the regional scale in recent years and oak die-off is currently widespread. This phenomenon is a major problem for forest owners and threatens sustainability of these woodlands (Carrasco, 2009). Pathogenic fungi are a factor of oak decline (Sánchez et al., 2002). Additionally, although there is a lack of experimental evidence of the effect of management on oak mortality, management is very intense in these ecosystems (thinning, livestock management, pruning, soil tillage) and may also be involved in this decline process.

The increase in drought an heat-induced tree die-off at the global scale indicates that climate change is an emerging factor of tree mortality processes (Allen et al., 2010; Choat et al., 2012; Anderegg et al., 2013). Increases in drought can predispose trees to mortality, or directly cause tree death, through different interrelated physiological mechanisms, including carbon starvation and hydraulic failure (McDowell et al., 2008, 2011). In the Iberian Peninsula, climate has become drier and warmer in recent decades (Sumner et al., 2003; Rodrigo and Trigo, 2007; Kovats et al., 2014). In Southern Spain, evergreen oaks grow under Mediterranean-type climates where meteorological drought (i.e. period in which P<2T, where “P” is mm of monthly precipitation and “T” is mean temperature in Celsius degrees) lasts for up to 5 months (Vázquez-Piqué, 2011) and is the most important limiting factor for vegetation. Moreover, narrow soils in many stands can amplify the impact of extreme climatic events like severe droughts (David et al., 2007; de Sampaio e Paiva Camilo-Alves et al., 2013). Atmospheric warming and climatic instability can increase pathogen activity and aggravate oak diseases (Brasier and Scott, 1994; Sanchez et al., 2002; Corcobado et al., 2013). Research indicates that climate change is a factor involved in forest mortality in some Spanish forests at higher latitudes (Martínez-Vilalta and Piñol, 2002; Linares et al., 2009; Hereş et al. 2012; Ruiz-Benito et al., 2013; Gea-Izquierdo et al., 2014), but a link between climate change and widespread increase of oak mortality in Southwestern Spain has not been established.

Dendrochronological data provide useful information to investigate forest dynamics in relationship with the environment (Fritts, 1976; Schweingruber, 1996). The xylem of Mediterranean evergreen species has anatomical features that make it difficult to establish chronologies (Cherubini et al., 2003), yet dendrochronological studies of *Q. ilex* has become well-established especially in recent times (Zhang and Romane, 1991; Cherubini et al., 2003; Campelo et al., 2009; Gea-Izquierdo et al., 2009, 2011). These studies have demonstrated that *Q. ilex* ring formation is very sensitive to climate, indicating the suitability of this species for dendroecological investigations. On other species, tree rings have been used to investigate growth patterns in declining forests and dead trees (see Schweingruber, 1996, p.369-391), to model mortality risk (e.g. Bigler and Bugmann, 2004) and to find relationships between mortality processes and external factors (e.g. Pedersen, 1998; Camarero et al., 2003; Bigler et al., 2006). Moreover, annual tree-ring widths can be used to estimate the basal area increment (BAI), as an indicator of forest productivity (Piovesan et al., 2008; Di Filippo et al., 2010). The inverse relationship between ring width and age is eliminated when radial growth is calculated as BAI (Biondi and Qeadan, 2008). In the absence of major ecological constraints, changes in BAI should be positive or approach an asymptote in adult trees (Poage and Tappeiner, 2002; Biondi and Qeadan, 2008; Sillet et al., 2010). Thus, recent studies have interpreted negative BAI trends in adult trees as evidence that trees have entered a declining phase (Piovesan et al., 2008; Di Filippo et al., 2010; Gea-Izquierdo et al., 2014).

In this paper, our objective was to assess the role of climate change on the widespread mortality of holm oaks occurring in the SW Iberian Peninsula. We used century-long tree ring chronologies of dead holm oaks (*Quercus ilex* ssp. *Ballota* [Desf.] Samp.) from two managed open woodlands. We examined the climate change-related growth variability to verify whether negative impacts of climate change were reflected in the growth patterns before tree death. We analyzed (*i*) the relationship between climate and growth to determine the climatic variables that mostly influenced tree growth, (*ii*) the shifts in climate-growth relationships over time to evaluate the sensitivity of trees to the changing climate, and (*iii*) the low-frequency growth variability to identify its connections with climate trends.

## Materials and methods

### *Study sites*

The study sites are located in the province of Huelva, Spain (Fig. 1). Oak samples were collected from two monitoring experimental plots (2.9 ha per plot): Calañas (CA, 37º 31’ N; 6º 55’ W; 165 m a. s. l.) and Huerto Ramirez (HR, 3º 34’ N; 7º 20’ W; 200 m a. s. l.). The two stands are representative of oak open-woodlands in the SW Iberian Peninsula that are primarily used for livestock management. In the two stands the understory layer is composed of

*Cistus ladanifer, C. crispus , C. monspeliensis* and an herbaceous layer of grasses. Soils in CA are shallower Regosols, Leptosols and Cambisols (25 to 50 cm depth) and deeper soils in HR range from Regosols and Cambisols (40-70 cm depth) to Acrisols, Alisols and Lixisols (60-100 cm depth). The stand density was 54 trees ha$^{-1}$ (basal area: 4.5 m$^{2}$ ha$^{-1}$) till 2006 in CA and 74 trees ha$^{-1}$ (basal area: 5.2 m$^{2}$ ha$^{-1}$) till 2010 in HR. Dead trees were logged since 2007 in CA and since 2011 in HR, and this led to decreases of stand density (Supplementary material 1). Similar to holm oak open woodlands in the province of Huelva, both stands present canopy dieback, widespread mortality and no regeneration.

### *Inventory of defoliation and mortality*

Tree inventories were performed in the two plots to characterize canopy defoliation and tree mortality. Tree defoliation, defined as the loss (i.e. fall or complete dryness) of leaves, twigs, and side branches, was monitored between November and December in 2010 at HR and in 2001, 2005, and 2006 in CA; additional observations were performed in both plots in June 2013. All living trees were classified as “slightly affected” when defoliation was 10-20% of the crown, partially affected when defoliation was 30-60%, heavily affected when canopy defoliation was greater than 60% (López and Sanchez, 2011). A tree was classified as healthy when the crown was undamaged or defoliation was less than 10%. Furthermore, tree inventories reported the decrease in stand density due to the logging of dead trees. A tree was assumed to be dead when it was completely defoliated for at least two successive growing seasons.

### *Sampling and dendrochronological analyses*

Complete cross-sections are needed for dendrochronological analysis of *Q. ilex* due to the complex xylem anatomy of this species (narrow rings, missing rings, and intra-annual density fluctuations [Cherubini et al., 2003; Campelo et al., 2007, 2009; Gea-Izquierdo et al. 2009]). Previous dendroecological studies on tree mortality in Iberian forests included tree ring data from dead and healthy trees for comparative analyses (e.g. Hereş et al. 2012; Gea-Izquierdo et al., 2014). In both sites of this study, the whole stand had signs of decline, thus establishing a chronology from healthy trees was not possible. Furthermore, obtaining stem sections of living *Q. ilex* trees is difficult because this species is protected in the region. Therefore, only cross-sections from dead trees were used for this study. In particular, we used basal stem sections from 30 trees logged during 2007 in CA and 12 trees logged during 2011 in HR. The complex xylem anatomy also made difficult to measure and cross-date ring sequences along different radii on each section. Thus, 11 of the 30 disks were discarded in CA because cross-dating was impossible. In HR, discarding disks could have leaded to a low replication of samples, so cross sections at breast height of the same trees were also collected and used for cross-dating. Rings from different stem heights did not provide different results because the rings are proportional and provide coherent climatic signals (Zhang and Romane, 1991; Chhin and Wang, 2005).

The cross-sections were air-dried, sanded, and polished with progressively finer grits (60 to 1200) to make the rings visible. Ring widths were measured with a stereomicroscope connected to a LINTAB$^{TM}$ table (Rinntech®). Ring width curves were plotted for visual checks and cross-dated using a coefficient of parallel variation (*Gleichlaeufigkeit* - Glk) (Speer, 2010: p. 107-109), *t*-value, and the cross-date index (CDI) as a combination of the *t*-value and Glk, which are executed in the software TSAP-Win$^{TM}$ (Rinntech®). The cross-dating was then verified using COFECHA (Grissino-Mayer, 2001). Missing rings were detected by cross-dating chronologies from different trees and inspecting ring boundaries along the whole circumference on the stem sections. Tree ages were estimated by counting the number of annual rings on the cross-dated chronologies. To assure that annual rings were correctly identified and dated, we compared the chronologies from CA and HR with a previously established chronology of *Pinus pinea* from a close site ("Valverde del Camino", see Natalini et al., 2015) and a *Q. ilex* chronology from an open-woodland in a neighboring region of Spain (Cáceres, West-Central Spain; see Gea-Izquierdo et al., 2011). Similar procedures to validate *Q. ilex* chronologies were used by Campelo et al. (2009) and Gea-Izquierdo et al. (2009).

The individual cross-dated ring-width series were detrended by applying a smoothing spline with a 50% frequency cutoff at 32 years. The growth index was computed using the ratio between the measured raw ring width and the value of the smoothing spline (Cook et al., 1990a). An autoregressive model was used to remove the autocorrelation, and a mean chronology for each stand was obtained by averaging the pre-whitened indexed series with a biweight robust mean to reduce the influence of outliers (Cook et al., 1990b). The mean indexed series were used to analyze the high-frequency response to climate. The expressed population signal, with a minimum threshold of 0.85 (EPS; Wigley et al., 1984), and the inter-series correlation coefficients (*r*-bar) were used for additional quality control and computed over 30-year windows lagged by 15 years along the chronologies.

To study the long-term growth trends, we used the cross-dated ring-width series to compute basal area increments (BAI). Past BAI were estimated by subtracting twice the annual ring width from the annual diameter, starting from the measured diameter outside the bark (see Piovesan et al., 2008).

All computations were done using the dplR library within the software R (Bunn, 2008).

### *Climate-growth relationships*

Climatic data were from the Huelva station (time span: 1920–2010; 37° 16' N; 6° 54' W; 19 m a.s.l.), and included daily precipitation, and minimum and maximum temperatures. To analyze the high-frequency responses of trees to climate, we computed bootstrapped correlations and response functions using DENDROCLIM2002 (Biondi and

Waikul, 2004) between the mean indexed chronologies of CA and HR and monthly climate data (monthly cumulative precipitation and averages of minimum and maximum temperatures). To determine whether growth-climate relationships changed over time, we computed correlations for running windows of 30 years between the chronologies and seasonal climate data. In this analysis, the critical α value was modified using a Bonferroni correction to account for multiple comparisons.

### *Growth history and climatic changes*

For analysis of the low-frequency climatic signal in growth trends, we used the average of the Palmer Drought Severity Index (PDSI) from November of the previous year to the current June, a period in which we expected to find the strongest growth response to climate (Gea-Izquierdo et al., 2011). Data of PDSI were obtained from the CRU 3.21 dataset (van der Schrier et al., 2006). The PDSI and BAI curves were compared to identify synchrony. We considered synchronous shifts of the BAI and PDSI curves to suggest that growth variations were induced by changes in drought. We used cross-wavelet analysis to compare the long-term (low frequency) changes in the PDSI and BAI series (Grinsted et al., 2004). This method identifies the common signal power of two time series in the time-frequency domain. The cross-wavelet analysis was performed between BAI series, pre-whitened with a 1st-order autoregressive model, and PDSI values standardized to a mean of 0 and a standard deviation of 1. This analysis was performed in R using the biwavelet package (Gouhier and Grinsted, 2013).

Additionally, we analyzed the percentage of growth changes (%GC; Nowacki and Abrams, 1997) in HR and CA to assess the effects of major disturbances or strong responses to periods of extreme climate (dry or wet periods). Yearly %GC was calculated between successive 10-year means of ring widths (Nowacki and Abrams, 1997):

$$\%GC = \frac{RW_2 - RW_1}{RW_1} \times 100$$

where $RW_1$ is the mean ring width of the preceding 10 years and $RW_2$ is the mean ring width of the subsequent 10 years. The yearly %GC was fixed to the last year of the preceding 10-year period. The threshold used to characterize a significant negative or positive peak in the %GC chronology depends on factors that influence the ability of a tree to respond to disturbances, including species, age, and diameter (Nowacki and Abrams, 1997; Black and Abrams, 2003; Gea-Izquierdo and Cañellas, 2014). In our analysis we considered a threshold of 50% as significant (Gea-Izquierdo and Cañellas, 2014). To adequately evaluate the relationship of climatic change with %GC, cumulative precipitation from the previous November to the current June was calculated for 10-year window differences:

$$P_{diff} = P_2 - P_1$$

where $P_2$ and $P_1$ are the amounts of precipitation of preceding and subsequent 10-year windows. Positive and negative peaks of differences indicated major shifts in precipitation that could impact growth.

## Results

### *Inventory of defoliation and mortality*

The tree inventories at both sites indicated increased defoliation and decreased stand density over time (Supplementary material 1). More specifically, the stand density in CA declined from 54 trees ha$^{-1}$ in 2001 to 22 trees ha$^{-1}$ in 2011. Large portions of this plot were treeless grasslands in 2011. Stand mortality in HR was less severe, but the measurements of defoliation indicated a deterioration of tree health. In fact, in this plot there was a marked increase in the number of heavily affected trees and a decrease in the number of healthy and slightly affected trees from 2010 to 2013. Remarkably, in 2013 only 5% of the trees in HR were healthy while there were no healthy trees in CA.

### *Tree-ring chronologies*

Tree ages ranged from 73 to 113 in CA, and from 41 to 149 in HR. Thus, dying trees were not old relative to standards of this species (Gea-Izquierdo et al., 2011). The statistics of the *Q. ilex* tree ring chronologies are in Table 1. The indexed chronologies are shown in Figure 2. The last ring common to all *Q. ilex* series was in 2004 at CA and in 2008 at HR, so tree death occurred after 2005 and 2009, respectively. The HR and CA chronologies were highly correlated between them (Glk = 82, $p < 0.01$; CDI = 131; Pearson’s $r = 0.79$, $p < 0.01$) and verified by the comparison with the reference chronologies (see Table 2). The *r*-bar and EPS confirmed the quality of the HR and CA chronologies (Supplementary material 2). The chronologies used for subsequent dendroecological analyses only included years replicated with at least five series (1903-2005 in CA and 1896-2010 in HR).

### *Climate-growth relationships*

Holm oak growth correlated with cumulative precipitation from October of the year prior to ring formation (t-1) to March-April of the year of ring formation (t), but there was no significant correlation with precipitation in summer and autumn of the year t (Fig. 3). Holm oaks had significant responses to autumn/winter temperatures (positive to Oct/Nov$_{t-1}$-Dec$_{t-1}$/Jan$_t$ minimum temperatures, negative to Nov$_{t-1}$ and Jan$_t$ maximum temperatures), and negative response to high temperatures during May and November of the year t (Fig. 3).

The relationship between climate and tree growth changed over time (Fig. 4). In particular, since the 1970s, the correlation between growth and precipitation during November and winter of the year t-1 became increasingly positive, while the correlation of growth with precipitation during the spring of the year t declined.

### *Growth history and climatic changes*

Overall, the changes in BAI and %GC were similar in trees from both sites (Fig. 5), suggesting the presence of a common low frequency climatic signal. In particular, trees from both stands had minor fluctuations from the 1930s to the 1960s, but a decline of BAI from the 1970s to the early 1980s. This growth decline corresponded to a downturn in PDSI (Fig. 5A), suggesting a connection between increasing drought and reduced growth. This interpretation is confirmed by the cross-wavelet analysis (Supplementary material 4), which indicates that both sites had similar growth responses to PDSI. In particular, the common power at lower frequencies in the 1970s and 1980s indicates a connection between shifts in the long-term trends of BAI and PDSI.

Analysis of the %GC in both stands indicates major declines of growth in the 1970s, corresponding to a negative peak of the 10-year differences in precipitation (Fig. 5B). Tree growth in both stands increased in the late 1980s, corresponding to an upturn in precipitations during these years (Fig. 5B), although the growth recovery was larger in the site with deeper soil HR (%GC > 50%) than in the shallower site CA (%GC ≈ 25%). At both sites, a second and final phase of growth decline started during a dry period in the mid-1990s (Fig. 5A, B). Trees died in the mid/late-2000s, when PDSI, nonetheless, was increasing (Fig. 5A).

The meteorological records showed an increasing trend of maximum temperature and a decreasing trend of spring precipitation since the 1970s (Supplementary material 3).

## Discussion

### *Trees show sensitivity to increasing drought*

Previous studies of *Q. ilex* stands in the Iberian Peninsula indicated that precipitation from autumn of the year t-1 to spring of the year t had a strong influence on growth (Campelo et al., 2009; Gea Izquierdo et al., 2011). In our study region, maximum rainfall occurs from November to January (Fig. 1), thus annual growth largely depends on this rainfall. There was also a relationship of growth with temperatures of autumn and winter of the year t-1 in other *Q. ilex* populations (Zhang and Romane, 1991; Gea Izquierdo et al., 2009, 2011). The positive relationship with minimum temperatures may be explained by photosynthesis, which can take place in these seasons in evergreen species (Baldocchi et al.,2010; Gea-Izquierdo et al. 2015). In fact, photosynthesis rates in winter were measured in holm oaks in HR (Carevic, 2010), in line with other studies in Italy (Gratani et al., 2013; Catoni and Gratani 2014). Moreover, the positive response to temperatures in winter may indicate sensitivity to low temperatures leading to photoinibition (Oliveira and Peñuelas, 2000) and damage of the xylem (Lo Gullo and Salleo, 1993). On the other hand, the negative response to maximum temperatures in autumn/winter may indicate respiration-induced loss of carbohydrates. Gratani et al. (2013) reported positive respiration/photosynthesis ratio in winter. Ecosystem respiration and net carbon losses in autumn have been observed in evergreen oak open woodlands in Southern Portugal (Pereira et al., 2007). Moreover, in our study areas heat-induced evapotranspiration had a negative effect on radial growth of holm oaks in all seasons, including wet autumn and winter (Martín et al., under review). Therefore, the coupled positive response to minimum temperature and negative response to maximum temperatures from autumn to winter may reflect the contribution of carbon gain during these seasons to radial growth in subsequent months.

The trees responded positively to rainfall until March/April, but growth during May did not correlate with precipitation and correlated negatively with temperature. For Mediterranean trees (Campelo et al., 2009; Gea-Izquierdo et al., 2011; De Luis et al., 2013), water availability is important during spring when growth is maximal (Pereira et al.,2007; Vaz et al,. 2010). However, in our study region drought can occur during May (Fig. 1). Heat and low rainfall amounts in this month, which can induce water deficit and limit the photosynthetic capacity of trees (Baquedano and Castillo, 2007), can explain the sensitivity of trees to high temperatures and the absence of significant relationships with precipitation in our sites. The absence of a growth response to summer climate, which was also reported for trees growing in other Iberian *Q. ilex* ecosystems (Campelo et al., 2009; Gea-Izquierdo et al., 2011), can be explained by the duration and intensity of summer drought, which can suppress radial growth (Cherubini et al., 2003; Camarero et al., 2010). The correlation of growth with temperature during November could suggest a re-activation of cambial activity at this time, as in other Mediterranean species (Campelo et al., 2007; Battipaglia et al., 2010; Camarero et al., 2010).

The temporal changes in the relationship between growth and precipitation suggest that the holm oaks were sensitive to variations in the growing conditions. Shifts in the correlation between growth and climate can reflect climate change impacts on tree phenology (Morin et al., 2010) and have been related to warming and increasing aridity in previous studies on Iberian *Q. ilex* (Gea-Izquierdo et al., 2009) and other Mediterranean species (e.g. Di Filippo et al., 2010; Natalini et al., 2015). In our study region, meteorological records did not describe any long-term increase in winter precipitation (Supplementary material 3), which thus do not explain the increase in the growth response. On the other hand, rainfall amounts during spring decreased and maximum temperatures increased since the 1970s. The observed shifts in the growth-climate relationships may indicate the limitation of radial growth during the warmer and drier spring was increasingly dependent on water availability from the previous months.

### *Climate change could have determined the inception of the mortality process*

The mortality process in HR and CA is representative of the current increase in oak die-off occurring in the province of Huelva (personal observation), which is one of the most affected areas in SW Spain (Carrasco, 2009).

Research indicates an increase of forest decline in Iberian woodlands (Martínez-Vilalta and Piñol, 2002; Linares et al., 2009; ; Hereş et al. 2012; Carnicer et al., 2011; Gea-Izquierdo and Cañellas 2014). Nevertheless, the increase in oak mortality occurring in our study region is, to our knowledge, the first case in the Iberian Peninsula of massive population-level die-off threatening the sustainability of a forest ecosystem. Increasing oak mortality exacerbates existing problems of regeneration failure in the Spanish evergreen oak open woodlands (Pulido et al., 2001; Plieninger et al., 2004).

In recent decades, climatic changes have exerted a more intense synchronizing control on the growth trends of the studied holm oaks. Tree growth decreased during dry periods as expected in Mediterranean forests (Piovesan et al., 2008; Di Filippo et al., 2010; Gea-Izquierdo and Cañellas, 2014). On the other hand, growth changes (%GC) were positive and BAI did not decline in the late 1980s, when there was an upturn in precipitation and PDSI values were positive (Fig. 5). This suggests a recovery of growth favored by the attenuation of aridity. The response to wetter climate after drought-induced growth suppression also occurred in *Quercus* trees from other Mediterranean woodlands (Di Filippo et al., 2010; Gea-Izquierdo and Cañellas, 2014). The different extent of growth recovery between HR and CA in the late 1980s remains unexplained. It could be related to different soil depth and, hence, different soil water retention. Additionally, in HR some trees (e.g. dead or senescent trees) might have been logged in the 1980s, and growth release in neighboring trees could have been the result of reduced stand density and lower competition, which actually exists even with the low tree densities found today in the studied stands (Gea-Izquierdo et al., 2009, 2011; Martín et al., 2014). However, timber inventories are not available and we cannot verify this hypothesis based on our data.

The observed correlation of climate and growth, the increase of this correlation over time, and the synchronizing control of climatic variations on growth trends indicate that our trees were sensitive to warming and increasing aridity. In addition, they suggest that these changes in climate could have an important role in the mortality process in our study sites. Drought-induced decline processes preceding tree death simultaneous with drier and warmer climate have been recognized as an emerging factor involved in the increase of tree mortality (Pedersen, 1998; Bigler et al., 2006; Hogg et al., 2008; Gea-Izquierdo et al., 2014). The fundamental mechanisms underlying tree mortality during drought are still incompletely understood (Allen et al., 2010). Theoretically, plants regulate their water status *via* stomatal closure and can undergo carbon starvation and/or hydraulic failure when drought is severe and protracted, and this could lead to metabolic problems and defense limitations (Martínez-Vilalta et al., 2002; McDowell et al., 2008; McDowell, 2011). For instance, Breshears et al. (2008) reported water stress during a protracted period before death, suggesting carbon starvation and associated increases in susceptibility to other disturbances. The susceptibility of trees to mortality seems to be related to tolerance thresholds in tree physiology in a complex way that is not yet completely understood (Allen et al., 2010; McDowell et al., 2011). Warming and increasing aridity could force trees beyond certain thresholds from which they cannot recover (D' Arrigo et al., 2004; Wilmking et al., 2004; McDowell et al., 2011).

Based on our data, we cannot directly verify whether these mechanisms occurred in our trees. However, Alejano et al. (2008) and Carevic et al. (2010) demonstrated how holm oaks at the same studied sites underwent water stress when water potentials fell below critical levels during the driest periods. Carevic et al. (2010) also indicated stomatal closure as a reaction to water shortage. Following these findings, we may hypothesize that droughts during the last decades affected our trees by inducing water stress. Holm oaks can undergo loss of hydraulic conductivity and reduction of carbon gain in conditions of water stress (Tognetti et al., 1998; Ogaya and Peñuelas, 2003; Ogaya et al., 2003). These mechanisms could be associated to the growth decline observed during the dry periods in the 1970s-1980s and mid-1990s. In contrast to the recovery following the dry period of the 1970s-1980s, growth did not recover after the droughts of the mid-1990s, notwithstanding the return of wetter conditions (upturn of the PDSI trend and precipitation in the late 1990s). This may suggest that performance decreased below some critical level and trees were unable to regain vigor. Sharp decreases in precipitation occurred in 2005 and 2009, inducing to water stress and growth reduction in our study plots and neighboring sites (Alejano et al., 2008; Carevic et al., 2010; Martín et al., 2014). Thus, drought may have helped to trigger the inception of tree mortality events in these years.

Debilitated trees may have been exposed to the effect of additional factors, including biotic agents and disturbances related to site ecology and land use. The activity of pathogenic fungi, which have been recognized as agents of oak decline in SW Spain, is enhanced by climatic instability and stressed hosts (Sánchez et al., 2002). The effect of climate change on tree mortality is also mediated by site characteristics, including edaphic conditions, microclimate, stand structure and composition (Ruiz-Benito et al., 2013; Gea-Izquierdo et al., 2014). In our study sites, soils are shallow (particularly at CA); additionally, they have low levels of nutrients, and are susceptible to erosion, desiccation and waterlogging. These soil conditions, together with a negative impact of the intensive land use carried out during decades at the studied stands (e.g. livestock management, soil tillage), might have contributed to amplify the impact of drought on trees (Corcobado et al., 2013; de Sampaio e Paiva Camilo-Alves et al., 2013). Intense management is also considered a possible factor influencing the tree health in these ecosystems. However, experiment-based assessment of the implication of management in the increase of oak mortality in Iberian open woodlands is lacking (Sánchez and López, 2011). Finally, as an additional factor, shrubs (*Cistus* spp.) could have a competitive advantage under extreme droughts and could help synergistically to reduce resilience of oaks (Rivest et al., 2011; Caldeira et al., 2015). The negative impacts of all these factors may have been aggravated in the last years before tree death, due to the increased vulnerability of trees to enhanced water stress, and likely contributed to the mortality process (Pedersen 1998; Bigler et al., 2007; Breshears et al., 2009). The causal relationships between different factors actually triggering tree death merits further research for the development of urgent mitigation practices to prevent the widespread die-off observed in the studied ecosystem.

## Conclusions

We investigated the role of climate change in the current widespread oak mortality in open woodlands in Southwestern Spain. Based on ring chronologies of dead holm oaks, we assessed the sensitivity to climate. Trees strongly responded to water availability. The increased temperature and aridity appeared to drive the temporal changes in tree growth response to climate. The trees had a common pattern in growth variability, suggesting they had a common response to climate change. Droughts in recent decades induced growth decline, but climate was wetter in the last years before death, suggesting that trees were unable to recover despite the return of wetter conditions. Droughts may have caused water stress beyond a critical level, hindering tree resilience. However, physiological mechanisms associated to water stress cannot be confirmed by our data, and the existence of tolerance thresholds also merits further investigation. Moreover, other factors in addition to the enhanced water stress (including pathogens, limiting site conditions and intense management) probably contributed synergistically to the mortality process. Including tree ring data from healthy and dead trees may permit a comparative analysis of the growth trends in relation to climate, but this could not be accomplished in our study sites. However, our results indicate that climate change may have a significant role in the tree die-off process. Finding a clear causal relationship between stress factors and tree death is difficult to achieve and understanding the mechanisms underlying tree mortality remains challenging. Thus, the current widespread oak mortality in SW Spain is most probably the result of different factors acting in a complex interplay. We assess climate change as a likely factor of this process. Our observations could suggest that increasing oak mortality in the Iberian Peninsula may occur in northern and colder sites if aridity further increases as it is projected by climate change scenarios (Kovats et al., 2014).

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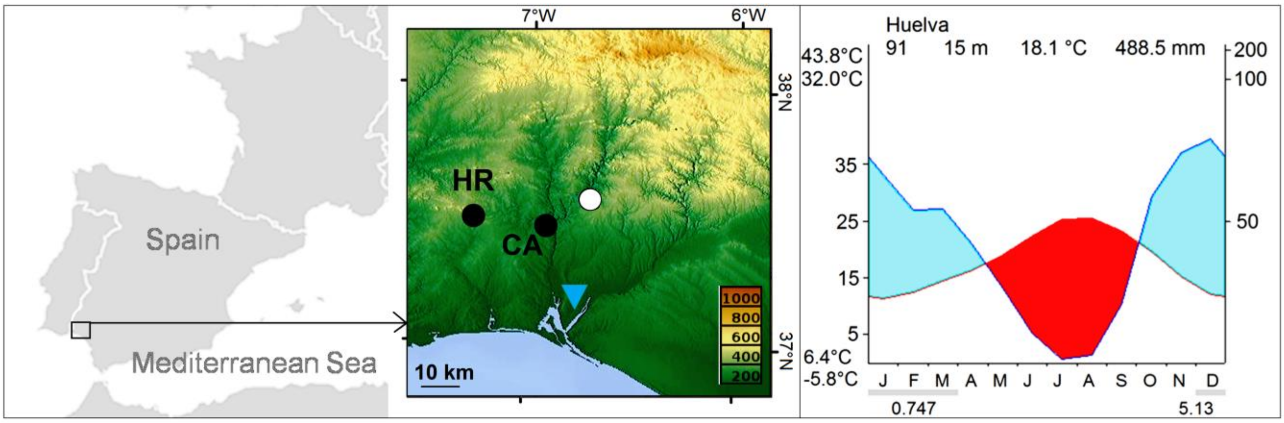
Fig.1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18.1 °C
488.5 mm
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32.0°C
6.4°C
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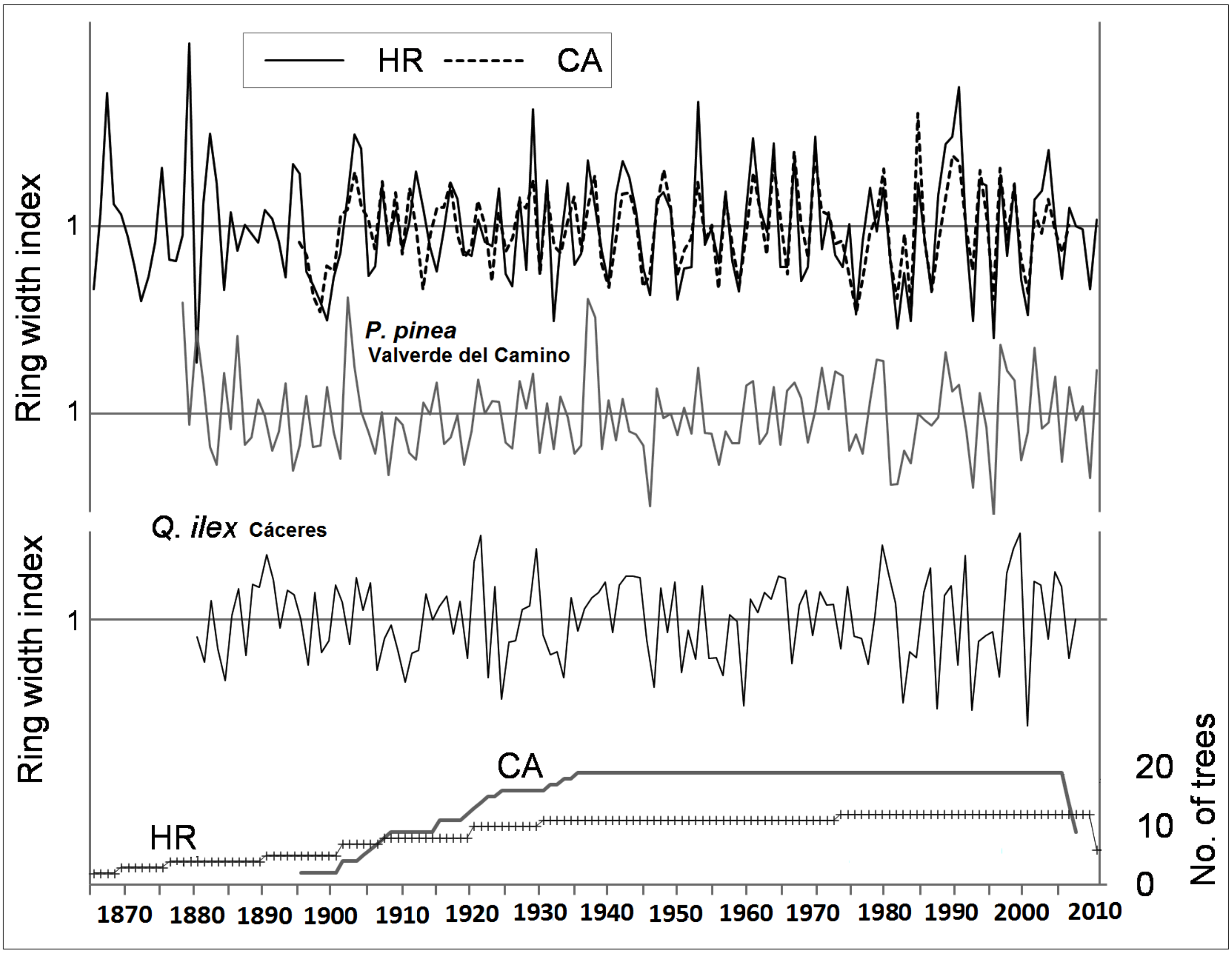
Fig.2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P. pinea
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Fig.3

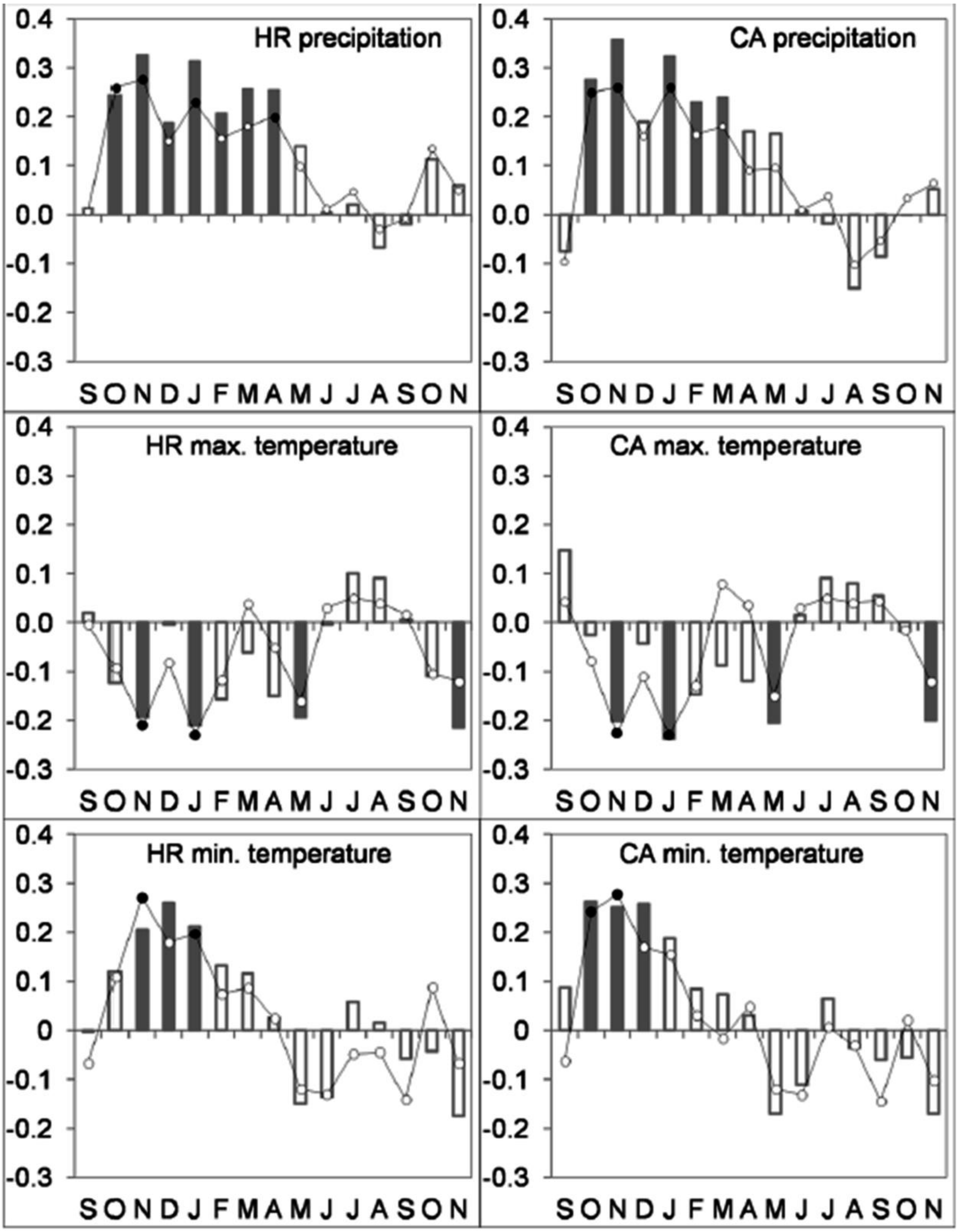
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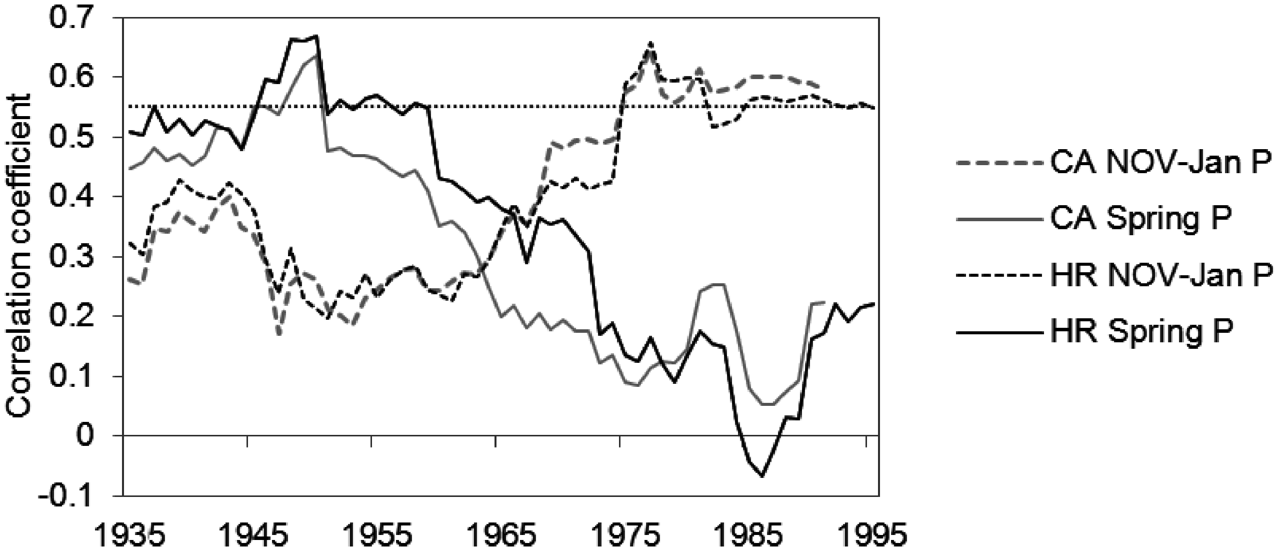
Fig.4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HR Spring P

Fig.5

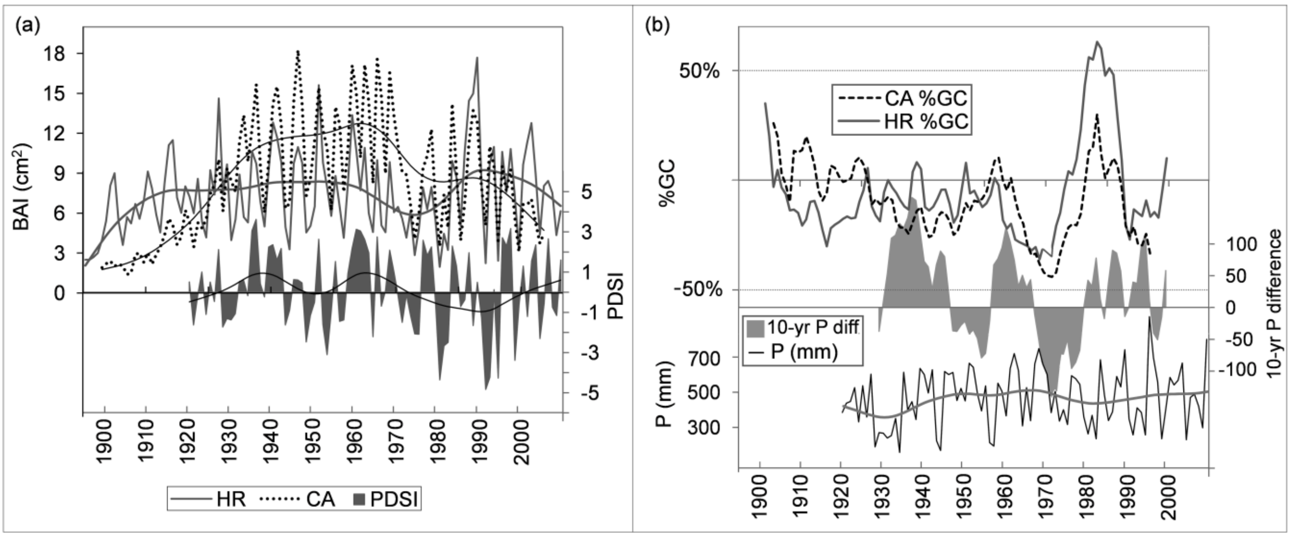
(a)
BAI (cm$^2$)
18
15
12
9
6
3
0
5
3
1
-1
-3
-5
PDSI
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
2000
HR
CA
PDSI
(b)
50%
%GC
-50%
CA %GC
HR %GC
100
50
0
-50
-100
10-yr P difference
10-yr P diff
P (mm)
700
500
300
P (mm)
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
2000

**Table 1.** Tree ring statistics of holm oaks in the HR plot and CA plot. Time span and chronology length indicate the period with at least two cross-dated series. The mean inter-series correlation is the average of the pair-wise correlations (Pearson’s *r* coefficients) computed between individual tree chronologies over the maximum common time period.

| **Parameter** | | **HR** | **CA** |
|---|---|---|---|
| Time span | | 1862-2010 | 1894-2006 |
| Chronology length (years) | | 149 | 113 |
| Trees (no. of radii) | | 12 (36) | 19 (57) |
| Mean ring width (mm) | | 1.36 | 1.74 |
| Mean inter-series correlation | | 0.55 | 0.57 |
| Mean sensitivity | | 0.41 | 0.35 |
| Expressed population signal | | 0.92 | 0.94 |
| 1st order autocorrelation | Ring width series | 0.63 | 0.70 |
| | Indexed series | -0.01 | 0.03 |

**Table 2.** Comparison between the holm oak chronologies (HR and CA) and the reference chronologies of *P. pinea* from Valverde del Camino (Natalini et al., 2015) and *Q. ilex* from Cáceres (Gea-Izquierdo et al., 2011). Glk is the coefficient of parallel variation (“Gleichlaeufigkeit”); CDI is the cross-date index.

| | HR | CA |
|---|---|---|
| *P. pinea* Valverde del Camino | Glk = 66 ($p<0.01$)<br>CDI = 41<br>Pearson $r = 0.65$ ($p<0.05$) | Glk = 67 ($p<0.01$)<br>CDI = 47<br>Pearson $r = 0.77$ ($p<0.01$) |
| *Q ilex* Cáceres | Glk = 61 ($p<0.05$)<br>CDI = 38<br>Pearson $r = 0.40$ ($p<0.05$) | Glk = 66 ($p<0.01$)<br>CDI = 38<br>Pearson $r = 0.60$ ($p<0.05$) |