Sensitivity to water stress drives differential decline and mortality dynamics of three co-occurring conifers with different drought tolerance

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1. Introduction

Global warming is expected to increase the intensity and frequency of drought episodes worldwide (IPCC, 2018). Drought affects tree performance both directly by constraining photosynthesis and hydraulic conductivity in plants (Adams et al., 2017; Gea-Izquierdo et al., 2017; McDowell et al., 2018) and indirectly by modification in life-cycles of biotic factors (Anderegg et al., 2015; Calvao et al., 2019; Gaylord et al., 2019). Thus, one of the negative potential expressions for forests of climate change is drought-induced decline and increased mortality as reported worldwide (Allen et al., 2015, 2010). Although adult mortality in closed-canopy forests creates gaps that allow the establishment of new cohorts in natural dynamics, the success of recruitment is also highly influenced by climate (Redmond et al., 2018). Lack of compensation between adult mortality and recruitment due to increased drought frequency and intensity may lead to shift in species and new plant communities dominated by more drought-tolerant species (Lenoir et al., 2008; Zhang et al., 2018). In mountain areas, warming temperatures can induce species shifts to higher, cooler altitudes (Lenoir et al., 2008; Lloret et al., 2004; Martinez-Vilalta and Lloret, 2016).

Tree survival to drought events is influenced by multiple factors that may affect species differently depending on their ecological plasticity and drought tolerance. Tree survival can be related to individual tree characteristics, behaviour after disturbance, growth dynamics (Bigler and Veblen, 2009; Caillet et al., 2014; Macalady and Bugmann, 2014), and site conditions including the microtopography, competition and productivity (Gitlin et al., 2006; Young et al., 2017). Tree ring proxies, particularly the low radial growth and negative growth trends preceding tree mortality (e.g. Bigler and Bugmann, 2004a; Caillet et al., 2017; Pedersen, 1998) have been widely used as indicators of tree vitality (Dobbertin, 2005). These proxies allow relating tree mortality to droughts occurring years before the mortality is observed.

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Understanding how different factors are involved in tree decline is crucial to forecast future changes in the landscape and identify which species and individuals will be more prone to die after drought.

The Mediterranean Basin is considered one of the regions most affected by climate change (Cramer et al., 2018; Lionello and Scarascia, 2018). Several studies have reported tree mortality and associated distribution shifts following droughts and warming temperatures since 1980 (Martínez-Vilalta and Lloret, 2016). In the Mediterranean region, pines are among the most abundant forest species. *Pinus pinaster* Ait. and *Pinus pinea* L. are naturally widespread in medium and low elevations, respectively, over the West Mediterranean Basin (Figure S1). Their current distribution has been greatly affected by humans for centuries (Barbero et al., 1998; López-Sáez et al., 2014). Presence and abundance of *P. pinaster* and *P. pinea* have been favoured through management (e.g. plantation, selective logging, thinning) for resin and seed production, respectively (Rodríguez-García et al., 2016). Although both species can share similar ecological niches, a higher drought tolerance has been attributed to *P. pinea* in terms of higher hydraulic performance and gene expression under water stress (Martínez-Vilalta et al., 2004; Perdiguero et al., 2015; Picon et al., 1996). These two pine species can coexist with *Juniperus oxycedrus* L., which is widespread in arid and semi-arid areas of the Mediterranean Basin (Vilar et al., 2016) (Figure S1). Similar to the high drought tolerance of many *Cupressaceae*, *J. oxycedrus* exhibits higher drought tolerance compared to co-occurring pines (Gaylord et al., 2013). More anisohydric junipers can maintain higher gas exchange rates and lesser stomatal control than pine trees under water stress due to their higher cavitation resistance (Gaylord et al., 2013; Koepke and Kolb, 2013; Plaut et al., 2012). In the Iberian Peninsula, *P. pinaster* decline has been observed in different areas recently. While in some stands biotic agents can be responsible for *P. pinaster* decline (Álvarez

![Fig. 1. Study area location and climate. A) Location of the plots. B) Climate diagram with average monthly precipitation and mean temperature for the period 1901–2017. C) Annual mean temperature, total precipitation and SPEI12Jun referred to the period 1901–2017. Vertical dashed lines in C show extreme dry years (i.e. SPEI12Jun < -1.3) from 1970.](image-url)
species have contrasting drought tolerances and show different decline health status in a Mediterranean mixed coniferous forest. These three species have contrasting drought tolerances and show different decline health status in the area. Species decline was assessed through canopy defoliation, infection by mistletoe (Viscum album L.), low regeneration rates and accelerated mortality (Gea-Izquierdo et al., 2019). The only species exhibiting decline at the stand level was P. pinaster while the two more drought-tolerant species P. pinea and J. oxycedrus exhibited no symptoms of species decline, i.e. low defoliation, any expression of biotic infection or widespread mortality. We analysed the role of drought in the decline and mortality patterns of these three species using a combination of dendrochronological and modelling approaches. Specifically, we tested the following hypotheses related to the potential roles of different factors (climate, tree, species and site characteristics) in tree decline and mortality: 1) radial growth declines reflect legacies from past extreme drought events; 2) growth of non-hardy trees exhibits higher sensitivity to drought than healthy trees; 3) stand features expressing low water stress (e.g. taller trees in soils with higher water retention) will increase the tree survival probability particularly in the species exhibiting decline (P. pinaster); 4) regeneration of species with higher drought tolerance will be more abundant than that of declining P. pinaster.

2. Materials and Methods

2.1. Study site and climatic data

The study area was located in the Central Mountain Range in Spain (40.5° N; 4.29° W) (Fig. 1A) where forests are dominated by maritime pine (P. pinaster) mixed with stone pine (P. pinea) and other species like juniper (J. oxycedrus) and holm oak (Quercus ilex L.). Drought tolerance of the three coniferous species follows a gradient: P. pinaster < P. pinea < J. oxycedrus (Barberó et al., 1998; Blanco et al., 2005). This gradient agrees with a previous study revealing higher post-drought mortality rates in P. pinaster than in P. pinea and J. oxycedrus across Spain (Penuelas et al., 2001). Our study site comprises the local altitudinal lower limit (i.e. species-wise dry, warm) of P. pinaster and upper limit of P. pinea in the area (i.e. species-wise humid, cold). P. pinaster and J. oxycedrus are considered to behave like pioneers, shade-intolerant species in open forests, while P. pinea can be more shade-tolerant (Abad Vinas et al., 2016). Intense human use, including livestock grazing, resin extraction, pinecone collection and frequent human-induced forest fires, have shaped species composition and structure, possibly extending P. pinaster and P. pinea distributions beyond their natural ranges in the studied area (López-Saez et al., 2014; Rodríguez-García et al., 2016).

We used monthly precipitation and minimum, maximum, and mean temperature from CRU TS 4.02 gridded data product for the period 1901–2017 (Harris et al., 2014). From these climate data, we estimated the Standardized Precipitation and Evaporation Index (SPEI) with the SPEI package in R (Seguera et al., 2014) using Thornthwaite’s equation to estimate potential evapotranspiration. After an exploratory analysis using SPEI with different time lags, we used SPEI June for 12-month periods because it showed the highest correlations with annual stem growth (Figure S2). The region has a typical Mediterranean climate with a three-month summer dry period (Fig. 1B). Annual total precipitation for 1901–2017 averaged 533 mm and mean temperature 12.3 °C. Temperature has significantly increased since the early 1980s (Fig. 1C) at 0.25 °C per decade (p < 0.05) while precipitation remained fairly stable, resulting in an intensification of water stress (i.e. more negative SPEI values). Extreme drought years since 1980 (1986, 1995, 2005, 2012, 2014) were identified as those years with June SPEI12 (hereafter SPEI12Jun) ≤ -1.30 (Fig. 1C).

2.2. Field methods and stand characteristics

In fall-winter of 2016 and 2017 we set up 75 circular plots of 10-m radius in the study area across an elevational gradient ranging between 790 and 1200 m a.s.l. (Table 1) Of the total plots, 45 plots were coincident with those in Gea-Izquierdo et al. (2019). Plots were centred on a target tree, defined as a tree belonging to one of the two pine species with minimum diameter at breast height (DBH) of 20 cm. Target trees were classified according to their canopy defoliation and level of mistletoe infection in one of three categories: healthy, declining, and dead (Gea-Izquierdo et al., 2019). Crown defoliation was characterised ranging from 0 to 4, being 0 full crown and 4 complete defoliation. Mistletoe infection – only present in P. pinaster – was expressed from 0 to 4 with 0 being absence of mistletoe and 4 heavy mistletoe infection in branches (Galiano et al., 2016). Healthy status corresponds to trees with defoliation below 25% (level 0–2) and mistletoe presence below level 2; dead implies 100% defoliation and declining any intermediate situation. In contrast with P. pinaster, in the elevations within the study area the health status of P. pinea was good so that we had to actively search for recently dead individuals, which were scarce, and we did not characterise any P. pinea tree as declining.

Within each plot, we characterised stand structure, species composition and health status of all trees. We recorded the position of all trees with DBH ≥ 5 cm and measured their DBH and height. In addition, to assess plot regeneration, we tallied saplings (height ≥ 1.3 m and DBH < 5 cm) and seedlings (height < 1.3 m) in five 1x1m quadrats located in the plot centre and the four cardinal directions 10 m away from the plot centre. We extracted three cores per target tree with increment borers. We included target trees in the sampling until we reached a minimum number of 20 individuals per status and species. Thus, the total number of target trees was 60 for P. pinaster (20 for each health status) and 41 for P. pinea (21 healthy and 20 dead) (Table 1 and Table 2). Additionally, we extracted core samples from 22 healthy J. oxycedrus, the most drought-tolerant of the studied species, which exhibited no signs of decline and no dead individuals were found.

2.3. Dendrochronological methods

Cores were progressively sanded before rings were visually cross-dated and ring width measured using LINTAB device and TSAP software. Visual crossdating was statistically verified with COFECHA (Holmes, 1983). Annual basal area increments (BAI, cm² t-1) were estimated from ring width and field-measured DBH as: BAI = π(Rt² - R0²) where R0 and Rt are the radius of a tree at t and t–1, respectively. To analyse the influence of the inter-annual variability in climate on tree growth, we used chronologies of ring width indices (RWI) separately for each combination of species and health status. Ring-width series were detrended using spline functions with a 50% variance cut-off of 30 years. Growth indices were computed using ratios and chronologies calculated using bi-weight robust estimations of the mean using the R package dplR (Bunn, 2008).

Seasonal climate-growth relationships were analysed for the common period 1950–2017 using bootstrap Pearson correlations in the R package treeclim (Zang and Blondi, 2015). We used those climatic variables that limit the most the cambial activity in Mediterranean species, i.e. winter, spring and early-mid summer temperature and spring precipitation (Campepo et al., 2015; Viestra et al., 2014). To explore potential changes of the influence of climate on growth over time, we also calculated moving correlations between chronologies and seasonally aggregated climate variables for 30-year periods lagged 1 year since 1950. In addition, we performed a piecewise regression between BAI...
Individual response to SPEI12

and to investigate the existence of tipping points expressing the start of growth declines in the BA1 growth series with the R package segmented (Muggeo, 2008).

To analyse the possible effect of disturbance legacies on tree decline and mortality, we explored the occurrence of past disturbances. Disturbances that reduce competition around surviving trees are recorded in tree-ring width series as abrupt and sustained faster growth rates (i.e. releases). To detect these releases, we used the radial-growth averaging method (Nowacki and Abrams, 1997) for any given year i as follows: GCi (% = (M2–M1)/M1, where M1 is the mean radial growth in mm for the 10 years before year i, and including i, and M2 is the mean radial growth for the 10 following years (Nowacki and Abrams, 1997). Here, we only considered major release events defined as GCi > 100%.

### 2.4. Indicators of tree decline and delayed mortality

We analysed whether individual and stand features, as well as early-warning signals (EWS) derived from tree-rings could explain the decline and mortality patterns (i.e. the health status) of the two pine species. Extending the four main hypotheses presented above, we tested covariate associations with the WTs. Using the R package segmented (Muggeo, 2008) to fit continuous regression models, we included several variables that are known to influence tree growth and survival (e.g. climatic variables, soil properties, disease pressure, etc.). To assess the influence of each covariate on tree health, we performed a series of regression analyses using the function segmented (Muggeo, 2008).

For each variable, we fitted a simple linear regression model, and then compared the models using the Akaike information criterion (AIC). We considered variables that had a significant effect on tree health (p < 0.05) as potential predictors. To select the best model, we used a forward selection approach, starting with the simplest model and adding variables one at a time until the AIC criterion was minimized.

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>P. pinaster</th>
<th>P. pinea</th>
<th>J. oxycedrus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Status</td>
<td>healthy</td>
<td>declining</td>
<td>dead</td>
</tr>
<tr>
<td>Plots</td>
<td>20</td>
<td>8</td>
<td>17</td>
</tr>
<tr>
<td>DBH (cm)</td>
<td>42.81 b</td>
<td>40.47 b</td>
<td>39.76 b</td>
</tr>
<tr>
<td>Height (m)</td>
<td>15.74 b</td>
<td>13.91 b</td>
<td>13.09 b</td>
</tr>
<tr>
<td>Age (years)</td>
<td>82 a</td>
<td>88 a</td>
<td>95 a</td>
</tr>
<tr>
<td>Hdo (m)</td>
<td>18.01 b</td>
<td>15.37 ab</td>
<td>14.11 a</td>
</tr>
<tr>
<td>YG 25 (cm² y⁻¹)</td>
<td>16.81 b</td>
<td>16.91 b</td>
<td>14.02 b</td>
</tr>
<tr>
<td>IRprec₀5₁₇</td>
<td>0.32 b</td>
<td>0.38 b</td>
<td>0.25 b</td>
</tr>
<tr>
<td>relBAI₀5₁₇</td>
<td>0.10 a</td>
<td>0.11 a</td>
<td>0.08 a</td>
</tr>
<tr>
<td>mBAI₀5₁₇</td>
<td>23.56 bc</td>
<td>15.51 b</td>
<td>16.01 b</td>
</tr>
<tr>
<td>relBAI₀5₁₇</td>
<td>0.48 bc</td>
<td>0.34 ab</td>
<td>0.36 ab</td>
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<tr>
<td>G (m² ha⁻¹)</td>
<td>25.98 a</td>
<td>19.95 a</td>
<td>16.16 a</td>
</tr>
<tr>
<td>Hegyi</td>
<td>1.78 ab</td>
<td>1.31 a</td>
<td>1.35 a</td>
</tr>
<tr>
<td>Defoliation</td>
<td>0-2</td>
<td>2-3</td>
<td>4</td>
</tr>
<tr>
<td>Mistletoe</td>
<td>0-2</td>
<td>0-4</td>
<td>0-4</td>
</tr>
</tbody>
</table>

### Table 2

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean chronology</th>
<th>Individual series</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. pinaster</td>
<td>Cores (trees)</td>
<td>Interval (trees &gt; 5)</td>
</tr>
<tr>
<td>healthy</td>
<td>40 (20)</td>
<td>1918 – 2016</td>
</tr>
<tr>
<td>declining</td>
<td>40 (20)</td>
<td>1896 – 2016</td>
</tr>
<tr>
<td>dead</td>
<td>40 (20)</td>
<td>1895 – 2016</td>
</tr>
<tr>
<td>P. pinea</td>
<td>healthy</td>
<td>42 (21)</td>
</tr>
<tr>
<td>dead</td>
<td>40 (20)</td>
<td>1856 – 2017</td>
</tr>
<tr>
<td>J. oxycedrus</td>
<td>healthy</td>
<td>41 (22)</td>
</tr>
</tbody>
</table>
(2) Non-healthy trees show lower mean growth sensitivity. Mean sensitivity (MS) (Fritts, 1976) is a measure of year to year variability in time series of tree-ring proxies that can be used to estimate tree susceptibility to exogenous factors since declining trees have less ability to maintain stable growth level along time (Beck, 2009; Cailleret et al., 2019).

(3) Non-healthy trees have higher early growth rates. For each tree, we calculated average BAI for their first 25 years of life (YG25) to assess the influence of juvenile growth rates on tree mortality (Bigler and Veblen, 2009).

(4) Non-healthy trees exhibit stronger radial growth relationships with drought and climate (defined hereafter as climate sensitivity) (Suarez et al., 2004). We tested the individual tree responses (bootstrap Pearson correlations) to different climatic covariates, including spring precipitation (IRpre) and SPEI2Jun (IRspei) in the periods 1950–2017 and in 1995–2017.

(5) Non-healthy trees are smaller. Pine trees with smaller diameters at a given age are expected to exhibit higher mortality rates, due to more limiting growing conditions (Hülsmann et al., 2018). Additionally, tree height (H) has been described to be an indicator of a deeper, more extensive root system, allowing the tree for further access to nutrient and water in the soil (Prieto-Reco et al., 2015; Stahl et al., 2013). Tree height is also commonly related to site quality and moisture availability (Assmann, 1970; Fontes et al., 2003; King, 1990). Plot dominant height (Hdo) is a commonly-used forestry proxy of site productivity (Assmann, 1970). Taller trees may reflect better growing conditions, particularly higher moisture availability. Both DBH and height were expected to be positively related to tree health. However, as shown by several studies, during water stress situations trees with larger DBH (Benett et al., 2015) or height (Stovall et al., 2019) could have a higher mortality risks.

(6) Non-healthy trees are expected to be less resilient to drought (DeSoto et al., 2020). Growth resilience (R) is the capacity of an individual to recover pre-disturbance growth levels (Holling, 1973). Resilience indices (resistance, recovery, resilience) were calculated following Lloret et al. (2011). We calculated resilience indices for all dry years between 1980 and 2012 but only tested resilience indices to the 1986 drought to avoid potential biases related to pre-mortality negative growth trends (Schwarz et al., 2020).

(7) Non-healthy trees withstood greater stand disturbances in the past (e.g. fire, thinning, drought-induced mortality of neighbouring trees), hence they expressed releases from competition as indirectly estimated by positive growth changes (PGC).

(8) Stand competition influences tree performance. Higher stand density negatively affects tree survival by increasing competition for resources, mainly for water. We used plot basal area (Gj) and the Hegyi index, a competition index depending on tree diameter and distance (Hegyi, 1974) to test the influence of competition in the mortality models.

2.5. Statistical analyses and models of mortality

We used logistic regressions to model the probability of survival of each individual tree of each species based on the different covariates described above. First, a binary logistic regression (BLR) with a binomial error distribution was fitted for each species P. pinea and P. pinaster using healthy and dead trees (Bigler and Bugmann, 2004b; Cailleret et al., 2016). The model used was the following:

\[
\log \left( \frac{P(Y_i = 1)}{1 - P(Y_i = 1)} \right) = \alpha + \beta_1 x_1 + ... + \beta_n x_n
\]

(1)

\[
P(Y_i = 1|X) = \frac{\exp(X \beta)}{1 + \exp(X \beta)}
\]

(2)

Where \(P(Y_i = 1)\) is the probability of the tree \(i\) to be alive, while \(Y_i = 0\) indicates that tree \(i\) is dead. \(\alpha\) is the intercept, and \(\beta_1, ..., \beta_n\) are fitted parameters for \(x_1, ..., x_n\) covariates.

Because trees of three health categories in a sequential order (healthy, declining and dead) were observed for P. pinaster, we also fitted an ordinal logistic regression model (OLR) for that species. OLR is an extension of BLR to an ordinal scale. We assumed the parallel slopes model with same coefficients \(\beta_i\) but different intercepts \(\alpha_j\) (Weiiskittel et al., 2011). Equation (2) represents the probability that an observation \(Y\) will be less or equal to ordinal level \(Y_j (j = 1–3\) levels), with \(X\) being a vector of explanatory variables where the probability of an individual to be included in class \(j\) is \(P(Y \leq Y_j | X) = P(Y \leq Y_j - 1 | X)\).

Models were selected according to the following criteria: (i) all variables included were significant at \(p \leq 0.05\), (ii) model had the minimum Akaike information criterion (AIC), (iii) in case of two models with \(\Delta AIC < 2\), the most parsimonious one was selected. We used ANOVA to compare nested models with different number of covariates. The goodness-of-fit of the final models was evaluated using three indexes: the McFadden pseudo-\(R^2\) (\(d^2\)) calculated as 1- (Residual deviance/Null deviance) with values between 0.2 and 0.4 considered to represent a good fit (McFadden, 1979); the receiving operating characteristics curve (ROC) and the associated area under the curve (AUC). A model with AUC < 0.7 is considered a poor model whereas AUC between 0.7 and 0.9 is considered a fair model and AUC over 0.9 an excellent model (Swets, 1988). Finally, we included contingency graphs of model results for each health status and species and we ran a leave-one-out cross-validation (LOOCV) to test the predictive power of the selected models. Validation was tested using accuracy (% of correctly predicted trees) on each LOOCV iteration (Zuur et al., 2009).

3. Results

P. pinea trees were significantly older and larger than P. pinaster and J. oxycedrus trees (Table 1 and Table 2). The age distribution of the trees cored revealed that there were non-healthy individuals in all age-classes in both pine species (Figure S3). Average basal area of all sampled plots was 20.15 ± 10.95 m² ha⁻¹ ranging between 16.16 ± 9.27 m² ha⁻¹ and 25.98 ± 11.12 m² ha⁻¹ in dead and healthy P. pinaster plots, respectively (Table 1). Nonetheless, P. pinaster regeneration was exclusively located in 5% of quadrats of P. pinaster plots (representing about 3% of total quadrats) (Fig. 2). In contrast, P. pinea and J. oxycedrus seedlings were present in 12% and 13% of all quadrats, respectively, with presence of P. pinea in 8% and 4% of quadrats located in P. pinaster and P. pinea plots, respectively, and J. oxycedrus found in 7% of quadrats placed in P. pinaster plots and in 6% of quadrats from P. pinea plots. The dominant species in the understory was Q. ilex, tallied in 35% of quadrats (Fig. 2).

3.1. Growth trends and disturbance events

The mean BAI chronologies of non-healthy P. pinaster diverged from that of healthy trees since 1995 (Fig. 3 and Fig. 4), while in P. pinea this divergence started later in 2005. Declining and dead P. pinaster individuals showed identical trends. The analysis of breaking points confirmed that there was a tipping point expressing the start of growth decline in 1994 ± 1.2 (estimate ± standard error) for P. pinaster and in 2005 ± 1.5 for P. pinea (p < 0.001 in both cases). Hence, for further analysis, we considered the droughts in 1995 and 2005 as the starting points of growth declines for P. pinaster and P. pinea, respectively. These two drought years in 1995 and 2005 had SPEI2Jun values of −1.6 and −1.3, respectively, and were also characterized by very low precipitation during spring (Table S3).

During the 20th century, P. pinaster trees exhibited two release events (Fig. 5A). The first one, around 1955 was mainly recorded in today-declining and today-dead individuals (Fig. 5B and Fig. 3). A smaller one, between 1990 and 1995, was recorded only in healthy individuals. Growth profiles for P. pinea revealed only one release event around 1935 that affected 27% of healthy individuals and 10% of dead trees. Many of the P. pinaster and J. oxycedrus sampled (70% and 77%,
respectively) recruited (at height 1.3 m) immediately after 1955, which could be associated to that disturbance (Fig. 3). In contrast, increase in P. pinea sample depth (a proxy for recruitment) remained fairly constant during the whole period (Fig. 5).

3.2. Influence of climate on tree growth

Growth of the two pine species was positively influenced by winter temperature, spring precipitation and SPEI12<sub>Jun</sub> while growth of J. oxycedrus was only enhanced by SPEI12<sub>Jun</sub> (Fig. 6). High summer temperatures negatively affected P. pinea and P. pinaster growth. The growth response to winter minimum temperature during the period 1950–2017 remained constant and similar for both species except in the case of dead P. pinaster, whose response was weaker in the last period (Fig. 7). Both P. pinea and P. pinaster became more sensitive to spring precipitation since the early 1980s (Fig. 7), but again growth of dead P. pinaster became less reactive in the last part of the period. Temporal trends of climate-growth correlations of the two pine species revealed an increasing response to SPEI12<sub>Jun</sub> while the J. oxycedrus response remained stable (Figure S4).

3.3. Effects of stand and individual features on tree mortality and decline

We reduced to 11 the number of variables to include in the models. For those hypotheses for which we had more than one variable calculated, we performed exploratory analysis to select the one that explained more variance in tree surviving to avoid collinearity. Thus, we selected relBAI for tree growth trend and Gj for plot competition. From all the covariates tested, the same three variables were selected in OLR and BLR for P. pinaster (Table 3, Table S1 and Table S2). Higher relative BAI during the period 1995–2017 (relBAI<sub>9517</sub>) and higher responses to spring precipitation (IRprec<sub>9517</sub>) increased probabilities of survival for P. pinaster. In relation to site conditions, the tree probability of being healthy increased in trees within plots with taller dominant height (Hdo,
Fig. 4. Annual basal area increments in *Pinus pinaster*, *Pinus pinea* and *Juniperus oxycedrus* from 1970. Solid lines represent mean values and smooth area the confidence intervals ($y \pm 1.96 \cdot \varepsilon$, being $y$ the mean growth and $\varepsilon$ the standard error of the mean). Dashed vertical lines indicate the tentative year where the mean BAI between health status start to diverge: 1995 in *P. pinaster* and 2005 in *P. pinea*.

Fig. 5. Mean growth changes per health status and species. A) Mean growth change (MGC) calculated in 5-year periods. B) Percentage of trees showing a growth release > 100% calculated in 5-year periods. The percentage of trees showing a growth release is represented by bars/polygons area. The solid lines indicate sample depth (number of trees) that could potentially exhibit a release in each period, that is, trees that presented a minimum of 10 rings at 1.3 m height. Minimum individuals shown per status is five.
which can be used as a proxy to stand productivity). The OLR for *P. pinaster* classified correctly 60% of healthy and 60% of dead trees (Fig. 8A) while it misclassified 63% of declining individuals (40% as dead and 23% as healthy). All declining *P. pinaster* trees misclassified as dead by the OLR model exhibited medium to high mistletoe infection levels (an ordinal variable that was not tested in the models because it was used to classify a priori the health status of the cored trees), while all but one declining *P. pinaster* trees misclassified as healthy by the OLR had no mistletoe infection (Figure S5). The BLR for *P. pinaster* correctly classified 80% of healthy trees and 95% of dead individuals (Fig. 8B). The BLR for *P. pinea* correctly classified 65% of dead and 70% of healthy trees (Fig. 8C). In the BLR for *P. pinea*, more positive growth trends before death (relBAI \textsuperscript{0517}) were also associated to increased probability of survival (Table 3). The likelihood of survival in *P. pinea* trees also increased with increasing DBH, in contrast to the *P. pinaster* survival likelihood, which was not affected by individual tree size.

The leave-one-out cross-validation suggested that all of the three models had medium predictive power: logistic models successfully predicted 45% of the tree status in the case of OLR *P. pinaster*, 66% in BLR *P. pinaster* and 58% in BLR *P. pinea* (Table 3).

4. Discussion

In the study area, *P. pinaster* and *P. pinea* showed differing evidences of decline and mortality, whereas we observed no mortality at all for *J. oxycedrus* in the study forest. Legacy effects from exceptional droughts after 1980s seemed to be the main factors initiating periods of reduced growth, >20 years in the case in *P. pinaster* and >10 years in *P. pinea*, leading to mortality. These results suggest that longer growth declines were exhibited with decreasing species drought tolerance in dead trees. The least drought-tolerant of the three species, *P. pinaster*, showed widespread evidences of decline at the landscape level. Descriptive logistic models revealed that higher growth rates since 1995, stronger response to spring precipitation and higher site productivity increased *P. pinaster* probability of survival. Factors increasing the likelihood of survival in *P. pinea* were higher growth rates after 2005 drought and larger diameters.

4.1. Longer negative growth trends preceding death in the least drought-tolerant species

Trees commonly reduce growth in response to increasing environmental stress, as expressed by dead trees for variable periods before death (Bigler and Bugmann, 2004b; Cailleret et al., 2017). However, unequivocally identifying the factors producing tree growth declines prior to death is challenging. In our results, two different drought years could have triggered growth declines for the two pine species analysed. BAI series of non-healthy individuals started diverging from those of healthy individuals after 1995 in *P. pinaster* and 2005 in *P. pinea*. Increasing water stress forced by warming temperatures in the area since the early 1980s may have acted as a long-term factor predisposing trees to higher damages due to subsequent extreme droughts (Anderegg et al., 2013), which probably acted synergistically with warming to incite tree decline. In contrast to healthy individuals, growth of non-healthy trees started declining immediately after the exceptional 1995 drought in *P. pinaster* (over 20 years before death) and in 2005 in *P. pinea* (over 10 years before death). Longer declining periods post-drought, like those observed in *P. pinaster*, may be considered as a consequence of higher sensitivity to water stress in comparison to the more drought-tolerant *P. pinea*, which might have required higher levels of water stress to surpass an ecological threshold triggering individual death (Zimmermann et al., 2015).

The extreme 1995 drought, which was preceded by a five-year period of low precipitation (Fig. 1 C), caused damage and mortality in multiple tree and shrub species across the Iberian Peninsula (Penuelas et al., 2001). Pine species exhibit high xylem vulnerability to low water potential despite their isohydric behaviour (Martínez-Vilalta et al., 2004). Among our study species, *P. pinaster* is considered a drought-avoiding species (Pison et al., 1996) with high xylem vulnerability compared to other co-occurring species like *P. pinea* (Martínez-Vilalta et al., 2004).
et al., 2004). Previous studies reported rapid stomatal closure of *P. pinaster* in response to mild-water stress, leading to decreased photosynthetic rates (Ripullone et al., 2007). Progressive decline in C assimilation can change the C allocation pattern, reducing its availability for non-essential processes such as secondary growth and cambial activity (Dobbertin, 2005; Oribe et al., 2003). Crown defoliation, observed in *P. pinaster* trees in the area but not in the other two species, may express water and carbon constraints under high water

Table 3
Parameters, estimates and p-values of selected models for each species. OLR = ordinal logistic regression; BLR = binary logistic regression. All estimates were significant at alpha < 0.05. All covariates included are defined in Materials and Methods and in Table S3. McFadden $d^2 = 1 - (\text{Residual deviance/Null deviance})$. AUC: Area under the curve. Accuracy: Overall model accuracy for the leave one out cross-validation.

<table>
<thead>
<tr>
<th>Species</th>
<th>Equation</th>
<th>$d^2$</th>
<th>AUC</th>
<th>Accuracy</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>OLR P. pinaster</strong></td>
<td>$\text{Logit}(P) = \alpha + \beta_1 \text{relBAI}<em>{0517} + \beta_2 \text{IRprec}</em>{0517} + \beta_3 \text{Hdo}$</td>
<td>0.13</td>
<td>0.79</td>
<td>45%</td>
</tr>
<tr>
<td>Parameter</td>
<td>Estimate</td>
<td>p-value</td>
<td></td>
<td></td>
</tr>
<tr>
<td>dead-declining</td>
<td>4.298</td>
<td>0.002</td>
<td></td>
<td></td>
</tr>
<tr>
<td>declining-healthy</td>
<td>6.035</td>
<td>&lt; 0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>relBAI$_{0517}$</td>
<td>2.895</td>
<td>0.020</td>
<td></td>
<td></td>
</tr>
<tr>
<td>IRprec$_{0517}$</td>
<td>2.686</td>
<td>0.050</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hdo</td>
<td>0.203</td>
<td>0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>BLR P. pinaster</strong></td>
<td>$\text{Logit}(P) = \alpha + \beta_1 \text{relBAI}<em>{0517} + \beta_2 \text{IRprec}</em>{0517} + \beta_3 \text{Hdo}$</td>
<td>0.40</td>
<td>0.89</td>
<td>66%</td>
</tr>
<tr>
<td>Parameter</td>
<td>Estimate</td>
<td>p-value</td>
<td></td>
<td></td>
</tr>
<tr>
<td>healthy</td>
<td>-12.820</td>
<td>0.003</td>
<td></td>
<td></td>
</tr>
<tr>
<td>relBAI$_{0517}$</td>
<td>8.131</td>
<td>0.007</td>
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</tr>
<tr>
<td>IRprec$_{0517}$</td>
<td>5.953</td>
<td>0.050</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hdo</td>
<td>0.489</td>
<td>0.004</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>BLR P. pinea</strong></td>
<td>$\text{Logit}(P) = \alpha + \beta_1 \text{DBH} + \beta_2 \text{relBAI}_{0517}$</td>
<td>0.15</td>
<td>0.75</td>
<td>58%</td>
</tr>
<tr>
<td>Parameter</td>
<td>Estimate</td>
<td>p-value</td>
<td></td>
<td></td>
</tr>
<tr>
<td>healthy</td>
<td>-5.493</td>
<td>0.029</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DBH</td>
<td>0.059</td>
<td>0.042</td>
<td></td>
<td></td>
</tr>
<tr>
<td>relBAI$_{0517}$</td>
<td>15.033</td>
<td>0.025</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 7. Moving correlations between ring width index and climatic variables for 30-year segments lagged by 1 year for the period 1950–2017 (final year of the segment represented in the X-axis). DJF Min T: Minimum temperature in winter. MAM Prec: Spring precipitation. Significant correlations are indicated with symbols, different colours define different status.
stress. Although reduced leaf area may contribute to acclimate the tree-water balance in the plant (Bréda et al., 2006), repeated dry episodes likely cause further leaf reduction, which in combination with low C uptake can leave negative legacies evident in tree performance years after drought (Allen et al., 2010; McDowell et al., 2018; Ogle et al., 2000). By weakening trees, water stress may also modify host-pathogen relationships. The high transpiration rates maintained by mistletoe, for example, increase water stress in host pines (Zweifel et al., 2012) and contribute to increase defoliation in affected trees (Galiano et al., 2010). The additional drought stress experienced by weakened trees could explain why eight declining trees infected with mistletoe were classified as dead in the OLR for P. pinaster (Figure S5). Nevertheless, the presence of dead and declining individuals without mistletoe suggests that mistletoe may be a secondary factor affecting previously water-stressed trees (Gea-Izquierdo et al., 2019).

Although P. pinea has a higher tolerance to drought than P. pinaster (Martínez-Vilalta et al., 2004; Perdiguero et al., 2015; Picón et al., 1996), the 10-year decline observed in dead P. pinea started right after an extraordinary drought, therefore suggesting that it was also likely triggered by drought. P. pinea has greater safety margins to xylem embolism than P. pinaster (Martínez-Vilalta et al., 2004) and performs an intermediate stomatal conductance between water-saving and water-consuming patterns under water stress, maintaining C uptake levels for intermediate stomatal conductance between water-saving and water-bolism. The high transpiration rates maintained by mistletoe, for example, increase water stress in host pines (Zweifel et al., 2012) and contribute to increase defoliation in affected trees (Galiano et al., 2010). The additional drought stress experienced by weakened trees could explain why eight declining trees infected with mistletoe were classified as dead in the OLR for P. pinaster (Figure S5). Nevertheless, the presence of dead and declining individuals without mistletoe suggests that mistletoe may be a secondary factor affecting previously water-stressed trees (Gea-Izquierdo et al., 2019).

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4.2. Stress expressions related to drought explain the mortality pattern of different species

Drought stress is one of the most common factors behind tree mortality in forests worldwide (Allen et al., 2010; Carnicer et al., 2011). Contrary to our hypothesis, in our study area, a higher probability of survival was related to stronger growth response to spring precipitation of the least drought-tolerant species, P. pinaster, but not on P. pinea. Both P. pinaster and P. pinea have increased their response to spring precipitation since the late 1970s similar to other species in the Iberian Peninsula (Andreu et al., 2007; Gea-Izquierdo et al., 2009). As a consequence of higher temperatures, more intense and frequent droughts make trees more dependent on spring precipitation to grow (Martín-Benito et al., 2010). Although higher responses to climate in healthy trees vs. dead trees were reported in several studies (Gea-Izquierdo et al., 2014; Macalady and Bugmann, 2014), the opposite trend has also been described (Suarez et al., 2004). Contrary to reported by other studies, we found no effect of plot density on tree climatic
response (Gea-Izquierdo et al., 2014; Viá-Cabrera et al., 2013). Secondary growth in \textit{P. pinaster} is enhanced by abundant spring precipitation (Vieira et al., 2020, 2014). Higher sensitivity to spring precipitation may represent a flexible tree response to adapt to variable resource availability and increase the tree probability of survival under stressful conditions. Some Mediterranean conifers exhibit a bimodal xylogenesis limited by temperature and precipitation, with maximum radial growth rates in spring and autumn (Camarero et al., 2010; Vieira et al., 2019). \textit{Juniperus} species are thought to feature a very plastic bimodal pattern and a general response to rainfall patterns along the year, even during summer, rather than a clear seasonal growth (Camarero et al., 2010). This pattern may confer junipers an additional feature to outperform pine species when coping with arid conditions (Camarero et al., 2010; Gaylord et al., 2013).

The positive effect of larger diameters on \textit{P. pinea} survival, as previously reported for other species (Hilsmann et al., 2018), can be interpreted as a proxy of the extension of the root system with increased access to resources, particularly soil moisture (Grote et al., 2016). Similarly, \textit{P. pinaster} trees growing in more productive sites (those with taller dominant height) had higher likelihood of survival. Therefore our results suggest that, at the stand scale, height is reflecting better microenvironmental conditions related to higher moisture availability (King, 1990). The positive effect of site conditions in tree survival has been broadly described (Gülin et al., 2006; Martinez-Vilalta et al., 2019; Young et al., 2017). As it has been shown for other species and ecosystems (Crouchet et al., 2019; Preisler et al., 2019), our results suggest that the microtopography in our study area allows the existence of pockets of deeper soil favouring higher nutrient content and water holding capacity, hence reducing drought stress. Despite the observed decline in \textit{P. pinaster}, under increasing drought stress with climate change, the species may be able to persist in the landscape in these favourable microsites. Our results agree with previous studies that recommend to include variables related to site heterogeneity to model tree mortality (Schwantes et al., 2018). These results can be applied to management, particularly in mixed afforestation with species of different drought tolerance distributed according to the local microtopography.

4.3. Low regeneration shows regression of species with the lowest drought tolerance

Species survival and distributional shifts are ultimately determined by the species ability to produce viable seeds and regenerate. \textit{P. pinaster} and \textit{J. oxycedrus} are considered pioneer species and their establishment is generally related to disturbances (Jovellar Lacambra et al., 2013; Tapia et al., 2004) as shown by the increase in the number of sampled trees in both species after the release in 1950s (Fig. 3 and Fig. 5). This disturbance could have been a consequence of the 1949 drought-induced mortality reported in different areas of the Iberian Peninsula (de Sampaio e Paiva Camilo-Alves et al., 2013). Extensive mortality may have created gaps in the canopy that favoured \textit{P. pinaster} and \textit{J. oxycedrus} regeneration. In contrast, more shade-tolerant \textit{P. pinea} exhibited constant establishment rates, regardless of disturbance intensity. The medium-low density of the stands, typical for Mediterranean pine forests (Tiscar et al., 2017) did not affect tree survival significantly (Table S1) while it would favour the regeneration of all three species. Nevertheless, \textit{P. pinaster} seedlings were very scarce in the study area and exclusively found in \textit{P. pinaster} plots located above 980 m (Figure S6). Yet, the age distribution of \textit{P. pinaster} in our study site indicates that the species successfully regenerated up to the 1990s (Figure S5), the same period when growth decline of dead and declining \textit{P. pinaster} started. Given the structure of the current forest with open canopies, major gaps, presence of fire scars in standing trees and abundance of pyrophilous species such as \textit{Cistus ladanifer} L. it seems that the presence of \textit{P. pinaster} in the area and the current status of the study forest was influenced by frequent wildfires in the past (Gea-Izquierdo et al., 2019). Fire and grazing have strongly shaped Mediterranean landscapes (López-Sáez et al., 2014), favouring adapted species, e.g. those with serotinous cones or those able to resprout or disseminate after fire or disturbance. Serotiny in \textit{P. pinaster} cones contributes to its post-fire regeneration, whereas neither \textit{P. pinea} nor \textit{J. oxycedrus} present serotinous cones (Tapia et al., 2004, 2001). Along with increasing temperatures and water stress, land-use legacies and lack of management in the last decades possibly shaped the current forest (Vayreda et al., 2016). The observed \textit{P. pinaster} decline may be a consequence of human intervention favouring its presence in areas that are currently out of the species natural ecological range due to climate change (Barbero et al., 1998; López-Sáez et al., 2014). In the case of \textit{J. oxycedrus}, the reduction of rural activities such as grazing may also have favoured its expansion in the area (Jovellar Lacambra et al., 2013). Our results suggest that \textit{P. pinaster} prevalence at its lowest altitudinal margin in the area may be compromised in concordance with reported altitudinal species shift in Europe (Lenoir et al., 2008; Lloret et al., 2004; Martínez-Vilalta and Lloret, 2016). Altogether, adult tree survival and regeneration dynamics suggest that increasing water stress, legacies and land-use changes may result in future lower presence of \textit{P. pinaster} at its lower altitudinal limit in favour of more drought-tolerant species (\textit{P. pinea, J. oxycedrus} and \textit{Q. ilex}).

5. Conclusions

The decline and regeneration dynamics of three co-occurring coniferous species observed suggested that water stress may be leading changes in species composition and dominance at the landscape scale. The currently dominant species, \textit{P. pinaster}, shows extensive signs of decline and mortality and little or no regeneration while it is being replaced by \textit{Q. ilex}, \textit{P. pinea} and \textit{J. oxycedrus}. Drought events under a warmer climate since the 1980s incited tree growth decline that differed between species. Non-healthy individuals of \textit{P. pinaster} exhibited negative growth trends since 1995. In dead \textit{P. pinea} trees, a growth decline started later since 2005. Different site structural and tree functional covariates expressing higher moisture availability increased the probability of \textit{P. pinaster} survival, while \textit{P. pinea} survival was mainly increased by tree size. Despite the slower growth of \textit{J. oxycedrus}, its higher drought tolerance would help this species to outcompete the pine species under increasingly arid conditions. Regeneration patterns in the area revealed that water stress along with land-use legacies are also limiting \textit{P. pinaster} establishment in comparison to more abundant regeneration of \textit{P. pinea} and \textit{J. oxycedrus}. Under global change in our study area, \textit{P. pinaster} will be replaced at its lower altitudinal limit by more drought-tolerant species like \textit{P. pinea, J. oxycedrus} and \textit{Q. ilex}.

CRediT authorship contribution statement

Macarena Férriz: Data curation, Formal analysis, Writing - original draft. Dario Martin-Benito: Conceptualization, Methodology, Formal analysis, Writing - review & editing. Isabel Canellas: Writing - review & editing. Guillermo Gea-Izquierdo: Conceptualization, Methodology, Formal analysis, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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