Dendroecology in common gardens: Population differentiation and plasticity in resistance, recovery and resilience to extreme drought events in *Pinus pinaster*

Running title: **Maritime pine resilience to extreme droughts**

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Word count (main text from intro to discussion): 5787
Refs: 76

Abstract

Quantifying intraspecific genetic variation and phenotypic plasticity of traits involved in drought tolerance is essential to forecast forest tree vulnerability to climate change. Tree ring analysis was applied to retrospectively assess the resistance, recovery and resilience of a Mediterranean pine in the face of extreme climate episodes. We combined a dendrochronological approach with the analysis of common-garden tests to disentangle genetic, environment and genetic-by-environment effects in growth responses of 10 *P. pinaster* populations to two extreme climatic events. Trees were 43 years old and had experienced two intense droughts, in 1995 and 2005. Drought events caused drastic reductions in secondary growth, but trees showed high capacity to recover pre-drought growth rates. The differences in the characteristics of the two drought events and the environmental distance between sites strongly modulated maritime pine responses to extreme droughts. However, a common among-population signal across sites and events was detected in the drought response strategy. Among-population variation in response to extreme droughts was evident for the resistance and recovery components, two strategies that appeared to trade-off between each other. Populations from Atlantic climates showed higher resistance but lower recovery capacity, whereas Mediterranean origins prioritised recovery over resistance. Mediterranean populations showed a more conservative strategy that indicated an adaptive advantage under water stress, reflected in greater long-term survival. The abovementioned relationships were clear in the site where the impact of the drought events was strongest, but not in the more favourable site. Differences in relationships between sites reflect that strategies of populations to cope with drought are strongly context dependent. Based on these results, we infer that future extreme droughts will differentially affect *P. pinaster* populations across the natural range of the species. Immediate effects will be more evident in Mediterranean areas but, in the long term, population persistence in the face of climate change will be more compromised for Atlantic origins. Because local environmental conditions can considerably modulate responses to extreme events, special attention is required to define appropriate management practices to mitigate the impact of future droughts.

Key words: Adaptive variation, Common garden, Climate change, Dendroecology, Drought tolerance, Extreme drought events, Phenotypic plasticity, Recovery, Resilience, Resistance

Introduction

Ongoing climate change is imposing serious constraints on forest productivity and persistence worldwide (Parmesan, 2006). The increasing frequency and intensity of extreme climate events such as droughts, heat waves and storms drastically impact tree growth and trigger forest dieback (Allen et al., 2010; Neumann et al., 2017). Extreme droughts are notably relevant in Mediterranean climate areas, where evidence is accumulating of forest decline due to drought (Camarero et al., 2015; Martínez-Vilalta and Piñol, 2002; Sánchez-Salguero et al., 2010).

Forest persistence in the face of climate disturbance may depend on the ability of trees to tolerate and recover from disturbance and maintain their function during and after the event (Ingrisch and Bahn, 2018). Drought tolerance relies on a wide range of physiological plastic responses to water deficit (McDowell et al., 2008; Ryan, 2011). In conifers, these physiological responses include mechanisms intended to (i) avoid hydraulic failure by stomata closure regulation, (ii) prevent cell damage under low water potential by osmotic adjustments, (iii) prevent carbon starvation by reallocating carbon reserves, and (iv) improve water uptake and use efficiency by changes in growth allocation priorities (Moran et al., 2017). Individual plastic responses may, however, be insufficient to cope with severe, prolonged or concatenated droughts, resulting in increased vulnerability to drought and high mortality rates (Navarro-Cerrillo et al., 2018). In these cases, tree populations can persist only by adaptive genetic changes. Selection pressure on adaptive traits related to drought tolerance may result in long-term changes in the mean and variance of population tolerance to drought. Gene flow from drought-adapted genetic pools may also help to enhance the drought tolerance of a population. However, migration and natural selection operate more slowly than the current pace of climate change, compromising forest persistence in the face of climate disturbances (Jezkova and Wiens, 2016).

Considerable effort has been made in recent decades to determine the quantitative genetic basis of drought adaptation. Most studies have focused on manipulative experiments on young trees (Moran et al., 2017), reporting large among- and within-population variation in drought tolerance (e.g. de la Mata et al., 2014; Gaspar et al., 2013; Lamy et al., 2014). Particularly, populations of maritime pine (*Pinus pinaster* Ait.) from dry climates were reported to be adapted to drought through larger biomass allocation to roots (Corcuera et al., 2012), higher water use efficiency with lower dependence on stomata closure regulation (Correia et al., 2008), higher resistance to cavitation (Corcuera et al., 2011; but see Lamy et al., 2014), and higher osmotic adjustment (Nguyen-Queyrens and Bouchet-Lannat, 2003) than populations from mild climates. Conversely, populations from mild climates were reported to grow faster when conditions were favourable and exhibited a less conservative strategy against abiotic stress (Corcuera et al., 2012; de la Mata et al., 2014). Tolerance at young ages is, however, not necessarily transferable to older ages (Cavender-Bares and Bazzaz, 2000; He et al., 2005). Because drought is also an important selective agent in mature stages, either directly, by causing hydraulic failure (Martínez-Vilalta and Piñol, 2002), or indirectly, by contributing to interactions with biotic stress (Netherer et al., 2015), quantitative analysis of drought tolerance genetics in mature trees is required.

Dendrochronological approaches have recently been applied to examine climate sensitivity and responses to extreme drought events in mature trees (Gazol et al., 2017; Gazol et al., 2018; Rubio-Cuadrado et al., 2018; Sánchez-Salguero et al., 2018; Serra-Maluquer et al., 2018). Dendrochronology provides an annually-resolved record of tree responses to climate variation across the tree lifespan. This technique can be applied to assess the impact on trees and their recovery capacity in the face of extreme climate events by analysing annual radial growth before, during and after a single extreme climate event (Lloret et al., 2011). Recent studies have shown that the ability of trees to cope with extreme climate events varies greatly among species (e.g. Gazol et al., 2018) and across the natural range of a given species (e.g. Sánchez-Salguero et al., 2018). Specifically, maritime pine populations growing in dry sites were less resistant to drought but recovered faster than trees growing in mesic sites (Sánchez-Salguero et al., 2018). However, these studies were not able to properly disentangle environmental from genetic effects as they were based on surveys of natural populations. Disentangling plastic from genetic variation is mandatory to properly assess the impact of climate change across the distribution range of a species. This can be achieved only by quantitative genetic approaches in which different populations are grown together in a common environment (Montwe et al., 2016).

Several studies have analysed intraspecific variation in resilience to extreme drought events in common garden tests using dendrochronological approaches (George et al., 2017; George et al., 2015; Heer et al., 2018; Housset et al., 2018; Montwe et al., 2016; Montwé et al., 2015; Taeger et al., 2013; Trujillo-Moya et al., 2018). These studies suggested that patterns of within-species variation in strategies to cope with extreme droughts differ greatly depending on the species considered, as has been previously observed in across-species surveys in natural systems (Gazol et al., 2018). Most of the previous studies focused on a single extreme event (Montwe et al., 2016) or a single test site (Housset et al., 2018), but responses to extreme events are dependent on the event itself (Gazol et al., 2018; Serra-Maluquer et al., 2018) and the environmental conditions of the test site (Savva et al., 2007). Moreover, the among-population patterns of variation in the response to extreme events can be affected by variable plastic responses to the environment of the test site (Savva et al., 2007). To assess the potential of local adaptation of tree species or populations to climate change, it is essential to understand the stability of the strategies and components of genetic variation in drought tolerance traits across a range of extreme climate events and across sites.

We analysed the influence of genetic (G, i.e. population differentiation), environment (E, site-to-site plasticity) and G×E interaction (i.e., among-population variation in phenotypic plasticity) in the growth responses of maritime pine (*Pinus pinaster* Ait.) populations to two episodes of extreme drought using a dendrochronological approach. Annual increment in basal area in the last 30 years was quantified in adult pine trees from 10 populations covering most of the distribution range of the species, planted in two replicated common garden tests in central Spain. Resistance (i.e. the impact of an extreme event on current growth relative to previous growth), recovery (i.e. the relative increase of growth rates after the event) and resilience (i.e. the capacity to reach pre-episode growth levels) in the face of the two extreme drought events identified were estimated following Lloret et al. (2011). Quantitative genetic analysis allowed us to estimate population differentiation across sites and events in these resilience components and identify signs of adaptation associated with the environmental conditions at the origin of each population.

Material and Methods

Study system

Maritime pine (*Pinus pinaster* Ait.) is an important Mediterranean tree that covers more than 4 Mha in Southwest Europe and North Africa. Across its natural range, this species grows in variable environmental conditions, from mild environments in the Atlantic to harsh, dry Mediterranean climates, and from sea level to more than 2000 m in the southern regions. Its natural distribution is highly fragmented and, either because of neutral demographic processes or local adaptation, populations are strongly differentiated in many life history traits, including primary (height) and secondary (radial) growth (Benito-Garzon et al., 2013; Di Matteo and Voltas, 2016) and tolerance to abiotic stress (Chambel et al., 2007; de la Mata et al., 2014; but see Lamy et al., 2014). Radial growth of mature maritime pine trees was shown to be sensitive to water availability (Arzac et al., 2018; Bogino and Bravo, 2008), and this effect varied among populations depending on their local environmental conditions (Caminero et al., 2018; Rozas et al., 2011).

Plant material and common garden experiments

The present study is based on data collected from two provenance trials established in 1967 as part of a larger series of test sites where 52 maritime pine populations from the complete natural range of the species were planted in five different sites in central Spain (Alia et al., 1997; Benito-Garzon et al., 2013). Each trial shared the same populations, and each population was represented by seed lots from 30 unrelated mother trees. The experimental design in each test site comprised a complete block design with four blocks of experimental units of 16 trees per population, planted at 2.5 × 2.5 m spacing.

We focused on the Cabañeros and Riofrío sites, in Ciudad Real province (Fig. 1a) and on 10 contrasting populations belonging to seven of the eight genetic pools identified by neutral markers for this species (Bucci et al., 2007) (Table ST1). The populations were selected to cover as much of the environmental variation across the natural distribution range of maritime pine as possible (Fig. 1b, Table ST1). The conditions at origin for these populations were highly variable, ranging from 28 to 1600 m in elevation, 336 to 1555 mm in total annual precipitation, and 9.7 to 15.6 ºC in mean annual temperature (Table ST1).

The two test sites are located in central Spain under Mediterranean continental climate, although Cabañeros is slightly wetter and colder than Riofrío (Table ST1). The two sites have acidic soils (pH ~ 5) derived from quartzite bedrock, but soils in Riofrío are stonier and shallower than in Cabañeros. Additionally, Cabañeros is on a homogeneous hilltop plain while Riofrío is on a mid-hill with irregular topography. Altogether, although the environmental differences between the two sites are not that big (Fig. 1b), they were enough to imprint notable differences in pine performance, with higher growth and survival rates of pines in Cabañeros than in Riofrío (Table ST1).

For both sites, monthly weather records from tree establishment to sampling was estimated using data from nearby meteorological stations of the National Agency of Meteorology (AEMET, Spanish Government; see details in Supplementary Information Methods SM1). Standardised precipitation-evapotranspiration index (SPEI) was calculated from the monthly temperature and precipitation series using the *SPEI* package of the software R 3.5.2 (Vicente-Serrano et al., 2010). Extreme drought events in the last three decades at both test sites were identified as minimum values of mean SPEI from October to May, the rainy period in the central Iberian Peninsula. Two extreme drought events were identified in 1995 and 2005 at both sites (Fig. 2a). These events were identified and used in previous studies that analysed drought responses in central and southern Spain (Rubio-Cuadrado et al., 2018; Sánchez-Salguero et al., 2010).

Climate data

Monthly mean climate data at each population origin were obtained for the period 1950-2000 from a regional climate model (Gonzalo-Jimenez, 2008)in the case of the seven Spanish populations, and from the Climate Explorer of the Royal Netherlands Meteorological Institute (CRU TS 4.01 data set; http://climexp.knmi.nl; Mitchell and Jones (2005)) for the French, Italian and Moroccan populations. The model of Gonzalo-Jimenez (2008) is known to be more accurate in the Iberian Peninsula than world-level models because it takes into consideration a dense network of meteorological stations (Jaramillo-Correa et al., 2015). Both models have a resolution of 1 x 1 km; for each population, data from the corresponding pixel was retrieved. The climate variables were annual mean temperature, maximum temperature in the warmest month, minimum temperature in the coldest month, temperature seasonality, annual and summer precipitations, and average number of frost days per year. To minimise Type I error in the correlation analyses between population performance and climate (see below), the information from these seven climate variables was summarised into two main components through a PCA using PROC PRINCOMP in SAS. The two first PCs (hereafter 'climate indices') explained ~84% of the overall variation. Climate index 1 explained 46.5% of the variance and was positively related to high minimum temperatures and precipitation and inversely related to temperature seasonality, suggesting a proxy of Atlantic climate for higher values of the index and of Continental and Mediterranean climates for lower values of the index (Fig. 1b). Climate Index 2 explained 37.2% of the variance and was positively related to mean temperatures and negatively related to frost frequency, suggesting a thermal gradient from cold to warm conditions (Fig. 1b).

Sampling and tree-ring data processing

In summer 2011, when trees were 43 years old, tree survival of the populations was assessed and wood samples were taken from 12-18 trees per population (3-5 trees per block) at each test site. Trees were cored at 1.3 m above ground using 5-mm Pressler increment borers. Two to four wood cores were sampled from each tree. Wood cores were sanded until tree rings were clearly visible and tree-ring series were visually cross-dated by assigning calendar years to the rings through identification of characteristic wide and narrow ring sequences (Speer, 2010). Tree-ring widths were measured to the nearest 0.001 mm on 2–4 radii per tree using a binocular microscope and a linear stage (Velmex Inc., Bloomfield NY, USA) interfaced with a computer. The accuracy of cross dating and ring width measurement was checked using the COFECHA programme (Holmes, 1983).

After averaging all ring width series from each tree on an annual basis, individual basal area increment (BAI, $cm^2 yr^{-1}$) series were calculated from ring widths, assuming circularity of the rings section and considering all available rings in each core (Biondi and Qeadan, 2008). BAI chronologies for each population and test site were calculated as a year-by-year arithmetic mean of individual BAI series. To avoid missing segments in the BAI series at young ages, the 31-year common period to all series from 1980 to 2010 was considered for the analyses.

Pointer years

To assess the impact of drought events on growth stability, we calculated the negative pointer years, i.e., years with extremely low annual growth in relation to previous years in a high proportion of trees (Schweingruber et al., 1990), using the *dplR* package

(Bunn, 2010). Negative pointer years were calculated considering BAI data for each individual tree at each test site. When more than 50% of trees at a site exceeded 50% BAI reduction in comparison to mean BAI for the previous three years, the year was considered a negative pointer year.

Drought resilience components

To quantify tree growth response to extremely dry conditions, we calculated the four resilience components proposed by Lloret et al. (2011): resistance (Rt), recovery (Rv), resilience (Rs) and relative resilience (rRs), calculated from BAI data as:

$$Rt = \frac{BAI_{DY}}{BAI_{PreDY}}$$

$$Rv = \frac{BAI_{PostDY}}{BAI_{DY}}$$

$$Rs = \frac{BAI_{PostDY}}{BAI_{PreDY}}$$

$$rRs = \frac{BAI_{PostDY} - BAI_{DY}}{BAI_{PreDY}}$$

where BAI_{DY} is the BAI during the drought year, BAI_{PreDY} is the mean BAI during the three pre-drought years, and BAI_{PostDY} is the mean BAI during the three post-drought years. Rt quantifies the capacity of trees to buffer drought stress and continue growing during drought. Rv quantifies the growth reaction during the three years following the drought year. As recommended, Rv was not calculated when BAI_{DY} was zero (Lloret et al., 2011). Rs quantifies the capacity of trees to recover pre-drought growth rates, and rRs quantifies the net balance between growth during extreme drought and the three following years. As the different indices share some elements in their equations, it should be noted that they are not completely independent (e.g. resistance and recovery could tend to be negatively related).

Inter-tree competition

As response to drought events may be contingent on the amount of resources each tree has available (Martinez-Vilalta et al., 2012), we accounted for competition interference in our statistical models. For that purpose, we assessed the surrounding basal area of each tree before each climatic event as a proxy of neighbouring competition (Serra-Maluquer et al., 2018). To estimate this competitive index, we took advantage of tree survival and dendrometric assessments done in 1985 (Alia et al., 1995) and 1998 (Alía et al., 2001). To homogenize the interval between the previous assessments and the two drought climatic events (occurring in 1995 and 2005), tree diameter in 1995 was interpolated from the assessments done in 1985 and 1998, assuming a constant growth rate during this period. Basal area surrounding each core-sampled tree was then estimated by adding the basal area at breast height of the immediately surrounding trees that were alive (8 neighbours at most) ten years before each climatic event.

Statistical analyses

A repeated mixed model analysis applied to tree-level BAI data was used to compare mean BAI before (three years before), during (event year) and after (three years after) the drought event and to explore whether differences among these three periods depended on the test site, the pine population and their interaction (see details in Methods SM2). In these models, the drought factor (three levels: before, during, after) accounts for the plastic response in BAI to the drought event (i.e. temporal plasticity within each subject) while the interactions between this factor and the sites and the populations represent spatial plasticity to environmental variation between sites and among-population variation in this spatial plasticity, respectively.

Resilience components were analysed by repeated measures mixed models but, in this case, the models were fitted for the two drought events (1995 and 2005) together. Individual trees were the subjects for which two repeated measures (one for each event) were obtained. The events and their interaction with sites and populations were thus considered within-subject repeated measures. The mixed model used was (random effects in italics):

$$RC = \mu + S + POP + POP\times S + Ev + Ev\times S + Ev\times POP + Ev\times POP\times S + \mathit{B(S)} + \mathit{B\times POP(S)} + \mathit{Tree(B\times POP\times S)} + NBA + \varepsilon$$

where RC is the resilience component of each tree and event, μ is the overall mean; S, POP, and POP×S are across-subject fixed effects that account for global common differences in the resilience component between sites, populations and their interaction; Ev is the within-subject fixed effect (repeated measures on the same trees) of the extreme event (1995, 2005); B(S) and B×POP(S) represent the random variation between the blocks within sites and between the whole plots of the multi-tree block design, respectively; *Tree(B×POP×S)* is a random effect identifying each tree that account for the autocorrelation among the repeated measures within trees; NBA is a continuous fixed covariate that accounts for neighbouring basal area, and ε is the random residual. The event factor indicates differences in the resilience component between the two events, while the Ev×S, Ev×POP and Ev×POP×S interactions reveal whether variation in the resilience component between sites and populations is contingent on each particular event. Covariation with neighbouring basal area accounts for the modulation of the resilience components by competitive effects. Mixed models were fitted with the MIXED procedure of the SAS System (Littell et al., 2006).

To determine whether variation among populations in response to drought events was related to climate conditions at the origin of the populations, across-population Pearson correlations (CORR procedure in SAS) were carried out between the resilience components and the two climate indices obtained from the principal component analysis described previously. Relationships between the different resilience components at the population level were also tested with Pearson correlation analysis. Correlation analyses were conducted using the across-extreme-events least square means of the resilience components for each population at each test site as derived from the previous mixed models.

Results

Standardised precipitation-evapotranspiration indices from previous October to current May varied greatly from year to year across the study period (1980-2010), and two extreme drought episodes in 1995 and 2005 at both the Cabañeros and Riofrío test sites were identified (Fig. 2a). In Cabañeros, considerable reduction in radial growth rates of more than 50% of sampled trees (i.e., negative pointer year) was observed only in 2005 (Fig. 2b). However, in Riofrío, both dry years coincided with negative pointer years (Fig. 2c).

Growth before, during and after the drought events

Basal area increment (BAI) drastically declined during the extreme drought events but recovered afterwards (Fig. 3). Growth responses to the drought events were, however, contingent on the site (Fig. 3) and the population (Fig. SF1). Reductions of BAI during the two extreme drought events were more pronounced in Riofrío than in Cabañeros, but growth recovery after the events was stronger in Riofrío than in Cabañeros (Fig. 3).

For both extreme events, all populations showed a drastic decrease in radial growth during the drought year but later recovered normal pre-drought growth rates (Fig. SF1). However, growth rates of the PRAV, COCA and TAMJ populations were significantly higher after the 2005 drought event than before (Fig. SF1).

Variation in resilience components

Resistance, recovery and relative resilience of growth to the drought events were significantly influenced by the sum of basal areas of neighbouring trees, a proxy of inter-tree competition (Table 1). Trees subjected to higher inter-tree competition showed reduced resistance to the extreme events, but higher recovery afterwards as well as higher relative resilience. No effect of competition on drought resilience was observed (Table 1).

Large differences were observed in the resilience components between the two extreme events (event factor in Table 1). Significant variation between sites and among populations was also observed across events for most of these components (site and population factors in Table 1). Site differences were particularly high for resistance, recovery and relative resilience (Table 1), with trees in Cabañeros consistently showing higher resistance but lower recovery and relative resilience than trees in Riofrío for the two events (Fig. 4). Differences between sites in resistance and relative resilience were, however, greater for the 1995 event than for the 2005 event (Fig. 4). Population resilience did not differ between sites for either event (Table 1, Fig. 4).

After accounting for the potential bias generated by variable competitive effects, resistance to and recovery from drought events also varied significantly among pine populations, although this variation differed between events or sites (see interaction terms with the population factor in Table 1). Despite these interactions, both population resistance and population recovery were positively correlated between events in Riofrío ($r = 0.89$, $N = 10$, $p < 0.001$ for resistance, and $r = 0.89$, $N = 10$, $p < 0.001$ for recovery) but not in Cabañeros (Fig 4a,b). In general, populations from the Atlantic climate (e.g., LEIR, PRAV, CAMB) showed higher resistance but lower recovery than populations from drier conditions (e.g., CARA, TAMJ) (Fig. 4). Population resistance across the two events was negatively related to population recovery, although the relationship was significant in Riofrío ($r = - 0.73$, $N = 10$, $p = 0.018$) and not in Cabañeros ($r = - 0.37$, $N = 10$, $p = 0.286$), where the recovery values and their among-population variation were very low (Fig. SF2). It should be noted that the CARA population, from southeast Spain, showed outstanding capacity for growth recovery after drought events, and this outstanding recovery may be forcing the previously reported relationship. However, the relationship between resistance and recovery in Riofrío remained significant after removing this population from the analysis ($r = 0.76$, $N = 9$, $p = 0.017$).

Among-population variation in resilience and relative resilience was site- and/or event-dependent (population × site and population × event interactions, respectively, in Table 1), resulting in no overall differences among populations in these parameters.

Dependence of drought resilience components on climate conditions at origin

Population resistance to the extreme drought events in Riofrío was significantly and positively related to climate index 1 (Fig. 5a), a proxy of Atlantic conditions at positive values of the index and of continental Mediterranean conditions at negative values. Growth resilience in Cabañeros was also positively related to climate index 1 (Fig. 5c), although this relation should be interpreted with caution because no significant overall variation among populations or population × site interactions were detected for this trait

(Table 1). No other significant relations were detected between resilience components and climate conditions at population origin (Fig. 5) except for a negative correlation (r = - 0.74, N = 10, p = 0.013) between growth recovery in Cabañeros and climate index 2, a proxy of thermal conditions (Fig. SF3).

Interestingly, among-population variation in growth resistance to drought events in Riofrío was negatively correlated with accumulated survival at age 43 (Fig. 6a). Population survival was also positively related to recovery from drought events in Riofrío, although this relationship was forced by the CARA population, without which the relationship becomes non-significant (Fig 6b). No significant relationships between the resilience indices and long-term survival were observed in Cabañeros (Fig. 6).

Discussion

This study made it possible to disentangle the effects of environment (i.e., site-to-site plasticity), genetics (population differentiation) and G×E (i.e., population differences in plasticity) on maritime pine responses in radial growth to two severe drought events. Using two common garden trials, we were able to account for relevant factors that are known to modulate tree responses to drought events, such as tree age, competitive status and inter-tree competition (Fernández-de-Uña et al., 2015; Martín-Benito et al., 2008; Martinez-Vilalta et al., 2012; Serra-Maluquer et al., 2018). These sources of variation were discarded because we sampled dominant trees established simultaneously under common environmental conditions according to a completely regular design. Inter-tree competition was accounted for by incorporating an index of competition (surrounding basal area to each experimental tree) as a covariate in the statistical models. Quantifying plasticity and true genetic differentiation among populations is essential to examine the adaptive value of drought-tolerance traits and strategies, and to suggest mitigation management tools such as assisted migration (Aitken et al., 2016; Alberto et al., 2013).

Drought response varies greatly across sites and drought events

A first important finding of this study is that radial growth response to extreme drought events largely depended on site. For each drought event, site was the most relevant factor explaining variation in resilience components, even when environmental differences between the test sites were not substantial (see Table ST1, Fig. 1).

Climate sensitivity and growth responses to drought have been shown to differ across test sites in other conifer species, with differences attributed to contrasting climate conditions across sites (McLane et al., 2011; Suvanto et al., 2016; Taeger et al., 2013). In our study, however, the intensity, timing and duration of each extreme event (1995 and 2005) were similar between sites (see Fig. 2). Thus, differences between sites in response to extreme drought events should not be attributed to differences associated to the extreme event itself, but to other environmental differences that must exist between sites.

Environmental conditions in the two test sites were similar but not equal. These differences were enough to imprint notable differences between sites in pine growth and survival (Alia et al., 1997). Cabañeros was slightly wetter and colder than Riofrío, and Riofrío has stonier and shallower soils, with higher slopes and irregular topography than Cabañeros. The lower overall quality for pine development of the Riofrío test site may have increased the impact of the drought events on all populations, as evidenced by the greater reduction of radial growth rates during the event year and lower resistance to drought at this site. Accordingly, pointer years coincided with the two drought events in Riofrío, but only with the 2005 event in Cabañeros. Differences in edaphic and geomorphological characteristics between sites may have particularly influenced early seedling development affecting for example root development or biomass partitioning (Chambel et al., 2007; de la Mata et al., 2014). This effect could have lasted to mature ages and magnified after a drought event amplifying site differences in response to climate stressors (Andivia et al., 2018). Little environmental differences triggering large differences in how trees responded to climate extremes may have important consequences when forecasting forest responses to climate change. Microenvironmental factors such as topography, soil depth and stoniness –typically unexamined in previous studies– may be much more relevant than previously recognized.

A second important finding of this study is that maritime pine responses to drought were strongly dependent on the particular characteristics of the event. Previous studies identified the intensity, timing and duration of the drought event as major drivers of forest drought resilience components (Gazol et al., 2018; Taeger et al., 2013). The two drought events studied here showed different intensity, timing and duration: 1995 was the last of six consecutive years of water deficit, while 2005 was a single very dry year preceded and followed by several drought-free years (see Fig. 2a). These differences likely explain the variable growth responses to the two drought events. For example, the longer duration and higher intensity of the 1995 drought event is likely behind the lower recovery observed for this event.

Inter-tree competition also influenced the resilience of maritime pine trees to the extreme drought events as evidenced by the significant correlation with surrounding basal area. According to previous findings (Linares et al., 2010; Martinez-Vilalta et al., 2012), trees growing under stronger neighbouring competition were less resistant to drought, probably because of reduced resource availability. However, the effect of competition on recovery and relative resilience was positive. A possible explanation for this counterintuitive result arises from the positive autocorrelation in growth that occurs in experimental designs with multi-tree plots (16 trees, 4 rows × 4 columns in our case) (e.g. Zas, 2006). Besides microenvironmental effects, in multi-tree plot designs, most trees that surround each experimental tree are from the same population and thus tend to grow similar to the focal tree. This results in a positive autocorrelation which, based on what was observed here, seems to surpass the negative autocorrelation between competition and growth responses to drought. Previous studies also failed to detect consistent and strong negative effects of competition on resilience components (Serra-Maluquer et al., 2018).

Patterns of growth response to drought among populations

Sites and events not only influenced overall growth responses to drought and resilience components, but also altered the variation observed among pine populations in their drought resilience strategies (see significant interactions with populations in Table 1). Patterns of among-population variation in recovery and relative resilience were dependent on site, and variation in all resilience components except recovery was dependent on the drought event. Repeatability across events in resilience components in *Larix decidua* populations was low, reflecting a high event × population interaction (George et al., 2017). Similarly, in *Abies alba*, among-population variation in response to different drought events varied greatly from one event to another, resulting in no overall common patterns of variation (George et al., 2015). Viewed together, these results highlight the importance of common-garden tests for exploring intraspecific patterns of variation in drought responses and the need to analyse responses to multiple events at different sites, irrespective of the environmental distance between them (de Villemereuil et al., 2016).

Despite the significant site × population and event × population interactions, global general patterns of among-population variation were detected in growth responses to drought and resilience components. Resistance and recovery in the face of the extreme events showed a common population signal across sites and events. In Riofrío, where the impact of the extreme events was more evident, population resistance and recovery were strongly correlated across events. This is an important result when inferring the adaptive value of the observed intraspecific variation. Maritime pine populations from drier environments were less resistant to drought but recovered faster than populations from mesic environments, a result that has been previously suggested upon natural population surveys in maritime pine (Sánchez-Salguero et al., 2018), and other tree species (Gazol et al., 2017; Stuart-Haentjens et al., 2018). Moreover, in the site where the impact of drought was strongest (Riofrío), resistance and recovery were negatively correlated, suggesting a trade-off between both components, as reported elsewhere (Gazol et al., 2017; Zang et al., 2014).

These observations are consistent with results from physiological studies on young pine trees, where the growth of populations from mild climates were less sensitive to water deficit (i.e. they were more ‘resistant’ to drought) while populations from drier conditions rapidly stop growing in response to water deficit (de la Mata et al., 2014; Klein et al., 2014). This risky strategy of the Atlantic populations may lead to cavitation and higher mortality rates under long-lasting or intense drought (Klein et al., 2013). This is consistent with the negative correlation between population resistance and long-term survival observed in Riofrío, where the intensity and impact of the drought events were slightly higher. Moreover, higher plasticity in stomatal regulation (Feinard-Duranceau et al., 2018) and/or greater capacity to accumulate carbohydrate reserves (Suárez-Vidal et al., 2017) in populations from drought-prone environments may explain their greater recovery capacity, as suggested in among-species studies (Gazol et al., 2018). Recovery emerges as a key adaptive strategy for coping with severe water deficit, and the significant positive correlation between recovery and long-term survival (Fig. 6b) points into this direction. The relationship between recovery and survival may be, however, overrated by values of recovery and survival of a single population (CARA, from the driest region of the Iberian Peninsula, Fig. 6b). The outstanding recovery of this population is likely due to the interruption of radial growth during the year of the drought event, resulting in very large recovery estimates. As mentioned before, minimizing growth in response to water deficit is a conservative strategy typically shown by drought-adapted origins of Mediterranean pines (de la Mata et al., 2014; Klein et al., 2014). Other pine species, however, may show contrasting adaptations to drought, with trees adapted to stressful environments showing less growth plasticity, and less plastic trees surviving better after extreme droughts (Ogle et al., 2000). It should be noted that removing the CARA population from the analyses makes the relationship between recovery and survival non-significant. The interpretation of the recovery-survival relationship should be, thus, considered with caution.

Adaptive significance of growth resilience to drought

Determining whether the observed patterns of intraspecific differentiation are consequences of local adaptation processes is an important milestone for forecasting the impact of climate change across the natural range of a given species and developing management tools to mitigate its effect (de Villemereuil et al., 2016). As observed in other conifer species such as *Pinus sylvestris* (Taeger et al., 2013), *Pseudotsuga menziesii* (Montwé et al., 2015), or *Larix decidua* (George et al., 2017), we found intraspecific genetic variation in drought resilience components among the studied populations. Particularly, resistance to and recovery from the extreme drought events showed consistent among-population variation. Because the main drought coping strategies of a given species tend to be those that are differentiated among populations as a consequence of local adaptation to environmental heterogeneity (Zang et al., 2014), we hypothesize that both resistance and recovery are key adaptive drought-tolerance strategies in this Mediterranean species.

Differentiation among populations can arise not only by divergent selection across a heterogeneous environment, but also by neutral processes like drift, associated with the demographic history of the species (George et al., 2017). Marked and structured neutral differentiation can be especially important in Palearctic species that suffered strong genetic bottlenecks during the last ice age, which is the case of maritime pine (Jaramillo-Correa et al., 2015). Neutral and adaptive variation could be disentangled by gathering information on neutral genotypic markers and using population genetics approaches such as Fst-Qst comparisons (Alcaide et al., 2019), or accounting for neutral variation in the statistical model fitting (López-Goldar et al., 2019). Although we lack genotyping information of our material, several of our results suggest that the patterns of variation observed are the result of adaptive processes. On the one hand, the conserved patterns across sites and drought events of among-population variation in resistance to and recovery from the extreme climate events points to a marked genetically-driven pattern of variation. On the other hand, the consistent and biologically meaningful relations between variation in resilience components and climate conditions at origin and the relationships between population resistance and population recovery with long-term survival suggest that the genetic variation in these resilience indices has an adaptive origin. The later relationships suggest that the resilience components may be relevant for tree fitness, and could therefore be subjected to selective pressures associated with extreme drought events. However, several limitations of these relationships must be recognized. First, survival was evaluated at the time of core sampling (when trees were 43 years old), and it can't be assumed that the cumulated mortality of trees to this date was totally related to the occurrence of the two extreme drought events. Early mortality during the first years after establishment could, for example, be disturbing the biological meaning of these relationships. Second, the relationship between recovery and survival was overridden by the outstanding values of one population (see discussion above), diminishing the reliability of the relationship. Finally, the different population survival rates may have generated different competition levels among populations which, in turn, may have affected tree responses to the drought events. This potential bias was, however, accounted for by including inter-tree competition in the statistical models and adjusting population least square means for variation in competition among trees. Altogether, although providing relevant information, the relationships between the resilience components and survival must be managed with caution. Further studies are needed to confirm the adaptive value of the resilience components in response to extreme drought events.

Other studies reported evidence that the components of resilience to extreme climate events assessed here are integrative traits reflecting drought-coping adaptations. For example, resilience components have been associated with functional molecular markers related to drought (Heer et al., 2018; Housset et al., 2018; Trujillo-Moya et al., 2018), and several studies have shown marked relations between among-population variation in resilience components and climate conditions at origin (Housset et al., 2018; Stuart-Haentjens et al., 2018; Trujillo-Moya et al., 2018). Moreover, repeatability of resilience components across sites and events has been found to vary significantly among populations (George et al., 2017), and this has been interpreted as a sign of adaptation, given that populations subjected to strong selective pressure (i.e., inhabiting drought-prone environments) showed lower within-population variation and higher repeatability across sites and environments (George et al., 2017).

Data Accessibility Statement

BAI chronology data are currently being submitted to DIGITAL.CSIC repository, and accession numbers will be supplied once available.

Acknowledgements

This research was funded by Spanish Government (MINECO/FEDER) grants FENOPIN (AGL2012-40151-C03-01) and FUTURPIN (AGL2015-68274-C03-02-R) and Xunta de Galicia-GAIN grant (IN607A2016/013). Language edition was funded by the European Regional Development Fund (ERDF, 'A way to achieve Europe') and the Government of Extremadura (Ref. GR18193). M. Vivas was supported by a “Juan de la Cierva program” funded by the Ministry of Economy, Industry and Competitiveness of the Spanish Government. The authors thank José Climent (INIA-CIFOR, Madrid, Spain) for providing basic information and data from the provenance trials, Jane McGrath for English edition of the manuscript, and Carla Vázquez for her help in climate data processing and figure editing. The staff of Cabañeros National Park is acknowledged for their logistic assistance in field work. César Cendán (MBG-CSIC) and David Castañe (USC) also helped in field work.

Conflict of interest

The authors declare no conflict of interest.

Author contributions: RZ , VR and LS conceived the ideas; RA contributed with previous data from the field trials; all authors participated in field sampling; VR processed the samples and did the dendrochronology assessments; RZ and VR analysed the data; RZ led the writing with assistance from all authors.

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Table 1. Main effects of test Site (Cabañeros and Riofrío), Population (10 levels) and drought Event (1995 and 2005) and their interactions on the drought resilience components, defined as resistance, recovery, resilience and relative resilience (Lloret et al., 2011). Effect of the drought event and the corresponding interactions were analysed as within-subject effects. Inter-tree competition (estimated as the sum of the basal area of neighbouring living trees) was included as a covariate in the model and, in case of a significant effect, the sign of the covariation indicated within brackets. Degrees of freedom (DF), F ratios and associated probability levels are shown. Significant effects (p < 0.05) are shown in bold.

		Resistance		Recovery		Resilience		Relative resilience	
	DF	F	P>F	F	P>F	F	P>F	F	P>F
Across subjects									
Site	1, 6	138.8	<**0.001**	119.2	<**0.001**	3.5	0.111	127.4	<**0.001**
Population	9, 44	4.0	**0.001**	3.2	**0.005**	1.4	0.223	0.7	0.723
Site x Pop	9, 44	1.5	0.198	4.3	<**0.001**	1.4	0.237	2.4	**0.024**
Within subjects									
Event	1, 252	84.6	<**0.001**	16.0	<**0.001**	13.9	<**0.001**	105.7	<**0.001**
Event x Site	1, 252	115.4	<**0.001**	0.1	0.818	2.5	0.116	48.9	<**0.001**
Event x Pop	9, 252	4.7	<**0.001**	0.3	0.961	3.9	<**0.001**	5.6	<**0.001**
Event x Site x Pop	9, 252	3.6	<**0.001**	1.2	0.277	2.2	**0.023**	2.6	**0.008**
Neighbouring competition	1, 252	10.9	**0.001** (-)	15.5	**0.000** (+)	0.0	0.891	5.1	**0.024** (+)

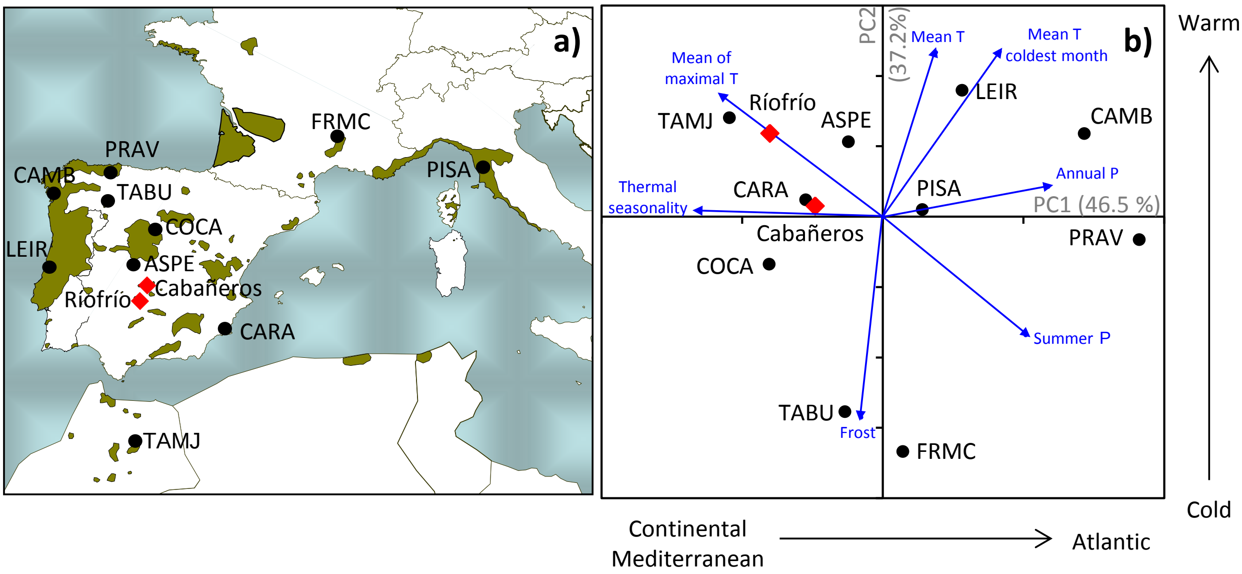

Fig. 1. a) Location of the two *Pinus pinaster* genetic test sites (red diamonds) in central Spain and origin of the 10 populations (black dots) across the species range of distribution [green area, EUFORGEN 2009, www.euforgen.org]. See Table ST1 for population abbreviations. b) Principal component analysis of climate data showing the loadings of the climate variables on the first two principal components (blue arrows) and the spread of the 10 maritime pine populations (black dots) and the test sites (red diamonds) along the resulting bi-dimensional space.

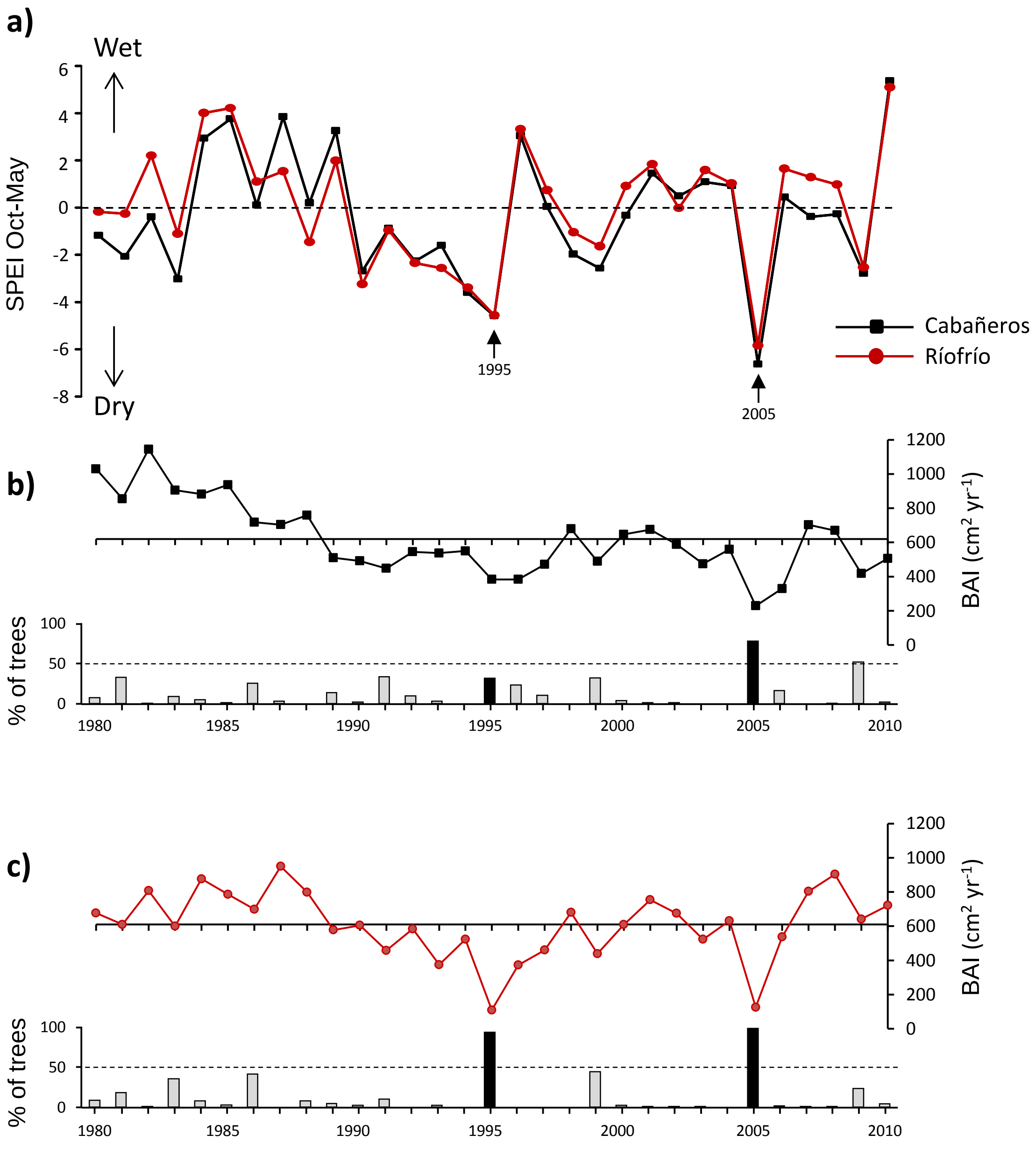

Fig. 2. Annual variation in the standardised precipitation-evapotranspiration index (SPEI) of the wet period of the year in the area (October to May) (a), and annual patterns basal area increment (BAI) and negative pointer years at the Cabañeros (b) and Riofrío (c) test sites. The extreme negative values of SPEI in 1995 and 2005 are indicated by arrows. Negative pointer years (bars) are expressed as a percentage of trees showing a sharp growth reduction (≥ 50% BAI reduction) in comparison with growth in the previous three years, according to the *dplR* package (Bunn, 2010). Black bars indicate the extreme drought events of 1995 and 2005 considered in this work.

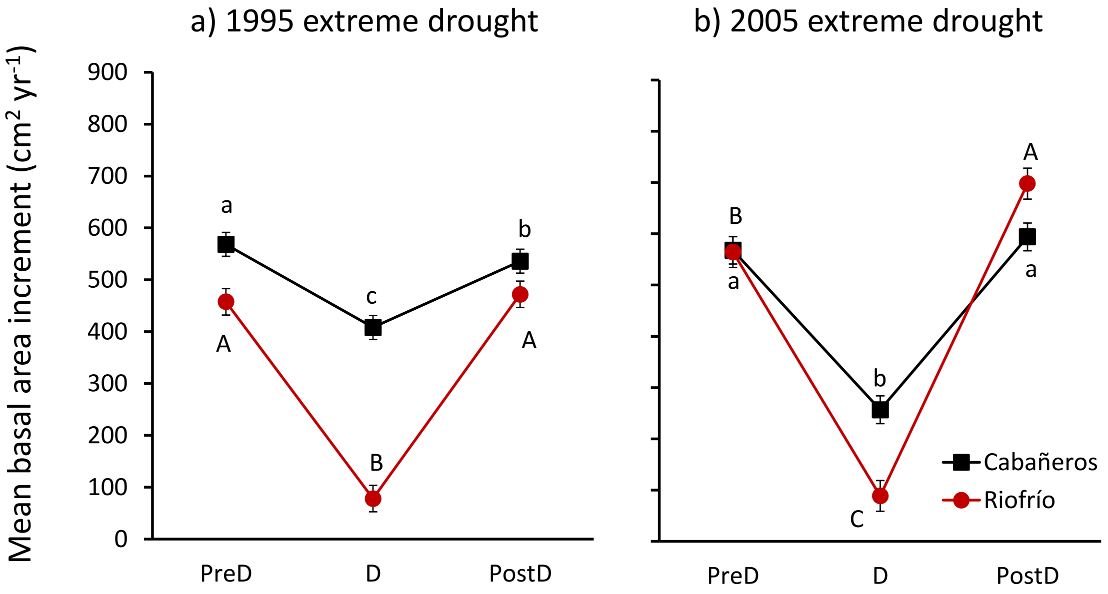

Fig. 3. Least square means (± s.e.) of basal area increment three years before (PreD), the year during (D) and three years after (PostD) the drought events of 1995 (a) and 2005 (b) events at Cabañeros (black squares) and Riofrío (red dots) test sites. Growth during the three periods were significantly different for both events ($F_{2,507} = 396.7$, $p < 0.001$ for the 1995 drought; $F_{2,507} = 564.8$, $p < 0.001$ for the 2005 drought) but differences varied depending on the test site (drought × site effect, $F_{2,507} = 85.3$, $p < 0.001$ for the 1995 drought; $F_{2,507} = 41.3$, $p < 0.001$ for the 2005 drought). Different lowercase and uppercase letters indicate significant differences (Tukey's HSD post-hoc test) between the three periods compared at Cabañeros and Riofrío, respectively.

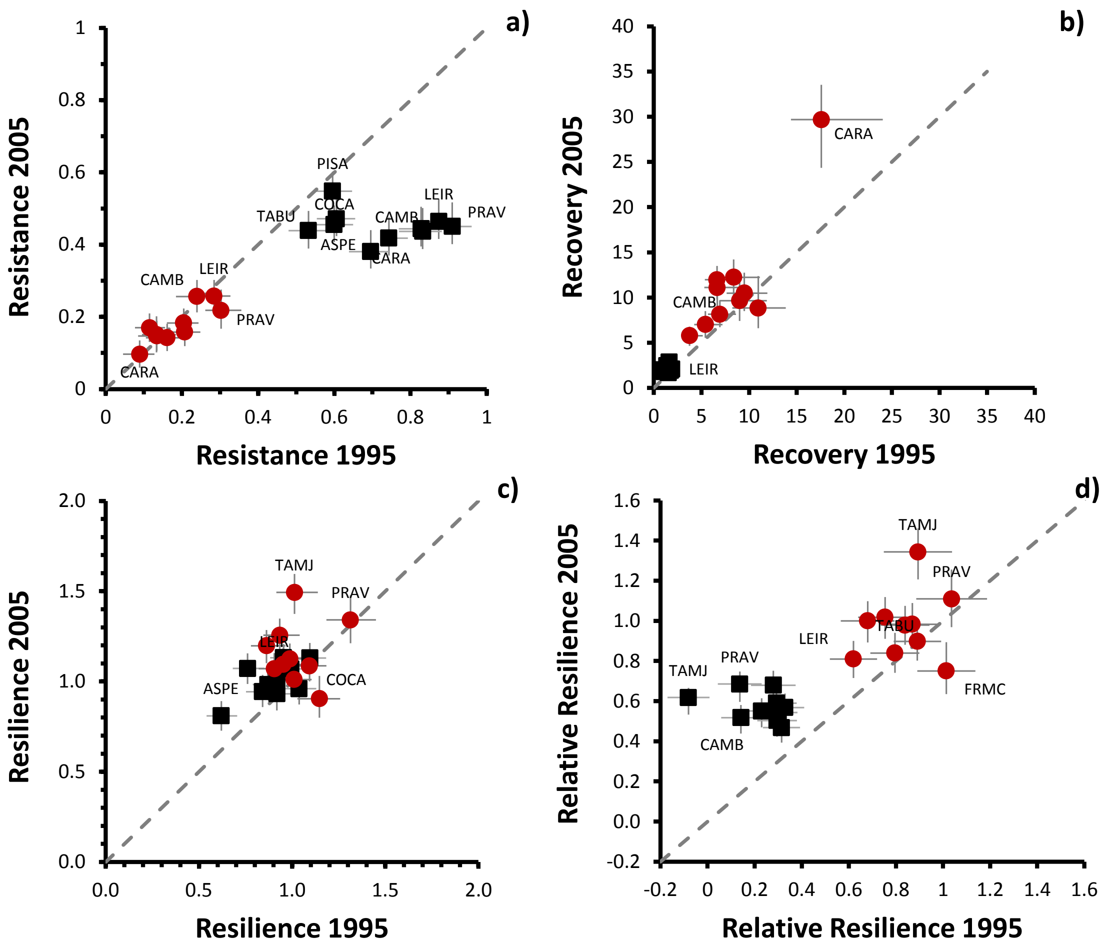

Fig. 4. Components of tree resilience in response to the extreme drought events of 1995 (horizontal axes) and 2005 (vertical axes) for 10 maritime pine populations established at two test sites (Cabañeros: black squares; Riofrío: red dots). Least square means ± standard errors are shown for (a) resistance, (b) recovery, (c) resilience and (d) relative resilience. The diagonal dashed line represents the 1:1 relation between the drought events. See Table ST1 for population abbreviations.

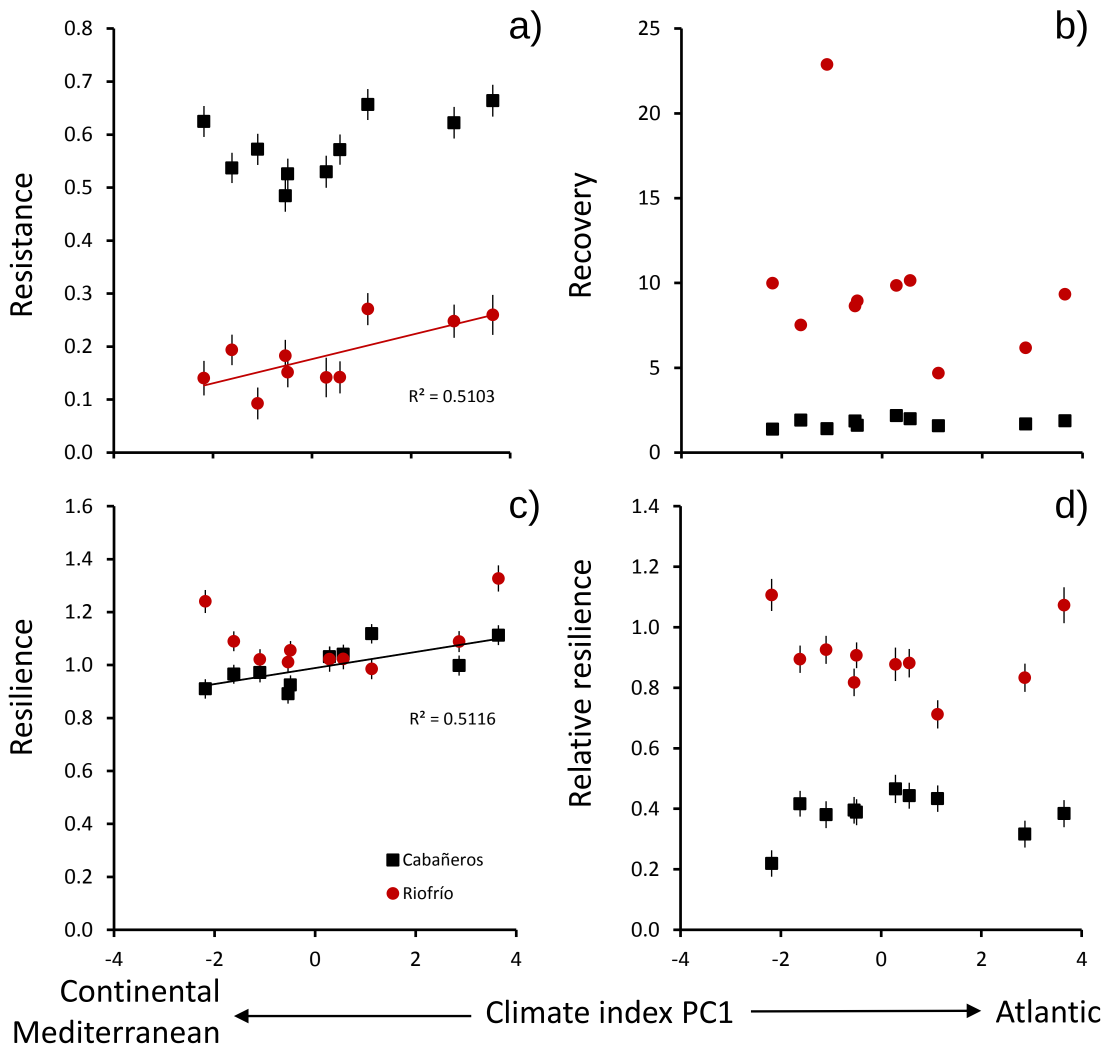

Fig. 5. Relation between climate conditions at origin (PC1 climate index) of the 10 *P. pinaster* populations in Cabañeros (black squares) and Riofrío (red dots) test sites and the corresponding population least square means for the resistance (a), recovery (b), resilience (c), and relative resilience (d) calculated across the extreme drought events studied (1995 and 2005). Linear trends and the corresponding r^2 values are shown for significant relations ($p < 0.05$).

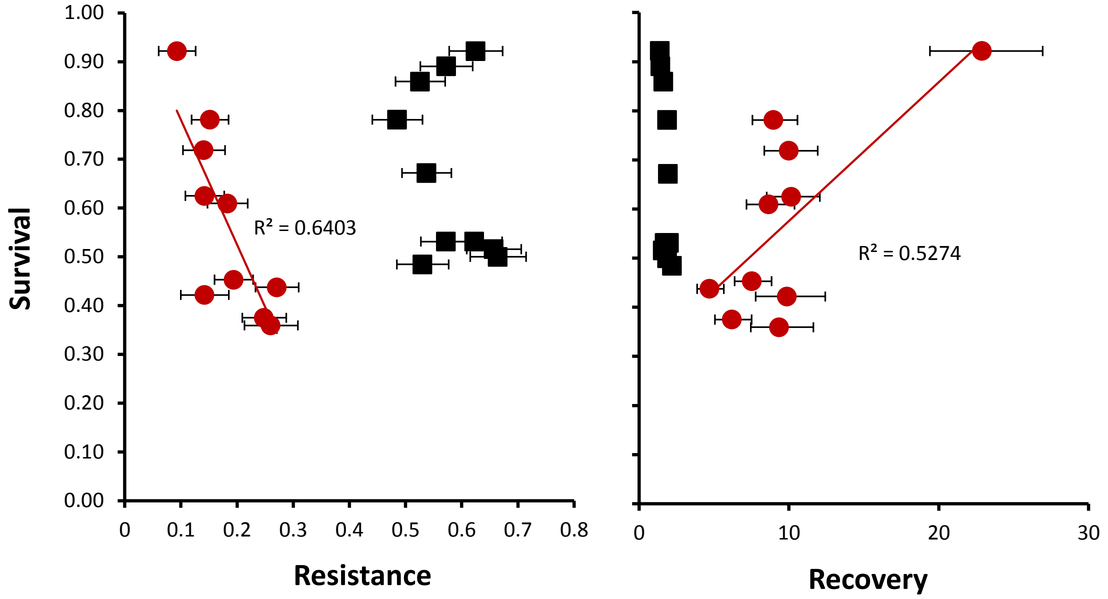

Fig. 6. Relations between (a) resistance and (b) recovery of the 10 maritime pine populations and overall provenance survival at age 43 at the Riofrío (red circles) and Cabañeros (black squares) test sites. Linear trends and the corresponding r^2 values are shown ($p < 0.05$). Dots are the least square means ± standard errors across the two drought events, 1995 and 2005.

Supplementary material

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Ricardo Alía, Vicente Rozas

Methods SM1. Estimating monthly climatic data in the two test sites during the studied period (1980-2010)

Monthly temperature series (mean, maximum, minimum, mean of maximums and mean of minimums) and precipitation series (monthly precipitation and number of rainy days per month) in the two test sites were estimated upon data of different climatic stations of the National Agency of Meteorology (AEMET, Ministerio para la Transición Ecológica, http://www.aemet.es) situated in the proximities of the two test sites. Temperature series in Cabañeros and Riofrío were estimated using data from 4 and 3 nearby stations, respectively (Table SM1), while precipitation series were estimated upon the 2 closest climatic stations of each test site (Table SM1). Stations were selected based not only in their proximity but also in the correspondence between the altitude and the relative geomorphological position in relation to the test sites.

Climatic stations (AEMET, http://www.aemet.es) used for the estimation of monthly temperature (T) and precipitation (P) series in the two test sites (CAB: Cabañeros, and RIO: Riofrío).

Station Code	Station Name	Altitude (m)	Long	Lat	Variables	Site
3298X	San Pablo de los Montes	917	383957	4378346	T	CAB
4123	Los Cortijos de arriba	775	407846	4352300	T	CAB
4193Y	El Robledo (Automática)	580	389109	4341690	T	CAB/RIO
4202E	Piedrabuena (El Casarejo)	660	382783	4330928	T	RIO
4316	Tamurejo	550	331393	4317335	T	RIO
4189	Pantano de Torre Abraham	697	391809	4358241	T	CAB
4171I	Retuerta del Bullaque	760	382188	4364610	P	CAB
4189	Pantano de Torre de Abraham	697	391809	4358241	P	CAB
4224	Arroba de los Montes (1)	615	366706	4334761	P	RIO
4224A	Arroba de los Montes (2)	615	366588	4334856	P	RIO

Monthly temperatures were obtained as the inverse distance-weighed means of the temperatures of the selected climatic stations for each site, applying a correction factor of -0.005 ºC per meter of altitude difference between the climatic station and the test site. Missing data in the original stations was previously predicted by regression models fitted between the available temperatures in the climatic station and the CRU TS 4.01 data set (Mitchell and Jones, 2005). CRU climate time series for the period 1901–2016 were taken from the Climate Explorer of the Royal Netherlands Meteorological Institute (http://climexp.knmi.nl/) for the 0.5º longitude × 0.5º latitude sector in which every climatic station was located.

Monthly precipitations in each site were estimated directly from climatic stations that were very close to the test sites. In the case of Riofrío, precipitations were obtained as the mean value of the data of the two closest stations, both sited <2 Km from the test site. In Cabañeros, data from the closest climatic station (<5 km from the test site) was largely incomplete. Missing data in this station was completed by regression models fitted between the precipitation series in this climatic station and those in the next closer station (12.5 km from Cabañeros). Additionally, remaining missing data in the two test sites were filled upon CRU TS 4.01 data using a similar procedure as that describer for temperatures.

References

Mitchell, T.D., Jones, P.D. 2005. An improved method of constructing a database of monthly climate observations and associated high resolution grids. International Journal of Climatology 25, 693–712.

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Methods SM2. Statistical mixed model for the analysis of growth responses to the extreme drought events

Growth responses to each extreme drought event were analysed separately by repeated mixed model analysis applied to tree-level BAI data. The following statistical mixed model was fitted (random effects in italics):

$$\mathrm{BAI} = \mu + \mathrm{S} + \mathrm{POP} + \mathrm{POP}\times\mathrm{S} + \mathrm{Dr} + \mathrm{Dr}\times\mathrm{S} + \mathrm{Dr}\times\mathrm{POP} + \mathrm{Dr}\times\mathrm{POP}\times\mathrm{S} + B(S) + B\times POP(S) + Tree(B\times POP\times S) + \mathrm{NBA} + \varepsilon$$

where μ is the overall mean basal area increment, S, POP, and POP×S stand for the across-subject fixed effects of the site, the population and their interaction, Dr represent the within-subject fixed effect (repeated measures on the same subjects, the trees) of the drought factor (PreD, D and PostD), B(S) and B×POP(S) represent the random variation between blocks within sites and between whole plots of the multi-tree block design, respectively, *Tree(B×POP×S)* is a random factor identifying each tree within each block, population and site and was included in the model to account for the autocorrelation among the repeated measures, NBA is a continuous fixed covariate accounting for the basal area surrounding each tree ten years before each climatic event as a proxy of competition, and ε is the random residual.

The across-subject effects of populations, sites and their interaction accounts for global differences among populations and sites in mean annual radial growth, and has nothing to do in relation to the extreme drought events.

Responses to the drought events are tested by the within-subject factors. The drought factor accounts for the plastic response in BAI to the drought event (temporal plasticity) while the interactions between this factor and the sites and the populations represent (spatial) plasticity to environmental variation between sites and among-population variation in these responses to drought, respectively.

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Table ST1. Characteristics of the ten *Pinus pinaster* provenances at their origin and the two experimental test sites. Average population and site survival and growth are also shown.

Site name	Code	Genetic group[1]	Elevation (m)	Latitude (º)	Longitude (º)	Annual precipitation (mm)	Mean annual temperature (ºC)	Survival (%) [4]	Total height (m) [5]	Diameter (cm) [5]
Populations										
Arenas	ASPE	Central Spain	634	40.209	–5.058	1217 [2]	13.7	85.9	11.2	20.4
Tabuyo	TABU	Central Spain	1019	42.314	–6.220	734 [2]	9.7	78.1	9.6	17.9
Pravia	PRAV	Northern Spain	146	43.555	–6.211	1299 [2]	13.3	50.0	10.6	18.4
Cambados	CAMB	Northern Spain	28	42.526	–8.770	1550 [2]	14.7	53.1	10.4	17.4
Coca	COCA	Central Spain	783	41.248	–4.493	454 [2]	12.3	67.2	9.8	19.4
Pisa	PISA	Northern Italy	100	43.717	10.384	860 [3]	13.9	53.1	10.0	17.7
Massif Central	FRMC	Atlantic France	400	45.001	3.75	839 [3]	13.1	48.4	11.4	17.5
Tamjout	TAMJ	Western Africa	1600	33.867	-4.033	336 [3]	14.2	92.2	10.3	18.6
Leiría	LEIR	Atlantic	60	39.751	-8.917	934 [3]	15.6	51.6	11.5	19.3
Caravaca	CARA	Eastern Spain	1063	38.145	-1.984	481 [2]	13.0	89.1	10.9	19.8
Test sites										
Cabañeros			1023	39.396	–4.475	796	12.4	65.9	11.0	18.8
Riofrío			725	39.134	–4.536	719	14.2	57.0	10.1	18.5

[1] Bucci et al. (2007)

[2] Data from CRU TS 4.01 model for the period 1950-2000

[3] Data from the model of Gonzalo (2007) for the period 1950-2000

[4] Survival at the time of sampling (age 43)

[5] Diameter at breast height and total tree height at age 32 (data recalculated from Alía et al., 2001)

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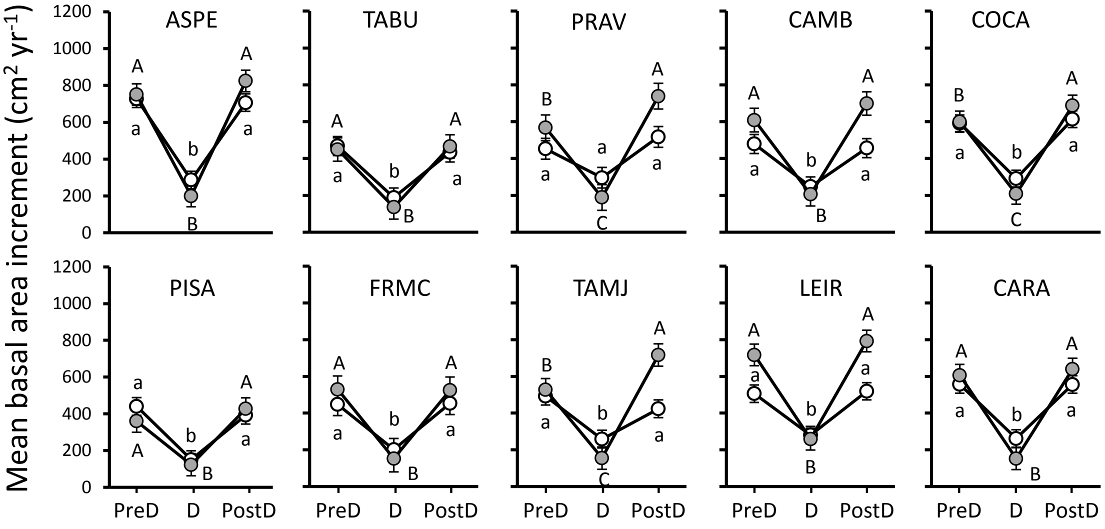

Fig. SF1. Least square means (± s.e.) of basal area increment three years before (PreD), the year during (D) and three years after (PostD) the drought events of 1995 (white dots) and 2005 (grey dots) of the ten studied populations averaged across the two test sites. Growth during the three periods were significantly different for both events ($F_{2,507} = 396.7$, $p < 0.001$ for the 1995 drought; $F_{2,507} = 564.8$, $p < 0.001$ for the 2005 drought) but differences varied depending on the population (drought × population interaction, $F_{18,507} = 3.6$, $p < 0.001$ for the 1995 drought; $F_{18,507} = 3.3$, $p < 0.001$ for the 2005 drought). See Table ST1 for abbreviations of provenances. For each population, different letters indicate significant differences between the three compared periods based on Tukey's HSD post-hoc test (lowercase letters for the 1995 event and uppercase for the 2005 event).

Supplementary material

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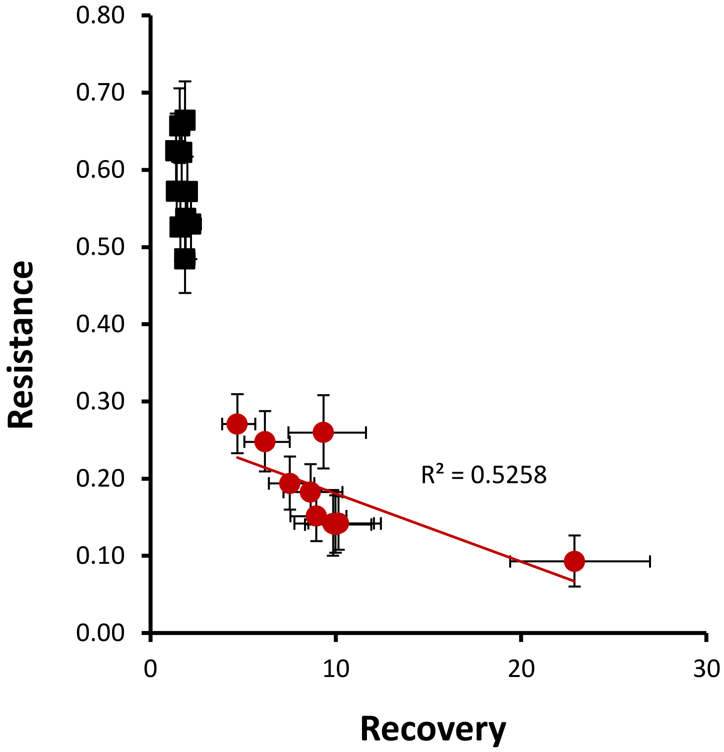

Fig. SF2. Relationship between resistance to and recovery from extreme drought events across 10 maritime pine populations established at two test sites (Cabañeros: black squares; Riofrío: red dots). Least square mean ± standard errors (polled across the two drought events, 1995, 2005) are shown. For significant relationships, linear trend and the corresponding r^2 value are shown.

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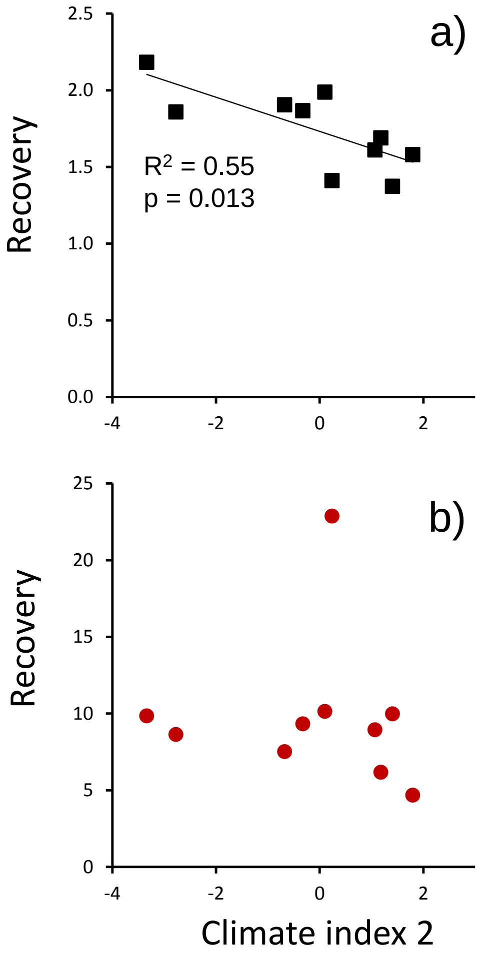

Fig. SF3. Relation between climate index 2 (a proxy of thermal conditions) at origin of the 10 *P. pinaster* populations and the corresponding population least square means for growth Recovery after the two extreme drought events (1995 and 2005) in Cabañeros (a, black squares) and Riofrío (b, red dots) test sites. Linear trends and the corresponding r^2 values are shown for significant relations ($p < 0.05$).

Figure1

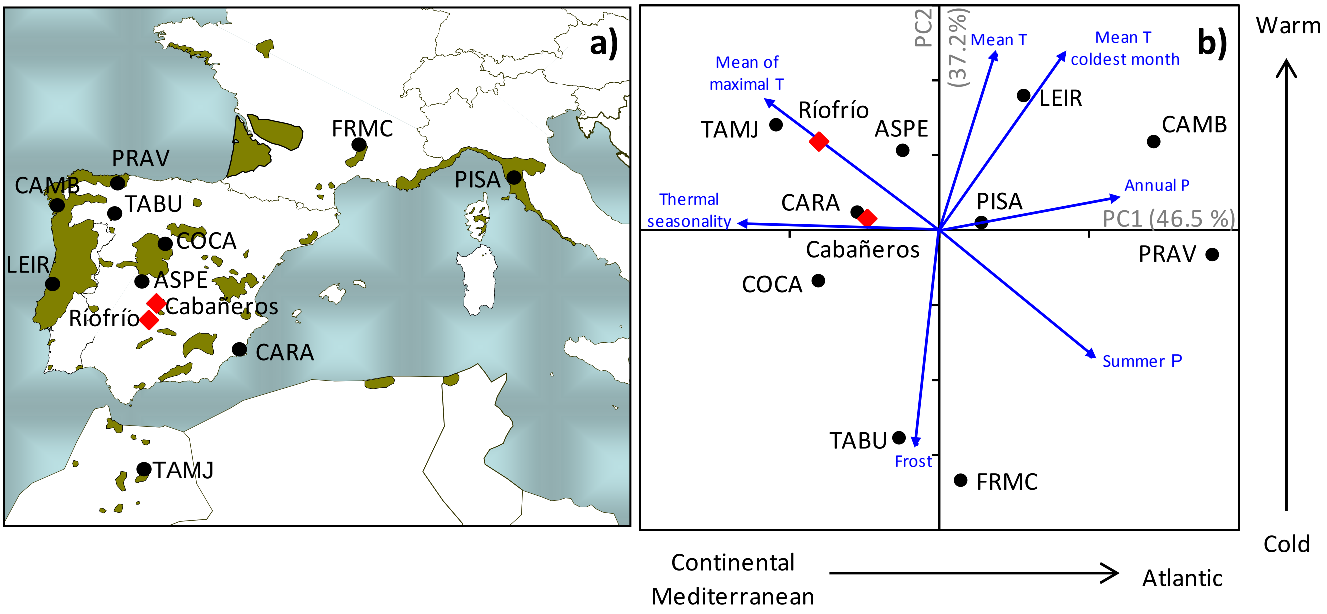

Figure 1

Figure2

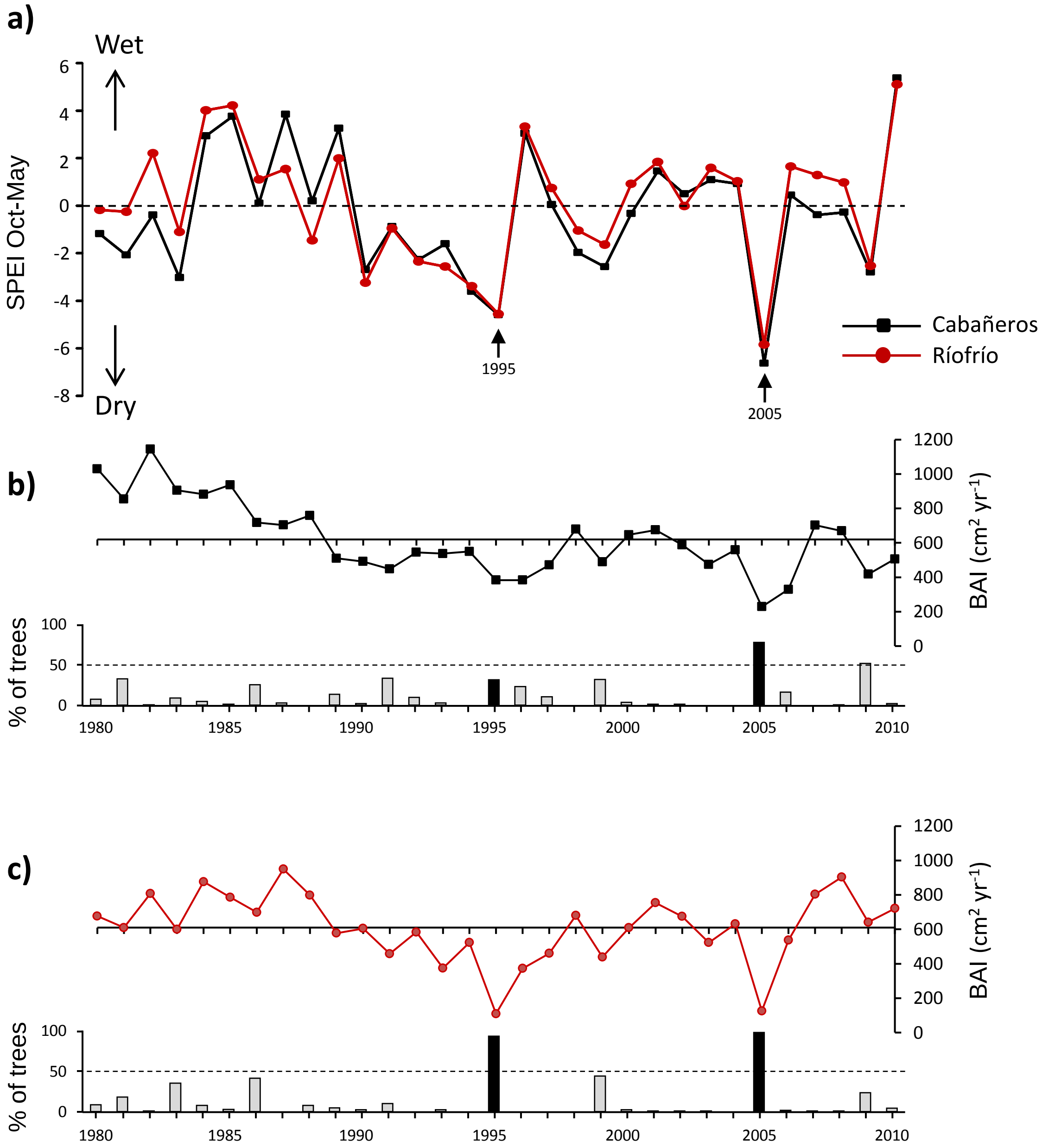

Figure 2

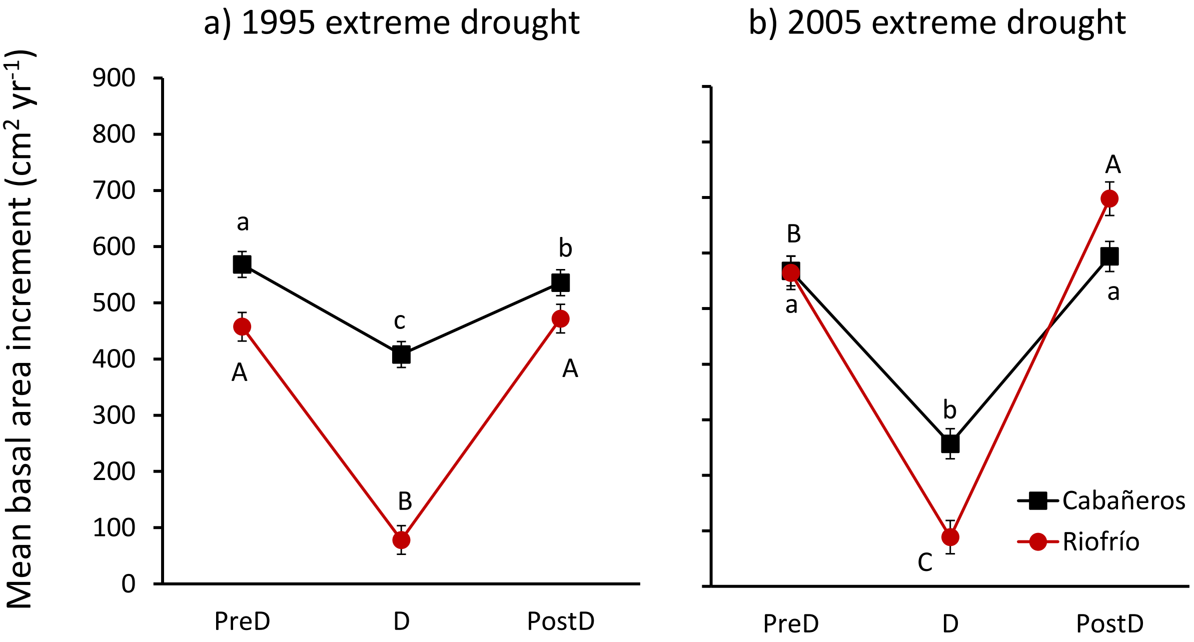
a) 1995 extreme drought
b) 2005 extreme drought
Mean basal area increment (cm² yr⁻¹)
900
800
700
600
500
400
300
200
100
0
a
c
b
A
B
A
B
a
b
C
A
a
PreD
D
PostD
PreD
D
PostD
Cabañeros
Riofrío

Figure 3

Figure4

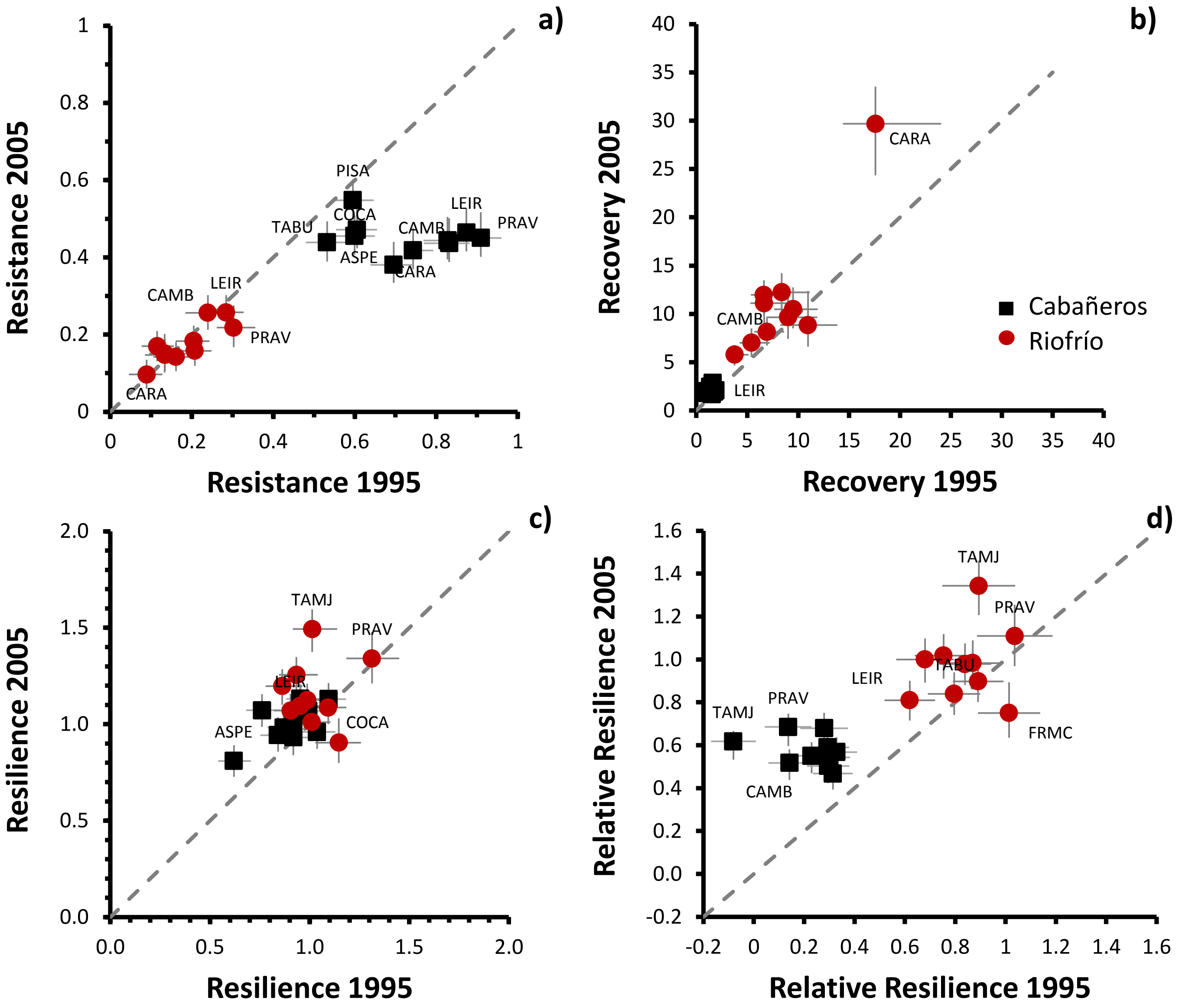

Figure 4

Figure5

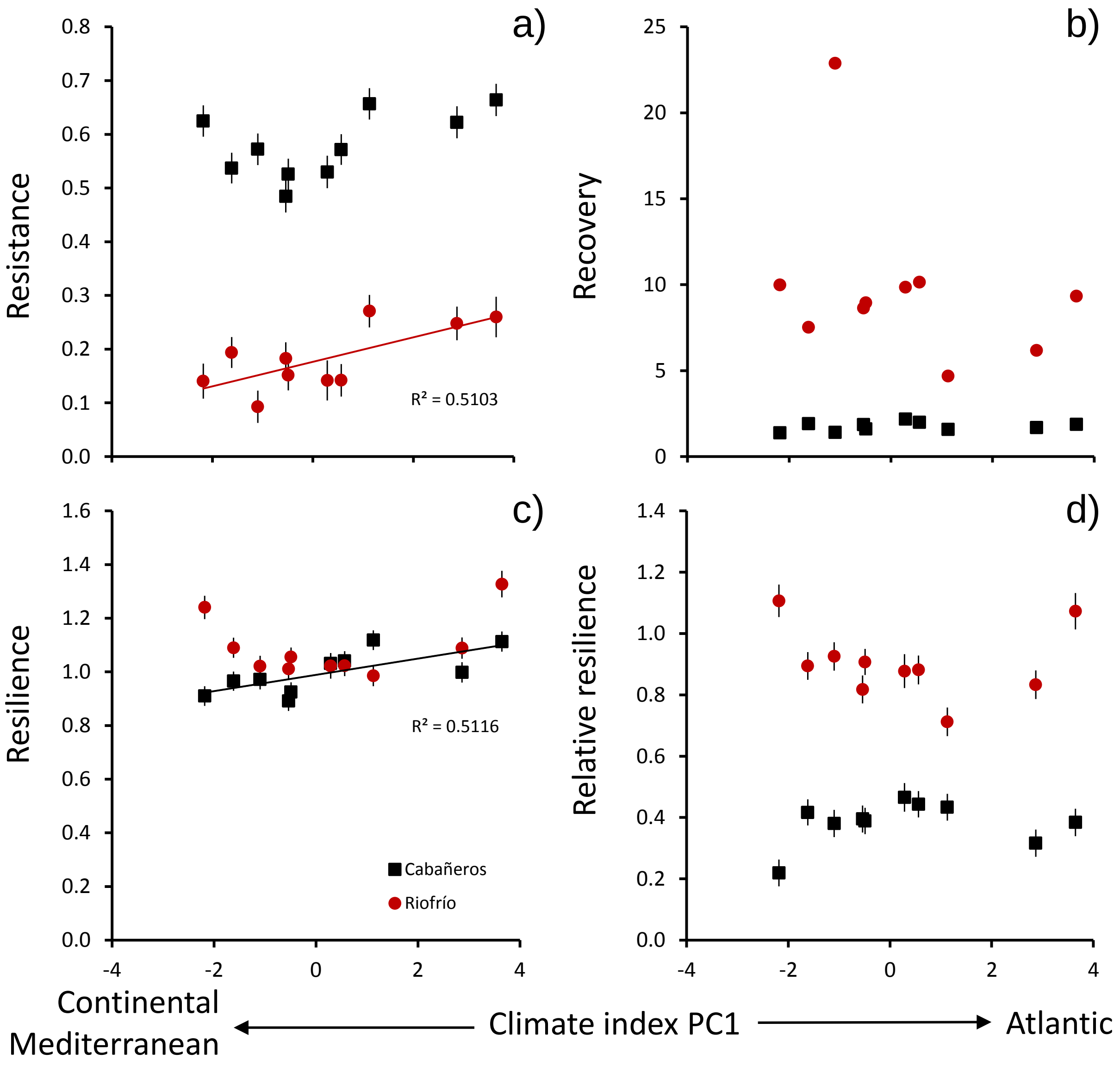

Figure 5

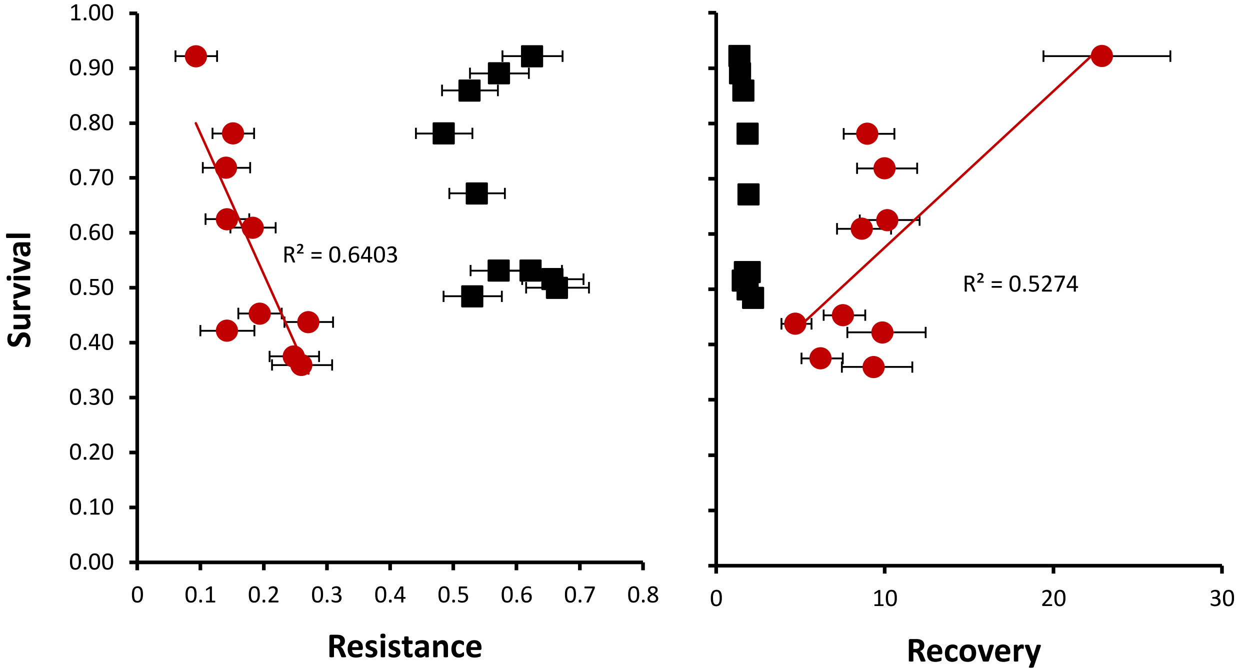
Survival
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Resistance
R² = 0.6403
0
10
20
30
Recovery
R² = 0.5274

Figure 6