New evidence for population-specific responses to drought events from tree ring chronologies of *Pinus nigra* ssp. *laricio* across the entire distribution range

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ABSTRACT

The increased frequency and severity of drought events due to climate warming is negatively affecting tree radial growth, particularly in drought-prone regions, such as, e.g., the Mediterranean. In this climate change hotspot, populations of the same tree species may show different growth responses to climate, due to the great variety of microclimates and environments that characterise this biogeographic region. In this study, we analysed growth-climate relationships and growth responses to drought events (i.e., resistance, recovery, and resilience) in 13 forest stands of black pine (*Pinus nigra* Arnold), encompassing the whole and peculiar distribution range of the ssp. *laricio* (Calabria, Sicily, Sardinia, and Corsica). Analysis focussed on the 1981–2010 period, which is commonly covered at all sites. Stem radial growth of trees increased under a positive spring/summer water balance. However, abundant winter precipitation had a negative impact on stem radial growth. Populations in Corsica were more sensitive to drought, showing lower resistance and resilience than those in Sicily and Sardinia. Older trees were more resistant to drought events than younger trees. Our results highlight that population-specific responses to drought events are mainly explained by tree age and local environment, suggesting geographically related patterns in tree growth and forest productivity correspond to different populations. Intraspecific variability in sensitivity to drought events should be included in species distribution models to predict the range of forest productivity responses to climate change.

1. Introduction

Drought periods are becoming more frequent and extended worldwide due to global warming (IPCC, 2018). Greater intensity, frequency, and duration of drought lead to an increase in evapotranspiration rates and an alteration of the start and duration of the growing season (Colangelo et al., 2018; Andersson et al., 2011), with negative impacts on tree growth and forest productivity (Allen et al., 2015). Southern Europe is predicted to experience increasing aridity in the 21st century mainly due to rising temperatures, and an increase of intensity, frequency, and duration of heatwaves and droughts (Giorgi and Lionello,

2008). Tree populations in drought-prone regions, such as the Mediterranean, are particularly vulnerable. The Mediterranean Basin is a climate change hotspot, in which the occurrence of intense and prolonged drought episodes may compromise the ecological resilience of tree species (Peñuelas et al., 2011). The great variety of microclimates, and the mutual interaction of temperature, precipitation, and evapotranspiration, determining water availability, challenge our predicting capacity of the potential of trees to cope with climate change across this biogeographic region (Pasho et al., 2012; Linares et al., 2011; Martín-Benito et al., 2010).

The Mediterranean region has a complex and heterogeneous climatic

system and regime, with a northern temperate climate and a southern semi-arid climate (Sangüesa-Barreda et al., 2019). This geographic variability, accompanied by variations in regional precipitation regimes (i.e., higher precipitation in the north-east than in the south-west), may differently influence the sensitivity of tree populations of the same species to drought (Dorado-Liñán et al., 2019), entailing different growth responses to global warming across geographic regions and genetic provenances (Camarero et al., 2020; Gazol et al., 2017). Furthermore, the complexity of the Mediterranean environment, linked to changes in atmospheric circulation patterns, is not only observable on a regional scale, but also on a local scale. For example, variations in air temperatures and precipitation within a very short distance, caused by different elevations and slopes in mountainous areas, may lead to local-specific responses to climate (Römer, 2021; Doğan and Köse, 2019).

The phenotypic plasticity of tree species determines their capacity to tolerate and recover from stress, influencing their resilience, although still difficult to be well-defined (Schwarz et al., 2020), and survival to climate change and disturbance events (Sánchez-Salguero et al., 2018; Gazol et al., 2017). Regardless of the ecophysiological and growth strategies adopted by tree species to withstand xeric conditions in summer, they may have limited capacity to tolerate severe drought events. For instance, black pine (*Pinus nigra* Arnold) has higher frost tolerance than other pines occurring in the Mediterranean region (Fernández-Pérez et al., 2018), but it is considered less able to cope with drought (e.g., González de Andrés and Camarero, 2020; Serra-Maluquer et al., 2018). Several studies revealed that black pine is highly sensitive to drought (Janssen et al., 2018; Köse et al., 2017; Granda et al., 2013; Linares and Tíscar, 2010; Martín-Benito et al., 2008). In Spain and France, tree-ring studies have shown that the radial growth of black pine is positively influenced by prior wet and cold autumns, warm winters, and cool and wet springs (Camarero et al., 2015, 2013; Amodei et al., 2013; Andreu et al., 2007; Lebourgeois, 2000). In Turkey, spring-/summer precipitation was shown to be the main driver of radial growth of black pine (e.g., Köse et al., 2017, 2012). Yet, in temperate regions, black pine is considered a relatively drought-tolerant species and, as such, a possible candidate for assisted migration in dry forest sites of Central Europe and a potential substitute for indigenous conifers under future climate scenarios, being able to adapt to various soil types and climate conditions (Quézel and Barbéro, 1988). These studies suggest that drought tolerance may differ between seed sources, determining the capacity of black pine to acclimate to local environmental conditions.

Black pine has a wide and fragmented distribution range, extending throughout the Mediterranean basin and central-eastern Europe, because of several glacial and interglacial climatic oscillations and geological events (Thompson, 2005). Probably because of its fragmented distribution range, the diversity in black pine's morphological, physiological, and ecological traits has led to the classification of this species into six different subspecies (Quézel and Médail, 2003). According to karyological (Cesca and Peruzzi, 2002) and biochemical studies (Afzal-Rafii et al., 1996; Scaltsoyiannes et al., 1994), black pine ssp. *laricio* has been regarded both as a very divergent subspecies and a taxonomically independent species. Black pine ssp. *laricio* has a unique distribution range, encompassing two big islands and an isolated peninsula (i.e., Sicily, Corsica, and Calabria). It has been regarded both as a very divergent black pine subspecies and a taxonomically independent species, and in Corsica shows a strong genetic distance from the subspecies *nigra* and *salzmannii* (Aguinagalde et al., 1997) and a distinct genetic variation even within the same subspecies, in terms of absolute growth (i.e., lower total height increment in Corsican populations than in those of southern Italy; Thiel et al., 2012). Black pine ssp. *laricio* has a conservative water-use strategy (Cinnirella et al., 2002) and a durable wood, which is rich in resin and easy to process (best log quality, in terms of stem form, branch quality, and timber volume). Due to its central position within the distribution range of black pine ssp. *laricio* can be considered an excellent model to study intraspecific growth-climate relationships and cope with climate-smart forestry requirements (Tognetti et al., 2022). Although populations of black pine ssp. *laricio* from their main range areas have been studied at molecular (Bonavita et al., 2016) and genetic levels (Scaltsoyiannes et al., 2009; Afzal-Rafii and Dodd, 2007), a comprehensive analysis of climate-growth relationships for this subspecies is currently lacking. Indeed, dendrochronological studies conducted on this subspecies have focused on certain localities (e.g., Mazza et al., 2018; Szymczak et al., 2014), though they have never considered climate-growth relationships and drought responses across the entire distribution range of black pine ssp. *laricio*. Therefore, insights on climate-growth relationships and drought responses in black pine ssp. *laricio* across its entire distribution range may become crucial to assess and implement adaptive management strategies aimed at increasing forest resilience to climate change in a peculiar environmental setting, like the one in central Mediterranean.

In this study, we analyse climate-growth relationships and tree growth responses to drought, in black pine ssp. *laricio*. We focus on 13 forest stands located in four regions (Calabria, Sicily, Sardinia, and Corsica), embracing the whole distribution range of this black pine ssp., in the southern Mediterranean Basin. We hypothesize that i) mild winters and relatively moist spring/summer months increase stem radial growth; and ii) responses to drought in Corsican populations are different from those in southern Italy, with a higher sensitivity and a lower resilience to drought events. To describe tree growth responses to drought episodes, we use three different indices: resistance (Rt), recovery (Rc), and resilience (Rs; Lloret et al., 2011). Resistance is the capacity to reduce the impact of the disturbance (e.g., drought event). Recovery is the ability to return to pre-disturbance growth levels after the drought event. Resilience is the capacity of trees to maintain their functions after the impact of a disturbance. Growth-based resilience indices for drought responses of trees provide useful information in the analysis of disturbance events and the application of silvicultural treatments (e.g., selective thinning).

2. Materials and methods

2.1. Study sites and forest stands

The natural distribution areas of black pine ssp. *laricio* are extremely fragmented. The study was conducted in three regions of southern Italy (Calabria, Sicily, and Sardinia) and in one region of southern France (Corsica). The study area encompasses a total of 13 forest stands situated in 11 locations (Fig. 1; Table 1). Four forest stands were in Calabria, two in the Sila National Park (Gallopane and Ponticelli) and two in the Aspromonte National Park (Bagaladi); four forest stands were in Sicily (two in Piano Provenzana, Citelli and Monte Nespole), in the Etna Park; one forest stand was in Sardinia, in the state-owned forest of Fiorentini (Su Tassu); four forest stands were in Corsica, in the Regional Natural Park of Corsica (Capannelle, Col de Verde, Col de Vizzavona, and Vivario).

Forest stands are mainly dominated by black pine ssp. *laricio*, except in Capannelle and Vivario, where black pine coexists with European beech (*Fagus sylvatica* L.) and maritime pine (*Pinus pinaster* Ait.), respectively. Elevations of the study sites range between 444 and 1844 m a.s.l., with mean annual precipitation ranging from 612 to 1227 mm and mean annual temperature from 6.4 to 13.8°C (Table 1). Forest stands are uneven aged forests, except for the experimental plantation in Su Tassu, established in 1919 (Bosa and Portoghesi, 2013), with seed sources from Calabria.

Sites show different terrain slopes, ranging from low (2°) to high (35°; Table 1). Soils are: Dystrudepts with a predominance of granite (Gallopane and Ponticelli) and metamorphic rocks (Bagaladi) in Calabria; Andisoil with a sandy-loam texture and vitric characteristics in Sicily (Seiler et al., 2017); Lithic Xerorthents with granite rocks in Sardinia; Cambisols of varying depths on granitic rocks in Corsica (Szymczak et al., 2020).
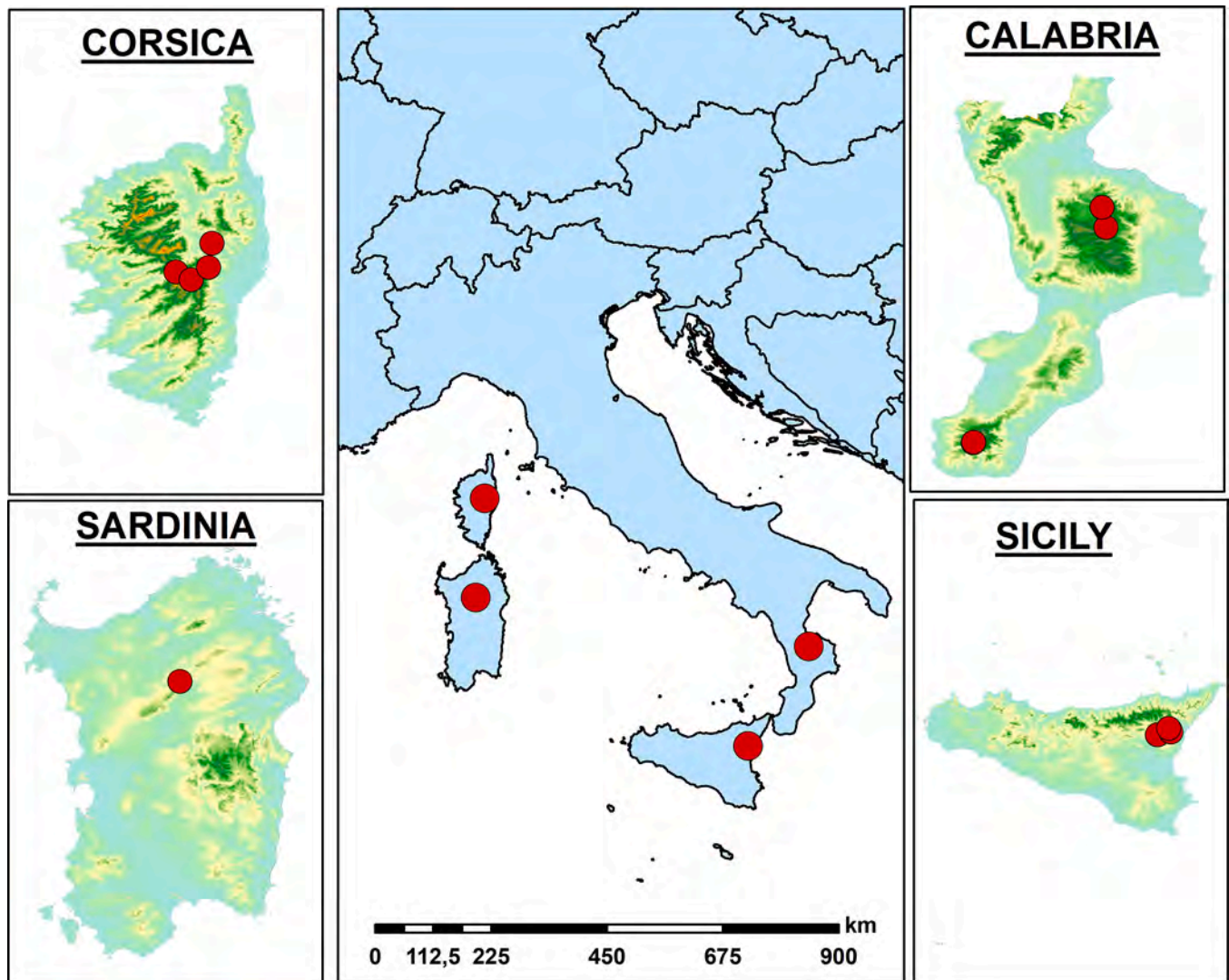
Fig. 1. Location of the 13 forest stands of black pine ssp. *laricio* at 11 locations in Corsica, Sardinia, Calabria, and Sicily.

Table 1
Characteristics of the 11 locations in which trees were sampled. Exposure (°); altitude (m) and slope (°).

Region	Location	Latitude (N)	Longitude (E)	Exposure (°)	Altitude (m a.s.l.)	Slope (°)	Precipitation (mm)	Temperature (°C)
Calabria	Bagaladi	38°06'50.53"	15°51'53.25"	244	1610	8	1136	8.2
		38°6'39.9"	15°51'43.7"	217	1609	2	1136	8.2
	Gallopane	39°24'39.977"	16°34'25.348"	198	1486	16	1227	8.3
	Ponticelli	39°17'53.9"	16°35'41.3"	349	1450	9	882	8.9
Sicily	Piano Provenzana	37°48'18.094"	15°2'27.6"	114	1844	4	881	6.4
		37°47'6.051"	15°3'18.034"	27	1642	8	766	7.9
	Citelli	37°45'54.062"	15°3'54.083"	70	1600	13	733	7.9
	Monte Nespole	37°48'18.063	15°2'27.585	321	1598	35	1031	8.3
Sardinia	Su Tassu	40°30'50.253"	9°4'1.436"	238	952	8	748	11.6
Corsica	Capannelle	42°08'	9°16'	93	782	18	696	12.9
	Col de Verde	42°04'25.39"	9°11'02.87"	158	927	18	612	11.5
	Col de Vizzavona	42°06'40.9"	9°06'39.89"	230	1140	19	790	9.5
	Vivario	42°15'	9°17'	164	444	21	738	13.8

Note: Average annual precipitation (mm) and mean temperature (°C) derive from CHELSA dataset for the period 1981–2010.

2.2. Data collection and tree-ring analysis

We sampled 162 trees from nine forest stands (70 in Calabria, 21 in Sardinia and 71 in Corsica). Additionally, we complemented this dataset with chronologies from four forest stands in Sicily (International Tree-Ring Databank, ITRDB; https://www.ncdc.noaa.gov/paleo-search) to cover the distribution area of black pine ssp. *laricio* in southern Italy. In detail, for each forest stand in Sicily, we used 28 trees (ITRDB code PINIital046) and 57 trees (ITRDB code PINIital048) for Piano Provenzana, 49 trees (ITRDB code PINIital047) for Citelli, and 44 trees (ITRDB code PINIital049) for Monte Nespole.

For the dendrochronological analysis, we considered dominant and

co-dominant trees. At all forest stands, two cores per tree were collected at breast height (1.3 m), at 120° from each other, with a minimum of 11 sampled trees for forest stands. Tree cores were processed according to standard dendrochronological procedures (Schweingruber, 1988). Tree cores were mounted on wooden supports, air-dried, and sanded. Ring-width series were measured with 0.01 mm precision through LINTAB-measurement equipment coupled to a stereomicroscope (Leica MS5). The TSAP software package (Rinn, 2003) was used for the analysis. Individual chronologies were cross dated visually against each other and statistically against the respective mean chronology. This allowed us to evaluate the quality of cross dating and measurement accuracy of tree-ring series through the software COFECHA (Holmes, 1983). The standardization of tree-ring width time series was performed using the ARSTAN program (Cook and Holmes, 1984). The standardization procedure was used to eliminate the so-called age-related trend; cubic smoothing splines curve functions with a 50% frequency cut-off were used. For all sites, a fixed 32-year cubic smoothing spline was applied, because of the variable tree age and growth rate (we tried different detrending options and chose this rather flexible spline function for its better statistical performance); mean standard chronologies for each forest stand were calculated as the bi-weight robust mean of detrended individual series (Cook, 1985).

To compare properties of each mean chronology, several descriptive statistics were used: (1) the mean sensitivity (MS), which is able to assess high-frequency variations; (2) the first order autocorrelation (AC) to detect the persistence retained before and after the standardization; (3) the mean correlation coefficient (RBAR), calculated for a common time interval between the single series in a chronology, and (4) the expressed population signal (EPS), which indicates the reliability of a given chronology by comparing it with the theoretical chronology based on an infinite number of trees, with a threshold of 0.85 (Wigley et al., 1984). We selected the period 1981-2010, which is common to all forest stands, to model the growth-climate relationships.

2.3. Climate data and selection of specific drought events

CHELSA (Climatologies at high resolution for the earth's land surface area) data were used to obtain climatic chronologies (Karger et al., 2017). CHELSA data are obtained from downscaling processes of the temperature, from a global circulation model of precipitation and Era - Interim reanalysis, at a spatial resolution of 30 arc seconds (approximately 1 km^2) over a period of 34 years (1979–2013; Karger et al., 2017). Climatic data of our forest stands were obtained through an extrapolation function between the grid data (1 × 1 km) and the coordinates of each forest stand, using the package raster of the R software (Hijmans, 2019). This allowed us to extrapolate average maximum and minimum monthly temperatures and total monthly precipitation, from 1981 to 2010.

In addition, we calculated the standardized precipitation evapotranspiration index (SPEI; Hadad et al., 2021; Vicente-Serrano et al., 2010), using the package SPEI of the R software (Beguería and Vicente-Serrano, 2012). This drought index is considered particularly appropriate to evaluate tree-ring growth responses to drought events (Huang et al., 2015). Furthermore, the SPEI is a multi-scalar drought index that enables identification of different types and impacts of drought on diverse systems (Vicente-Serrano et al., 2013, 2012) and provides a measure for aggregated climatic water balance over multiple months or years. The monthly climatic water balance values for the calculation of the SPEI were estimated by the monthly difference between precipitation and potential evapotranspiration (PET). PET was estimated based on average maximum and minimum monthly temperatures, total monthly precipitation, and latitude, using the Hargreaves equation (Hargreaves and Samani, 1985).

In this study, SPEI values were calculated for each month of each year from 1981 to 2010. To identify the SPEI with the best performance, mixed linear models were developed that considered the cumulative

water balance from 1 to 24 previous months with a step of 1 (see Appendix S2 in Supplementary material). Akaike's information criterion (AIC) was used to identify the timescale in which the SPEI best reflects radial growth (Fig. A1). The estimated values of SPEI with the best performance, on the other hand, were used to identify the month that had the highest influence on ring widths (Table A1). The timescale with the lowest AIC value was the SPEI of four months (SPEI4) and the month of July was the most important variable that influenced the radial growth.

The SPEI4$_{July}$ values were thus used to identify the drought events from 1981 to 2010. There are several approaches for selecting a threshold of SPEI value to identify drought years. For example, several studies have used a SPEI value <-1.5 (e.g., Serra-Maluquer et al., 2022; Camarero, 2021), while others have considered a SPEI value <-1.0 (e.g., Gillerot et al., 2021; Bose et al., 2021; Pardos et al., 2021). In this study, we chose a threshold of SPEI <-1.0 to retain all the study sites in the analysis, ensuring a greater replicability of the sites, at least in three regions (four sites in each of Calabria, Sicily, and Corsica), and obtain a response to drought of black pine ssp. laricio across its entire distribution range. Furthermore, the study sites are representative of relatively humid mountain environmental conditions, thus, selecting a more restrictive SPEI value would have completely excluded several sites from the analysis (e.g., Piana Provenzana, Citelli, and Monte Nespole). Therefore, years with SPEI4$_{July}$ below - 1 were considered as drought years with values ranging from - 1.00 (mild drought) to - 2.10 (severe drought), according to the classifications of McKee et al. (1993) and Paulo et al. (2012); Table A2. Selected drought years were pooled in subsequent analyses and their severities were considered by including their SPEI4$_{July}$ values in the models of drought responses (resistance, recovery, resilience).

2.4. Components of drought response

Growth responses to drought for each specific drought event and sampled tree were quantified using the components of drought resilience described by Lloret et al. (2011). The three components reflecting growth before, during, and after a drought event were calculated as follows:

$$Resistance = \frac{Dr}{preDr} \tag{1}$$

$$Recovery = \frac{postDr}{Dr} \tag{2}$$

$$Resilience = \frac{postDr}{preDr} \tag{3}$$

where Dr corresponds to the drought period, preDr corresponds to the average of years before the drought event, and postDr corresponds to the average of years after the drought event.

We averaged the ring width index of two years before and after a drought event for preDr and postDr. Although the calculation of preDr and postDr periods often considers three-four years before and after the drought event (e.g., Jiang et al., 2019; Anderegg et al., 2015), black pine may recover from stress within two years, due to its capacity to rapidly counterbalance drought-induced growth declines (Granda et al., 2013). Therefore, we considered that two years may represent a good trade-off between the time being sufficiently long to ensure a good estimation of the mean growth before and after the drought event. In addition, to minimise bias, we avoided the risk of an overlap of preDr and postDr periods with adjacent drought events (e.g., 2003 in Capannelle and Col del Verde) and excluded incomplete drought events (as 1982 in Gallopane and Su Tassu, and 2009 in Col de Vizzavona and Vivario; Table A2). However, 2003 and 2006, in Vivario and Col de Vizzavona, respectively, were included in the analysis, as they are considered severe drought years (Table 2). The final number of years with drought events

Table 2
Specific drought events and values of the standardized precipitation and evapotranspiration index (SPEI4$_{July}$) identified for each population of black pine ssp. *laricio* from 1981 to 2010 and used to calculate resistance (Rt), recovery (Rc), and resilience (Rs).

	Location										
	Bagaladi	Gallopane	Ponticelli	Piano Provenzana	Citelli	Monte Nespole	Su Tassu	Capannelle	Col de Verde	Col de Vizzavona	Vivario
Drought events	1995	1988	1988	1997	1997	1997	1987	1993	1987	2006	2003
	2003	2003		1998	1998	1998			1993		
	2008			2008	1999	2003					
					2008	2008					
Values of SPEI4$_{July}$	-1.24693	-1.81458	-1.91623	-1.22381	-1.26359	-1.24705	-1.14158	-1.00188	-1.00022	-2.03229	-1.97511
	-1.5168	-1.12819		-1.24989	-1.25185	-1.04455			-1.03988		
	-1.4048			-1.15276	-1.03534	-1.37046					
					-1.07017	-1.07602					

ranged from one to four (Table 2).

It must be pointed out that, although the Lloret growth-based indices for characterising drought responses of trees have been widely used, there has been some critique regarding the interpretation of the results using these indices, as it is not clear which index between the resistance and recovery is more important to overall resilience (Schwarz et al., 2020). Schwarz et al. (2020) proposed alternative indices to account for the time needed to reach pre- and post-drought growth levels and help identify suitable tree species and management options under climate change. Based on this study, we have also considered a framework analysis based on pooling sites for each region, which allows an integrated interpretation of the three Lloret indices (Schwarz et al., 2020), assuming that resistance could be the most important index, because highly resistant forest stands need less recovery than forest stands with lower resistance (Hoffmann et al., 2018; Kunz et al., 2018). To verify if there is a universal trade-off between resistance and recovery of radial growth to drought, we analysed the relationship between resistance and recovery. Then, we compared the observed relationship between resistance and recovery with a theoretical relationship, representing full resilience (value of 1) at any given resistance value and calculated the recovery at a given resistance value with the equation Rc = 1/Rt.

2.5. Modelling approach

Linear mixed-effects models were applied to derive (i) the response of stem radial growth, based on several climatic variables used as predictor, and (ii) the different drought response components based on specific drought events. Models were fitted separately using ring-width index (RWI), resistance (Rt), recovery (Rc), and resilience (Rs) as response variables. In all models, we tested the incidence of multicollinearity between the independent variables, removing the variables with a variance inflation factor ≥ 3 (Zuur et al., 2010). The incidence of multicollinearity was evaluated with the "VIF" function of the R package "car" (Fox, 2012). The models were fitted through the "lmer" function of the R package "lme4" (Bates et al., 2014). The sampling site was added as a random effect, to consider the non-independence associated with each location. We also included the sampling year as a random effect, to account for stochastic year variation in RWI, Rt, Rc, and Rs values that could be uncaptured by environmental variables (Milner et al., 1999).

To identify the best random structure, we used three different configurations (i) separate random terms, (ii) nested random terms, and iii) separate random terms plus their interaction. The comparison between the three configurations was performed through a likelihood ratio test (LRT; "anova" function in the "lmer4″ package) based on maximum likelihood estimation (Bates et al., 2014; Zuur et al., 2013). Models goodness-of-fit was assessed by calculating the conditional and marginal coefficients of determination, obtained through the "r.squared.GLMM" function of the "MuMIn" package (Barton, 2010). Conditional coefficient of determination (R^2c) indicates the variance explained by the entire model, both fixed and random terms, whereas marginal coefficient of determination (R^2m) refers to the variance explained only by the fixed factors (i.e., excluding the random effect).

2.5.1. Climate-growth modeling

As a dependent variable in the climate-growth models, we used RWI values calculated for each forest stand within the 1981–2010 interval. The dependent variable was log-transformed to improve normality. In this analysis, the predictors were: total precipitation (*P*), mean maximum (*Tmax*) and minimum (*Tmin*) temperatures of the current year (January to December), *Elevation, Slope, Northness* and *Eastness*. Climatic predictors are referred to each month and forest stand, while topographic predictors are referred to each forest stand. Topographic predictors were calculated from a digital elevation model provided by Earthdata website (https://search.earthdata.nasa.gov) at a spatial resolution of ca. 30 m. For each sampling forest stand, we derived the elevation, the slope, and the aspect in terms of eastness and northness

through the "terrain" function of the "raster" package.

The full model was characterized by 40 independent variables, as shown by Eq. (4):

$$\log(y) = a_0 + a_1 P + a_2 Tmax + a_3 Tmin + a_4 Elevation + a_5 Slope \\ + a_6 Northness + a_7 Eastness + r + \varepsilon \quad (4)$$

where y is the dependent variable (RWI), a_0 is the intercept and $a_{1\ to\ 7}$ are the parameter coefficients: a_{i1}: precipitations of each month; a_{i2}: maximum temperatures of each month; a_{i3}: minimum temperatures of each month; a_{4-7}: parameter coefficients referring to the topographic predictors as detailed in the formula. Again, r represents the random effect (separate random terms sampling year and location, plus their interaction), and ε indicates the model residuals.

Afterwards, through the VIF function, only the variables with a low multicollinearity were identified, obtaining a final set of 17 variables (Table A4, Model 1). The final set of 17 variables indicated that the best random structure was the separate random terms *sampling year* and *location*, plus their interaction (Table A3). The model was fitted through the likelihood criterion (ML – Pinheiro and Bates, 2000) and Akaike's information criterion was used to identify the variables with high explanatory power. To remove the first variables from the final set, we used the "stepAIC" function of the "MASS" package (Ripley et al., 2013), thus obtaining nine variables (Table A4, Model 2). Subsequently, the nine variables were used to obtain the most explanatory variables, considering all the possible combinations (Table A4). Among the compared models (based on the variables specified above), the model with the lowest Akaike's Information Criterion (AIC) value was selected (Model 44). Finally, the best model was fitted using the maximum likelihood criterion (ML), with a significance threshold of $p < 0.1$.

2.5.2. Drought response modeling

As dependent variables in drought response models, we used resistance (Rt), recovery (Rc), and resilience (Rs) values calculated for each sampled tree within the 1981–2010 interval. The mixed models were constructed with Rt, Rc and Rs values of drought events specific to each forest stand. The number of drought events for each forest stand ranged from one to four (Table 2). We performed a log-transformation of response variables to improve normality in all models. The predictors included *age* of each tree, $SPEI4_{July}$ of each forest stand and *Region* (i.e., Calabria, Sicily, Sardinia, and Corsica) as dummy variables.

According to the LRT performed on random effect configurations, the best random structure in the model of resistance and resilience was when separating the random terms *sampling year* and *location*; while in the model of recovery, the best random structure was *sampling year* nested in *location* (Table A5). Models were fitted using the maximum likelihood criterion (ML), with a significance threshold of $p < 0.1$.

The final model constructed is shown in Eq. (5).

$$\log(y) = a_0 + a_1 \frac{1}{Age} + a_2 SPEI4_{July} + a_3 Region + r + \varepsilon \quad (5)$$

where y is the response variable, i.e., the analysed drought response index (Rt, Rc, and Rs), a_0 is the intercept, a_{1-3} are parameter coefficients, r is the random effect (Rt and Rs *sampling year* and *location;* Rc *sampling year* nested in *location*), and ε the indicate model residuals.

The overall region-specific responses to drought were compared by a multiple comparison test. The Kruskal-Walli's test ("coin" package; Hothorn et al., 2017) and the pairwise Conover's test ("PMCMR" package; Pohlert, 2018) were used to detect differences in drought response (resistance, recovery, resilience) among regions. More specifically, these are non-parametric tests and require no assumptions. In all comparisons, the significance was associated with the critical value $p \le 0.05$.

3. Results

3.1. Tree-ring width chronologies

Descriptive statistics of the 13 ring-width chronologies are shown in Table 3. Mean tree-ring widths showed high growth values in all forest stands (from 1.15 to 3.63), except in Bagaladi (0.25; Table 3). Mean sensitivity (MS) for all chronologies was relatively low (from 0.128 to 0.241). The first order autocorrelation (AC1) indicates low to moderate variation in annual stem radial growth (from 0.147 to 0.521), except in Col de Verde (0.903). The correlation of mean intersections (RBAR) ranged from 0.212 to 0.511. These values of RBAR suggest a good agreement between the individual series in each forest stand chronology (Table 3). The EPS statistics show that the 13 ring-width chronologies were robust (EPS > 0.85).

3.2. Influence of climate on stem radial growth

Overall, relationships between spring/summer precipitation and tree-ring width showed a positive trend, whereas those between autumn/winter precipitation and tree ring width had a negative trend (Figs. A2 and A3). The climate-growth model, on the other hand, identified the climatic variables that mainly influenced the stem radial growth. The final model (Table 4) identified *P_March, P_April, P_June, P_July, P_December*, and *Tmax_December* as those climatic variables reflecting a significant association with stem radial growth (Table 4). Particularly, stem radial growth increases with increasing *P_April* and *P_June*, while decreasing with increasing *P_March, P_December*, and *Tmax_December*. Furthermore, the model showed differences between *sampling year* nested in *location*, with R^2 of 0.70, when all effects were included, and R^2 of 0.07, when only fixed effects were considered.

3.3. Influence of drought index and tree age on drought response

Models for drought response showed a significant negative influence of $SPEI4_{July}$ in terms of resilience (Rs; $p < 0.05$); while tree age had a slightly significant negative influence only in terms of resistance (Rt; $p < 0.1$), with higher resistance values in trees aged between 1/389 and 1/100 (Fig. A4). The model comparisons showed a lower resistance and resilience in Corsican populations than in those from Sardinia and Sicily (Table 5). No differences emerged between Corsican and the other populations in terms of recovery. The models showed differences between the separate random terms sampling year and location, with R^2 of 0.30 (Rt), 0.52 (Rc), and 0.44 (Rs), when all effects were included, and R^2 of 0.06 (Rt), 0.07 (Rc), and 0.11 (Rs), when only fixed effects were considered.

Three models were constructed according to the three components of resilience (Lloret et al., 2011) as log-transformed variables. $SPEI4_{July}$ = standardized precipitation evapotranspiration index (SPEI) of the month of July with an aggregation period of 4 months. Calabria, Sicily, and Sardinia are part of a four-level categorical variable, with Corsica as a reference (sometimes considered a separate subspecies; Santini et al., 2019). Significance levels: .$p < 0.1$; *$p < 0.05$; **$p < 0.01$.

Overall, non-parametric tests confirmed the results of models for drought response, showing that Corsican had lower mean values for resistance and resilience, but not for recovery, than the other populations (particularly in Sicily and Sardinia; Fig. A5). Furthermore, drought responses significantly differed among the other populations, in terms of resistance, recovery, and resilience (Fig. A5).

After pooling sites for each region (only one site was sampled in Sardinia), Fig. A6 shows the patterns of the observed relationship between resistance and recovery, and the theoretical line of full resilience. In general, a negative power function (black line) provided the best fit (Table A6). Therefore, in all sites, trees (or forest stands) with large growth reductions during drought (lower resistance) were able to recover faster than trees (or forest stands) with higher resistance.

Table 3
Descriptive statistics of mean ring widths (MRW) with the standard deviation (SD) calculated on the series of raw annual ring widths of black pine ssp. *laricio* in 13 forest stands.

Location	N° tree	Time Span	Maximum age	Minimum age	MRW ± SD (mm)	MS	AC1	RBAR	EPS
Bagaladi	23	1894-2016	123	38	0.25 ± 0.17	0.166	0.319	0.366	0.89
	17	1874-2020	147	101	1.77 ± 0.78	0.128	0.420	0.436	0.92
Gallopane	15	1740-2016	277	123	1.66 ± 1.02	0.134	0.508	0.366	0.89
Ponticelli	15	1889-2019	131	79	3.33 ± 1.85	0.132	0.222	0.212	0.87
Piano Provenzana	28	1884-2010	127	50	2.72 ± 1.55	0.229	0.329	0.418	0.94
	57	1820-2014	191	39	3.14 ± 2.03	0.226	0.484	0.419	0.95
Citelli	49	1896-2013	117	38	3.63 ± 1.45	0.204	0.147	0.385	0.95
Monte Nespole	44	1886-2014	129	54	2.00 ± 1.43	0.241	0.466	0.473	0.97
Su Tassu	21	1919-2019	100	82	2.46 ± 2.02	0.148	0.517	0.472	0.95
Capannelle	19	1605-2017	413	42	1.15 ± 0.78	0.150	0.404	0.443	0.87
Col de Verde	20	1615-2018	403	150	1.43 ± 1.10	0.151	0.903	0.336	0.93
Col de Vizzavona	21	1651-2018	367	59	1.31 ± 0.93	0.199	0.528	0.496	0.91
Vivario	11	1825-2017	192	97	1.38 ± 0.87	0.215	0.521	0.511	0.92

Note: Maximum and minimum age are relative to the oldest tree and the youngest tree, respectively; MS = mean sensitivity; AC1 = first-order autocorrelation; RBAR = correlation of mean intersections; EPS = expressed population signal computed on the indexed tree-ring series.

Table 4
Results of the best climate-growth model using the maximum likelihood criterion (ML).

	log(RWI)	VIF
Intercept	-0.054*	
P_March	-0.031*	1.109361
P_April	0.026*	1.115726
P_June	0.029*	1.054146
P_July	0.016	1.055970
P_December	-0.021.	1.202176
Tmax_December	-0.027*	1.145901
Observations	390	
R^2_m	0.07	
R^2_c	0.70	

Note: The model was constructed with ring-width index (RWI) as log-transformed variable. P = total precipitation; Tmax = mean maximum temperatures. Significance levels: .p < 0.1; *p < 0.05.

Table 5
Results of drought response (Rt, Rc, and Rs) models using the maximum likelihood criterion (ML).

	log(Rt)	log(Rc)	log(Rs)
Intercept	-0.1938*	0.2036 *	-0.0829
Age	-0.0185 .	0.0154	-0.0038
Spei4_July	-0.0019	-0.0361	-0.0756 *
Calabria	0.0293	0.0110	0.0439
Sicily	0.1790 .	-0.1231	0.3314 *
Sardinia	0.2914 *	0.1663	0.4188 **
Observations	662	662	662
R^2_m	0.06	0.07	0.11
R^2_c	0.30	0.52	0.44

In Corsica, for resistance values below 0.7, the recovery of resilience was not complete (values < 1). The deviation from the line of full resilience increased with the decrease in resistance, leading to the conclusion that the populations of this region should be assigned a relatively lower drought resilience in comparison with the other regions.

In Sicily and, to a lesser extent, in Calabria, the observed relationship between resistance and recovery showed a closer fit to the line of full resilience in comparison with the other regions. A prompt recovery at any resistance value was revealed and even trees showing a marked reduction in their growth were able to fully recover from drought.

In Sardinia, for almost all resistance values, the observed relationship between resistance and recovery was clearly above the theoretical curve, indicating a prompt recovery of growth after the dry period.

Regardless of the numerosity of the forest stands considered, all the four regions showed similar resistance values (about 0.7), point in which

the observed relationship starts to be above the theoretical relationship, but with different recovery values. This would indicate that, depending on the prevailing climatic conditions in the drought and post-drought periods, the same resistance value might lead to a different recovery pattern in black pine ssp. *laricio*.

4. Discussion

4.1. Growth-climate relationship

The climate-growth model shows that precipitation was the main driver for stem radial growth in the studied populations of black pine ssp. *laricio* (Table 4). Several studies conducted both on black pine ssp. *laricio* (e.g., Mazza et al., 2018; Lebourgeois, 2000) and ssp. *salzmannii* (e.g., Sangüesa-Barreda et al., 2019; Camarero et al., 2013) highlighted the importance of water availability in determining stem radial growth, especially in late winter and spring months. Mazza et al. (2018) and Lebourgeois (2000) observed that an increase of water availability in winter and in spring precipitation may support earlywood formation in black pine ssp. *laricio*. In the Mediterranean environment, adequate water supply in winter months may recharge soil water storage, positively influencing growth resumption in spring before the onset of summer drought (Camarero et al., 2013).

Nevertheless, our results show a positive relationship between spring/summer precipitation (April and June) and stem radial growth, and a negative relationship in late winter (March; Table 4). This suggests that, in our case, winter precipitation was less important in determining stem radial growth of black pine ssp. *laricio* than water availability in early spring and summer, which determines xylem phenology and its capacity to cope with drought (Delzon et al., 2010). This observation supports our first hypothesis to some extent. A negative influence of excess precipitation in February on stem radial growth in black pine ssp. *pallasiana* was also found in Turkey (Doğan and Köse, 2019). Indeed, Doğan and Köse (2019) found a negative relationship between stem radial growth and precipitation mainly on the southern slope of the mountain, probably related to higher exposure to winter snowfall brought by southerly winds coming from the Mediterranean Sea in comparison with the northern slope. High snowfall may delay the beginning of the vegetative period at high altitudes due to decreasing soil temperature and frost drought. Furthermore, if high snowfall is accompanied by low temperature, a reduction or interruption of the water cycle may occur (Thomsen, 2001; Tranquillini, 1982), with impacts on growth resumption. These climatic conditions (more snow and greater persistence of the snowpack on the ground) may provide explanation for the observed response of trees in forest stands at high altitudes. In forest stands at low altitude, on the other hand, a possible explanation of the negative relationship between stem radial growth and

precipitation in March can be linked to the local environmental conditions that characterize these forest stands. In Corsica, for example, precipitation is very unevenly distributed throughout the year, with maximum precipitation in autumn and winter (Bruno et al., 2001). The high intensity and duration of precipitation events during the autumn and winter months may lead to soil saturation or surface runoff (Szymczak et al., 2020), with consequent loss of most precipitation, in turn inducing a negative influence on stem radial growth.

It is worth noting that most of the maximum temperature variables, including those of winter months (i.e., January, February, and March), were removed in the climate-growth model due to the strong collinearity among the variables. For this reason, our first hypothesis cannot be completely supported. Only maximum temperatures in December of the current year were included among the variables of the climate-growth model, showing a significant negative influence (Table 4).

4.2. Responses to drought events

Black pine ssp. *laricio* was able to recover within two years after drought events, except in Vivario (Table A7). According to Granda et al. (2013) and Martín-Benito et al. (2008), black pine ssp. *salzmannii* may recover two years after periods of drought, rapidly counterbalancing drought-induced growth declines (Granda et al., 2013). However, the capacity to recover the stem radial growth can be severely compromised if consecutive periods of severe drought occur (Allen et al., 2010). Therefore, the incomplete recovery two years after the drought event observed in Vivario (Table A7), can be related to consecutive severe drought events that occurred in 2003 and 2006 (Table A2), compromising the capacity of this species to offset drought induced growth declines.

The models for drought response show that black pine ssp. *laricio* populations in Corsica were more sensitive to drought events than populations in southern Italy, supporting our second hypothesis. Corsican populations displayed lower resistance and resilience values than those of Sicily and Sardinia (Table 5; Fig. A5), which was confirmed by the framework analysis based on pooling sites in each region (Table A6; Fig. A6). The geographical pattern in the response to drought suggests a local adaptation to disturbance events in black pine ssp. *laricio*. Impacts of severe drought events and the plasticity of growth responses to these events can be population-specific and depend on site characteristics. Adaptation potential to drought events have been found in other Mediterranean pine species (e.g., Sánchez-Salguero et al., 2018). Nevertheless, our results contrast with observations by Thiel et al. (2012), who detected significant differences only in tree growth and survival rates within and among provenances of black pine, but not in the response to drought and warming. These authors suggested marginal adaptation capacity to local conditions in black pine. According to Soto et al. (2010), diversity within black pine ssp. *salzmannii* populations may depend on high water availability during summer months, as regions with regular precipitation support larger and demographically more stable populations than regions with lower precipitation. In Corsica, precipitation is very unevenly distributed, with short high intensity rainfall events, which occur also during the summer. Szymczak et al. (2014) underlined that only long-lasting low intensity rainfall events during the summer contribute to improve soil water availability and, therefore, favour stem radial growth in black pine ssp. *laricio*. Therefore, low resistance and resilience values in Corsican populations can be caused by the scarce water availability needed for tree growth during drought events. Furthermore, if black pine ssp. *laricio* behaved like black pine ssp. *salzmannii*, i.e., showing increased genetic diversity in populations with regular water availability, Corsican populations should have less genetic variation than those in Sicily and Sardinia.

4.3. Influence of tree age on drought responses

Based on our analysis, older trees (aged 1/389-1/100 years) were

found to be more resistant to drought-related disturbance than younger trees (Table 5; Fig. A4). Older/larger trees may have deeper root systems and thus gain better access to water in deeper soil layers than young/smaller trees, thereby decreasing drought stress (Pretzsch et al., 2018). Yet, older/larger trees can also be more resilient to short-time variations in evaporative demand due to their larger internal water storage (Liu et al., 2020). A decline in leaf-sapwood area ratio with increasing tree age/height is expected in conifer trees (e.g., Poyatos et al., 2007; McDowell et al., 2002), which may help avoid excessive transpiration and xylem embolism. Several studies have reported tree age/height-related decline in stomatal conductance in pine species (e.g., Martínez-Vilalta, 2009; Magnani et al., 2008Magnani et al., 2008), associated with decreasing leaf area- and mass-based assimilation rate as tree height/age increases (Niinemets, 2002). More conservative gas exchange in older/larger pine trees may also imply higher water use efficiency (e.g., Drake et al., 2010). Older trees/larger face increased hydraulic challenges compared to younger/smaller trees, as the resistance to water flow through the xylem increases due to a longer hydraulic pathway through the tree stem and a greater gravitational effect on the water column (Bennett et al., 2015; Ryan and Yoder, 1997).

Our results agree with studies conducted on black pine (e.g., Camarero et al., 2018) and other conifer and broadleaved species (e.g., Pardos et al., 2021; Thurm et al., 2016; Carrer and Urbinati, 2006), in which older trees showed lower sensitivity to drought events than younger trees. Camarero et al. (2018) observed that an extreme drought induced a marked growth reduction in declining black pine individuals when accounting for age effects on growth rates (younger declining and older non-declining individuals). Nevertheless, these results are in contrast with other studies conducted both on black pine (e.g., Lucas-Borja et al., 2021; Granda et al., 2018; Martin-Benito et al., 2008) and other tree species (e.g., Bose et al., 2021; Bennett et al., 2015; Dorman et al., 2015). In these studies, older trees were found to be less resistant to drought than younger trees and the impact of drought events on growth and mortality rates in larger trees was relatively greater than in smaller trees. Contradictory results on the responses of different tree ages/sizes to drought show the complexity of climate-growth relationships and the importance of clarifying how height-diameter allometric relations and the age effect may vary locally under different disturbance regimes (Marziliano et al., 2019). It is important to note that in our study the effect of tree size on drought responses was not considered. The lack of measurements of tree stem diameters in previous years did not allow us to accurately calculate the effect of tree size for the years in which drought events occurred.

5. Conclusion

The main driver of stem radial growth in black pine ssp. *laricio* is early spring and summer precipitation, probably determining xylem cell production and elongation and the capacity of xylem conduit to withstand water stress. Conversely, severe conditions triggered by excessive winter precipitation, both in terms of rain and snow, have negative impacts on stem radial growth in black pine ssp. *laricio*. Corsican populations showed a lower drought resistance and resilience than those in Sicily and Sardinia. This implies a trade-off between growth resistance to drought stress and resilience after disturbance release, probably regulated by local environmental conditions. Older trees were more resistant to drought events than younger trees, which emphasises the importance of considering ontogenetic effects and their impacts on tree growth.

This work, therefore, shows that tree age and local environmental conditions influenced stem radial growth and drought responses in our populations of black pine ssp. *laricio*. The population-specific sensitivity to spring-summer water availability and the age-(size)-mediated growth responses to drought may indicate different impacts of predicted climate change scenarios on different geographic regions. Furthermore, enrichment planting and assisted regeneration in degraded forests

should exploit intraspecific diversity and rely on better adapted populations or subspecies of black pine instead of non-native tree species. It is worth noting that further studies on drought-growth relationships in black pine ssp. *laricio* are needed to draw more solid conclusions and inform adaptive measures for managing this Mediterranean forest tree under a warming climate.

Declaration of Competing Interest

The authors have no relevant financial or non-financial interests to disclose.

The authors have no conflicts of interest to declare that are relevant to the content of this article.

All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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Supplementary materials

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References

Afzal-Rafii, Z., Dodd, R.S., Zavarin, E., 1996. Genetic diversity in foliar terpenoids among natural populations of European black pine. Biochem. Syst. Ecol. 24, 325–339.

Afzal-Rafii, Z., Dodd, R.S., 2007. Chloroplast DNA supports a hypothesis of glacial refugia over postglacial recolonization in disjunct populations of black pine (*Pinus nigra*) in western Europe. Mol. Ecol. 16, 723–736.

Aguinagalde, I., Llorente, F., Benito, C., 1997. Relationships among five populations of European black pine (*Pinus nigra* Arn.) using morphometric and isozyme markers. Silvae Genet. 46, 1–5.

Allen, C.D., et al., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. 259, 660–684.

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6, 1–55.

Amodei, T., Guibal, F., Fady, B., 2013. Relationships between climate and radial growth in black pine (*Pinus nigra* Arnold ssp. *salzmannii* (Dunal) Franco) from the south of France. Ann. For. Sci. 70, 41–47.

Anderegg, W.R., et al., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349, 528–532.

Andersson, M., Milberg, P., Bergman, K.O., 2011. Low pre-death growth rates of oak (*Quercus robur* L.)—Is oak death a long-term process induced by dry years? Ann. For. Sci. 68, 159–168.

Andreu, L., Gutierrez, E., Macias, M., Ribas, M., Bosch, O., Camarero, J.J., 2007. Climate increases regional tree-growth variability in Iberian pine forests. Glob. Change Biol. 13, 804–815.

Barton, K., 2010. MuMIn: multi-model inference. R package version 0.13. 17. http://CRAN.R-project.org/package=MuMIn.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2014. Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823.

Beguería, S., Vicente-Serrano, S.M., 2012. SPEI: Calculation of the Standardised Precipitation-Evapotranspiration Index. R Foundation for Statistical Computing, Vienna, Austria. R package version 1.2.

Bennett, A.C., McDowell, N.G., Allen, C.D., Anderson-Teixeira, K.J., 2015. Larger trees suffer most during drought in forests worldwide. Nat. Plants 1, 15139.

Bonavita, S., Vendramin, G.G., Bernardini, V., Avolio, S., Regina, T.M.R., 2016. The first SSR-based assessment of genetic variation and structure among *Pinus laricio* Poiret populations within their native area. Plant Biosyst. 150, 1271–1281.

Bosa, B., Portoghesi, L., 2013. Igiganti della sardegna: la particella pavari della foresta demaniale di fiorentini. L'Italia Forestale e Montana 57 (6), 553–560.

Bose, A.K., Rohner, B., Bottero, A., Ferretti, M., Forrester, D.I., 2021. Did the 2018 megadrought change the partitioning of growth between tree sizes and species? A Swiss case-study. Plant Biol. J. https://doi.org/10.1111/plb.13380.

Bruno, C., Dupré, G., Giorgetti, J.P., 2001. Chì tempu face? Météorologie, Climatet Microclimates de la Corse. CNDP-CRDP de Corse/Meteo France, Ajaccio.

Camarero, J.J., Gazol, A., Tardif, J.C., Conciatori, F., 2015. Attributing forest responses to global-change drivers: limited evidence of a CO₂-fertilization effect in Iberian pine growth. J. Biogeogr. 42, 2220–2233.

Camarero, J.J., Manzanedo, R.D., Sanchez-Salguero, R., Navarro-Cerrillo, R.M., 2013. Growth response to climate and drought change along an aridity gradient in the southernmost *Pinus nigra* relict forests. Ann. For. Sci. 70, 769–780.

Camarero, J.J., et al., 2021. Differences in temperature sensitivity and drought recovery between natural stands and plantations of conifers are species-specific. Sci. Total Environ. 796, 148930.

Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Cantero, A., Sánchez-Salguero, R., Sánchez-Miranda, A., Granda, E., Serra-Maluquer, X., Ibáñez, R., 2018. Forest growth responses to drought at short- and long-term scales in Spain: squeezing the stress memory from tree rings. Front. Ecol. Evol. 6, 9. https://doi.org/10.3389/fevo.2018.00009.

Camarero, J.J., Sánchez-Salguero, R., Ribas, M., Touchan, R., Andreu-Hayles, L., Dorado-Liñán, I., Meko, D.M., Gutiérrez, E., 2020. Biogeographic, atmospheric, and climatic factors influencing tree growth in Mediterranean Aleppo pine forests. Forests 11, 736.

Carrer, M., Urbinati, C., 2006. Long-term change in the sensitivity of tree-ring growth to climate forcing in *Larix decidua*. New Phytol. 170, 861–872.

Cesca, G., Peruzzi, L., 2002. *Pinus laricio* Poir. and *P. leucodermis* Antoine: karyotype analysis in Calabrian populations (Southern Italy). Caryologia 55, 21–25.

Cinnirella, S., Magnani, F., Saracino, A., Borghetti, M., 2002. Response of a mature *Pinus laricio* plantation to a three-year restriction of water supply: structural and functional acclimation to drought. Tree Physiol. 22, 21–30.

Colangelo, M., Camarero, J.J., Ripullone, F., Gazol, A., Sánchez-Salguero, R., Oliva, J., Redondo, M.A., 2018. Drought decreases growth and increases mortality of coexisting native and introduced tree species in a temperate floodplain forest. Forests 9, 205.

Cook, E.R., 1985. A Time-Series Analysis Approach to Tree-Ring Standardization. University of Arizona, Tucson, AZ, p. 175. Ph.D. Thesis.

Cook, E.R., Holmes, R.L., 1984. Program ARSTAN users manual. Labo. Tree-Ring Res. Univ. Ariz. 15, 50–65. Tucson.

Delzon, S., Douthe, C., Sala, A., Cochard, H., 2010. Mechanism of water-stress induced cavitation in conifers: Bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant Cell* Environ. 33, 2101–2111.

Doğan, M., Köse, N., 2019. Influence of climate on radial growth of black pine on the mountain regions of southwestern Turkey. Plants 8, 276.

Dorado-Liñán, I., et al., 2019. Geographical adaptation prevails over species-specific determinism in trees' vulnerability to climate change at Mediterranean rear-edge forests. Glob. Change Biol. 25, 1296–1314.

Dorman, M., Svoray, T., Perevolotsky, A., Moshe, Y., Sarris, D., 2015. What determines tree mortality in dry environments? A multi-perspective approach. Ecol. Appl. 25, 1054–1071.

Drake, J.E., Raetz, L.M., Davis, S.C., DeLucia, E.H., 2010. Hydraulic limitation not declining nitrogen availability causes the age-related photosynthetic decline in loblolly pine (*Pinus taeda* L.). Plant Cell Environ. 33, 1756–1766. https://doi.org/10.1111/j.1365-3040.2010.02180.x.

Fernández-Pérez, L., Villar-Salvador, P., Martínez-Vilalta, J., Toca, A., Zavala, M.A., 2018. Distribution of pines in the Iberian Peninsula agrees with species differences in foliage frost tolerance, not with vulnerability to freezing-induced xylem embolism. Tree Physiol. 38, 507–516.

Fox, J, 2012. Package 'car'. R foundation for statistical computing, Vienna. https://cran.r-project.org/web/packages/car/car.pdf.

Gazol, A., Camarero, J.J., Anderegg, W.R.L., Vicente-Serrano, S.M., 2017. Impacts of droughts on the growth resilience of Northern Hemisphere forests. Glob. Ecol. Biogeogr. 26, 166–176.

Gillerot, L., Forrester, D.I., Bottero, A., Rigling, A., Lévesque, M., 2021. Tree neighbourhood diversity has negligible effects on drought resilience of European beech, silver fir and Norway spruce. Ecosystems 24 (1), 20–36.

Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region. Glob. Planet. Change 63, 90–104.

González de Andrés, E., Camarero, J.J., 2020. Disentangling mechanisms of drought-induced dieback in *Pinus nigra* Arn. from growth and wood isotope patterns. Forests 11, 1339.

Granda, E., Camarero, J.J., Gimeno, T.E., Martinez-Fernandez, J., Valladares, F., 2013. Intensity and timing of warming and drought differentially affect growth patterns of co-occurring Mediterranean tree species. Eur. J. For. Res. 132, 469–480.

Granda, E., Gazol, A., Camarero, J.J., 2018. Functional diversity differently shapes growth resilience to drought for co-existing pine species. J. Veg. Sci. 29, 265–275.

Hadad, M.A., González-Reyes, Á., Roig, F.A., Matskovsky, V., Cherubini, P., 2021. Tree-ring-based hydroclimatic reconstruction for the northwest Argentine Patagonia since 1055 CE and its teleconnection to large-scale atmospheric circulation. Glob. Planet. Change 202, 103496.

Hargreaves, G.H., Samani, Z.A., 1985. Reference crop evapotranspiration from temperature. Appl. Eng. Agric. 1, 96–99.

Hijmans, R.J., 2019. *raster: geographic data analysis and modeling.* R package version 3.0-7.

Hoffmann, N., Schall, P., Ammer, C., Leder, B., Vor, T., 2018. Drought sensitivity and stem growth variation of nine alien and native tree species on a productive forest site in Germany. Agric. For. Meteorol. 256, 431–444.

Holmes, R.L., 1983. Computer assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43, 69–78.

Hothorn, T., Hornik, K., van de Wiel, M.A., Zeileis, A., 2017. Package 'coin'. Pages 1–98. https://cran.r-project.org/web/packages/coin/coin.pdf.

Huang, K., et al., 2015. Tipping point of a conifer forest ecosystem under severe drought. Environ. Res. Lett. 10, 024011.

IPCC, 2018. Chapter 3: impacts of 1.5 C global warming on natural and human systems.

Janssen, E., et al., 2018. Recent growth trends of black pine (*Pinus nigra* JF Arnold) in the eastern mediterranean. For. Ecol. Manag. 412, 21–28.

Jiang, P., Liu, H., Piao, S., Ciais, P., Wu, X., Yin, Y., Wang, H., 2019. Enhanced growth after extreme wetness compensates for post-drought carbon loss in dry forests. Nat. Commun. 10, 1–9.

Karger, D.N., et al., 2017. Climatologies at high resolution for the earth's land surface areas. Sci. *Data* 4, 1–20.

Köse, N., Akkemik, Ü., Dalfes, H.N., Özeren, M.S., Tolunay, D., 2012. Tree-ring growth of *Pinus nigra* Arn. subsp. *pallasiana* under different climate conditions throughout western Anatolia. Dendrochronologia 30, 295–301.

Köse, N., Güner, H.T., Harley, G.L., Guiot, J., 2017. Spring temperature variability over Turkey since 1800 CE reconstructed from a broad network of tree-ring data. Clim. Past. 13, 1–15.

Kunz, J., Löffler, G., Bauhus, J., 2018. Minor European broadleaved tree species are more drought-tolerant than Fagus sylvatica but not more tolerant than Quercus petraea. For. Ecol. Manag. 414, 15–27.

Lebourgeois, F., 2000. Climatic signals in earlywood, latewood and total ring width of Corsican pine from western France. Ann. For. Sci. 57, 155–164.

Linares, J.C., Tíscar, P.A., 2010. Climate change impacts and vulnerability of the southern populations of *Pinus nigra* subsp. *salzmannii*. Tree Physiol. 30, 795–806.

Linares, J.C., Delgado-Huertas, A., Carreira, J.A., 2011. Climatic trends and different drought adaptive capacity and vulnerability in a mixed *Abies pinsapo–Pinus halepensis* forest. Clim. Change 105, 67–90.

Liu, C., Hölttä, T., Tian, X., Berninger, F., Mäkelä, A., 2020. Weaker light response, lower stomatal conductance and structural changes in old Boreal conifers implied by a Bayesian hierarchical model. Front. Plant Sci. 11, 579319 https://doi.org/10.3389/fpls.2020.579319.

Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120, 1909–1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x.

Lucas-Borja, M.E., Bose, A.K., Andivia, E., Candel-Pérez, D., Plaza-Álvarez, P.A., Linares, J.C., 2021. Assessing tree drought resistance and climate-growth relationships under different tree age classes in a *Pinus nigra* Arn. ssp. *salzmannii* forest. Forests 12, 1161.

Magnani, F., Bensada, A., Cinnirella, S., Ripullone, F., Borghetti, M., 2008. Hydraulic limitations and water-use efficiency in *Pinus pinaster* along a chronosequence. Can. J. For. Res. 38, 73–81. https://doi.org/10.1139/X07-120.

Martín-Benito, D., Cherubini, P., Del Río, M., Cañellas, I., 2008. Growth response to climate and drought in *Pinus nigra* Arn. trees of different crown classes. Trees 22, 363–373.

Martín-Benito, D., Del Río, M., Heinrich, I., Helle, G., Cañellas, I., 2010. Response of climate-growth relationships and water use efficiency to thinning in a *Pinus nigra* afforestation. For. Ecol. Manag. 259, 967–975.

Martínez-Vilalta, J., et al., 2009. Hydraulic adjustment of scots pine across Europe. New Phytol. 184, 353–364. https://doi.org/10.1111/j.1469-8137.2009.02954.x.

Marziliano, P., Tognetti, R., Lombardi, F., 2019. Is tree age or tree size reducing height increment in *Abies alba* Mill. at its southernmost distribution limit? Ann. For. Sci. 76, 17.

Mazza, G., Sarris, D., Chiavetta, U., Ferrara, R.M., Rana, G., 2018. An intra-stand approach to identify intra-annual growth responses to climate in *Pinus nigra* subsp. *laricio* Poiret trees from southern Italy. For. Ecol. Manag. 425, 9–20.

McDowell, N.G., et al., 2002. The relationship between tree height and leaf area: sapwood area ratio. Oecologia 132, 12–20. https://doi.org/10.1007/s00442-002-0904-x.

McKee, T.B., Doesken, N.J., Kleist, J., 1993. The relationship of drought frequency and duration to time scales. Preprints. In: Proceedings of the 8th Conference on Applied Climatology,. Amer. Meteor. Soc., Anaheim, CA, pp. 179–184.

Milner, J.M., Elston, D.A., Albon, S.D., 1999. Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. J. Anim. Ecol. 68, 1235–1247.

Niinemets, Ü., 2002. Stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size in *Picea abies* and *Pinus sylvestris*. Tree Physiol. 22, 515–535. https://doi.org/10.1093/treephys/22.8.515.

Pardos, M., et al., 2021. The greater resilience of mixed forests to drought mainly depends on their composition: analysis along a climate gradient across Europe. For. Ecol. Manag. 481, 118687.

Pasho, E., Camarero, J.J., Vicente-Serrano, S.M., 2012. Climatic impacts and drought control of radial growth and seasonal wood formation in *Pinus halepensis*. Trees 26, 1875–1886.

Paulo, A.A., Rosa, R.D., Pereira, L.S., 2012. Climate trends and behaviour of drought indices based on precipitation and evapotranspiration in Portugal. Nat. Hazards Earth Syst. Sci. 12, 1481–1491.

Peñuelas, J., Terradas, J., Lloret, F., 2011. Solving the conundrum of plant species coexistence: water in space and time matters most. New Phytol. 189, 5–8.

Pinheiro, J.C., Bates, D.M., 2000. Linear Mixed-Effects Models: Basic Concepts and Examples. In: Mixed-Effects Models in S and S-PLUS. Statistics and Computing. Springer, New York, NY. 10.1007/0-387-22747-4_1.

Pohlert, T., 2018. *PMCMRplus: calculate pairwise multiple comparisons of mean rank sums extended.* Available at: https://cran.r-project.org/web/packages/PMCMRplus/PMCMRplus.pdf.

Poyatos, R., et al., 2007. Plasticity in hydraulic architecture of Scots pine across Eurasia. Oecologia 153, 245–259. https://doi.org/10.1007/s00442-007-0740-0.

Pretzsch, H., Schütze, G., Biber, P., 2018. Drought can favour the growth of small in relation to tall trees in mature stands of Norway spruce and European beech. For. Ecosyst. 5, 1–19.

Quézel, P., Barbero, M., 1988. Signification phytoécologique et phytosociologique des peuplements naturels de Pin de Salzmann en France. Ecol. Mediterr. 14, 41–63.

Quézel, P., Médail, F., 2003. Ecologie et Biogéographie du Bassin Méditerranéen. Elsevier, Paris.

Rinn, F., 2003. TSAP-Win. Time series analysis and presentation for dendrochronology and 409 related applications. *User reference.*

Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., Ripley, M.B., 2013. Package 'MASS'. *CRAN Repository*. See http://cran.r-projectorg/web/packages/MASS/MASS.pdf.

Römer, P., et al., 2021. Reduced temperature sensitivity of maximum latewood density formation in high-elevation Corsican pines under recent warming. Atmosphere 12, 804.

Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to tree height and tree growth. Bioscience 47, 235–242.

Sánchez-Salguero, R., et al., 2018. Resist, recover or both? Growth plasticity in response to drought is geographically structured and linked to intraspecific variability in *Pinus pinaster*. J. Biogeogr. 45, 1126–1139.

Sangüesa-Barreda, G., et al., 2019. Droughts and climate warming desynchronize black pine growth across the Mediterranean Basin. Sci. Total Environ. 697, 133989.

Santini, F., Serrano, L., Kefauver, S.C., Abdullah-Al, M., Aguilera, M., Sin, E., Voltas, J., 2019. Morpho-physiological variability of *Pinus nigra* populations reveals climate-driven local adaptation but weak water use differentiation. Environ. Exp. Bot. 166, 103828.

Scaltsoyiannes, A., Rohr, R., Panetsos, K.P., Tsaktsira, M., 1994. Allozyme frequency distributions in five European populations of black pine (*Pinus nigra* Arnold). (I) Estimation of genetic variation within and among populations. (II) contribution of isozyme analysis to the taxonomic status of the species. Silvae Genet 43, 20–30.

Scaltsoyiannes, A., Tsaktsira, M., Pasagiannis, G., Tsoulpha, P., Zhelev, P., Iliev, I., Rohr, R., 2009. Allozyme variation of European Black (*Pinus nigra* Arnold) and Scots pine (*Pinus sylvestris* L.) populations and implications on their evolution: a comparative study. J. Biol. Res.-Thessalon 11, 95–106.

Schwarz, J., Skiadaresis, G., Kohler, M., Kunz, J., Schnabel, F., Vitali, V., Bauhus, J., 2020. Quantifying growth responses of trees to drought—a critique of commonly used resilience indices and recommendations for future studies. Curr. For. Rep. 6, 185–200.

Schweingruber, F.H., 1988. Tree Rings: Basics and Applications of Dendrochronology. Reidel, D., Publishing Co., Dordrecht, the Netherlands, p. 276.

Seiler, R., et al., 2017. Insensitivity of tree-ring growth to temperature and precipitation sharpens the puzzle of enhanced pre-eruption NDVI on Mt. Etna (Italy). PLoS One 12, e0169297.

Serra-Maluquer, X., Mencuccini, M., Martínez-Vilalta, J., 2018. Changes in tree resistance, recovery and resilience across three successive extreme droughts in the northeast Iberian Peninsula. Oecologia 187, 343–354.

Serra-Maluquer, X., Gazol, A., Anderegg, W.R., Martínez-Vilalta, J., Mencuccini, M., Camarero, J.J., 2022. Wood density and hydraulic traits influence species' growth response to drought across biomes. Glob. Change Biol. 28, 3871–3882.

Soto, A., Robledo-Arnuncio, J.J., González-Martínez, S.C., Smouse, P.E., Alía, R., 2010. Climatic niche and neutral genetic diversity of the six Iberian pine species: a retrospective and prospective view. Mol. Ecol. 19, 1396–1409.

Szymczak, S., Hetzer, T., Bräuning, A., Joachimski, M.M., Leuschner, H.H., Kuhlemann, J., 2014. Combining wood anatomy and stable isotope variations in a 600-year multi-parameter climate reconstruction from Corsican black pine. Quat. Sci. Rev. 101, 146–158.

Szymczak, S., et al., 2020. How do Mediterranean pine trees respond to drought and precipitation events along an elevation gradient? Forests 11, 758.

Thiel, D., Nagy, L., Beierkuhnlein, C., Huber, G., Jentsch, A., Konnert, M., Kreyling, J., 2012. Uniform drought and warming responses in *Pinus nigra* provenances despite specific overall performances. For. Ecol. Manag. 270, 200–208.

Thompson, J.D., 2005. Plant Evolution in the Mediterranean. Oxford University Press, New York, USA.

Thomsen, G., 2001. Response to winter precipitation in ring-width chronologies of *Pinus sylvestris* L. from the northwestern Siberian plain, Russia. Tree-Ring Res. 57, 15–29.

Thurm, E.A., Uhl, E., Pretzsch, H., 2016. Mixture reduces climate sensitivity of Douglas-fir stem growth. For. Ecol. Manag. 376, 205–220.

Tognetti, R., Smith, M., Panzacchi, P., 2022. Climate-Smart Forestry in Mountain Regions. Springer Nature, p. 574.

Tranquillini, W., 1982. Frost-drought and its ecological significance. Physiological Plant Ecology II. Springer, Berlin, Heidelberg, pp. 379–400.

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Clim. 23, 1696–1718.

Vicente-Serrano, S.M., et al., 2012. Performance of drought indices for ecological, agricultural, and hydrological applications. Earth Interact. 16, 1–27.

Vicente-Serrano, S.M., et al., 2013. Response of vegetation to drought time-scales across global land biomes. Proc. Natl. Acad. Sci. 110, 52–57.

Wigley, T.M., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Appl. Meteorol. Climatol. 23, 201–213.

Zuur, A.F., Hilbe, J.M., Ieno, E.N., 2013. A Beginner's Guide to GLM and GLMM with R: A Frequentist and Bayesian Perspective for Ecologists. Highland Statistics Ltd, Newburgh, UK, p. 270.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14.