



Short- and long-term growth response to climate in mixed and monospecific forests of *Pinus pinea* and *Pinus pinaster*

Marta Vergarechea^{1,2,6} · Rafael Calama^{1,2} · Hans Pretzsch³ · Josu G. Alday^{4,5} · Miren del Río²

Received: 7 April 2020 / Revised: 6 November 2020 / Accepted: 12 November 2020 / Published online: 2 January 2021
© Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

Over recent decades, climate change has been particularly severe in the Mediterranean basin, where the intensity and frequency of drought events have had a significant effect on tree growth and mortality. In this context, differences in structural and physiological strategies between tree species could help to mitigate the damage inflicted by climate variability and drought events. Here, we used dendroecological approaches to observe common associations (synchrony) between indexed ring width in *Pinus pinea* and *P. pinaster*, as a measure of degree of dependence on climate variation or growth sensitivity to climate, as well as to analyze species growth responses to drought events through the Lloret's indices of resistance, recovery and resilience. Based on data from 75 mixed and pure plots installed in the Northern Plateau of Spain, we used modeling tools to detect the effect of the mixture, along with climate and stand-related variables, on the short-term responses and long-term growth sensitivity to climate. Our results showed a trade-off between resistance and recovery after the drought episodes. In addition, different attributes of tree species, such as age and size as well as stand density seemed to act synergistically and compensate drought stress in different ways. The presence of age and quadratic mean diameter as covariates in the final synchrony model for *P. pinaster* reflected the influence of other variables as modulators of growth response to climate. Furthermore, differences in growth synchrony in mixed and monospecific composition suggested the existence of interactions between the two species and some degree of temporal niche complementarity. In mixed stands, *P. pinaster* exhibited a lower sensitivity to climate than in monospecific composition, whereas *P. pinea* enhanced its resistance to extreme droughts. These results allowed us to identify the species-specific behavior of *P. pinea* and *P. pinaster* to mitigate vulnerability to climate-related extremes.

Keywords Resilience · Mediterranean forests · Drought · Synchrony · Mixed forests

Communicated by Lluís Coll.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10342-020-01336-x>) contains supplementary material, which is available to authorized users.

✉ Marta Vergarechea
vergarechea.marta@gmail.com

Rafael Calama
rcalama@inia.es

Hans Pretzsch
hans.pretzsch@tum.de

Josu G. Alday
josu.alday@udl.cat

Miren del Río
delrio@inia.es

² Sustainable Forest Management Research Institute
UVa-INIA, Av de Madrid 503, 34004 Palencia, Spain

³ Chair of Forest Growth and Yield Science, Technische
Universität München, Freising, Germany

⁴ Joint Research Unit CTFC - AGROTECNIO, Av. Alcalde
Rovira Roure 191, E25198 Lleida, Spain

⁵ Department Crop and Forest Sciences, University of Lleida,
Av. Alcalde Rovira Roure 191, E25198 Lleida, Spain

⁶ Norwegian Institute of Bioeconomy Research, Postboks 115,
NO1431 Ås, Norway

¹ Department of Forest Dynamics and Management, Forest
Research Center, INIA-CIFOR, Crta. de la Coruña km 7,
5 - 28040 Madrid, Spain

Introduction

Recent decades are characterized by dramatic increases in air temperatures and changes in precipitation regimes (IPCC 2018). Alarming, droughts are expected to occur more frequently, last longer and be more intense, affecting tree allometry, reducing tree and stand growth or even increasing tree and stand-level decline and mortality (Trenberth et al. 2014). These changing and uncertain future conditions pose a potential risk to forest species or ecosystems (Allen et al. 2010). Therefore, the capacity of forests to cope with such future conditions and extreme events is an issue which has become increasingly important in forest practice (Puettmann 2011).

Forest species display a wide spectrum of strategies (i.e., differences in xylem anatomy, plant allometry, stomatal behavior or rooting strategies) to cope with changing climate and drought events (Martínez-Vilalta et al. 2012; Grossiord 2019). All these different strategies might be beneficial in mixtures since, according to insurance hypothesis, biodiversity insures ecosystems against declines in their functioning because the presence of a larger number of species provides greater likelihood that some of them will continue functioning even if others fail (Yachi and Loreau 1999). Additionally, positive interactions between several cohabiting tree species could help them to cope with drought events (Pretzsch et al. 2013, 2014). However, contradictory findings have been reported, since certain responses being highly species composition dependent (Grossiord 2019). Other factors, such as tree size, competitive status of the tree, age, or site conditions also have an impact on tree growth response to drought (Lloret et al. 2011; Merlin et al. 2015). All the above factors can also act synergistically and may be dynamic, changing according to stand dynamics, resource availability or climate conditions (Belote et al. 2011; Astigarraga et al. 2020).

Furthermore, the legacy of past land use and management practices may exacerbate the impacts of drought on forests (Vernon et al. 2018) and lead to dieback due to continuous drought-induced conditions (Gazol et al. 2018). However, during recent years, forest management goals have shifted more generally toward enhancing ecosystem resilience (Nocentini et al. 2017). This paradigm shift (from management based mainly on the provision of goods and services toward favoring mitigation and adaptation of forest) is essential for forest ecosystems which are more vulnerable to climate change, such as Mediterranean forests (Palahi et al. 2008).

The effect of drought on forest systems may last for several years, since dry conditions reduce tree growth and often weaken trees by deteriorating their vigor (for

example, water and resource consumption, growth and root production) (Camarero et al. 2018; Colangelo et al. 2018). Hence, the analysis of tree growth based on annual rings represents a suitable approach for reconstructing the long-term effects of environmental variables on growth (González de Andrés et al. 2018), and provides a record, with annual resolution, of growth response to climate, which is also highly useful for the study of past known disturbances such as drought events (Fang and Zhang 2019). In this context, the concept proposed by Lloret et al. (2011) to quantify resilience components of tree growth through indices of resistance, recovery and resilience can be considered in order to assess species responses to disturbances. These indices have recently been applied to investigate how tree species diversity can be used as an effective silvicultural tool to counteract the adverse impacts of droughts on tree growth (Pretzsch et al. 2013; Grossiord 2019; Steckel et al. 2020).

Synchrony in inter-annual growth variation among trees has been used to analyze the response of tree species to climatic restrictions, since these constraints tend to strengthen growth–climate relationships. Harsher climate conditions might result in enhanced common ring width signals among stands, or greater spatial synchrony (Shestakova et al. 2016), as well as within-stand, or within-population synchrony (Tejedor et al. 2020). Similarly, analyzing synchrony in tree growth within and between species in pure and mixed forests may provide additional information about the species-specific degree of dependence on inter-annual climate fluctuations or growth sensitivity to climate, and possible species interactions which modify species-specific growth response to climate variation (del Río et al. 2014). Spatial synchrony analysis at regional level is highly relevant, since a certain relationship has been observed between spatial synchrony and the vulnerability of populations; the greater the synchrony between population dynamics, the greater the probability of extinction (Heino et al. 1997). Accordingly, within-stand synchrony was found to be a good indicator of the impact of climate change on tree growth stress (Tejedor et al. 2020). Although few methodological approaches currently exist to unravel the complexities of tree-ring signals (Alday et al. 2018); Shestakova et al. (2014) presented a sound methodology to analyze synchrony patterns in tree-ring networks, ranging from local (Shestakova et al. 2018) to sub-continental scales (Shestakova et al. 2016). Through this approach, it is possible to test the presence of contrasting tree-ring patterns in pre-established groups of chronologies, so it could be very useful to detect common temporal signals between different species across time and space.

In this study, we focus on the Mediterranean pinewoods of the Northern Plateau in Spain, where some symptoms of decay have been already reported (Prieto-Recio 2016; Calama et al. 2019). In this region, *Pinus pinea* L. and *P.*

pinaster Ait. populations have been favored due to the high economic importance of edible pine nut production in the case of *P. pinea*, and timber and resin production in the case of *P. pinaster* (Gordo et al. 2012), these populations having been managed in the area since Middle Ages (Prieto-Recio et al. 2015). Both species are found in monospecific and mixed stands, sharing territory as well as ecological conditions (Calama et al. 2017) and several studies have demonstrated that precipitation is the main growth-driving factor for the two species in these Mediterranean forests (Prieto-Recio 2016; Calama et al. 2019). The effect of water scarcity is more evident in *P. pinaster* which seems to display worse adaptation to the current environmental conditions than *P. pinea* (Vergarechea et al. 2019a, b). Furthermore, tree-ring formation in both species is very sensitive to drought events (Bogino and Bravo 2008; Mazza et al. 2014).

The main aims of this study were to examine the differences in short-term responses to several drought events as well as the long-term influence of climate variability on annual growth in two important Mediterranean species (*P. pinea* and *P. pinaster*). We examined the role of species composition, tree size, age and stand density in order to better understand how these factors interact with tree growth responses to climate and episodic drought stress. For this purpose, we used data from 75 mixed and monospecific plots installed in 2016 in the Northern Plateau of Spain. Our main hypotheses were that: i) tree growth response to drought differs between *P. pinea* and *P. pinaster* and for both species improves in mixed stands; ii) tree size, tree age or stand density negatively affect these responses in both species; iii) synchrony in tree growth response to inter-annual climate variability is species-specific and decreases in mixtures.

Materials and methods

Study area

The study area is located on the Northern Plateau of Spain. This region is defined by the river Duero Basin with typical soils presenting a large percentage of sand and low nutrient content. The study was centered in the province of Valladolid, where these species cover approximately 68.000 ha, with monospecific *P. pinea* stands covering 70% of the area, monospecific *P. pinaster* 10% and mixed forest of the two species, 20% (PORF 2008).

Up until the 1960's, *P. pinaster* was traditionally favored over *P. pinea* in the region, due to the economic importance of resin (Gordo 1999). As a consequence, the management of the area was conditioned by the production of resin, resulting in clearcutting methods with short rotation (80 years) and regeneration periods (10 years). Following the resin crisis in the 1980s there was as a shift toward favoring *P. pinea*

stands, a situation that has continued until the present. A uniform shelterwood system was proposed based on experience from other regions (e.g., Andalusia) (Montero et al. 2008). Rotations in monospecific stands of *P. pinea* currently range from 100 to 120 years, while for monospecific stands of *P. pinaster* the rotation is around 80–100 years (Calama et al. 2017). In mixed stands, management tends to mimic the practices proposed for the dominant species, since no specific guidelines for these mixtures currently exist.

Experimental design

The dataset consists of 75 plots installed by INIA-CIFOR in 18 public forests located in the province of Valladolid (Fig. 1). Mixed (25 plots) and monospecific *P. pinaster* plots (25 plots) were installed between the summer of 2015 and the spring of 2016. Monospecific, even-aged *P. pinea* plots (25 plots) were set up in 1996 in cooperation with the forest services of Valladolid (Junta de Castilla y León) and are regularly monitored. (The most recent inventory was carried out in 2016.) In order to achieve an accurate representation of stand variability in the region, plots were selected to cover the whole range of stocking, age and site conditions in even-aged stands. Furthermore, the plots were installed in stands with no signs of recent (< 5 years) thinnings, regeneration cuttings or pruning. Monospecific plots included 20 trees. The number of trees in mixed plots ranged from 20 to 36, with at least ten trees of the less represented species. Thus, the admixture proportion in the investigated plots ranged from 27 to 50% in *P. pinea* and 50% to 73% in *P. pinaster*. In each plot, tree measurements included tree coordinates, species, diameter at breast height (DBH, cm), total height (Height, m), height to crown base (Live_Branch, m) and four crown radius measurements (Crown Radius m) (Table 1). In addition, we calculated the quadratic mean diameter (D_g), which represent the level of tree space occupation (Corvalán and Hernández 2006), and the stand density index (SDI) proposed by Reineke (1933), which is an expression of relative stand density and it characterizes the degree of crowding with respect to standard conditions. This index was calculated using the following equation:

$$SDI = N \left(\frac{25}{D_g} \right)^E$$

where N is the number of trees per hectare and D_g is the quadratic mean diameter of the trees in the plot. We used the generic figure proposed by Reineke $E = -1.605$ for the coefficient E in eq. [1] for both species.

Two radial increment cores were extracted perpendicularly at breast height (1.30 m) from a subset of five sample trees per plot (the five closest to the center of the plot) in monospecific *P. pinaster* plots and of ten sample trees per

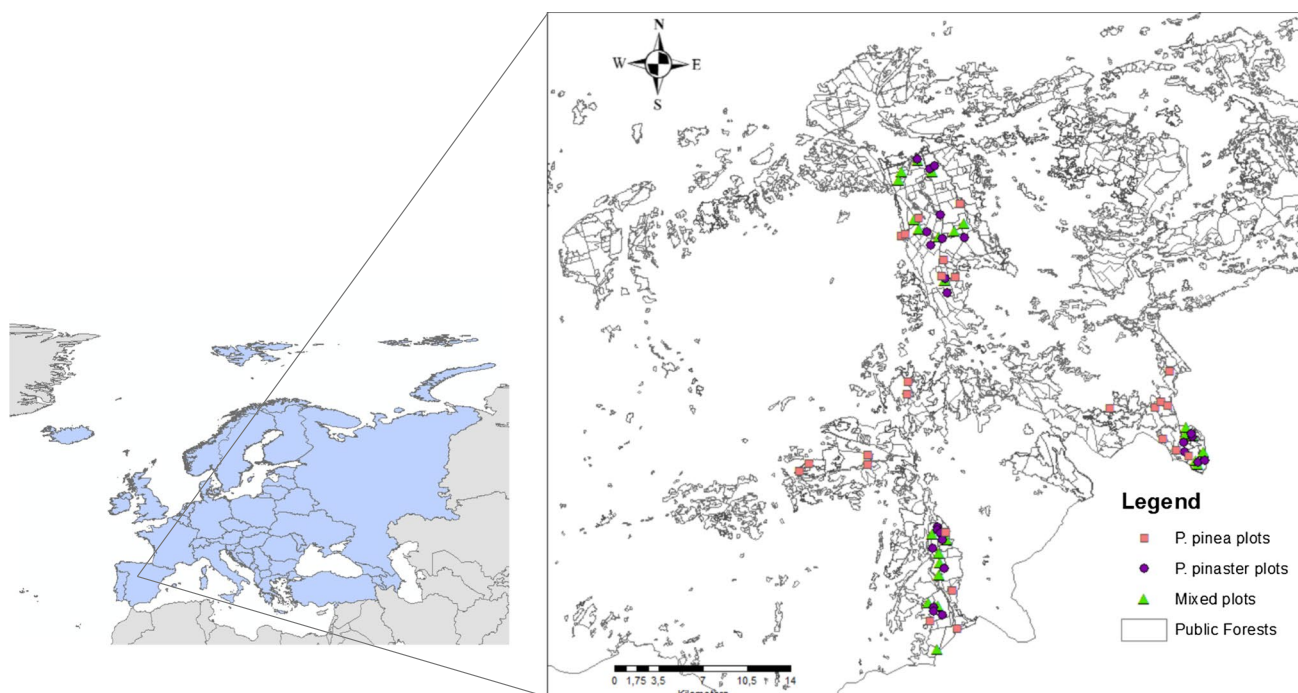


Fig. 1 Distribution of the monospecific and mixed *P. pinea* and *P. pinaster* permanent plots comprising our dataset for Valladolid province

Table 1 Main stand variables for *P. pinea* and *P. pinaster* in mixed and monospecific plots. Mean (\pm SD)

Composition	<i>N</i> (Trees/ha)	BA (m ² /ha)	DG (cm)	Ho (m)	SDI	Age	SI
Pure <i>P. pinea</i>	162.14 (72.13)	21.68(10.47)	41.26 (10.26)	13.25 (9.80)	316.10 (104.33)	88.12 (29.7)	14.16 (2.51)
Mixed <i>P. pinea</i>	58.22 (19.12)	7.35 (2.40)	41.15 (7.38)	13.90 (2.47)	121.84 (37.31)	63.04 (28.7)	17.15 (4.18)
Pure <i>P. pinaster</i>	181.38 (107.99)	22.92 (11.39)	40.81 (6.70)	16.62 (1.56)	374.82 (179.86)	57.66 (18.7)	11.48 (1.08)
Mixed <i>P. pinaster</i>	66.15(18.31)	7.38 (2.99)	37.74 (4.51)	15.11 (2.20)	123.74 (36.03)	51.64 (17.7)	10.34 (1.45)

N: number of trees; BA: basal area; DG: mean square diameter; Ho: Dominant height; SDI: standard density index; SI: site index for *P. pinea* (100 years) and *P. pinaster* (60 years)

plot (five of each species closest to the center of the plot) in mixed plots. The *P. pinea* sample trees were selected according to the protocol for the long-term network of permanent plots (see Calama et al. 2019 for further details), so the number of cored trees per plot varies from three to five. In order to estimate the stand age, one increment core per plot and species was taken from the base of the tree. The total number of cored trees was 250 for *P. pinaster* and 223 for *P. pinea*.

Climate data

The climate is continental-Mediterranean with a mean annual temperature of 11.2 °C and extreme absolute temperatures in summer (40 °C) and winter (− 10 °C). The mean annual precipitation is 435 mm, with a dry period between July and September. Frosts may occur from September to May. Due to the homogeneity of the climate over the whole

studied area, we used climate data from a single meteorological station (Sardon de Duero—Valladolid, 424202 E—413643 N, 725 a.s.l) for all the analyses. In addition to monthly data for mean, maximum and minimum temperature and precipitation, we calculated the Standardized Precipitation Evapotranspiration Index-SPEI (Vicente-Serrano et al. 2010) to estimate drought intensity according to its strength and duration in the studied area. Negative values below − 1 and positive values above 1 for this index correspond to dry and wet periods, respectively. To better identify the temporal variability of the SPEI in the studied area and its potential influence on tree growth we then calculated the SPEI for three accumulated periods: 6, 9 and 12 months, obtaining three SPEI values for each month of the year. For further analysis, monthly SPEI values were averaged into a single yearly value using; a) the period from 1 October of the previous year to 30 September of the current year

(hydrological year in the region) b) and from January to December (chronological year). The adequacy of the different accumulation periods was then determined through Pearson correlations with the dendrochronological master series (see Sect. 2.4) of *P. pinea* and *P. pinaster*, built using the data from monospecific plots. The SPEI index was calculated using the “SPEI” package in R (Berguería and Vicente-Serrano 2017).

Dendrochronological analyses

Increment cores were mounted on wooden supports and sanded until tree-ring boundaries were clearly visible and later measured using a LINTAB measuring table (Rinntech 2010) with an accuracy of 0.01 mm. The quality of cross-dating and synchronization of the growth series were then assessed using the “dplR” R package (Bunn 2010). This package was also used to calculate the mean series of annual radial increments for each individual, which were then transformed into series of basal area increments (BAI) since this variable is preferable for analyzing growth trends (Biondi and Qeadan 2008):

$$\text{BAI} = \pi(r_t^2 - r_{t-1}^2)$$

where r_t and r_{t-1} represent the stem radius at the end and the beginning of a given annual ring increment corresponding to rings formed in t and $t-1$ years. To eliminate the biological growth trends and to produce stationary and residual chronologies of dimensionless basal area increment indices (IBAI) (Fritts 1976), we applied a detrending procedure and autocorrelation removal using the Friedman supersmoother spline (Friedman 1984) and autoregressive modeling. In addition, to observe the reliability of the chronologies, we calculated standard dendrochronological statistics (mean tree-ring width, mean correlation with master series, mean sensitivity and expressed population signal (EPS)) (Speer 2010), grouped by species and species composition (monospecific vs mixed stands).

Selection of drought event years

In order to determine tree growth response to drought, we selected specific drought events, hereafter “pointer years”, with a notable effect on growth at individual level (Steckel et al. 2020). First, we used a function implemented in the pointRES R package (Cropper 1979; Van Der Maaten-Theunissen et al. 2015) to identify negative pointer years, by normalization of a moving window method. This method relates tree growth in a particular year to the average growth of a specific number of preceding years. In this study we determined the common pointer years as those years in which at least 60% of the *P. pinea* and *P. pinaster* trees

showed a basal area increment (BAI) decrease of at least 60% relative to the average BAI in the 3 previous years (windows length). We then compared those negative pointer years with values for previously calculated Standardized Precipitation Evapotranspiration Index (SPEI) in order to ensure that these periods correspond to droughts and were not caused by other local drivers. Based on the approach outlined in Potop et al. (2014), we considered specific drought years that displayed at least 1 month with a $\text{SPEI} \leq -1$ during the growing season. Additionally, given the limitations of the SPEI for detecting short-term periods of intense drought, we contrasted this information with the annual climatic diagrams and with monthly SPEI values calculated for 1 month accumulated period to explore the characteristics of the drought period (Fig. S1 and Table S1). In this way, years identified as both negative pointer years and drought years, were deemed to be drought events and used to assess tree growth responses to drought.

Tree growth response to drought

To evaluate the performance of individual trees under episodic drought stress, we calculated numerical indices for resistance, recovery, and resilience (Lloret et al. 2011) for all the sampled trees. The indices were obtained through the annual basal area increment indices (IBAI) for all individual trees. We then averaged the relative IBAI values for a period of 3 years prior to the drought period (PreDr), for the year of drought (Dr), and for a period of 3 years following the drought period (PostD). We used this period of three years because we consider that it represents a good trade-off between the period being sufficiently long to ensure a good estimation of the mean growth before and after the drought event while avoiding an overlap with pre- and post-drought periods. These values were used to calculate the resistance of trees to drought, determined as the ratio between growth during the drought event and growth during the respective pre-drought period ($R_r = \text{Dr}/\text{PreDr}$). This index (R_r) quantifies the decrease from the pre-drought period to the drought period and a value of R_r close to 1 indicates complete resistance, while values falling below 1 indicate lower resistance. The growth reaction following the drought event was explained by the recovery index. This index (R_c) is determined by the ratio between the post-drought growth and the growth during the respective drought event (PostDr/Dr). Here, $R_c = 1$ implies persistence of a low level of growth even after the drought, $R_c < 1$ implies further decline, and $R_c > 1$ can be interpreted as recovery after the drought period. Finally, the ratio between post-drought and pre-drought increment was represented by the resilience index, $R_s = \text{PostDr}/\text{PreDr}$. In this case, full recovery or even an increase after the episodic stress is indicated by values of $R_s \geq 1$, while $R_s < 1$ reveals growth decline and low resilience.

For contrasting hypothesis (i) we analyzed the possible effect of species on the components of resilience by checking for significant differences in these indices associated with the species (*P. pinaster* vs *P. pinea*) at each level of composition (mixed vs monospecific). Given the lack of normality observed in the distribution of the components of resilience, these paired comparisons were carried out using Mann–Whitney tests.

Tree growth synchrony

We defined synchrony, \hat{a}_c , as the presence of a relevant common signal for a time-varying trait, (in our case annual indices of basal area increment), in a group of tree-ring series. To study the behavior of the two species growing in mixed and monospecific stands, we estimated synchronies at plot level, that is, the synchrony between the tree-ring series in a specific plot, for a period covering the last 30 years. Synchrony was estimated as the inter-series temporal correlation, which may express the degree of dependence on inter-annual climate fluctuations.

To analyze the pattern of covariation among the tree-ring series by plot, between and within species in the case of mixed plots, we used different variance–covariance (VCOV) mixed models according to the approach by Shestakova et al. (2016). The different VCOV models for each plot were then compared using standard criteria for model selection (Akaike and Bayesian information criteria) (Burnham et al. 2002). We obtained the synchrony values (\hat{a}_c) from the VCOV of the best mixed model (Shestakova et al. 2018a, b; Alday et al. 2018). Values close to 1 represent a near-perfect synchrony between tree-ring series while values close to 0 indicate asynchrony. Thus, we obtained an intra-specific synchrony value for each monospecific *P. pinea* and *P. pinaster* plot, whereas for each mixed plot we estimated three synchrony values, the two intra-specific synchronies and the inter-specific synchrony (*P.pinea*—*P. pinea*/*P. pinea*—*P. pinaster*/*P.pinaster*—*P-pinaster*). The DendroSync package was used to calculate synchronies at plot level (Alday et al. 2019). To test the hypothesis (iii) we evaluated the following comparisons:

- A. Differences in intra-specific synchrony depending on of the type of forest (monospecific, mixed) where the tree population exists (i.e., monospecific *P. pinea* versus monospecific *P. pinaster* and mixed *P. pinea* versus mixed *P. pinaster*). These comparisons allowed us to identify whether the two species show different degree of dependence on inter-annual climate variation in both pure and mixed stands.
- B. To test whether mixing species modifies the species-specific degree of dependence on inter-annual climate fluctuation, we compared the synchrony of trees of the

same species (intra-specific synchrony) living in mono-specific or mixed plots (i.e., monospecific *P. pinea* versus mixed *P. pinea* and monospecific *P. pinaster* versus mixed *P. pinaster*).

- C. Finally, we compared differences in intra- and inter-specific synchronies of trees growing in mixed plots. If inter-specific synchrony is lower than intra-specific synchronies, it might reflect that two species respond in a different way to inter-annual climate variation.

Modeling approaches for the components of resilience

To check hypothesis (ii), we used linear mixed models to evaluate whether R_p , R_c and R_s were related to any of the following explanatory variables (X): tree age, tree size, species composition (mixed or monospecific), stand density index (SDI), and the year of the drought event. We proposed these separate analyses per species—instead of including species as a factor—in order to adequately describe the pattern of response of each species and avoid high-order interactions.

Given the hierarchical structure of the data, random plot effects were included in the model.

The expression of the models was then formulated as:

$$I_{ijk} = X_{ijk}\beta + u_i + \varepsilon$$

where I_{ijk} is the observation for the response variable (one of the three indices) recorded for the i th tree within the j th plot during the drought event year k th. In this case X_{ijk} is the vector containing the observed values for the explanatory covariates while β is the vector of the estimable parameters. Finally, u_j represents the plot random effect, normally distributed with mean zero and variance σ_u^2 , and ε represents the independent and identically distributed residual error.

Modeling Approaches for the Synchrony Values

To quantify the effects of stand characteristics on synchrony values of *P. pinea* and *P. pinaster*, we built a logistic regression model for each species. In this regard, the logit transformation is widely used in percentages, ratios and covariates ranging between 0 and 1. We related the \hat{a}_c values, previously obtained, to the different stand characteristics, such as age, species composition of the plot (mixed or monospecific), stand density index (SDI), and quadratic mean diameter (DG). The expression of the models was the following:

$$\text{logit}(\hat{a}_j) = \ln\left(\frac{a}{1-a}\right) = X_j\beta$$

where \hat{a}_j is the observation for the response variable (synchrony) recorded in the j th plot. In this case X_j is the vector

containing the observed values for the explanatory covariates while β is the vector of the estimable parameters.

In the case of linear mixed models (Lloret's indices), we fitted the complete model including all the explanatory variables in the fixed part and then we carried out a backward procedure for the selection of fixed effects in each model. Similar procedure (backward) was used in the selection of covariates in the logistic regression models (synchrony). Finally, we used the Akaike information criterion (AIC) as well as the significance of the parameter estimates to select the best model.

In order to avoid collinearity between all the exploratory covariates included in the models (both the Lloret models and the synchrony model), we checked the correlation between them by computing the variance inflation factor (or VIF). This procedure was performed using the R function *vif* from the *car* package (Fox and Weisberg 2019).

All models were processed using R version 3.3.3 (Team R Core 2018) and the *lme4* package, version 3.5.3 (Bates et al. 2015). Normality and homogeneity of the residual variance were checked by visual inspections of diagnostic plots of residuals against fitted values (Zuur et al. 2010).

Results

Tree growth and selection of drought events

We found that the increment in the mean tree basal area for both species was higher in mixed composition compared to monospecific plots. Similar results were obtained when we compared the mean tree-ring width in mixed and pure compositions (Table 2). These variations in tree-ring width as well as basal area increment might partly be explained by the differences found in tree age between pure and mixed stands (particularly for *P. pinea*), an in stand-level basal area, which was lower in the mixed stands than in pure stands (Table 1). The values of the expressed population signal (EPS) as well

as the mean correlation between separate tree-ring series and the master chronology, both in monospecific and mixed compositions (Table 2), revealed that all chronologies can be considered reliable and well replicated ($\text{EPS} > 0.85$) (Wigley et al. 1984).

Although the results of the Pearson correlations between the master chronologies and the different options for computing the Standardized Precipitation Evapotranspiration Index-SPEI were quite similar, the highest correlation was found for the SPEI-6 averaged over the hydrological year and an accumulation period of 6 months (Table S2, supplementary material), both in *P. pinea* and *P. pinaster*. Therefore, this was the SPEI value which was used for the rest of the study to evaluate drought severity in the studied area.

We identified the years 1992, 2005 and 2012 as pointer years using the normalization in a moving window method. These 3 years were used to evaluate the performance of individual trees under episodic drought stress. 2005 and 2012 were years with low average SPEI-6 values (Fig. 2), while 1992 showed negative SPEI-6 values ≤ -1 for at least one month during the growing season (Fig. S1 and Table S1, supplementary material). In this regard, although 1992 is not observed in Fig. 2 as a drought year and appears to be a normal year with SPEI-6 values close to 0, we observed a significant reduction in tree growth for all the individuals in that year. Since the dataset included different stands and forests located in different municipalities, we can discard the occurrence of a local disturbance as being the cause of the observed growth reductions in 1992. In addition, no references to pest outbreaks or extreme frost events resulting in growth reduction are recorded for that year. Furthermore, when examining the distribution of the precipitation over the year we observed a clear period of "dry conditions" during late winter and early spring, with negative SPEI-6 value from January to April (Fig. S1 and Table S1, supplementary material). Hence, we decided to maintain 1992 as a 'drought year' in order to explore the performance of tree species under these dry conditions.

Table 2 Description of structural and dendrochronological variables for cored trees in mixed and monospecific plots

	Pure_ <i>P. pinea</i>	Mixed_ <i>P. pinea</i>	Pure_ <i>P. pinaster</i>	Mixed_ <i>P. pinaster</i>
Number of cored trees	98	125	125	125
Number of sampled cores	195	375	375	375
Mean length of series (years)	53	60	59	52
Maximum length of series (years)	117	151	127	120
Mean tree-ring width (mm)	1.83	2.52	2.11	2.6
Mean basal area increment (cm ²)	3.87	5.67	4.75	6.18
Mean correlation with master series	0.5	0.61	0.63	0.62
Mean inter-series correlation	0.60	0.63	0.62	0.59
Mean sensitivity	0.41	0.38	0.35	0.34
Expressed population Signal	0.98	0.99	0.98	0.98

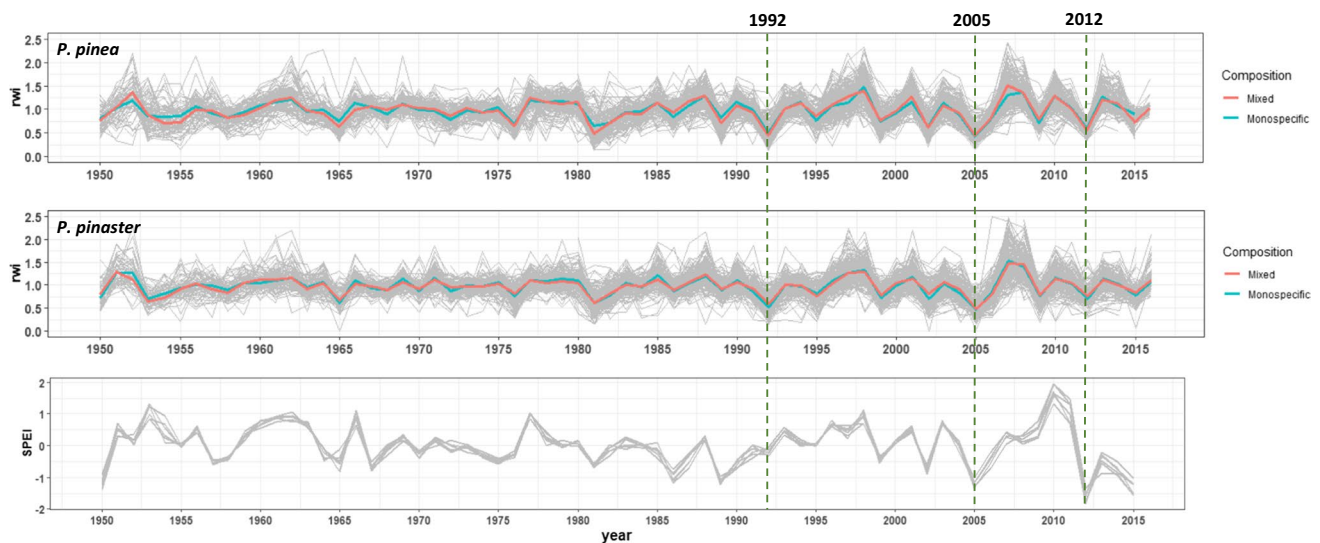


Fig. 2 Ring width indices for each sample (gray lines) of *P. pinea* and *P. pinaster*. Mean fluctuation of *P. pinea* (a) and *P. pinaster* (b) in monospecific and mixed stands. Different values for the Index-SPEI

(c) computed using various temporal windows (6, 9 and 12 months) and two options for the growth period (hydrologic and calendar year)

Table 3 Mann-Whitney test results for the Lloret indices comparing both species in mixed and monospecific composition

		P-value	Median <i>P. pinea</i>	Median <i>P. pinaster</i>
R_t	Mixed	< 0.0001	0.510	0.638
	Monospecific	0.001	0.525	0.590
R_c	Mixed	< 0.0001	2.208	1.664
	Monospecific	0.001	2.122	1.811
R_s	Mixed	0.006	1.105	1.075
	Monospecific	0.846	1.101	1.082

R_t : Resistance index; R_c : Recovery index; R_s : Resilience index

Species differences in growth response to drought events

We observed significant differences in resistance R_t (p value < 0.001) and recovery R_c (p -value < 0.008) after drought events between the two species, although not in resilience index R_s (p -value = 0.418). *P. pinea* showed lower R_t (0.54) than *P. pinaster* (0.63). In contrast, recovery in *P. pinea* was greater (2.43) than that of *P. pinaster* (2.11). When we applied the Mann–Whitney test separately in mixed and monospecific compositions, we found similar results for the resistance and recovery indices but not for resilience. Differences between species in term of resilience were only observed in mixed composition, with *P. pinaster* showing lower R_s than *P. pinea* (Table 3, Fig. 3).

Species differences in growth synchrony

When comparing the intra-specific synchronies of the two species, the results of the t test showed that they differed significantly in mixed composition but not in monospecific composition (Table 4, A). This result indicates that the strength of common signal is similar for the two species in monospecific stands, but not in mixtures where intra-specific synchrony in tree growth series was lower for *P. pinaster* than for *P. pinea*. Accordingly, there were significant differences in the synchrony values for *P. pinaster* between monospecific and mixed composition, with lower values for the latter, whereas this difference was not observed in the case of *P. pinea* (Table 4, B). Finally, the comparisons of the inter-specific and intra-specific synchronies in mixed plots only revealed significant differences in the case of *P. pinea*, with lower inter- than intra-specific synchrony (Table 4, C), indicating that the two species differ to some extent in their growth response to inter-annual climate variation (Fig. 4).

Resistance, recovery and resilience models

The estimated parameters of the fitted models for the three resilience components, by species, are shown in Table 5. We found a significant effect of the drought events for both species. The resistance of the two species was greater in the 2012 drought event, although this event was the worst in terms of recovery, both in *P. pinea* and *P. pinaster*. The best recovery in both species was observed following the 2005 drought event (Fig. 3). Note also that 1992 was the most

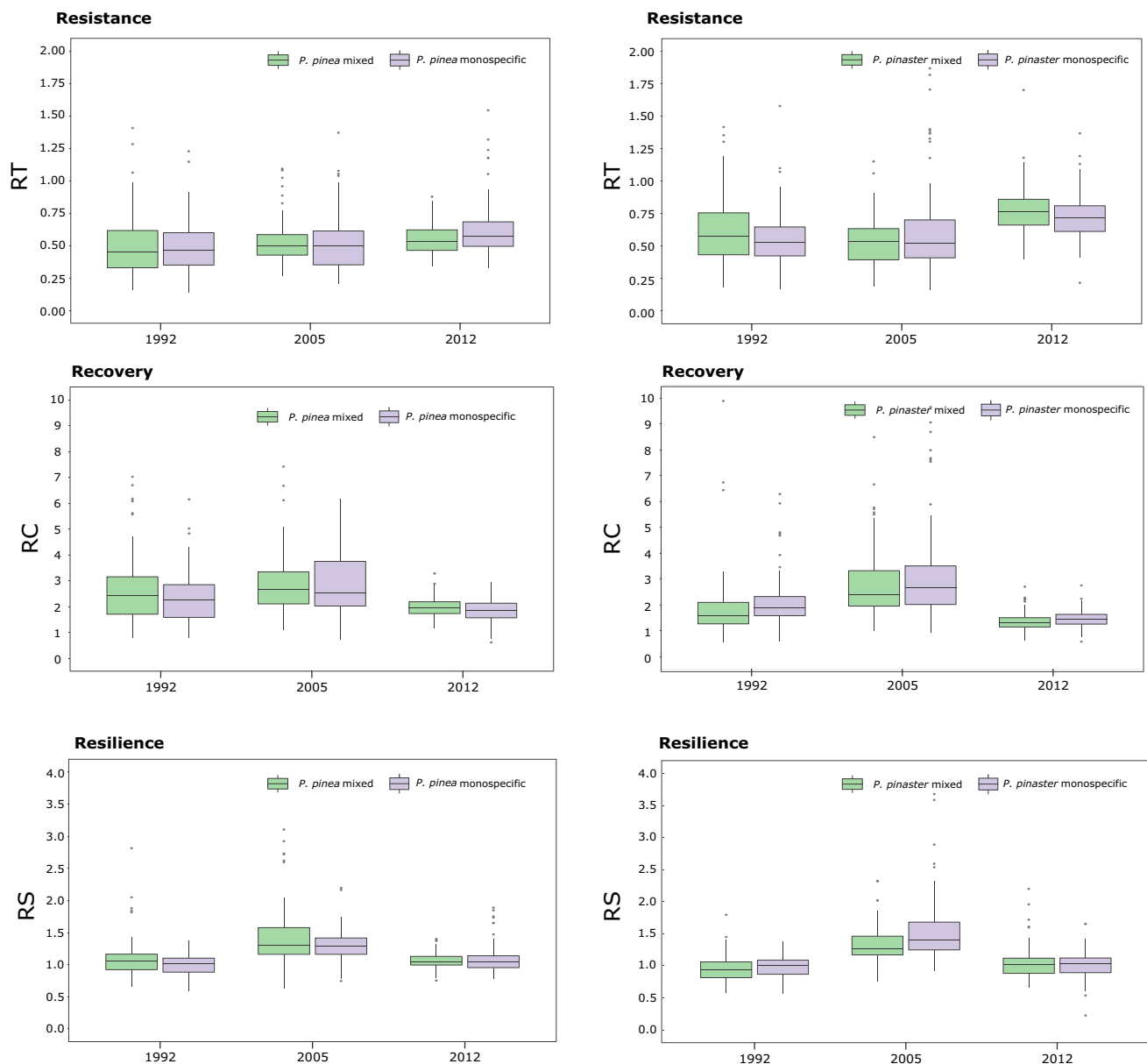


Fig. 3 Boxplots showing the median values and error bars for the different components of resilience calculated for *P. pinea* and *P. pinaster* in mixed and monospecific composition

negative drought event in terms of resilience, while 2005 was the most positive.

The modeling results also showed a positive effect of mixture on the resistance capacity of *P. pinea*, although it was mediated by tree size (negative interaction between mixture and tree diameter at breast height), leading to a lower mixing effect on large trees. In the case of *P. pinaster*, larger tree diameters led to lower resistance to drought events, but also to greater recovery. Species composition had no effect for *P. pinaster* (Table 5). As regards the stand density index (SDI), we detected a positive effect on recovery capacity in *P. pinaster*.

Synchrony models

As regards the fitted models for the synchrony components, none of the available covariates was found to be significant for *P. pinea*. The final model for *P. pinaster* indicated that both age and quadratic mean diameter significantly increased the intra-specific synchrony, and that the presence of mixture in the plot led to lower synchrony in this species (Table 6), in accordance with results in Table 4, B.

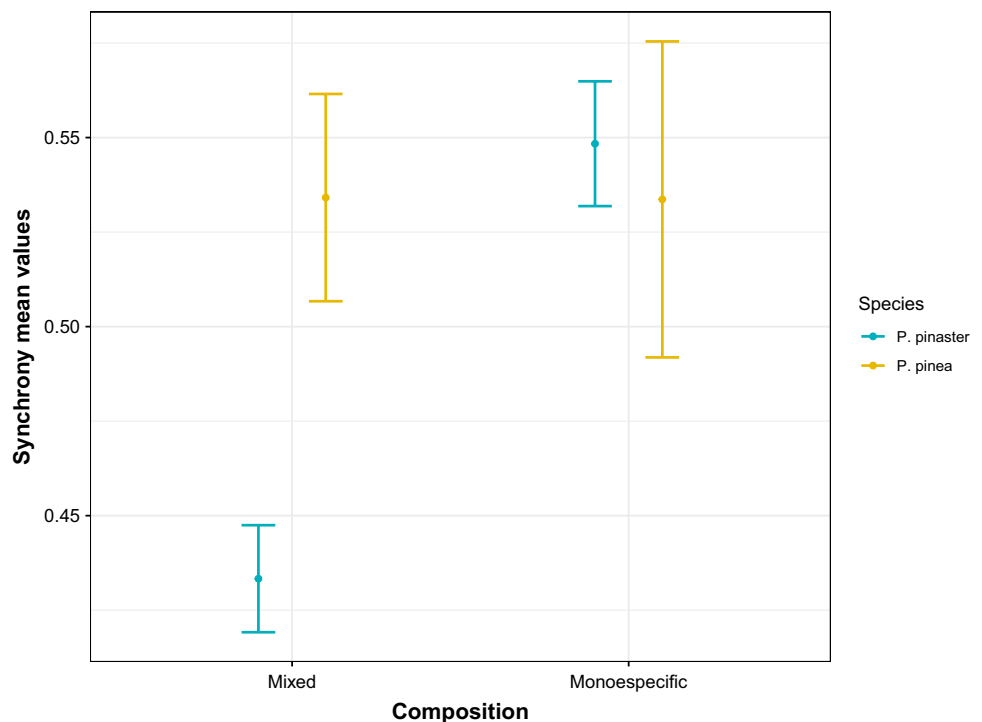
Table 4 Results for the t test analysis to evaluate different synchrony patterns. (A) Comparing the intra-specific synchrony of the two species in mixed and monospecific composition. (B) Comparing, separately for each species, the intra-specific synchrony between mixed and monospecific composition. (C) Comparing, for each species, the

intra-specific with inter-specific synchrony in mixed plots. Means of the two options in each case (i.e., in case A, mean of *P. pinea* synchrony values and mean of *P. pinaster* synchrony values in the first line in monospecific composition and in the second line in mixed composition)

Case	Unit of comparison	<i>p</i> -value	Mean1	Mean2
(A) <i>P. pinea</i> vs <i>P. pinaster</i>	Monospecific	0.7451	0.5336	0.5483
	Mixed	0.0013	0.5407	0.4317
(B) Mixed vs Monospecific	<i>P. pinea</i>	0.882	0.5341	0.5336
	<i>P. pinaster</i>	< 0.0001	0.4333	0.5483
(C) Inter vs intra	<i>P. pinea</i>	0.0007	0.4349	0.5341
	<i>P. pinaster</i>	0.9475	0.4349	0.4330

Where Mean 1: first element of the comparison (*P. pinea* in case A, Mixed in case B and inter in case C); Mean 2: second element of the comparison (*P. pinaster* in case A, Monospecific in case B and intra in case C)

Fig. 4 Mean values and standard deviation for synchrony values in *P. pinea* and *P. pinaster* in mixed and monospecific composition



Discussion

We provide different temporal-scale approaches (short-term impacts of extreme droughts and long-term strength of climate signal) to the analysis of tree species responses to climate. The results corroborate our two first hypotheses on the existence of different behaviors in *P. pinea* and *P. pinaster* to cope with drought stress based on variables such as age, composition (monospecific or mixed), stand density, size or drought intensity. The third hypothesis was corroborated only partially, as synchrony levels were different between species only in mixed stands.

Factors influencing tree responses to extreme drought

Results of the resilience components models showed a clear trade-off between resistance and recovery after the drought episodes. In this regard, Klein (2014) and Martínez-Vilalta et al. (2014) suggested that these different patterns of low resistance/high recovery vs. high resistance/low recovery represent different strategies of plants to cope with droughts. However, Schwarz et al. (2019) pointed that even if this trade-off exists, it is important to explore which of these two components is more important in the face of a drought event. In this regard, *P. pinea*

Table 5 Summary of final parameterization of the Lloret indices models for *P. pinea* and *P. pinaster*

Model	Sp	Effect	Parameter	Estimate	Standard error	<i>t</i> value	Pr > <i>t</i>	
Resistance	<i>P. pinea</i>	Intercept	α_0	0.7211	0.043	16.498	< 0.0001	
		DroughtYear_2005	β_{1_2005}	-0.0704	0.0158	-4.887	< 0.0001	
		DroughtYear_1992	β_{1_1992}	-0.1065	0.0181	-5.476	< 0.0001	
		DBH	β_2	0.00005	0.0004	0.426	0.6709	
		Mixed	B_3	0.2451	0.0730	3.354	0.0009	
		DBH x Mixed	β_{2_m}	-0.0004	-0.0001	-3.786	0.0001	
		Variance of random effects						
	plot	σ_1	0.0084					
	<i>P. pinaster</i>	Intercept	α_0	0.976	0.0533	15.46	< 0.0001	
		DroughtYear_2005	β_{1_2005}	-0.211	0.0204	-10.326	< 0.0002	
		DroughtYear_1992	β_{1_1992}	-0.226	0.0235	-9.593	< 0.0003	
		DBH	β_2	-0.0003	-0.0005	-2.599	0.00962	
		Age	β_3	-0.0015	-0.0001	-2.710	0.00762	
		Variance of random effects						
plot		σ_1	0.0041					
Recovery	<i>P. pinea</i>	Intercept	α_0	1.539	0.218	7.042	< 0.0001	
		DroughtYear_2005	β_{1_2005}	0.974	0.0882	10.867	< 0.0001	
		DroughtYear_1992	β_{1_1992}	0.605	0.0993	6.009	< 0.0001	
		Variance of random effects						
	plot	σ_1	0.1625					
	<i>P. pinaster</i>	Intercept	α_0	-1.478	0.9951	-1.485	0.1433	
		DroughtYear_2005	β_{1_2005}	1.625	0.0931	17.451	< 0.0001	
		DroughtYear_1992	β_{1_1992}	0.652	0.1051	6.208	< 0.0001	
		log (SDI)	β_2	0.396	0.1717	2.311	0.0249	
		DBH	β_3	0.002	0.0006	2.684	0.0075	
		Variance of random effects						
	plot	σ_1	0.1166					
	Resilience	<i>P. pinea</i>	Intercept	α_0	1.066	0.0218	48.823	< 0.0001
			DroughtYear_2005	β_{1_2005}	0.2848	0.0234	12.141	< 0.0001
DroughtYear_1992			β_{1_1992}	-0.028	0.0249	-1125	0.261	
Variance of random effects								
plot		σ_1	0.009					
<i>P. pinaster</i>		Intercept	α_0	1.020	0.025	40.166	< 0.0001	
		DroughtYear_2005	β_{1_2005}	0.418	0.0273	15.277	< 0.0001	
		DroughtYear_1992	β_{1_1992}	-0.052	0.027	-1.901	0.0577	
		Variance of random effects						
		plot	σ_1	0.013				

Where DBH: diameter at breast height of the tree in cm; Age: age of the tree; SDI: Reineke stand density index in the plot; Mix: dummy variable related to the presence or not of mixture; SPEI: Standardized Precipitation Evapotranspiration Index. Parameters with a p-value lower than 0.05 are in bold

showed lower resistance and greater recovery than *P. pinaster* (Table 4), reflecting certain distinct strategies of the two species. Although pine species show in general an isohydric behavior, some differences in physiological strategies to deal with water shortages are reported among pine species (Salazar-Tortosa et al. 2017), and consequently, in tree growth response to extreme droughts (Marqués et al. 2016; Salazar-Tortosa et al. 2018).

The impact of the drought event may be influenced by two factors; the moment at which the dry conditions arise (Michelot et al. 2012) and the availability of accumulated reserves (Morán-López et al. 2014). Here, there was a period of intense water deficit during early spring 1992 (value of SPEI below -1 in May), which probably had a negative effect on the cambial activity (Martin-Benito et al. 2013). Similarly, the years prior to 2005 were also characterized

Table 6 Summary of final parameterization of the synchrony model for *P. pinaster*

Effect	Parameter	Estimate	Standard error	<i>t</i> value	Pr > <i>t</i>
Intercept	α_0	0.2901	0.0698	4.153	< 0.0001
Mixed	β_1	-0.1029	0.0192	-5.357	< 0.0001
Age	β_2	0.0012	0.0005	2.105	0.0408
DG	β_3	0.0046	0.0017	2.649	0.0111

Where Mix: presence or not of mixture in the plot; Age: average age of the trees in the plot; DG: the quadratic mean diameter of the trees in the plot

as dry years, with an important heat wave in 2003. This fact likely influenced vigor, leaving the trees more vulnerable to the impact of drought. Conversely, the 2 years prior to 2012 were very wet, so these years probably influenced (positively) the resistance capacity of the species and could explain why the recovery capacity in 2012 is somewhat lower than in 1992 and 2005, since as Pretzsch et al. (2013) noted, the more a tree growth is decreased during the drought, the more it regrowth (recover) after the drought event. In this regard, Andivia et al. (2020) also observed that post-drought precipitation was lower after the 2012 than 2005 drought event, which would likely decrease the recovery capacity of the species during this year. This trend could reveal a cumulative effect of droughts on the capacity of these tree species to respond to consecutive droughts (Navarro-Cerrillo et al. 2018), which may compromise the resilience capacity of tree species due to loss of leaf area, depleted reserves of carbohydrate and hydraulic dysfunction (Anderegg and Anderegg 2013; Andivia et al. 2020).

However, note that the use of SPEI index neglects the importance of local soil characteristics as well as that of actual water availability, which could hamper the comparison of values for different periods (Zang et al. 2020). Accordingly, our results for the analysis of pointer years (i.e., anomalously wide or narrow rings), originating from extreme events, only partly coincide with the peaks obtained in the SPEI-6 values (Fig. 2), evidencing the limitations of using this index and the importance of considering additional information such as intra-annual climate conditions when defining drought events (Fig. S1, supplementary material).

Regarding the different variables modulating tree growth response to drought, we found that in the case of *P. pinaster*, young, smaller trees were more resistant than older, large trees, which confirm our second hypothesis for this species. This is in agreement with the results of previous studies which point to tree age and size having a possible influence on low-growth periods in *P. pinaster*, while also highlighting the complexity of these effects (Navarro-Cerrillo et al. 2018). Our results also revealed contrasting effects of increasing DBH in *P. pinaster*, with

resistance decreasing but the recovery capacity increasing. These findings agree with those of Merlin et al. (2015), who observed a better response in small trees in terms of resistance to drought and, as in our case, faster recovery in larger trees. Nonetheless, the findings of Pichler and Oberhuber (2007) contradict our results, since they found that small trees are more affected by drought events than larger trees because the shallow root system. A more extensive root system may allow larger trees to compete more effectively during drought events (Maluquer et al. 2018), however, taller trees can be exposed to elevated atmospheric water demands and present longer hydraulic path lengths, which exacerbate drought stress (McDowell et al. 2013). This opposing mechanism could explain the lack of uniformity in the effect of tree size and age on resistance to drought (Zang et al. 2014; Andivia et al. 2020).

The higher stand density (SDI) improved the ability to regain growth (recovery) to pre-drought levels in *P. pinaster*. However, the literature on this issue generally points to a negative effect of high stand densities on the resistance capacity of tree species due to decreased availability of resources (Thurm et al. 2016). This density effect agrees with the abovementioned theory concerning the existence of a trade-off between resistance and recovery after the drought episodes (Sun et al. 2018).

Although the results indicate that *P. pinea* trees in mixtures have a higher resistance to drought than trees in monospecific composition, we cannot confirm totally our first hypothesis since the negative interaction of DBH with mixtures suggests that this effect is attenuated in larger trees and mixture did not have any influence on *P. pinaster*. In this context, a positive effect of mixtures associated with drought episodes could indicate higher within species competition than between-species competition, with smaller differences for larger trees, in drought years. In mixtures, it could be argued that tree diversity contributes to reducing vulnerability to drought in *P. pinea*, as supported by numerous studies in recent years for other species (Pretzsch et al. 2013), although this is not the case for *P. pinaster*. In this regard, Grossiord (2019), in a recent review, reported that although positive effects of mixture are more commonly observed in relation to drought events, neutral and negative effects are also possible for some species. Forrester (2014) and Belote et al. (2011) also noted that tree diversity is not a fixed modulator of drought events and that the influence of mixture on tree growth response can shift from negative to positive under, for example, more benign climate conditions. Other factors related to the environmental conditions (local site characteristic or management practices) have been observed to influence the relationships between tree diversity and the impacts of drought (Grossiord 2019). Here, the differences in plot density and basal area between pure and mixed stands (Table 1), may be a reason why *P. pinea* in

mixtures displays higher resistance to drought than in mono-specific composition.

Drivers of synchrony

Our synchrony analysis revealed that growth patterns are affected by forest structure and species composition, since differences between species arise in mixed stands (Table 4, A). *P. pinaster* growth was less synchronous when growing mixed with *P. pinea* (Table 4, B), which implies that species mixing reduces its dependence on climate variation. This fact highlights the importance of competition-facilitation processes to mitigate climate effect (Sánchez-Salguero et al. 2015), which is particularly relevant in a restrictive habitat, such as the Mediterranean pinewoods studied. However, this effect was not identified during extreme events, possibly because growth in those extreme years was more limited by climate conditions than by competition. Conversely, *P. pinea* synchrony was not modified by *P. pinaster* admixture, although its intra-specific synchrony was greater than inter-specific synchrony (Table 4, C). This observations confirms our third hypothesis that to some extent the two species are affected by climate variation in a different way in mixed stands, suggesting some degree of temporal niche complementarity (Forrester 2014; del Río et al. 2021) which might benefit *P. pinea* growth, as found in extreme drought events.

The presence of age and quadratic mean diameter as covariates in the synchrony model for *P. pinaster* reflected the influence of other variables as modulators of synchrony patterns in forests. In this regard, findings in community ecology have led to disagreement on the role of age in the relationships between climate and radial growth. While some studies assumed that, once the biological growth function has been removed, these relationships are independent of tree age (Fritts et al. 1990), other studies maintain that trees respond in different ways to climate depending on their age (Thurm et al. 2016). Our results agree with the second assumption, since the significant positive effect of this covariate in the synchrony model for *P. pinaster* suggests greater sensitivity to climate variability in older trees than in younger trees. However, there is a lack of uniformity in the response of trees of different ages. While Natalini et al. (2015) observed that younger Mediterranean pine trees were less sensitive to climatic variability than older trees, Vieira et al. (2009) revealed that young *P. pinaster* trees responded faster (cambial activity) to climate than older trees. Similarly, the results of the model showed that in the case of *P. pinaster*, larger trees were more sensitive than small trees to climate, which agree with the previously mentioned findings on the size-resistance relationship. However, as previously

mentioned, it is important to consider that different soil or competition conditions within a stand can also modify the response thresholds of individual trees (Pichler and Oberhuber 2007; Merlin et al. 2015).

As regards *P. pinea*, the inability to build a model suggests a common growth response to annual climatic variability in the region, regardless of stand characteristics or composition. The low genetic variability found in *P. pinea* (Mutke et al. 2019) can reduce the individual response to climate and stand conditions, thus reducing variability and increasing synchrony.

Concluding remarks

Our findings highlight the complexity of tree species growth response to climate, which depends on stand characteristics, the nature of this dependence varying depending on the time scale (short or long term). Different attributes of tree species, such as age and size, as well as stand density seem to act synergistically and compensate drought stress in different ways. In monospecific stands, *P. pinaster* showed greater resistance to extreme drought than *P. pinea*, with both species displaying similar degree of dependence on climate variability. In mixed stands, *P. pinaster* growth is more influenced by inter-specific interactions than that of *P. pinea* and less conditioned by climatic conditions than in monospecific stands, i.e., mixed compositions could reduce *P. pinaster* tree-ring sensitivity, whereas *P. pinea* benefits from mixture, increasing its resistance to extreme drought events. Therefore, it could be argued that the interactions between climate and forests depend not only on the sensitivity of species to droughts, but also on the tree resilience. This fact poses a challenge for forest managers and researchers, who need to identify the specific thresholds, i.e., the conditions under which tree species are no longer able to recover, and the degree to which these thresholds depend on stand characteristics, such as monospecific vs mixed composition. Thus, the adaptation of forest management should be a dynamic as well as local process, designed on the appropriate scale and defined by local interactions between climate and tree species, that is, as a systematic learning process.

Acknowledgements We are grateful to the Forest Service of the Junta de Valladolid for their support during the field work. We also thank Adam Collins for revising the English. M. V. acknowledges the FPI scholarship program from the Spanish Ministry of Education. J.G.A. was supported by a Ramon y Cajal fellowship (RYC-2016-20528). This contribution has been supported within the framework of the projects PCIN2017-026, AGL2014- 51964-C2-2-R, AGL2017-83828-C2.1R and RTA2013-00011-C2.1, of the Spanish Ministry of Economy and Competitiveness, and 778322-CARE4C H2020. Finally, the authors are grateful to the anonymous reviewers whose comments and suggestions significantly improved both clarity and precision of the paper.

References

- Alday JG, Shestakova TA, Resco de Dios V, Voltas J (2018) DendroSync: an R package to unravel synchrony patterns in tree-ring networks. *Dendrochronologia* 47:17–22. <https://doi.org/10.1016/J.DENDRO.2017.12.003>
- Alday JG, Shestakova TA, Resco de Dios V, Voltas J (2019) DendroSync: a set of tools for calculating spatial synchrony between tree-ring chronologies. R package v (1) (2019), p 3. <https://CRAN.R-project.org/package=DendroSync>
- Allen CD, Macalady AK, Chenchouni H 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. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Anderegg WRL, Anderegg LDL (2013) Hydraulic and carbohydrate changes in experimental drought-induced mortality of saplings in two conifer species. *Tree Physiol* 33:252–260. <https://doi.org/10.1093/treephys/tpt016>
- Andivia E, Ruiz-Benito P, Díaz-Martínez P et al (2020) Inter-specific tolerance to recurrent droughts of pine species revealed in saplings rather than adult trees. *For Ecol Manag* 459:117848. <https://doi.org/10.1016/j.foreco.2019.117848>
- Astigarraga J, Andivia E, Zavala MA et al (2020) Evidence of non-stationary relationships between climate and forest responses: increased sensitivity to climate change in Iberian forests. *Glob Change Biol*. <https://doi.org/10.1111/gcb.15198>
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Belote RT, Prisley S, Jones RH et al (2011) Forest productivity and tree diversity relationships depend on ecological context within mid-Atlantic and Appalachian forests (USA). *For Ecol Manag* 261:1315–1324. <https://doi.org/10.1016/j.foreco.2011.01.010>
- Berguería S, Vicente-Serrano SM (2017) Package SPEI: calculation of the standardised precipitation-evapotranspiration index. R package v (1.7) (2017). <https://cran.r-project.org/web/packages/SPEI/SPEI.pdf>
- Biondi F, Qeadan F (2008) A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Res* 64:81–96
- Bogino SM, Bravo F (2008) Growth response of *Pinus pinaster* Ait. to climatic variables in central Spanish forests. *Ann For Sci*. <https://doi.org/10.1051/forest:2008025>
- Bunn AG (2010) Statistical and visual crossdating in R using the dplR library. *Dendrochronologia* 28:251–258. <https://doi.org/10.1016/J.DENDRO.2009.12.001>
- Burnham KP, Anderson DR, Burnham KP (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, Berlin
- Calama R, Manso R, Lucas-Borja ME et al (2017) Natural regeneration in Iberian pines: A review of dynamic processes and proposals for management. *For Syst* 26:eR02S. <https://doi.org/10.5424/fs/2017262-11255>
- Calama R, Conde M, de-Dios-García J et al (2019) Linking climate, annual growth and competition in a Mediterranean forest: *Pinus pinea* in the Spanish Northern Plateau. *Agric For Meteorol* 264:309–321. <https://doi.org/10.1016/j.agrformet.2018.10.017>
- Camarero JJ, Gazol A, Sangüesa-Barreda G et al (2018) Forest growth responses to drought at short- and long-term scales in Spain: squeezing the stress memory from tree rings. *Front Ecol Evol*. <https://doi.org/10.3389/fevo.2018.00009>
- Colangelo M, Camarero JJ, Borghetti M et al (2018) Drought and phytophthora are associated with the decline of oak species in Southern Italy. *Front Plant Sci*. <https://doi.org/10.3389/fpls.2018.01595>
- Corvalán P, Hernández J (2006) Densidad del Rodal. Universidad de Chile, Facultad de Ciencias Forestales. Cátedra de Dasometría. Chile. 5 p
- Cropper JP (1979) Tree-ring skeleton plotting by computer. *Tree-Ring Bull* 39:47–60
- del Río M, Schütze G, Pretzsch H (2014) Temporal variation of competition and facilitation in mixed species forests in Central Europe. *Plant Biol* 16:166–176. <https://doi.org/10.1111/plb.12029>
- del Río M, Vergarechea M, Hilmers T et al (2021) Effects of elevation-dependent climate warming on intra- and inter-specific growth synchrony in mixed mountain forests. *For Ecol Manag*. <https://doi.org/10.1016/j.foreco.2020.118587>
- Fang O, Zhang QB (2019) Tree resilience to drought increases in the Tibetan Plateau. *Glob Change Biol* 25:245–253. <https://doi.org/10.1111/gcb.14470>
- Forrester DI (2014) The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *For Ecol Manag* 312:282–292. <https://doi.org/10.1016/j.foreco.2013.10.003>
- Fox J, Weisberg S (2019) An {R} Companion to applied regression. Third Edition. Sage Publications, Thousand Oaks
- Friedman JH (1984) A variable span scatterplot smoother. Stanford University, Stanford
- Fritts HC (1976) Tree rings and climate, 2001st edn. Blackburn Press, Caldwell
- Fritts HC, Guiot J, Gordon GA, Schweingruber F (1990) Methods of calibration, verification, and reconstruction. *Methods of dendrochronology*. Springer, Dordrecht, pp 163–217
- Gazol A, Camarero JJ, Vicente-Serrano SM et al (2018) Forest resilience to drought varies across biomes. *Glob Change Biol* 24:2143–2158. <https://doi.org/10.1111/gcb.14082>
- González de Andrés E, Camarero JJ, Blanco JA et al (2018) Tree-to-tree competition in mixed European beech–Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions. *J Ecol* 106:59–75. <https://doi.org/10.1111/1365-2745.12813>
- Gordo FJ (1999) Ordenación y selvicultura de *P. pinea* L en la provincia de Valladolid. In: Madrigal A (ed) Ciencias y Técnicas Forestales. 150 años de aportaciones de los ingenieros de montes. FUCO-VASA, Madrid, pp 79–100
- Gordo F., Rojo LI, Calama R, Al E (2012) Selvicultura de regeneración natural de *Pinus pinea* L. en montes públicos de la provincia de Valladolid. In: J G, R C, Al PM et (eds) La regeneración natural de los pinares en los arenales de la meseta castellana. Instituto Universitario de Investigación en Gestión Forestal Sostenible, Valladolid, pp 145–159
- Grossiord C (2019) Having the right neighbors: how tree species diversity modulates drought impacts on forests. *New Phytol*. <https://doi.org/10.1111/nph.15667>
- Heino M, Kaitala V, Ranta E, Lindström J (1997) Synchronous dynamics and rates of extinction in spatially structured populations. *R Soc London Proc B Biol Sci* 264(1381):481–486
- IPCC (2018) Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pörtner H-O, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, Pidcock R, Connors S, Matthews JBR, Chen Y, Zhou X, Gomis MI, Lonnoy E, Maycock T, Tignor M, Waterfield T (eds) Global warming of 1.5°C. An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty, World Meteorological Organization, Geneva, Switzerland, 32 pp
- Klein T (2014) The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Funct Ecol* 28:1313–1320. <https://doi.org/10.1111/1365-2435.12289>

- Lloret F, Keeling EG, 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>
- Maluquer XS, Mencuccini M, Vilalta JM (2018) Changes in tree resistance, recovery and resilience across three successive extreme droughts in the northeast Iberian Peninsula. 343–354
- Marqués L, Camarero JJ, Gazol A, Zavala MA (2016) Drought impacts on tree growth of two pine species along an altitudinal gradient and their use as early-warning signals of potential shifts in tree species distributions. *For Ecol Manag* 381:157–167. <https://doi.org/10.1016/j.foreco.2016.09.021>
- Martin-Benito D, Beeckman H, Cañellas I (2013) Influence of drought on tree rings and tracheid features of *Pinus nigra* and *Pinus sylvestris* in a mesic Mediterranean forest. *Eur J For Res* 132:33–45. <https://doi.org/10.1007/s10342-012-0652-3>
- Martínez-Vilalta J, López BC, Loepfe L, Lloret F (2012) Stand- and tree-level determinants of the drought response of Scots pine radial growth. *Oecologia* 168:877–888. <https://doi.org/10.1007/s00442-011-2132-8>
- Martínez-Vilalta J, Poyatos R, Aguadé D et al (2014) A new look at water transport regulation in plants. *New Phytol* 204:105–115. <https://doi.org/10.1111/nph.12912>
- Mazza G, Cutini A, Manetti MC (2014) Site-specific growth responses to climate drivers of *Pinus pinea* L. tree rings in Italian coastal stands. *Ann For Sci* 71:927–936. <https://doi.org/10.1007/s13595-014-0391-3>
- McDowell NG, Ryan MG, Zeppel MJB, Tissue DT (2013) Feature: improving our knowledge of drought-induced forest mortality through experiments, observations, and modeling. *New Phytol* 200:289–293. [https://doi.org/10.1111/NPH.12502@10.1002/\(ISSN\)1469-8137\(CAT\)FEATUREISSUES\(VI\)DROUGHTINDUCEDFORESTMORTALITY](https://doi.org/10.1111/NPH.12502@10.1002/(ISSN)1469-8137(CAT)FEATUREISSUES(VI)DROUGHTINDUCEDFORESTMORTALITY)
- Merlin M, Perot T, Perret S et al (2015) Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. *For Ecol Manag* 339:22–33. <https://doi.org/10.1016/j.foreco.2014.11.032>
- Michelot A, Simard S, Rathgeber C et al (2012) Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree Physiol* 32:1033–1045. <https://doi.org/10.1093/treephys/tps052>
- Montero G, Calama R, Ruiz-Peinado R (2008) Selvicultura de *Pinus pinea*. In: Montero G, Serrada R, Reque J (eds) Compendio de Selvicultura de Especies. Ministerio de Educación y Ciencia, Madrid, pp 431–470
- Morán-López T, Poyatos R, Llorens P, Sabaté S (2014) Effects of past growth trends and current water use strategies on Scots pine and pubescent oak drought sensitivity. *Eur J For Res* 133:369–382. <https://doi.org/10.1007/s10342-013-0768-0>
- Mutke S, Vendramin GG, Bagnoli F (2019) Molecular and quantitative genetics of stone Pine (*Pinus pinea* L.) sustainable forest management Research Institute UVa-INIA *Correspondence: mutke@inia.es
- Natalini F, Correia AC, Vázquez-Piqué J, Alejano R (2015) Tree rings reflect growth adjustments and enhanced synchrony among sites in Iberian stone pine (*Pinus pinea* L.) under climate change. *Ann For Sci* 72(8):1023–1033
- Navarro-Cerrillo RM, Rodríguez-Vallejo C, Silveiro E et al (2018) Cumulative drought stress leads to a loss of growth resilience and explains higher mortality in planted than in naturally regenerated *Pinus pinaster* stands. *Forests*. <https://doi.org/10.3390/f9060358>
- Nocentini S, Buttoud G, Ciancio O, Corona P (2017) Managing forests in a changing world: the need for a systemic approach. A review. *For Syst* 26:eR01. <https://doi.org/10.5424/fs/2017261-09443>
- Palahi M, Mavsar R, Gracia C, Birot Y (2008) Mediterranean forests under focus. *Int For Rev* 10:676–688. <https://doi.org/10.1505/ifer.10.4.676>
- Pichler P, Oberhuber W (2007) Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. *For Ecol Manag* 242:688–699. <https://doi.org/10.1016/J.FORECO.2007.02.007>
- PORF (2008) Plan de ordenación de los recursos forestales de la provincia de Valladolid. Servicio Territorial de Medio Ambiente. Junta de Castilla y León. <http://www.jcyl.es/web/jcyl/MedioAmbiente/es/Plantilla100DetalleFeed/1246988359553/Noticia/1200229949988/Comunicacion>
- Potop V, Boroneanţ C, Možný M et al (2014) Observed spatiotemporal characteristics of drought on various time scales over the Czech Republic. *Theor Appl Climatol* 115:563–581. <https://doi.org/10.1007/s00704-013-0908-y>
- Pretzsch H, Schütze G, Uhl E (2013) Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biol* 15:483–495. <https://doi.org/10.1111/j.1438-8677.2012.00670.x>
- Pretzsch H, Rötzer T, Matyssek R et al (2014) Mixed Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* [L.] stands under drought: from reaction pattern to mechanism. *Trees - Struct Funct* 28:1305–1321. <https://doi.org/10.1007/s00468-014-1035-9>
- Prieto-Recio C (2016) Biotic, abiotic and management factors involved in *Pinus pinaster* decline in the Iberian Peninsula. Doctoral Thesis. University of Valladolid
- Prieto-Recio C, Martín-García J, Bravo F, Diez JJ (2015) Unravelling the associations between climate, soil properties and forest management in *Pinus pinaster* decline in the Iberian Peninsula. *For Ecol Manag* 356:74–83. <https://doi.org/10.1016/j.foreco.2015.07.033>
- Puettmann KJ (2011) Silvicultural challenges and options in the context of global change: “simple” fixes and opportunities for new management approaches. *J For Res* 109(6):321–331. <https://doi.org/10.1093/jof/109.6.321>
- Reineke L (1933) Perfecting a stand-density index for even-aged forests. *J Agric Res Wash* 46:627–638
- Rinntech (2010) TSAP-WIN. Time series analysis and presentation for dendrochronology and related applications (Version 0.55 ed.), Heidelberg, Germany. <http://www.rinntech.com>
- Salazar-Tortosa D, Castro J, Rubio De Casas R et al (2018) Gas exchange at whole plant level shows that a less conservative water use is linked to a higher performance in three ecologically distinct pine species. *Environ Res Lett* 13:045004. <https://doi.org/10.1088/1748-9326/aab18f>
- Sánchez-Salguero R, Linares JC, Camarero JJ et al (2015) Disentangling the effects of competition and climate on individual tree growth: a retrospective and dynamic approach in Scots pine. *For Ecol Manag* 358:12–25. <https://doi.org/10.1016/j.foreco.2015.08.034>
- Schwarz JA, Skiadaresis G, Kohler M et al (2019) Quantifying growth responses of trees to drought—a critique of the Lloret-indicators and recommendations for future studies. *Ecol Funct*. <https://doi.org/10.32942/OSF.IO/5KE4F>
- Shestakova TA, Aguilera M, Ferrio JP et al (2014) Unravelling spatiotemporal tree-ring signals in Mediterranean oaks: a variance-covariance modelling approach of carbon and oxygen isotope ratios. *Tree Physiol* 34:819–838. <https://doi.org/10.1093/treephys/tpu037>
- Shestakova TA, Gutiérrez E, Kiryanov AV et al (2016) Forests synchronize their growth in contrasting Eurasian regions in response to climate warming. *Proc Natl Acad Sci U S A* 113:662–667. <https://doi.org/10.1073/pnas.1514717113>

- Shestakova TA, Gutiérrez E, Voltas J (2018) A roadmap to disentangling ecogeographical patterns of spatial synchrony in dendrosciences. *Trees - Struct Funct* 32:359–370. <https://doi.org/10.1007/s00468-017-1653-0>
- Speer JH (2010) Fundamentals of tree-ring research. University of Arizona Press, Tucson
- Steckel M, del Río M, Heym M et al (2020) Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.)—Site water supply and fertility modify the mixing effect. *For Ecol Manag* 461:117908. <https://doi.org/10.1016/j.foreco.2020.117908>
- Sun S, Qiu L, He C et al (2018) Drought-affected *Populus simonii* Carr. Show lower growth and long-term increases in intrinsic water-use efficiency prior to tree mortality. *Forests*. <https://doi.org/10.3390/f9090564>
- Team R Core (2018) R: a language and environment for statistical computing. Team R Core, Vienna
- Tejedor E, Serrano-Notivol R, Luis M et al (2020) A global perspective on the climate-driven growth synchrony of neighbouring trees. *Glob Ecol Biogeogr* 29:1114–1125. <https://doi.org/10.1111/geb.13090>
- Thurm EA, Uhl E, Pretzsch H (2016) Mixture reduces climate sensitivity of Douglas-fir stem growth. *For Ecol Manag* 376:205–220. <https://doi.org/10.1016/j.foreco.2016.06.020>
- Trenberth KE, Dai A, Van Der Schrier G et al (2014) Global warming and changes in drought. *Nat Clim Change* 4:17–22. <https://doi.org/10.1038/nclimate2067>
- Van Der Maaten-Theunissen M, Van Der Maaten E, Bouriaud O (2015) Technical note pointRes: an R package to analyze pointer years and components of resilience. *Dendrochronologia* 35:34–38. <https://doi.org/10.1016/j.dendro.2015.05.006>
- Vergarechea M, Calama R, Fortin M, del Río M (2019a) Climate-mediated regeneration occurrence in Mediterranean pine forests: a modeling approach. *For Ecol Manag* 446:10–19. <https://doi.org/10.1016/j.foreco.2019.05.023>
- Vergarechea M, del Río M, Gordo J et al (2019b) Spatio-temporal variation of natural regeneration in *Pinus pinea* and *Pinus pinaster* Mediterranean forests in Spain. *Eur J For Res*. <https://doi.org/10.1007/s10342-019-01172-8>
- Vernon MJ, Sherriff RL, van Mantgem P, Kane JM (2018) Thinning, tree-growth, and resistance to multi-year drought in a mixed-conifer forest of northern California. *For Ecol Manag* 422:190–198. <https://doi.org/10.1016/j.foreco.2018.03.043>
- Vicente-Serrano SM, Beguería S, López-Moreno JI (2010) A multi-scalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J Clim* 23:1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>
- Vieira J, Campelo F, Nabais C (2009) Age-dependent responses of tree-ring growth and intra-annual density fluctuations of *Pinus pinaster* to Mediterranean climate. *Trees - Struct Funct* 23:257–265. <https://doi.org/10.1007/s00468-008-0273-0>
- Wigley TML, Briffa KR, Jones PD et al (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J Clim Appl Meteorol* 23:201–213. [https://doi.org/10.1175/1520-0450\(1984\)023%3c0201:OTAVOC%3e2.0.CO;2](https://doi.org/10.1175/1520-0450(1984)023%3c0201:OTAVOC%3e2.0.CO;2)
- Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc Natl Acad Sci U S A* 96:1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>
- Zang C, Hartl-Meier C, Dittmar C et al (2014) Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. *Glob Chang Biol* 20:3767–3779. <https://doi.org/10.1111/gcb.12637>
- Zang CS, Buras A, Esquivel-Muelbert A et al (2020) Standardized drought indices in ecological research: why one size does not fit all. *Glob Chang Biol* 26:322–324. <https://doi.org/10.1111/gcb.14809>
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1:3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.