Received: 18 December 2023 | Accepted: 22 May 2024

DOI: 10.1111/1365-2745.14355

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Similar climate–growth relationships but divergent drought resilience strategies in coexisting Mediterranean shrubs

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Funding information
Agencia Estatal de Investigación, Grant/Award Number: PID2021-123675OB-C43 and TED2021-129770B-C21; Ministerio de Ciencia, Innovación y Universidades, Grant/Award Number: RyC2020-030647-I; Consejo Superior de Investigaciones Científicas (CSIC), Grant/Award Number: PIE-20223AT003

Handling Editor: Bérangère Leys

Abstract

1. Anticipating future impacts of climate warming and aridification on drylands requires understanding how coexisting woody plant species respond to climate variability. However, we lack knowledge of the growth resilience capacity of Mediterranean shrubs. Do coexisting trees and shrubs differ in their response to climate? Do coexisting shrub species have comparable post-drought growth resilience?
2. This study was conducted in two Mediterranean shrublands with sparse trees in semi-arid north-eastern Spain. We selected sites situated in formerly agricultural or grassland areas in two regions subjected to semi-arid Mediterranean climate conditions. We sampled six shrubs' species (*Juniperus phoenicea*, *Juniperus oxycedrus*, *Pistacia lentiscus*, *Pistacia terebinthus*, *Rhamnus lycioides* and *Rhamnus alaternus*) and one tree species (*Pinus halepensis*) to measure their radial growth and to reconstruct their past growth patterns using dendrochronology. We quantified climate–growth relationships of trees and shrubs, as well as the growth resilience capacity after drought events of the six shrubs.
3. Growth patterns differed between species but a prevalent trade-off between growth and longevity was found. Growth responses to climate were comparable between species but differed between sites. Most species responded positively to precipitation and negatively to temperature. The most negative correlations of growth with drought severity were found at the driest Valcuerna site. Shrubs differed in their resilience capacity. Across sites, species were more resistant and resilient in Alcubierre, the wettest site. The shrubs *P. terebinthus* and *R. lycioides* were more resistant and resilient than the rest of species, which required longer growth recovery times and accumulated stronger growth reductions, particularly *J. phoenicea*.
4. *Synthesis*. These results highlight the importance of drought as a driver of growth in Mediterranean scrublands. Growth resilience strategies differed between species with junipers being less resilient to drought than other coexisting shrubs. Further research should investigate how this difference in post-drought resilience

is related to functional traits, particularly those related with plant water-use strategies.

KEYWORDS
climate, dendrochronology, drought, radial growth, resilience, root depth, SPEI, water deficit

1 | INTRODUCTION

Climate change is increasing the frequency, duration and intensity of droughts reducing forest growth and productivity (Lindner et al., 2010) and triggering the occurrence of dieback events in both forests and scrublands (Allen et al., 2015; Camarero et al., 2015; Colangelo et al., 2017; Hammond et al., 2022; Tamudo et al., 2021). Mediterranean forests and shrublands are considered to be vulnerable to future water shortages related to warmer conditions and increased aridity (Peñuelas & Sardans, 2021). Thus, it is necessary to generate scientific knowledge about how woody plant species respond to aridification.

Annual tree-rings represent a reliable archive of growth variation in woody plants and dendrochronology allows reconstruction of past growth patterns and how they depend on climate variability (Fritts, 1976). In the Mediterranean region, drought is considered an important driver of variability in tree and shrub radial growth (Gazol et al., 2017; Pasho et al., 2012). Drought impairs the normal functioning of woody plants and results in severe growth reductions, which can last for several years after drought cessation (Anderegg et al., 2015; Schweingruber, 1986; Veuillen et al., 2023), potentially modifying the resistance and resilience of species to future drought extremes (Bose et al., 2020). The growth resilience indices allow quantifying how woody plants respond to drought and whether they can recover pre-drought growth values (Lloret et al., 2011; Schwarz et al., 2020; Thurm et al., 2016). The resilience capacity of woody plants to drought vary between species (Gazol et al., 2017), and it is modulated by factors such as site characteristics (Gazol et al., 2020, 2022; Kannenberg et al., 2018), drought timing (Huang et al., 2018), species functional traits (Serra-Maluquer et al., 2022) and post-drought climate conditions (Veuillen et al., 2023). In trees, gymnosperms are less resistant to drought, that is they have more pervasive drought-induced growth reductions, than angiosperms (Anderegg et al., 2015), and taller tree species suffer more from drought than shorter ones (Trugmann et al., 2021). However, how shrub growth differs between species has been less studied (e.g. Gazol & Camarero, 2012; Gazol et al., 2017; Oladi et al., 2017). Thus, the more knowledge we gain on how co-occurring species respond to drought the closer we will be to understanding how they will thrive in a warmer and drier future.

The Mediterranean basin is considered a plant biodiversity hotspot (Myers et al., 2000), where historical land uses (agricultural, livestock and forestry) have profoundly altered the landscape and plant ecosystems (García-Ruiz et al., 2020). However, in some regions such as the conterminous Spain, formerly rural areas are rewilding after massive rural abandonment in the 1960s (Alfaro-Sánchez et al., 2019; Quintas-Soriano et al., 2022). This rapid rewilding is characterized by forest and shrubland encroachment, but there is a lack of data on how coexisting trees and shrubs will respond to extreme climate events such as droughts (Gazol & Camarero, 2012). Thus, knowledge of the growth responses of co-occurring trees and shrubs to climate stress is of primary importance to delimit their growth potentials in these secondary woodlands and scrublands. Particularly, we need more information on growth resilience capacity after extreme climate events such as droughts to forecast the responses of trees and shrubs to increasing aridity (Bose et al., 2020; Camarero et al., 2018; DeSoto et al., 2020).

Increasing the number of tree and shrub species showing different adaptive strategies should lead to more resilient ecosystems (Schnabel et al., 2021). In the Mediterranean region, woody species present different functional traits to deal with drought, based on different phenological, leaf, root and wood anatomical characteristics (Castro-Díez, 1996; Castro-Díez et al., 2003; Milla et al., 2010; Valeriano et al., 2023; Villar-Salvador, 2000). Species that coexist in these environments often adopt different resource use strategies, through different functional traits such as rooting depth or leaf phenology, leading to a better spatial and temporal use of limiting resources, such as water (Moreno-Gutiérrez et al., 2012; Palacio et al., 2017). Given that water availability is considered one of the main limiting factors for vegetation growth in the Mediterranean region, understanding whether there are differences in the radial growth responses to climate and drought severity of coexisting species in these environments could help to better understand their changes in structure and functioning under present and future conditions.

In this context, our main objectives were to study differences in growth patterns, responses to climate and post-drought resilience sampling six shrub species of three genera (*Pistacia lentiscus* L., *Pistacia terebinthus* L., *Rhamnus alaternus* L., *Rhamnus lycioides* L., *Juniperus phoenicea* L. and *Juniperus oxycedrus* L.) and one tree species (*Pinus halepensis* Mill.) co-occurring in two sites of the Monegros steppe, northeastern Spain. We selected shrublands and woodlands developed over formerly used agricultural or sparsely vegetated areas. We used dendrochronology to assess past radial growth of the studied woody species and analyse the relationships between ring width indices and climatic variability. We paid special attention to the relationship between growth and a drought index and aimed to detect differences in the short-term growth response of the studied species to dry years. We hypothesize that growth will be sensitive to water shortage resulting in growth reductions during dry years and that there will be differences in post-drought growth resilience between coexisting species and between shrubs and trees. We also expect lower growth and worse recovery after drought events in the driest site, particularly for gymnosperm species, which show stronger post-drought legacies.

2 | METHODS

2.1 | Study site and species

The study took place in two sites located in the Monegros steppe, a region with a dry-semiarid, meso-thermo-thermo-mediterranean climate (Rivas-Martínez et al., 2011) situated in the Middle Ebro Basin, northern Aragón, eastern Spain (Pedrocchi, 1998). The first site (Alcubierre, 41°49′6.59″ N, 0°30′32.25″ W, 550 m a.s.l.) is located on north-oriented gentle slopes (10%–15%), and it is considered the wettest site, while the second site (Valcuerna, 41°24′57.02″ N, 0°05′38.10″ E, 250 m a.s.l.) is situated on northwest-oriented slopes of similar steepness, and it is considered the driest site (Figure S1). The climate in the study area is characterized by cold winters and dry, warm summers where the annual precipitation is 550 mm in Alcubierre and 332 mm in Valcuerna. The mean annual temperature is 12°C and 14°C in Alcubierre and Valcuerna sites, with mean minimum and maximum monthly temperatures of 6–9°C (January) and 20–21°C (July–August), respectively. The annual climatic water balance is −400 and −800 mm in Alcubierre and Valcuerna, respectively. The water balance is negative from February to October in Valcuerna and from April to September in Alcubierre, with minimum values reached during July and August (Figure S1d,e) in the two sites (Atlas Climático de Aragón, 2007).

Soils are basic in both sites, mainly composed of marl, limestone and gypsum (Navas, 1998). The dominant vegetation is composed of Aleppo pine (*Pinus halepensis*) together with junipers (*Juniperus phoenicea*) and Kermes oak (*Quercus coccifera* L.). The understorey is dominated by different shrub species (e.g. *Pistacia lentiscus*, *Rhamnus alaternus*, *Rhamnus lycioides*, *Juniperus oxycedrus*, *Genista scorpius* L., *Ephedra nebrodensis* Tineo ex Guss. *Salvia rosmarinus* Spenn., *Thymus* spp.). Other species such as holm oak (*Quercus ilex* L.) and Portuguese oak (*Quercus faginea* Lam.) are found in Alcubierre (Camarero et al., 2021), whereas others such as *Pistacia terebinthus*, *Helianthemum myrtifolium* L., *Lithospermum fruticosum* L. are only found in Valcuerna (Gazol et al., 2017). The main woody plant species that compose the selected ecosystems show a wide variety of water-use strategies (Palacio et al., 2017), growth rates and capacity to tolerate drought (Camarero et al., 2021; Gazol et al., 2017). Some of these main functional traits have been collected from various literature sources (Table 1). The Valcuerna site was affected by a severe *J. phoenicea* drought-induced mortality event in the year 2012 (Gazol et al., 2017).

2.2 | Changes in land use

Changes in land use were analysed by comparing aerial images taken in 1956 and 2021. Specifically, images from the National Aerial Orthophotography Plan from the year 2021 were compared with those taken in 1956. The photographic sources were consulted in the National Geographic Institute download webpage (https://centrodedescargas.cnig.es/CentroDescargas/index.jsp) and the Spatial Data Infrastructure of Aragón (https://idearagon.aragon.es/visor/). Based on the orthophotos, a study area of 150 ha was delimited in each region. Land use types in Alcubierre and Valcuerna sites were digitalized and analysed using the ArcGIS 10.7.1 software (ESRI, 2019).

2.3 | Climate data and drought index

To characterize the climatic conditions of both sites, monthly maximum and minimum temperatures and total precipitation data were obtained from the E-OBS database (https://climexp.knmi.nl/start.cgi) with a resolution of 0.25° for the period from 1970 to 2020 (Cornes et al., 2018). We used this data set to avoid problems in homogeneity or gaps in local series, which usually do not cover periods longer than 30 years.

In addition, the Standardized Precipitation–Evapotranspiration Index (SPEI) was used to assess the severity and duration of droughts. This is a multiscale drought index that varies according to precipitation and evapotranspiration calculated monthly for different timescales (Vicente-Serrano et al., 2010). Positive and negative SPEI values indicate wet and dry conditions, respectively. SPEI data were downloaded, considering a spatial resolution of 1 km^2, (https://monitordesequia.csic.es/monitor/?lang=es#index=spei#months=1#week=4#month=10#year=2022) for a time scale of 12 months. According to the July 12-month SPEI values (i.e. from the previous August to July), 2005 and 2012 were dry years in both study areas (Figure S2).

2.4 | Field sampling

Fieldwork was undertaken in March–June 2021 and in August 2023, after obtaining the corresponding fieldwork permits from the government of Aragon. In each site, we sampled dominant individuals in apparent good state of health excluding *J. phoenicea* in Valcuerna where we included individuals with defoliated stems that survived the 2012 drought. In the case of shrubs, basal cross sections were taken from the thickest trunk using a handle saw. In the case of *P. halepensis*, two cores were extracted per individual at a height of 1.3 m using a Pressler increment borer. During the sampling, the height and diameter of each individual was measured using tapes. In Alcubierre, a total of 93 samples were collected from *P. lentiscus*, *R. alaternus*, *R. lycioides*, *J. phoenicea*, *J. oxycedrus* and *P. halepensis* (Table 1). In Valcuerna, a total of 101 samples were collected from *P. lentiscus*, *P. terebinthus*, *R. alaternus*, *R. lycioides*, *J. phoenicea and J. oxycedrus*. In addition, *P. halepensis* cores taken in 2014 were already available (Table 1).

TABLE 1 Descriptive data on the growth series of the species studied and qualitative and functional traits.

Species	No. samples (No. radii)		RW (mm)		AC		MS		EPS		Period		Clade	Form	Leaf habit	LA (mm^2)	WD (mg cm^{-3})	Root depth
	Al	Va	Al	Va	Al	Va	Al	Va	Al	Va	Al	Va						
P. lentiscus	10 (20)	17 (34)	1.19 ± 0.35	0.67 ± 0.23	0.42 ± 0.27	0.38 ± 0.19	0.27 ± 0.09	0.28 ± 0.06	0.68	0.96	1969–2020	1904–2020	A	Large shrub	E	142	0.65	Deep
P. terebinthus	–	15 (30)	–	0.61 ± 0.35	–	0.51 ± 0.21	–	0.39 ± 0.10	–	0.92	–	1954–2020	A	Large shrub	D	827	0.67	Deep
R. alaternus	14 (28)	15 (30)	0.67 ± 0.20	0.79 ± 0.31	0.21 ± 0.14	0.14 ± 0.21	0.31 ± 0.05	0.29 ± 0.06	0.86	0.91	1969–2020	1985–2020	A	Medium shrub	E	198	0.69	Shallow
R. lycioides	15 (30)	16 (32)	0.47 ± 0.09	0.39 ± 0.15	0.33 ± 0.15	0.26 ± 0.24	0.29 ± 0.05	0.29 ± 0.05	0.81	0.86	1944–2020	1882–2020	A	Medium shrub	E	25	1.00	Shallow
J. phoenicea	15 (30)	16 (32)	0.69 ± 0.19	0.44 ± 0.19	0.31 ± 0.24	0.14 ± 0.26	0.31 ± 0.05	0.27 ± 0.05	0.95	0.78	1974–2022	1957–2020	G	Small tree	E	1	0.66	Medium roots
J. oxycedrus	16 (32)	16 (32)	0.57 ± 0.24	0.33 ± 0.06	0.27 ± 0.15	0.28 ± 0.13	0.37 ± 0.04	0.34 ± 0.04	0.79	0.88	1939–2022	1914–2022	G	Medium shrub	E	13	0.70	Medium roots
P. halepensis	45 (46)	16 (35)	1.06 ± 0.41	1.53 ± 0.36	0.61 ± 0.17	0.47 ± 0.19	0.35 ± 0.06	0.34 ± 0.04	0.98	0.97	1869–2020	1926–2014	G	Tree	E	65	0.54	Deep

Note: Mean values ± standard deviation for the whole period studied is shown. Sources of functional data: Antunes, Chozas, et al., 2018, Antunes, Cruz Díaz-Barradas, et al., 2018, Canadell et al. (1996), De la Riva et al. (2021), Castro-Díez (1996), Filella and Peñuelas (2003), Flora Ibérica (2022), Guerrero-Campo et al. (2006), Moreno-Gutiérrez et al. (2012), Navarro-Cano et al. (2021), Pausas and Çağatay (2018), Silva et al. (2002) and Villar-Salvador (2000).

Abbreviations: A, Angiosperm; AC, first-order autocorrelation of ring-width data; Al, Alcubierre; D, Deciduous; E, Evergreen; EPS, Expressed Population Signal; G, Gymnosperm; LA, Leaf area; MS, mean sensitivity of standard ring-width indices; Period, period with maximum replication and EPS values; PM, Pre-Mediterranean origin; RW, ring width; Va, Valcuerna; WD, Wood density.

2.5 | Dendrochronological procedures

Wood samples were air-dried and sanded with sandpapers of different grains until annual rings were visible. Then, they were scanned at a resolution of 2400 dpi using an Epson Expression 10,000-XL scanner (Epson, Suwa, Japan). Two radii per individual were visually cross-dated, and ring widths were measured to the nearest 0.001 mm from the bark to the pith using the CooRecorder and CDendro software 9.8.1 (Larsson & Larsson, 2022). The quality of the visual cross-dating was checked and controlled by using the software COFECHA (Holmes, 1983), which calculates correlations between ring-width series of the same and different individuals and the mean site series.

The measured series of each individual were standardized, and their trend removed using a polynomial spline adjustment. Temporal autocorrelation was eliminated by fitting autoregressive models. For each species and site, standard- (RWIs) and residual or pre-whitened chronologies (RWIr) were obtained by averaging the standard and residual series of ring-width indices for each species, respectively.

In addition, ring-width data were transformed to basal area increment (BAI). The BAI removes the variation caused by adding volume to a circular stem, and it is considered a more accurate indicator of growth than ring widths if stem growth is considered approximately concentric (Biondi & Qeadan, 2008). We used the formula:

$$\mathrm{BAI} = \pi \left(r_t^{\,2} - r_{t-1}^{\,2}\right) \tag{1}$$

where r_t and r_{t-1} are the squared stem radial increments at the end and beginning of a given annual ring corresponding to rings formed in years t and $t-1$, respectively. Finally, a mean BAI series was calculated for each individual by averaging the BAI series of the two series measured in each disc (or core).

2.6 | Calculating resilience indices

To quantify short-term growth responses to drought at the individual level, we calculated resilience indices (Lloret et al., 2011; Schwarz et al., 2020). A collection of indices quantifying drought impacts and post-drought recovery capacity were calculated for each individual from standardized ring width series and considering the 2005 and 2012 droughts. First, resistance (Rt) was defined as the capacity to sustain growth levels during the stress episode. Second, recovery (Rc) was defined as the ability of tree growth to recover after disturbance. Third, resilience (Rs) was considered the ability of trees to reach pre-disturbance growth levels. Fourth, the relative resilience (RelRs) was the Rs weighted by the drought impact. Finally, we calculated the recovery period and total growth reduction, which are the time in years needed to recover pre-drought growth and the total growth loss during and after the drought event, respectively (Thurm et al., 2016). We also obtained the average recovery rate, which measures the percentage of recovery during the recovery period (Schwarz et al., 2020). These indices were calculated specifying

4 years for pre- and post-disturbance periods, and 6 years of maximum recovery period.

2.7 | Statistical analyses

To characterize the ring-width series for each species in each site, several statistics were calculated over the best-replicated period (1980–2020). These included (Fritts, 1976) the mean ring width and its coefficient of variation, the first-order autocorrelation, the mean sensitivity (a measure of the inter-annual variability in the width of consecutive rings), the mean correlation among indexed ring-width series, and the Expressed Population Signal (EPS) which quantifies how much the sample size from which the chronology was obtained is representative of a theoretical population, given an infinite number of individuals, (Wigley et al., 1984). We determined whether there were differences in growth and autocorrelation between species and sites using an ANOVA test followed by the multiple comparison Tukey Honestly Significant Difference (Tukey HSD; Miller, 1981) test, which was used to determine differences in mean values between groups.

To characterize the relationship between monthly climate variables (maximum and minimum temperatures and precipitation, and the 12-month SPEI) and growth variability, we calculated Pearson's correlation coefficients between the mean series of residual growth indices (RWIr) of each species, climatic variables and the SPEI. Correlations were obtained from September of the previous year of growth ($t-1$) to September of the current year (t). The significance associated with the correlation coefficients ($p<0.05$) was calculated using a permutation test. In our case, we used 1000 permutations to establish the significance of each correlation coefficient.

A linear model between residual growth indices (RWIr) and the 12-month June SPEI was fitted for each species in each site considering the period 1980–2020. The slope of the regression obtained for each species was compared between sites using ANOVAs to estimate whether growth was more limited by drought in the driest Valcuerna site.

To study the variation in growth resilience capacity between species, we analysed the difference in resilience indices (Rt, Rc, Rs, Rel.Rs., Rec. period, Rec. rate and Tot.grow.red.). First, a principal component analysis (PCA) was calculated considering the covariance–variance matrix of the seven resilience indices (Legendre & Legendre, 2012). The variables were standardized prior to the analyses and log-transformed to achieve normality if required. A PERMANOVA (McArdle & Anderson, 2001) considering factors of species identity and site was performed to quantify their capacity to explain the dispersion in the data. The analysis was performed considering a Euclidean distance between samples and the significance of each factor ($p<0.05$) was tested using 1000 randomizations.

After that, the first and second axes of the PCA (PC1 and PC2) were retained to further explore how the location in the resilience space varied between sites, species and depending on individual characteristics. To this end, we constructed regression models using the PC1 and PC2 as response variables and including the site and the species identity as factors as well variables accounting for the individual characteristics. In this respect, we included as covariates the age (number of rings from pith to bark) and diameter of each shrub, the first-order autocorrelation (AR1), and the coefficient of variation in growth (CV). The different models constructed for each species were compared in terms of the Akaike information criterion (AIC), and the model with the lowest value was retained as the final model. When species was retained as a factor in the final model, we performed post hoc analyses by means of estimated marginal means (Fox & Weisberg, 2018).

All statistical analyses were made in the R statistical environment (R Core Team, 2023). Tree-ring files were processed with the dplR package (Bunn et al., 2022), and resilience indices were calculated using the pointRes R package (Van der Maaten-Theunissen et al., 2015). Comparisons between groups were performed using the dplyr R package (Wickham et al., 2022), and climate growth relations with the treeclim R package (Zang & Biondi, 2015). The PCA was constructed and the PERMANOVA analyses were done using the vegan R package (Oksanen et al., 2022). Model selection and AIC calculations were done in the MuMIn R package (Bartoń, 2023) and post hoc analyses and graphs with the emmeans (Lenth, 2023) and Effects packages (Fox & Weisberg, 2018), respectively.

3 | RESULTS

3.1 | Growth characteristics

Growth patterns (Figure 1; Figure S3) and variability (Figure S4) differed between species, but growth reductions coincided with dry years (mainly 2005 and 2012; Figure S2) in both sites (Figure 1). The species with the highest radial growths were *P. lentiscus* in Alcubierre and *P. halepensis* in Valcuerna. In Valcuerna, *P. halepensis* showed the highest growth rate, whereas *R. lycioides* presented the lowest growth values at both sites. Overall, interspecific differences in growth were more pronounced in Valcuerna than at Alcubierre. The ring-width series showed mean sensitivity (MS) values around 0.28–0.39. The autocorrelation (AC) values ranged between 0.14–0.61 and the EPS between 0.70 and 0.98 (Table 1). In the case of shrubs, a negative relationship between mean growth and estimated age was observed in the two sites (Figure S5). Most individuals were established after 1956 in both sites and old individuals were more common in Valcuerna (Figure S6). This was related to differences in historical land uses observed in both sites (Table S1; Figures S7 and S8).

3.2 | Responses to climate and drought

The growth of all species responded to the climatic variables, but the responses were species- and site-specific (Figure 2). Overall, precipitation showed a higher positive influence on the growth of most species in Valcuerna than in Alcubierre, being significant for most

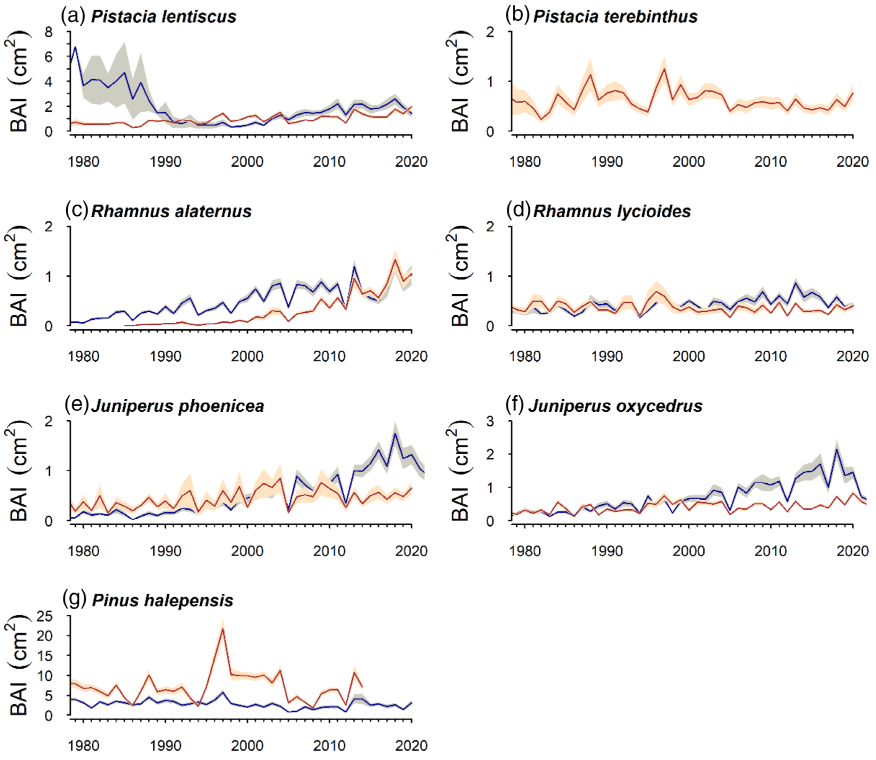

FIGURE 1 Basal area increment (BAI) of (a) *Pistacia lentiscus*, (b) *Pistacia terebinthus* (c) *Rhamnus alaternus*, (d) *Rhamnus lycioides*, (e) *Juniperus phoenicea*, (f) *Juniperus oxycedrus* and (g) *Pinus halepensis* in Alcubierre (blue lines) and Valcuerna (orange lines) in the period 1980–2020. Envelopes correspond to standard errors.

species except *R. alaternus* in winter (mainly January) and spring (April), as well as in June for *P. lentiscus*, *P. terebinthus* and *P. halepensis*. In Alcubierre, April minimum temperature showed a positive influence on the growth of all species exceptjunipers (Figure 2). On the other hand, in Valcuerna, maximum temperatures showed negative relationships with growth indices during March (*R. lycioides*), May (*P. lentiscus*, *J. phoenicea* and *J. oxycedrus*), June (*P. terebinthus* and *J. oxycedrus*) and July (*P. halepensis*). In this dry site, minimum temperature showed positive relationships with growth during January (*P. lentiscus*, *J. phoenicea*, *J. oxycedrus* and *P. halepensis*), April (*R. lycioides* and *P. halepensis*) and August (*R. alaternus*). However, correlations with June–July minimum temperatures were negative in the case of *P. terebinthus* (Figure 2).

The relationships between growth indices (RWIr) and the 12-month July SPEI (Figure 3) showed higher slopes for the species sampled in the driest Valcuerna site except in the case of *R. lycioides* (Figure S9; Table S2). In general, model fits (R^2) were also better in Valcuerna than in Alcubierre. This was noticeable in *P. lentiscus*, *J. phoenicea*, *J. oxycedrus* and *P. halepensis*, which were more drought-limited in Valcuerna than in Alcubierre. In addition, *P. halepensis* showed the steepest slopes at both sites.

3.3 | Resilience to drought

Overall, individuals for all species reduced their growth in response to droughts (i.e. $\text{Rt} < 1$; Figure 4a), but they were able to recover pre-drought growth values (i.e. $\text{Rc} > 1$; Figure 4b). Rt was higher in *P. lentiscus*, *R. lycioides* and *P. terebinthus* than in *J. oxycedrus* and *J. phoenicea* that presented higher Rc values, particularly in Alcubierre. Recovery took longer (Figure 4c) and total growth reductions were higher (Figure 4d) in Valcuerna, particularly for *J. phoenicea*, *J. oxycedrus* and *P. lentiscus*, than in Alcubierre (except for *R. alaternus*).

The PC1 and PC2 accounted for 48.9% and 35.2% of the variation in resilience indices, respectively (Figure 5). The dispersion of individuals in the PCA biplot was partially explained by the effects of site ($F=10.63$; $p<0.01$; $R^2=0.05$) and species identity ($F=4.88$; $p<0.01$; $R^2=0.12$), but their interaction was not significant ($F=1.65$; $p=0.09$; $R^2=0.03$). These factors accounted for 21.3% of the variation in the data. Overall, the PC1 separated individuals with strong growth reductions and longer recovery periods from more resistant and resilient individuals that presented also higher average recovery rates. The PC2 represented a trade-off between resistance and recovery and relative resilience indices.

The regression models showed that site and species were important factors explaining the variation in the two PCAs (Figure S10; Table S3). Besides species and sites, the first-order autocorrelation and the coefficient of variation in growth were included in the final model for PC2 (Table 2). The R^2 of the models was low and similar to that found with the PERMANOVA ($R^2=0.19$ and $R^2=0.23$ for the PC1 and PC2, respectively). The scores in the PC1 and PC2 were significantly higher ($p<0.01$ and $p<0.05$, respectively) in Valcuerna than in Alcubierre. That is, total growth reductions and the recovery period were higher in Valcuerna, while resistance was higher in Alcubierre. Between species, *P. terebinthus* and *R. lycioides* had lower loadings in PC1 than the rest of the species, while *J. phoenicea* had lower loadings in the PC2 than

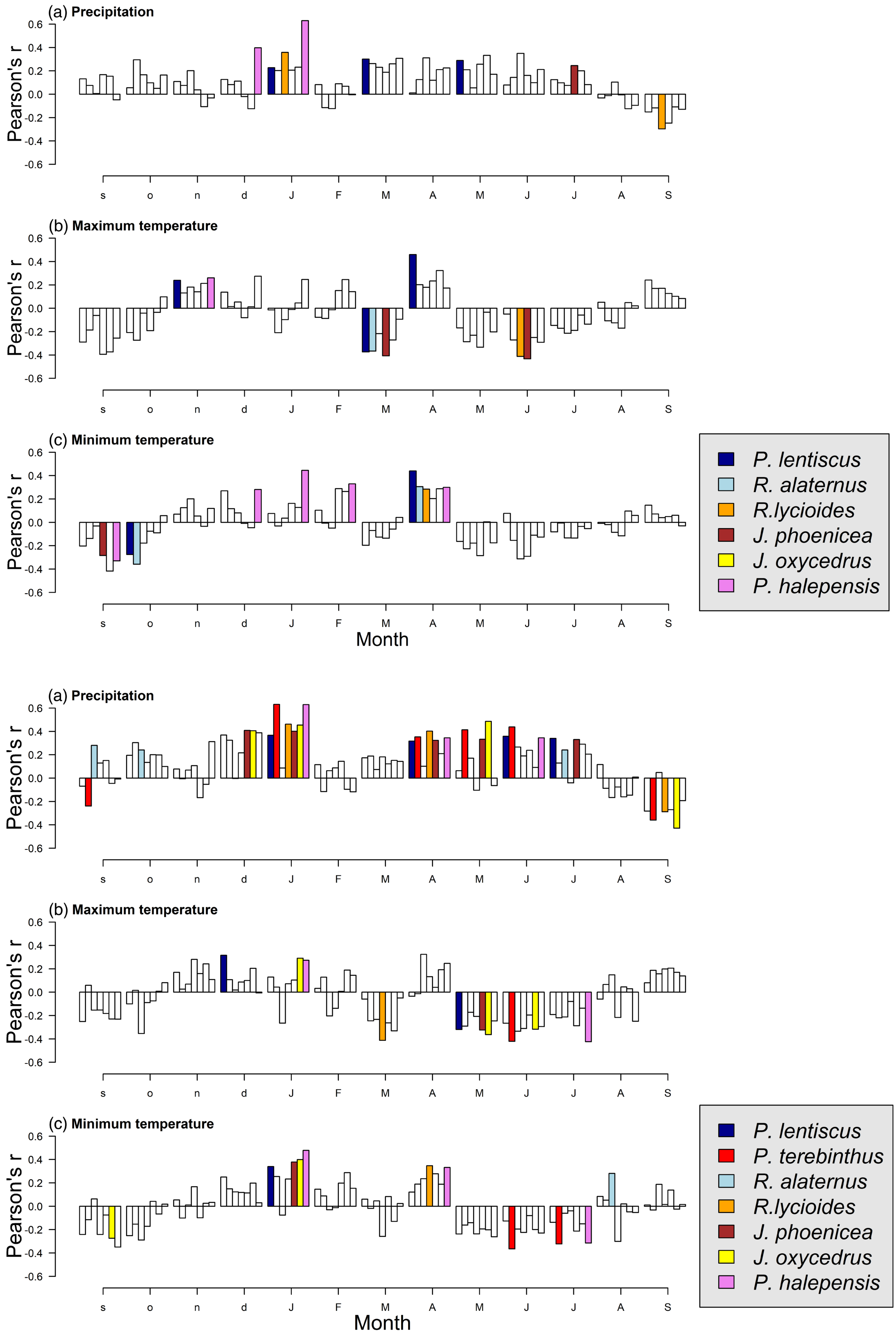

FIGURE 2 Climate–growth relationships (Pearson's correlation coefficients) of all species sampled in Alcubierre (upper plot) and Valcuerna (lower plot). Monthly climatic data correspond to: (a) precipitation, (b) mean maximum and (c) minimum temperatures. The time axis refers to the period from September (s) of the previous year ($t-1$) up to September (S) of the growth year (t). Significant relationships ($p<0.05$) are shown in colours.

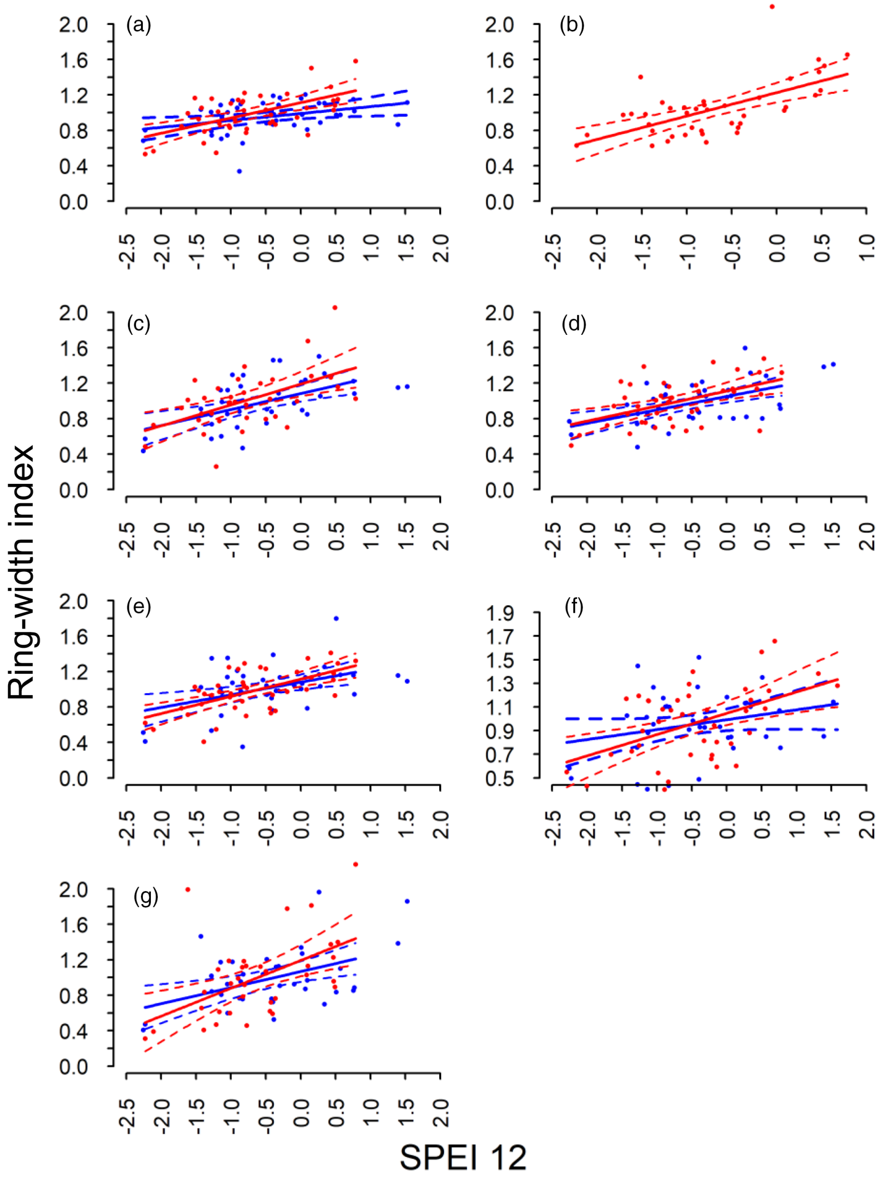

FIGURE 3 Linear regressions between the ring-width indices and the 12-month July SPEI (SPEI12) for: (a) *P. lentiscus*, (b) *P. terebinthus*, (c) *R. alaternus*, (d) *R. lycioides*, (e) *J. phoenicea*, (f) *J. oxycedrus* and (g) *P. halepensis* in Alcubierre (blue symbols and lines) and Valcuerna (red symbols and lines). Solid lines represent linear relationships and dashed lines confidence intervals according to the regression models.

the rest of species (Figure 5; Figure S10). That is, *P. terebinthus* and *R. lycioides* were more resistant while *J. phoenicea* accumulated higher growth reductions and presented higher recovery values. Regarding PC2, the coefficient of variation in growth had a negative effect ($p = 0.02$) and the first-order autocorrelation showed a positive effect ($p = 0.112$).

4 | DISCUSSION

This study advances our knowledge of the growth response to climate and drought resilience capacity of Mediterranean shrubs. According to our first hypothesis, we found significant relationships between climate and growth (including the drought index) for all species and marked growth reductions in dry years. The results also supported our second hypothesis as we found that growth responses to precipitation and the drought index were in general higher in Valcuerna, the driest site, than in Alcubierre. Accordingly, shrubs in Valcuerna were less resistant and accumulated higher total growth reductions. Besides, we found that growth resilience to drought varied at the intraspecific level, as indicated by the strong dispersion in resilience space between individuals, but that there were also significant differences between species, particularly in the case of *R. lycioides*, *P. lentiscus* and *J. phoenicea*.

Our results demonstrated that the precipitation in the months of January and April significantly impacted on the radial growth of several species. This fact was particularly remarkable in the case of *P. halepensis* which benefited from cool-warm winter–spring conditions and cool summer conditions as found before (Pasho et al., 2012; Veuillen et al., 2023).

In terms of photosynthesis rates, Baquedano and Castillo (2007) recognized two stress periods for *P. halepensis* and *J. phoenicea* throughout the year, winters with low temperatures and summers with drought and high radiation. The shrubs *J.*

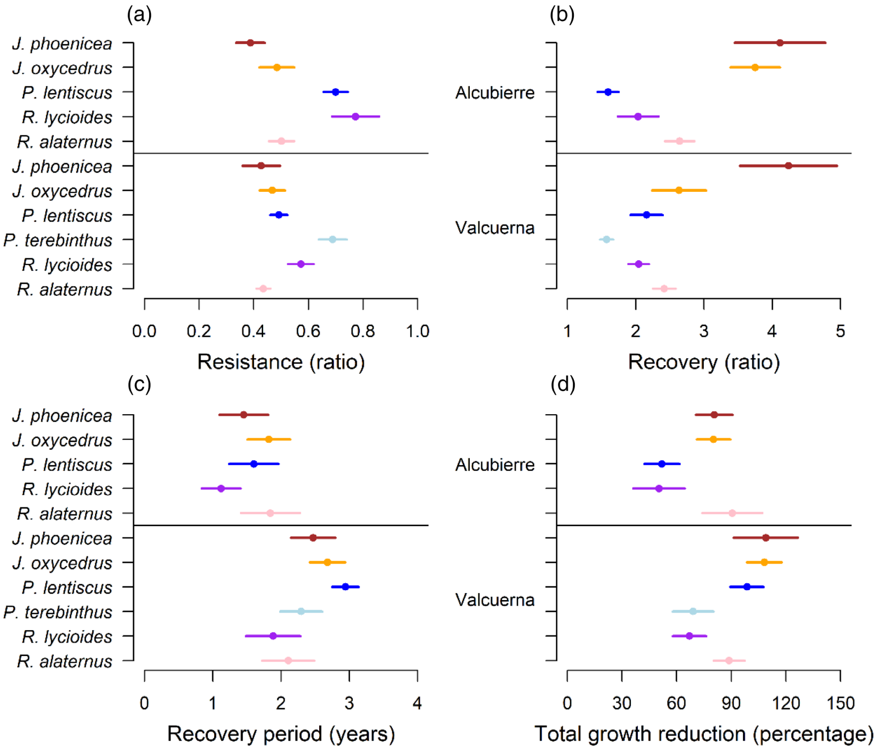

FIGURE 4 Resilience indices for the coexisting Mediterranean shrubs. Means (points) and standard errors (segments) for each species (different colours) are shown for the two study sites (Alcubierre and Valcuerna). The resistance (a) and recovery (b) indices are ratios between the growth of the pre-drought and the drought period and growth during the drought and the post-drought periods, respectively. The recovery period (c) represents the years needed to recover pre-drought growth values and the total growth reduction (d) is the percent growth reduction during the drought and the post-drought period.

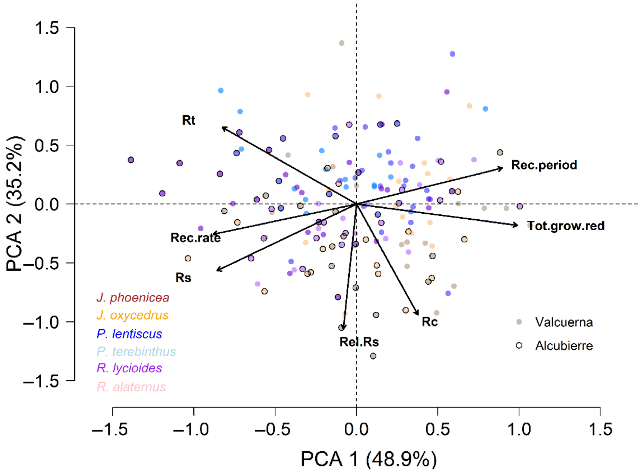

FIGURE 5 Resilience space for the coexisting Mediterranean shrubs. The biplot shows the ordination of individuals according to their resilience indices for the six shrub species (different colours) in the two sites (Valcuerna—symbols without lines; Alcubierre—symbols with lines). The abbreviations of the indices are as follows: Rt, resistance; Rc, recovery; Rs, resilience; Rel.Rs., relative resilience; Rec. period, recovery period; Rec. rate, average recovery rate; and Tot.grow.red., total growth reduction.

TABLE 2 Selected models to explain the variation in the growth resilience space (PC1 and PC2).

PC axes	Factor	df	Sum sq	F	p	R^2
PC1						0.193
	Site	1	2.08	12.01	<0.001	
	Species	5	4.48	5.17	0.01	
	Residuals	158	27.33	—	—	
PC2						0.230
	AR1	1	1.02	6.08	0.01	
	CV	1	1.12	6.70	0.01	
	Site	1	2.08	12.41	<0.001	
	Species	5	3.57	4.26	<0.001	
	Residuals	156	26.10	—	—	

Note: The variables included in the models to explain the variations in the first (PC1) and second (PC2) axis is shown together with the R^2 of the model and the variables included. For each variable, the associated degrees of freedom (df), sum of squares (sum sq), *F* statistic and associated probability (*p*) are shown. The variables are as follows: AR1, first-order temporal autocorrelation; CV, coefficient of variation in ring-width; Site, site factor (two levels); Species, species identity (six values).

phoenicea, *J. oxycedrus* and *P. lentiscus* are species whose growth is quite dependent on precipitation, and it is reduced by high spring–summer temperatures associated with higher evapotranspiration rates, as reflected in other studies (Altieri et al., 2015; Armas & Pugnaire, 2009). The growth of *P. terebinthus* was also dependent on rainfall, especially during spring and summer, and it was also reduced by high summer temperatures. The growth of *R. lycioides* shows a greater positive response to abundant rainfall during winter and spring (January and April) than *R. alaternus*, and the growth of both species is limited by cold spring temperatures. The strong dependence of the growth of *Rhamnus* species on precipitation is in accordance with results obtained in semi-arid areas from the the Irano-Turanian region (Oladi et al., 2017). The month of April seems to be determinant in relation to high minimum temperatures for several of the species at both studied sites suggesting these thermal conditions trigger cambial resumption. Our results suggest that the responses of growth to climate are similar between species, although with differences between sites. This synchrony in growth response to climate is expected in harsh environments (Gazol et al., 2020).

Despite similarities in growth response to climate, the variability of species responses to drought may indicate different strategies and functional thresholds for dealing with these extreme events (Pasho et al., 2011). Gazol et al. (2020) found greater growth reductions and more marked legacies in gymnosperms than in angiosperms, as well as higher capacities to recover after droughts. In this study, *J. phoenicea* showed significant growth reductions during dry years at both sites as well as relatively good recoveries. However, the resilience capacity observed by J. phoenicea was lower than several species studied, as also happened with *J. oxycedrus*, possibly due to the high dependence of its growth on rainfall. *P. lentiscus*, followed by *J. oxycedrus* and *J. phoenicea*, showed the lowest relationships of growth with the drought index at Alcubierre, but their growth was very suppressed by dry conditions in Valcuerna. This difference may be explained by the effect of more arid conditions in the second site, which may amplify the impact of drought on trees and shrubs and reduce their drought resistance (Gao et al., 2018). This effect of drought was more pronounced in junipers than in *P. lentiscus*, although the latter also showed a lower resistance and resilience after these events, supporting our hypotheses formulated in the previous section.

Furthermore, during the 2012 drought, Lloret and García (2016) reported mortality rates of around 50% in *J. phoenicea* populations in Valcuerna, indicating a high vulnerability of this species to this type of event, which was higher when compared with other coexisting species (Gazol et al., 2017). González de Andrés et al. (2021) observed that taller individuals took less time to recover growth levels before intense drought events, in contrast to other studies showing reduced resilience patterns and increased mortality risk with increasing height (Bennett et al., 2015; McGregor et al., 2020; Stovall et al., 2019). However, these studies focussed on interspecific patterns, which may be reversed when looking at intraspecific variability, as reported by other research in oak species (Camarero et al., 2016; Colangelo et al., 2017; Ripullone et al., 2020). We found no clear evidence that plant size (in this case diameter) was a factor explaining growth resilience potentially suggesting that size differences may not be so important for shrubs, and opening questions on why the responses of shrubs to drought varied across sites and between species.

The shrub *R. lycioides* showed little variation between sites in response to drought, remaining constant compared with several of the species considered. This could be related to its small leaves, dense wood and narrow vessels that allow it to adapt better to cold and arid conditions (Castro-Díez, 1996). Serra-Maluquer et al. (2022) also observed that species with higher wood density may have advantages and be less vulnerable to drought-induced mortality than species with less dense wood. *R. alaternus* showed similar relationships with drought events. However, the resilience indices of *R. lycioides* were higher than most of the species in both sites revealing the capacity of this species to grow equally well in xeric and mesic sites (Varone & Gratani, 2009). This could be thanks to its relatively high plasticity in its water strategy (El Aou-Ouad et al., 2014) and the ability to overcome water shortage in terms of adjusting its physiology and morphology (Zunzunegui et al., 2010).

Different water-use strategies could explain the different growth responses to climate (Kulmatiski et al., 2019). All the species in this work belong to lineages that developed under tropical environments during the Tertiary, prior to the establishment of dry Mediterranean-type climatic conditions and, therefore, most of them show conservative water-use strategies (Moreno-Gutiérrez et al., 2012), although with some differences. According to Antunes, Chozas, et al. (2018) and Antunes, Cruz Díaz-Barradas, et al. (2018), *P. halepensis* has deeper roots than shrub species allowing it to tap deeper water resources, which can be an advantage in times of water scarcity. Determining root depth is complex as it varies according to site conditions. Klein et al. (2013) reported that *P. halepensis* roots on dry sites reached 50–60 cm depth, while Canadell et al. (1996) found values up to 7.5 m. Other authors point out that *J. phoenicea* has shallower roots than *P. halepensis* (Altieri et al., 2015), which makes it dependent not only on rainfall but also on warm temperatures (Baquedano & Castillo, 2007; Castillo et al., 2002). Guerrero-Campo et al. (2006) obtained root depth values for *J. oxycedrus* of about 1.7 m. Furthermore, several studies indicate that *J. phoenicea* is one of the species most threatened by the current trend of rising temperatures and summer drought, due to poor stomatal regulation (Altieri et al., 2015; Armas & Pugnaire, 2009; Camarero et al., 2020), which may explain why *J. phoenicea* is most impaired in the driest location (Valcuerna).

Castro-Díez (1996) indicated that evergreen shrubs such as *P. lentiscus* are prepared to maintain relatively high activity rates during the summer, so they would be closer to opportunistic strategies. To exhibit this behaviour, they need to have deep root systems, in some cases up to 5 m, although it has been observed that soil structure and depth influence the use of water and the depth at which roots acquire it (Filella & Peñuelas, 2003). Silva et al. (2002) reported shallower root depths of *P. lentiscus*, around 0.5 m. Furthermore, several authors suggested that *P. lentiscus* had a competitive advantage over *J. phoenicea*, most likely due to differences in rooting patterns and salinity tolerance, which may determine the source of water available to each species and affect stomatal regulation (Armas et al., 2010; Armas & Pugnaire, 2009; Zunzunegui et al., 2010). This may lead to differences in the resilience of these species to drought events. *P. terebinthus* also has deep roots (Castro-Díez, 1996), but reduced water availability filters out the presence of deciduous species, which have wider vessels than evergreen species and are also less frequent in smaller growth forms (Villar-Salvador, 2000). Furthermore, in xerophytic environments, plants with small, persistent leaves dominate, unlike those of *P. terebinthus* (Castro-Díez, 1996), which could represent a problem for the perpetuation of this species in these environments.

Finally, according to Castro-Díez (1996), the two *Rhamnus* species are xerophytic shrubs with narrow leaves and low water loss through transpiration, and form dense wood in comparison with the rest of the species considered. They are therefore species highly adapted to aridity, which form both shallow (ca. 0.3 m; Antunes, Chozas, et al., 2018; Antunes, Cruz Díaz-Barradas, et al., 2018; Navarro-Cano et al., 2021) and well-developed deep main roots. Thus, the *Rhamnus* species illustrate a niche complementarity with the other species, as they do not compete for the same water resources (Araya et al., 2010; Kulmatiski et al., 2019). Determining the relationships between the growth resilience of species and the soil depth of water uptake by their roots is, therefore, a potential field of research of great relevance.

5 | CONCLUSION

Changes in land use have conditioned the natural dynamics of the plant communities in the dry ecosystems studied by favouring the establishment of woody species due to the reduction in the intensity of extensive livestock, farming and agriculture, particularly in Alcubierre. Shrub species show higher growth rates than trees in relative terms. There are differences in response to climate between species and sites, with stronger relationships found between growth and rainfall in the driest site (Valcuerna) and with temperatures in the least dry site (Alcubierre). Drought is the main limiting factor of the radial growth of shrubs and trees at both sites. Trees and shrubs show differences in the magnitude of resilience indices, with *P. halepensis* and *R. lycioides* showing the highest and lowest plasticity before and after drought events.

These results highlight the need to clarify how species coexisting in semi-arid environments respond to climate and extreme drought events, and how this response relates to functional traits such as water uptake depth, to improve the management and conservation of diverse Mediterranean scrublands.

AUTHOR CONTRIBUTIONS

Elisa Tamudo, Antonio Gazol and J. Julio Camarero designed the study and lead the writing; Antonio Gazol, J. Julio Camarero, Michele Colangelo and Ester González did the fieldwork and collected the samples, Cristina Valeriano, Elisa Tamudo and J. Julio Camarero processed the samples; Elisa Tamudo and Antonio Gazol analysed the data; Elisa Tamudo wrote the first draft and all authors commented on it.

ACKNOWLEDGEMENTS

We thank Aragón Government for sampling permissions.

FUNDING INFORMATION

AG is supported by the 'Ramón y Cajal' Program of the Ministerio de Ciencia, Innovación y Universidades under Grant RyC2020-030647-I, and by Consejo Superior de Investigaciones Científicas (CSIC) under grant PIE-20223AT003. This research was funded by the Science and Innovation Ministry and the AEI with projects PID2021-123675OB-C43 and TED2021-129770B-C21.

CONFLICT OF INTEREST STATEMENT

None of the authors have any conflict of interest in this article.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14355.

DATA AVAILABILITY STATEMENT

The data are available on Figshare: https://doi.org/10.6084/m9.figshare.25975381 (Tamudo et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Changes in area occupied by each type of land use in the two study areas.

Table S2: Slopes, significance levels ($p < 0.05$*, $p < 0.01$**, $p < 0.001$***) and coefficients of determination (R^2) of linear regression models calculated between series of ring-width indices and SPEI-12 July values.

Table S3: Proposed models to explain the variation in the resilience space (PC1 and PC2).

Figure S1: (a) Location of the sites studied in Aragón, north-eastern Spain.

Figure S2: SPEI-12 values for the month of July during the period 1980-2020 in Alcubierre (red line) and Valcuerna (blue line).

Figure S3: Log-transformed (log(x+1)) Basal area increment (BAI) of: (a) *Pistacia lentiscus*, (b) *Pistacia terebinthus* (c) *Rhamnus alaternus*, (d) *Rhamnus lycioides*, (e) *Juniperus phoenicea*, (f) *Juniperus oxycedrus* and (g) *Pinus halepensis* in Alcubierre (blue lines) and Valcuerna (orange lines) in the period 1980–2020.

Figure S4: Series of ring-width indices in (a) *Pistacia lentiscus*, (b) *Pistacia terebinthus*, (c) *Rhamnus alaternus*, (d) *Rhamnus lycioides*, (e) *Juniperus phoenicea*, (f) *Juniperus oxycedrus* and (g) *Pinus halepensis* in Alcubierre (blue lines) and Valcuerna (red lines) over the period 1979–2020.

Figure S5: Relationship between radial growth and estimated age for the sampled shrubs in the two sites.

Figure S6: Establishment decade for the shrubs sampled in Alcubierre and Valcuerna.

Figure S7: Land use classification maps of the sampling area located in Alcubierre (a, b) from CORINE Land Cover, on the 1956 (a) and 2021 orthophotos (b).

Figure S8: Land use classification maps of the sampling area located in Valcuerna (a, b) from CORINE Land Cover, on the 1956 (a) and 2021 orthophotos (b).

Figure S9: Relationships between the 12-month July SPEI and series of ring-width index of species sampled in Alcubierre (a): *Pistacia lentiscus*, *Pinus halepensis*, *Rhamnus alaternus*, *Rhamnus lycioides*, *Juniperus phoenicea* and *Juniperus oxycedrus*; and in Valcuerna (b): *P. lentiscus*, *Pistacia terebinthus*, *R. alaternus*, *R. lycioides*, *J. phoenicea* and *J.oxycedrus*.

Figure S10: Differences between species (SP effect) in the resilience space.

How to cite this article: Tamudo, E., Gazol, A., Valeriano, C., González, E., Colangelo, M., & Camarero, J. J. (2024). Similar climate–growth relationships but divergent drought resilience strategies in coexisting Mediterranean shrubs. *Journal of Ecology*, *00*, 1–14. https://doi.org/10.1111/1365-2745.14355