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Growth of tree (*Pinus sylvestris*) and shrub (*Amelanchier ovalis*) species is constrained by drought with higher shrub sensitivity in dry sites

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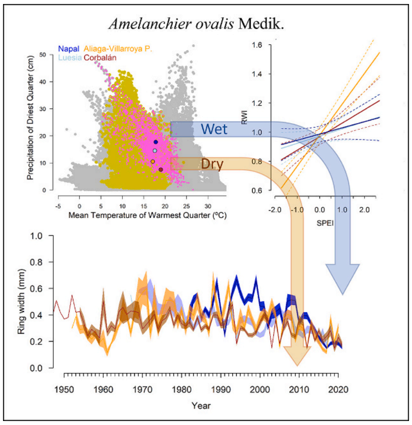
HIGHLIGHTS

- The winter deciduous shrub *A. ovalis* forms distinct annual growth rings.
- Lower growth synchrony of *A. ovalis* as compared to co-occurring *P. sylvestris*.
- *A. ovalis* growth is enhanced by wet spring-summer conditions.
- *A. ovalis* growth is more limited by water scarcity in dry sites.
- Coexisting tree and shrub species show different tolerances to drought.

GRAPHICAL ABSTRACT



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ABSTRACT

We lack understanding of how variable is radial growth of coexisting tree and shrub species, and how growth is constrained by drought depending on site aridity. Here, we compared the radial growth of two widespread and coexisting species, a winter deciduous shrub (*Amelanchier ovalis* Medik.) and an evergreen conifer tree (*Pinus sylvestris* L.). We sampled four sites in Northeastern Spain subjected to different aridity levels and used dendrochronological methods to quantify growth patterns and responses to climate variables. The growth of the two species varied between regions, being lower in the driest sites. The first-order autocorrelation (growth persistence) was higher in more mesic sites but without clear differences between species. Tree and shrub growth negatively responded to elevated summer temperatures and positively to spring-summer precipitation and wet conditions. However, negative growth responses of the shrub to drought were only observed in the two driest

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sites in contrast to widespread responses of the tree. Abrupt growth reductions were common in the drier sites, but resilience indices show that the two species rapidly recovered pre-drought growth levels. The lower growth synchrony of the shrub as compared to the tree can be due to the multistemmed architecture, fast growth and low stature of the shrub. Besides, the high dependency of the shrub growth on summer rainfall can explain why drought limitations were only apparent in the two driest sites. In any case, results point out to the dendrochronological potential of shrubs, which is particularly relevant giving its ability to inhabit woodlands and treeless regions under harsh climatic conditions. Nevertheless, further research is required to elucidate the capacity of shrub species to tolerate drought, as well as to understand how shrubs thrive in water- and cold-limited environments.

1. Introduction

Climate change includes increases in temperature and atmospheric evaporative demand triggering the occurrence of more severe droughts since the early 1980s, particularly in Mediterranean regions (Vicente-Serrano et al., 2022). This has important ecological implications because water shortage coupled with elevated temperatures increases drought stress which can ultimately lead to higher mortality in woody plants (Allen et al., 2015). Accumulated evidence indicates that the occurrence of “hotter-droughts” over the past decades have contributed to increase forest disturbances (Senf et al., 2018), to increase background mortality rates (Changenet et al., 2021; Cabon et al., 2023) and triggered the occurrence of dieback events (Gazol and Camarero, 2022). In the near future, climate change is expected to increase even more the occurrence of heatwaves and droughts (AghaKouchak et al., 2020), and this is particularly relevant in the Mediterranean region, a climate change hotspot, where temperature rises will be accompanied by more arid conditions (Tuel and Eltahir, 2020). In this scenario, a better understanding of the occurrence of drought-induced forest decline events (Doblas-Miranda et al., 2015) and the resilience capacity of forests to drought (Peñuelas and Sardans, 2021) is required to maintain Mediterranean ecosystems and the services they provide.

Dendrochronology provides the basis for reconstructing radial growth and allows quantifying growth responses to climate extremes such as droughts (Fritts, 1976). Thus, the formation of annual growth rings in shrubs and trees provides a natural archive on how the studied individuals have responded to climate variability. Tree radial growth is strongly linked to phenology (Delpierre et al., 2015), but it also reflects long-term changes in vitality and productivity (Dobbertin, 2005), which can be linked to the occurrence of drought events (Anderegg et al., 2015; Camarero et al., 2018). It is thus expected that changes in tree growth responses to drought and post-drought resilience can be used as early-warning signals of forest decline (Camarero et al., 2015; Cailleret et al., 2017; Cabon et al., 2023). Across tree populations, lower resilience capacity (Serra-Maluquer et al., 2021), and stronger linkages between climate and growth variability (Camarero et al., 2021a) is expected in stands exposed to drier or harsher conditions. Across tree species, more positive growth trajectories and less intense climate growth couplings are expected in drought-adapted species (e.g. Gazol et al., 2022). Besides, process-based growth models, such as the Vaganov-Shashkin model (Vaganov et al., 2006) can be used to determine limit to the growth potential and climatic tolerance of populations and species as well as to identify those which are more vulnerable to drought-induced dieback (Valeriano et al., 2021). Interestingly, these models, which explicitly account for non-linear climate-growth relationships, have been proven to be valid both for trees and shrubs (Camarero et al., 2021b; Valeriano et al., 2023a).

The abundance and ecological relevance of shrubs is particularly high in the Mediterranean basin, a region in which the coexistence between trees and shrubs is fairly common (Lombardo et al., 2020). Yet, while trees have been widely studied, our dendroecological knowledge on dwarf shrubs and shrubs (chamaephytes and phanerophytes) is still scarce (e.g. Montserrat-Martí et al., 2011; Götmark et al., 2016; Camarero et al., 2021a, 2021b). While several studies have evaluated how different coexisting tree species respond to drought in sites with contrasting climate conditions (e.g. Bohner and Diez, 2021), studies involving trees and coexisting shrubs are less common (e.g. Gazol and Camarero, 2012; Gazol et al., 2017; Camarero et al., 2021b) despite the importance that shrubs will have in a warmer and drier future, particularly in semi-arid, often treeless regions (Peñuelas and Sardans, 2021). If shrublands are expected to expand at the expense of forests as aridification develops, more information on the resilience capacity of trees and coexisting shrubs to drought is required to determine vulnerable forests prone to drought-induced dieback (Martinez del Castillo et al., 2022), and to infer which tree and shrub species will better tolerate drought so as to identify climate change winners and losers (Kasper et al., 2022).

The snowy Mespilus or serviceberry (*Amelanchier ovalis* Medik., *Rosaceae*) is a winter deciduous tall shrub widely distributed in in sub-Mediterranean areas of central and south Europe and south-west Asia (Karapatzak et al., 2023). This species is of ecological interest due to its transitional climatic distribution but also of agronomical importance due to the production of edible fruits (Ochmian et al., 2013; Karapatzak et al., 2023). The phenology of this species responds to climate by reducing activity during the dry summer (Milla et al., 2005). Vegetative growth occurs during spring and leaf shading in summer, a fact that might reduce its capacity to compete with evergreen Mediterranean species and can restrict its presence to favorable microsites (Milla et al., 2005). This species has a diffuse and semi-ring porous wood and forms distinct rings (Schweingruber, 1990) but, little is known on how its growth variability responds to climate. Here, we fill this knowledge gap by sampling *A. ovalis* populations and quantifying its radial growth (Fig. 1). Besides, we sampled coexisting Scots pine (*Pinus sylvestris* L., *Pinaceae*) trees in order to quantify the growth variability and its response to climate and drought in sites with contrasting climate conditions in NE Spain. Contrasting response to climate between trees and shrubs can be expected giving the differences in growth form, architecture and functional traits including leaf characteristics and wood type (Götmark et al., 2016). Besides, recent studies suggest that the distribution of gymnosperms strongly depend on temperature variations, while the distribution of angiosperms depends more on precipitation related variables at large spatial scales (Puchałka et al., 2023). Having a tall trunk, tree crowns will be more exposed to higher temperatures and direct sunlight than shrubs (Yang et al., 2020) showing closer aerodynamic coupling to air circulation and experiencing wider thermal amplitude than shrubs (Körner, 2012). Multistemmed, low-stature shrubs grow faster (Götmark et al., 2016) and have narrower rings and a smaller conductive area than trees (Treml et al., 2019), potentially allowing them to survive in hasher environments and depending more on microsite conditions (Gazol and Camarero, 2012). Architectural differences can also modify the root system allowing shrubs to invest more on fine roots and making them more responsive to changes in shallow soil water availability (Yang et al., 2020), although Mediterranean shrubs can be also deep-rooted (Peñuelas and Sardans, 2021). Finally, deciduous shrubs such as *A. ovalis* will require phenological adjustments and regulation of leaf nutrient content to cope with summer drought (Milla et al., 2005).

Thus, our aims are: 1) to evaluate the dendrochronological potential of the shrub *A. ovalis*; 2) to study its growth response to climate; and 3) to compare it with co-occurring *P. sylvestris* trees in sites subjected to different aridity located in NE Spain. Overall, we expect that growth synchrony between individuals within populations will be higher for *P. sylvestris* than for *A. ovalis* given that *A. ovalis* growth depends more on microsite conditions and will be more variable within each site. We also expect that *P. sylvestris* growth will be more tightly related to air temperature variations given that their crowns and stem meristems (e.g., cambium) are more coupled to air circulation (Körner, 2012), they have a longer hydraulic path and a larger root system than the low-stature shrub *A. ovalis*. However, we expect that the two species will reflect growth reductions in response to drought, which will be more marked in the driest sites regardless the considered species. In this sense, we expect that *A. ovalis* growth will respond to a drought index in the dry sites, thus reflecting the dependency of its growth to shallow water availability.

2. Material and methods

2.1. Study sites

We sampled four sites where the two species coexist along a wide climatic and latitudinal gradient in NE Spain (Fig. 1).

The study sites are subjected to Mediterranean climate conditions with a dry summer, cold winter conditions and wet-cool spring and autumn conditions. The Napal (42.712 N, 1.205 W, 694 m a.s.l.) and Luesia (42.378 N, 1.014 W, 819 m a.s.l.) sites are characterized by milder climate conditions due to Atlantic influence, whereas the Aliaga-Villarroya de los Pinares (40.652 N, 0.710 W, 1214 m a.s.l.) and Corbalán (40.442 N, 0.988 W, 1209 m a.s.l.) sites are more continental and drier due to higher elevation and stronger Mediterranean influence (Fig. S1). To characterize the distribution of the two species and to delineate their climate space, we used their distributions from different sources (Chorological map of *P. sylvestris*, Caudullo et al., 2017; GBIF *A. ovalis* records, GBIF.org), and bioclimatic variables from the WorldClim database (Fick and Hijmans, 2017) (see Fig. 1). The average climate conditions differ between sites (Fig. S1) being the annual precipitation values and mean annual temperatures higher in Napal and Luesia than in Aliaga-Villarroya de los Pinares and Corbalán.

In Napal, soils are basic and develop on Eocene marls with alternation of sandstone, lutites and limestone (Geological survey of Spain, IGME-CSIC; https://info.igme.es/visor/). Apart from *A. ovalis* and *P. sylvestris*, other tree and shrub species abundant in the study site are the common (*Juniperus communis* L.) and Prickly junipers (*Juniperus oxycedrus* L.) and the oak *Quercus humillis* Mill. The Luesia site is located in a Cenozoic basin dominated by conglomerates, sandstones, lutites, limestones, marls and gypsum. Other tree species present in the region are European beech (*Fagus sylvatica* L.), the oak *Quercus subpyrenaica* E. H. del Villar accompanied with other minor trees and shrubs such as *Ilex aquifolium* L., *Crataegus monogyna* Jacq., *Sorbus torminalis* L., *Buxus sempervirens* L. and *J. communis*. In Aliaga-Villarroya de los Pinares basic soils develop over Mesozoic limestones, marls and sandstones. Vegetation is dominated by shrubs such as Spanish juniper (*Juniperus thurifera* L.), *A. ovalis*, *Berberis vulgaris* L. and scattered trees such as the black pine (*Pinus nigra* J.F. Arn.) and *P. sylvestris*. In Corbalán, the soils develop on conglomerates, sandstones, red clays, marls and limestones from the Cenozoic. Forests are dominated by *Quercus ilex* subsp. *ballota* (Desf.) Samp., *P. nigra*, *Quercus faginea* Lam. and *J. thurifera* with presence of small shrubs such as *Lavandula latifolia* Medik. in the understory. In Corbalán, ongoing dieback and elevated mortality rates of *P. sylvestris* have been observed after the 2005 and 2012 droughts (Camarero et al., 2015; Valeriano et al., 2021).

Fieldwork was undertaken between 2016 and 2022. In each site, between 10 and 40 mature, apparently healthy individuals of each species were selected and sampled. In Napal and Luesia, *A. ovalis* shrubs were sampled in shrublands while *P. sylvestris* trees were sampled in pure (Napal) or mixed (Luesia) forests. In Aliaga-Villarroya de los Pinares and Corbalán shrubs were sampled in the understory of mixed forests where trees were also sampled. For *P. sylvestris*, two increment cores were extracted at breast height (1.3 m) using a Pressler increment borer (Haglöf Sweden AB). In the case of *A. ovalis*, cross basal sections were taken from the thickest trunk using a hand saw.

2.2. Dendrochronological methods

Wood samples were processed using standard dendrochronological methods. Cores of *P. sylvestris* and basal cross-sections of *A. ovalis* were air dried and sanded with sandpapers of different grain until annual rings were visible. Then, these samples were scanned at a resolution of

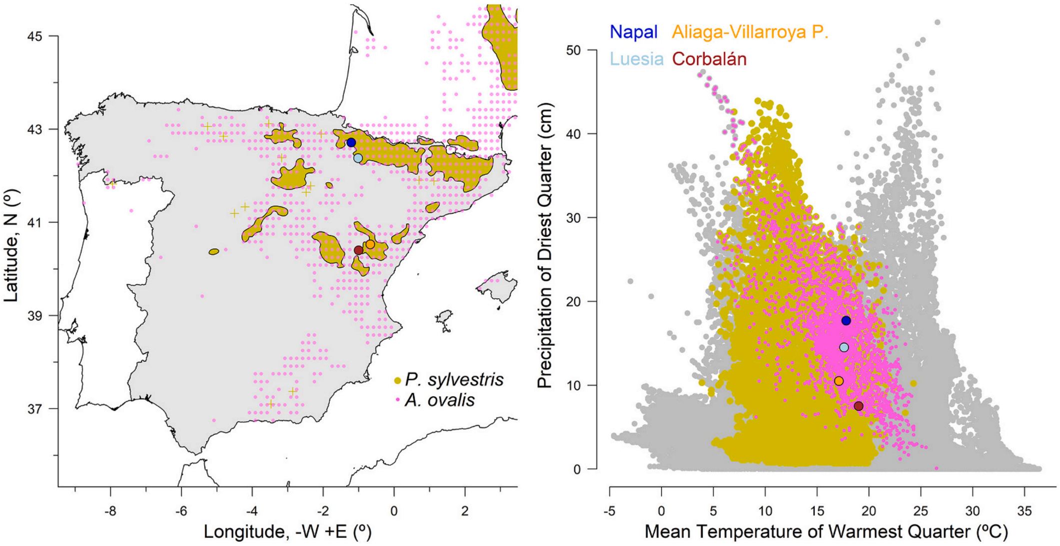

Fig. 1. Distribution of *Amelanchier ovalis* (pink dots) and *Pinus sylvestris* (green polygons). A) Distribution of the two species in Peninsular Spain and the Balearic Islands. Colored circles indicate study sites (Aliaga-Villarroya de los Pinares, Corbalán, Luesia and Napal) where the two species were sampled. B) Distribution of *Amelanchier ovalis* (pink small dots) and *Pinus sylvestris* (green polygons) in the climate space across their distribution ranges. The grey area indicates the entire climatic space and colored dots indicating the four study sites. The distribution of each species was obtained from different sources (Chorological map of *P. sylvestris*, Caudullo et al., 2017; GBIF *A. ovalis* records, GBIF.org) and the climate for each site according to WorldClim database (Fick and Hijmans, 2017).

2400 dpi using an Epson Expression 10000XL scanner (Epson, Suwa, Japan). After that, samples were visually cross-dated, and ring widths were measured to the nearest 0.001 mm from the pith to the bark considering two radii for each individual. For this purpose, we used the CooRecorder and CDendro software 9.8.1 (Larsson and Larsson, 2022). To assess the quality of the visual cross-dating we used the software COFECHA (Holmes, 1983), which calculates correlations between the resulting site chronology and the individual ring-width series of the measured individuals.

The measured ring-width series were standardized, and their trends removed, fitting a spline with a 50 % frequency cutoff at a frequency equal to 25 years for all individual series. Thus, individual series were transformed in standardized ring-width series (hereafter RWIs). In addition, temporal autocorrelation was eliminated by fitting autoregressive models to obtain residual ring-width series (RWIr). Standardized and residuals ring-with series were obtained across sites for each series considering the common period 1980–2020. Standardized and residual site chronologies were calculated with Tukey bi-weight robust mean for the same period.

For each species in each site, several dendrochronological statistics were calculated over the best-replicated period (1982–2020). For each individual, we considered the mean ring width as a proxy for growth rate and the first-order autocorrelation (AR1) as a measure of growth persistence. The quality and reliability of the site-chronologies was estimated by calculating the Expressed Population Signal (EPS), mean sensitivity and mean correlation among indexed ring-width series for each species in each site (Briffa and Jones, 1990; Wigley et al., 1984).

The presence of negative pointer years (extremely narrow rings) was scrutinized using standardized ring-width series (RWIs) of each species in each site. For this purpose, we used the abrupt growth change method proposed by Schweingruber (1990) which compares the value observed in a particular year with the values observed in the preceding *n* years. We compared each year with the preceding 4 years. For each species in each site, we considered negative pointer years when 75 % of the tree-ring series presented growth reductions higher than 40 % and positive pointer year when 75 % of the series presented growth enhancements higher than 60 %.

Short-term growth responses to drought were quantified using the resilience indices proposed by Lloret et al. (2011) and further modified (van der Maaten-Theunissen et al., 2015, 2021). In particular, we considered the resistance (Rt), recovery (Rc) and resilience (Rs) indices. They were computed for each RWIs as follows:

$$\mathrm{Rt} = RWId/PreRWI \tag{1}$$

$$\mathrm{Rc} = PostRWI/RWId \tag{2}$$

$$\mathrm{Rs} = PostRWI/PreRWI \tag{3}$$

Where *RWId* refers to the growth during the drought period, and *PreRWI* and *PostRWI* refer to the growth before and after the drought period, respectively. Resistance (Rt) is considered as the capacity to sustain growth levels during the stress episode and represents the decrease in growth from the pre-episode to the stress period. Recovery (Rc) is the ability of tree growth to recover after disturbance, whereas resilience (Rs) reflects the ability of trees to reach growth levels observed before the drought occurred (van der Maaten-Theunissen et al., 2015, 2021). We focused on the years 2005 and 2012 because they have been identified as abnormally dry years with strong impacts on forest productivity and tree growth across Spain (Gazol et al., 2020; Fig. S2).

2.3. Climate data and drought index

Maximum and minimum temperature and precipitation data were downloaded from the Spanish Meteorological Agency database (Agencia Estatal de Meteorología, AEMET) with a 5-km spatial resolution, which is calculated from >3200 and 1800 precipitation and temperature local stations, respectively, located in Spain (https://www.aemet.es/es/serviciosclimaticos/cambio_climat/datos_diarios?w=2). We consider these climate data to be representative of the actual climate at the sampling sites, given the high density of stations used to compute them and the closeness of the prediction points (i.e. the centers of the grid cells closest to each sampling point; see Table S1). In addition, the Standardized Precipitation-Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010) was downloaded at a spatial resolution of 1 km^2 from the Spanish SPEI database website (https://monitordesequia.csic.es/). The SPEI is a multi-scalar drought index with negative and positive values corresponding to dry and wet conditions, respectively. Thus, the SPEI was used to assess the severity and duration of droughts and its impact on growth.

2.4. Using the Vaganov-Shashkin model to identify climate constraints of growth

The Vaganov-Shashkin model (hereafter VS model) was used to pinpoint the main climate constraints of radial growth (Vaganov et al., 2006). The model calculates unitless partial growth rates due to either temperature (GrT) or soil moisture (GrM) which are used to produce an integral growth rate (Gr). This integral rate is defined as a standardized sum of integral growth rates during a year (Tychkov et al., 2019). The GrT and GrM indicate relative suitability of temperature and soil moisture for growth with lower values representing more stressful growth conditions. The lower partial growth rates are scaled by the daily photoperiod (GrE) which is constant and depends on site latitude.

Soil moisture was calculated by an integrated hydrological submodel from temperatures and precipitation totals considering several processes (interception, evaporation, transpiration, surface runoff, soil infiltration and snow dynamics). Model inputs included daily temperature and precipitation data and the RWI residual series. The VS-model was parameterized for each of the 8 residual site chronologies for the calibration period (Table S2) and tuned the model parameters to maximize the Pearson correlations (*r*) between simulated and observed ring-width chronologies (period 1980–2020; Fig. S3) using the VS-Oscilloscope software ver. 1.37 (Shishov et al., 2016). To reduce the risk of overfitting, we set parameters related to plant water balance (e.g., rooting depth, transpiration coefficients interval) and growth phenology (e.g., minimal cambial cell growth rate) to be constant across sites (cf. Tumajer et al., 2021).

We calculated several statistics for the calibration and verification periods to quantify the similarity between observed and simulated series of ring-width indices (RWIr) including: *r*, root-mean-square error (RMSE) and Gleichläufigkeit (Glk), which evaluates the year-to-year agreement as the percentage of synchronous growth changes between two tree-ring width series (Buras and Wilmking, 2015). Finally, the VS-model was used to quantify daily integral and partial growth rates due to temperature and soil moisture of the two study species in the four study sites (Fig. S4).

2.5. Statistical analyses

We first evaluated differences in growth capacity (mean ring-width) and growth persistence (AR1) for each species between sites. To this end, we used a Kruskal-Wallis rank sum test (Hollander and Wolfe, 1973) followed by a Pairwise Wilcoxon rank sum tests with Bonferroni corrections for multiple testing. We proceed by comparing the differences between sites (Aliaga-Villarroya de los Pinares, Corbalán, Luesia and Napal) for each species (*A. ovalis* and *P. sylvestris*). We also used the Kruskal-Wallis rank sum test to compare growth persistence (AR1) between species in each site. To compare the coherence between chronologies, Pearson correlation coefficients were calculated between all pairs of residual site chronologies.

To study the relationship between growth variability and climate, we calculated Pearson correlation coefficients between the residual site chronologies of each species and the climatic variables (maximum temperature, precipitation and SPEI). Correlations were obtained for each month of the year, 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.

Linear models were used to study how the responses of growth to the drought varied between species and sites. Residual site chronologies (RWIr) for each species in each site were used as the response variables and the 3-month long SPEI for July and a factor accounting for differences between sites was used as response variable. After fitting the model, post-hoc analyses were performed to test how growth responses to the drought index varies between sites. A similar procedure was applied to compare the responses of growth to drought between species (*A. ovalis* and *P. sylvestris*) in each site.

At the individual series level, we determined if there were differences in resilience indices between species and sites, using again Kruskal-Wallis rank sum test followed by a pairwise Wilcoxon rank sum tests with Bonferroni corrections for multiple testing. As done before, a factor accounting for site (Aliaga-Villarroya de los Pinares, Corbalán, Luesia and Napal) was used to study differences between sites for each species. In each case, separate analyses were done for the 2005 and 2012 droughts. To compare the resilience indices between years (2005 and 2012) for each species in each site, we applied linear-mixed effect models (Pinheiro and Bates, 2000). In the models, year was used as fixed factor and tree or shrub identity as random factor. In all cases, resilience indexes were log transformed ($log_{10}\, x + 1$) to meet normality assumptions. Finally, we compared the resilience components in the 2005 and 2012 droughts between species using Kruskal-Wallis rank sum test followed by a pairwise Wilcoxon rank sum tests with Bonferroni corrections for multiple testing.

All statistical analyses were performed using the R Studio platform and the R statistical software (R development core Team 2023). The dplR package was used to process dendrochronological data. The Res.comp function from PointRes package (van der Maaten-Theunissen et al., 2015, 2021) was used to calculate pointer years and resilience components. Climate-growth correlations were calculated using the “dcc” function of the treeclim package (Zang and Biondi, 2015) and the kruskal.test and pairwise.wilcox.test functions were used to perform non-parametric comparisons and post-hoc analyses. The nlme package (Pinheiro et al., 2023) was used to fit the linear-mixed effect models for resilience indices. Finally, the lstrend function of the lsmeans package (Lenth, 2016) was used to compare the trends in the response to SPEI between sites.

3. Results

3.1. Growth patterns in trees and shrubs

We found marked differences in the radial growth of the two species between sites (Table 1; Fig. 2; Table S3). In the case of *A. ovalis* the highest growth was found in Napal, and it was significantly higher than the growth found in Luesia and Corbalán. The AR1 was higher in Napal and Luesia than in Aliaga-Villarroya de los Pinares and Corbalán (Tables 1 and S3). In the case of *P. sylvestris*, mean growth was higher in Napal and Luesia than in Aliaga-Villarroya de los Pinares and Corbalán (Fig. 2; Table S3). The AR1 was higher in Napal than in Luesia, and no differences in AR1 were found between Corbalán and Aliaga-Villarroya de los Pinares (Tables 1 and S3). Between species, significant differences in AR1 were found in Napal where *P. sylvestris* had higher values than *A. ovalis*, and marginal differences ($P = 0.05$) in Luesia where *A. ovalis* had higher values than *P. sylvestris* (Tables 1 and S4). The rbar and EPS

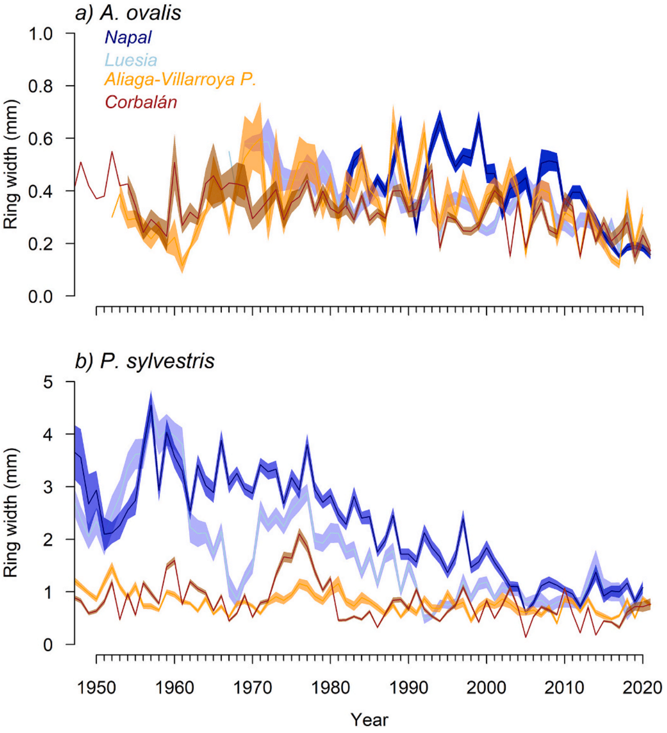

Fig. 2. Radial growth patterns (ring width) of the two species in the four sites. Each site is represented with a different color. Note that the units (y-axis) are different for each species. The solid line represents the average across the sampled individuals and the shaded area is the 95 % confidence interval for the mean.

Table 1
Summary of the dendrochronological properties of the sampled species in each site. For each site (abbreviated as AL – Aliaga-Villarroya P.; CO – Corbalán, LU – Luesia, NA – Napal) and each species the number of individuals and measured radii and the studied period are shown together with the mean ring width (± standard deviation) and first-order autocorrelation (± standard deviation) for the period 1982–2020. The Rbar (mean correlation among series) and the Expressed Population Signal for the period 1982–2020 are also shown. In the case of ring width and AR1 superscript letters indicate significant differences (P. < 0.05) for each species between sites (see Table S3).

Site (code)	Species	No. individuals (radii)	Period	Ring width (mm)	AR1	Rbar	EPS
Napal (NA)	*A. ovalis*	20 (38)	1982–2021	0.417 ± 0.235^{a1}	0.541 ± 0.153^{a1}	0.341	0.912
	P. sylvestris	20 (38)	1933–2020	1.49 ± 0.898^{a2}	0.64 ± 0.152^{a2}	0.457	0.944
Luesia (LU)	*A. ovalis*	21 (40)	1967–2020	0.323 ± 0.189^{b1}	0.539 ± 0.195^{a1}	0.242	0.858
	P. sylvestris	12 (24)	1902–2020	1.103 ± 0.638^{a2}	0.474 ± 0.135^{b2}	0.418	0.782
Aliaga-Villarroya de los Pinares (AL)	*A. ovalis*	15 (29)	1952–2020	0.339 ± 0.223^{ab1}	0.341 ± 0.179^{b1}	0.363	0.872
	P. sylvestris	11 (20)	1899–2021	0.704 ± 0.329^{b2}	0.271 ± 0.197^{c2}	0.511	0.92
Corbalán (CO)	*A. ovalis*	29 (55)	1947–2021	0.299 ± 0.171^{b1}	0.224 ± 0.206^{b1}	0.313	0.913
	P. sylvestris	40 (80)	1810–2021	0.622 ± 0.402^{b2}	0.22 ± 0.173^{c2}	0.742	0.991

were higher for *P. sylvestris*, excluding the EPS in Luesia (Table 1), suggesting that growth synchrony between individuals within populations is higher for *P. sylvestris*.

Ring-width chronologies and the occurrence of negative pointer years differed between species and sites (Fig. 3; Table S5 & Fig. S5). In the dry sites (Aliaga-Villarroya de los Pinares and Corbalán) growth reductions were common in the 2005 and 2012 dry years (Fig. 3) despite with strong variation between sites and years. Aliaga-Villarroya de los Pinares was the only site in with the chronologies of the two species showed a positive correlation (Table S5). The *P. sylvestris* chronology of Corbalán was positively related with that of *A. ovalis* in Aliaga-Villarroya de los Pinares, which was also related with the *P. sylvestris* Napal chronology and the *A. ovalis* Luesia chronology (Table S5).

Negative pointer years were only found in the two driest sites: Aliaga-Villarroya de los Pinares and Corbalán (Fig. S5). In the case of *A. ovalis*, these pointer years corresponded to the 2003 (Corbalán) and 2005 (Aliaga-Villarroya de los Pinares) years. In the case of *P. sylvestris* they were only observed in Corbalán and corresponded to the years 1981, 1999, 2005, 2012 and 2014.

3.2. Climate-growth relationships and resilience indices

Climate-growth relationships showed an overall positive effect of spring-summer precipitation on growth indices, and negative relationships with mean maximum temperature (Fig. 4). In the case of precipitation, positive relationships between April, May, June and July values and growth indices were more common in *P. sylvestris* than in *A. ovalis*. Elevated temperatures in March reduced the growth of *P. sylvestris* in Aliaga-Villarroya de los Pinares and of *A. ovalis* in Luesia, Aliaga-Villarroya de los Pinares and Corbalán. Elevated temperatures during summer negatively affected the growth of the two species, but in the case of *A. ovalis* these relationships were significant in the driest sites only. The linkages between growth and the 3-month long SPEI were observed for *P. sylvestris* in all sites except Luesia while for *A. ovalis* significant relationship were only observed in the two driest sites: Aliaga-Villarroya de los Pinares and Corbalán (Fig. 4). The regression analyses showed that there was a significant interaction between the SPEI and the factor reflecting differences between sites for each species (Table S6). The results showed that the growth of *A. ovalis* was more

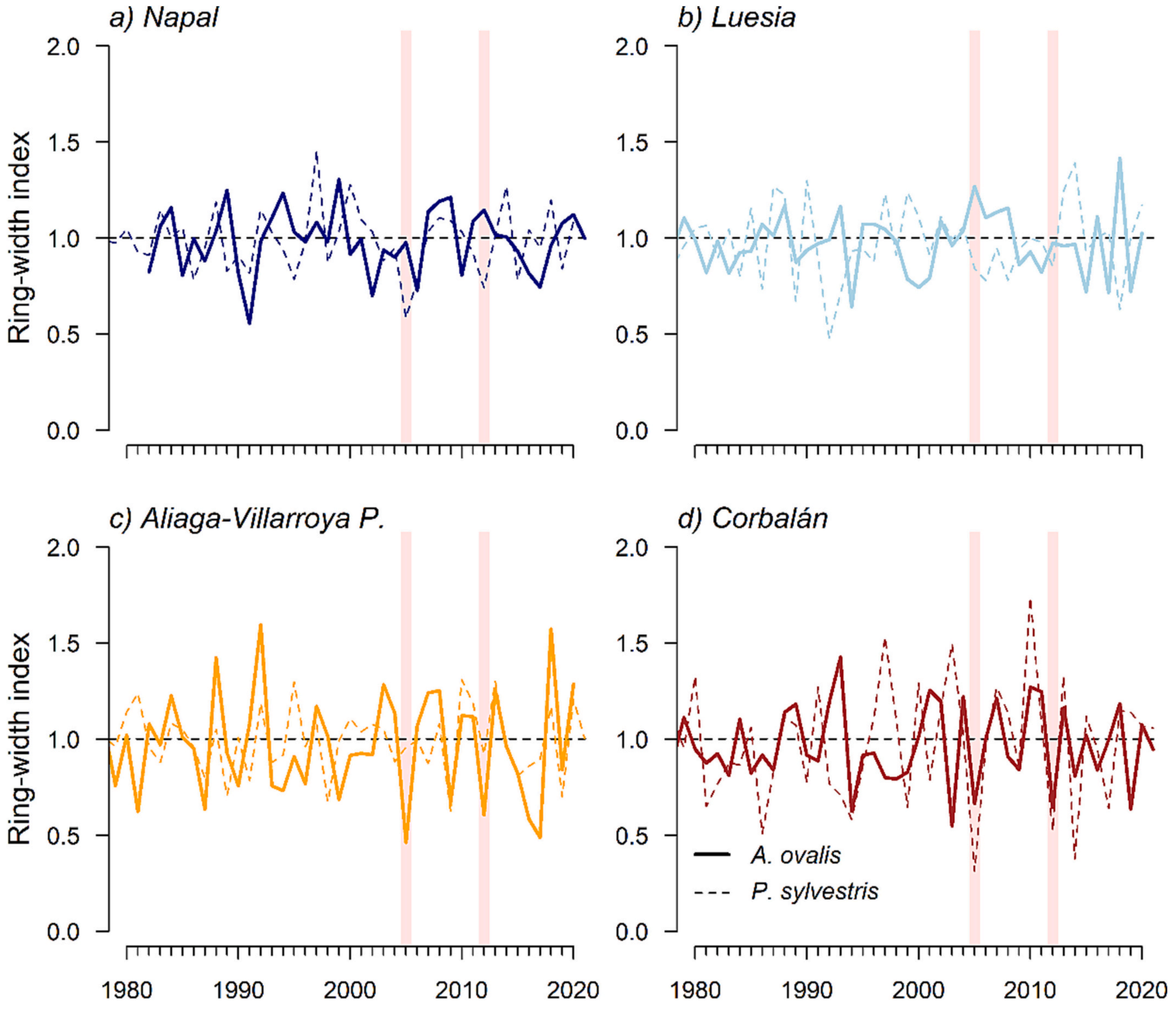

Fig. 3. Series of residual ring-width indices for each species (a, *A. ovalis*; b, *P. sylvestris*) in each site. Different sites are represented with different colors: AL – Aliaga-Villarroya de los Pinares, orange; CO – Corbalán, brown; LU – Luesia, light blue; NA – Napal, dark blue. Dashed lines are used for *P. sylvestris* and solid thicker ones for *A. ovalis*. The red vertical lines indicate the 2005 and 2012 droughts.

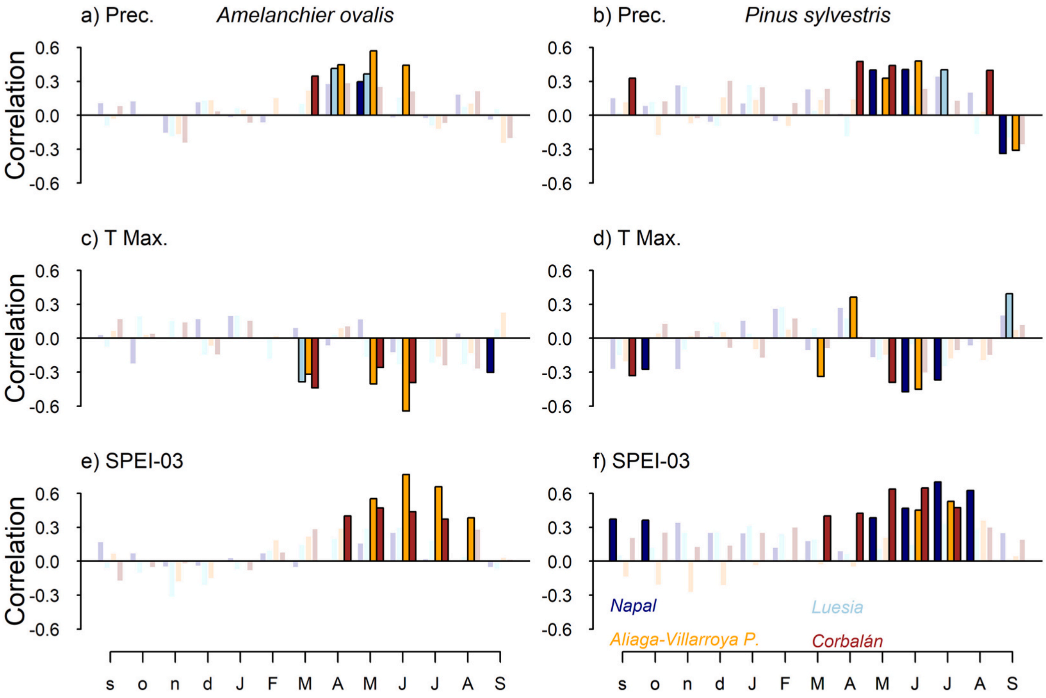

Fig. 4. Pearson correlations (bars) between *P. sylvestris* and *A. ovalis* ring-width chronologies with monthly total precipitation (Prec.), mean maximum temperature (Tmax.) and the 3-month SPEI. Different sites are represented with different colors. Significant correlations ($p. < 0.05$) are indicated in darker colors.

impacted by drought in the Aliaga-Villarroya de los Pinares site than in the other sites while the growth of *P. sylvestris* was more impacted by drought in Corbalán (Fig. 5; Table S6). Accordingly, differences between species in each site were only detected in Corbalán (higher response to drought for *P. sylvestris*) and Aliaga-Villarroya de los Pinares (higher response to drought for *A. ovalis*; Table S7).

Short-term responses to drought confirmed the stronger response of the two species to water shortage in the driest sites (Fig. 6; Table S8). Overall, resistance values varied around 1 for *A. ovalis* in Napal and Luesia, and for *P. sylvestris* in Aliaga-Villarroya de los Pinares and Luesia suggesting that drought impacts were minor in accordance with pointer year analyses (Fig. S5). Accordingly, the resistance of *A. ovalis* growth to the 2005 and 2012 droughts was lower in the dry Aliaga-Villarroya de los Pinares and Corbalán sites than in the wet Luesia and Napal sites. In

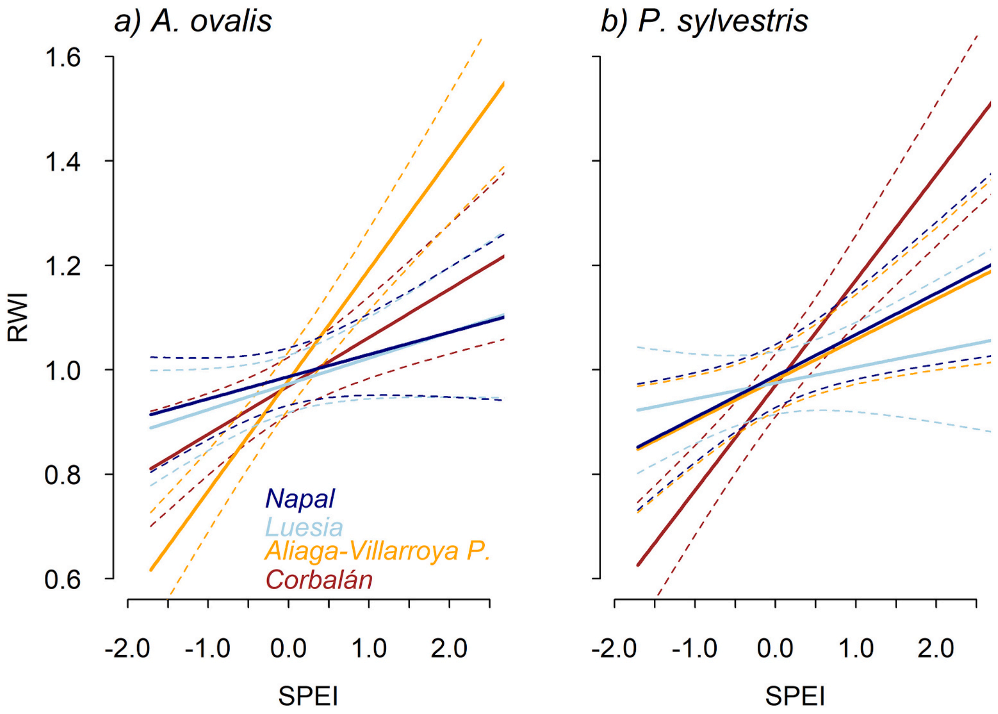

Fig. 5. Linear relationship between RWI and the 3-month July SPEI for each species in each site. For each species, the regression line (solid thicker line) and standard errors (dashed lines) are shown. Different sites are represented with different colors: AL, Aliaga-Villarroya de los Pinares, orange; CO, Corbalán, brown; LU, Luesia, light blue; NA, Napal, dark blue.

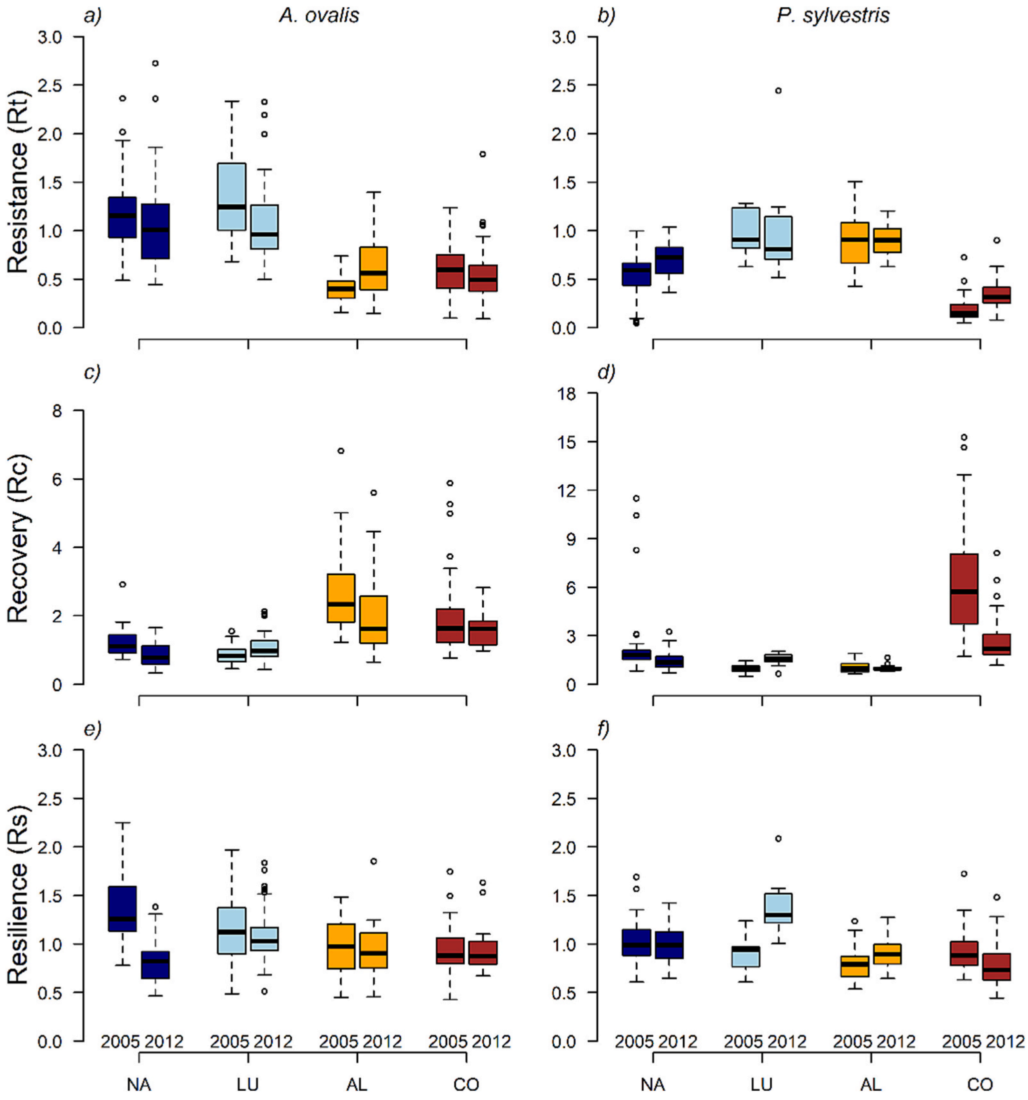

Fig. 6. Resilience components in the two dry years (2005 and 2012) for each species in each site. Different sites are represented with different colors: AL, Aliaga-Villarroya de los Pinares, orange; CO, Corbalán, brown; LU, Luesia, light blue; NA, Napal, dark blue. See Tables S8 and S9 for statistical comparisons.

2005, the resistance to drought was also lower in Aliaga-Villarroya de los Pinares than in Corbalán (Table S8). Temporal differences in resistance were found in Luesia and Aliaga-Villarroya de los Pinares but with different sign (Table S9). In the case of *P. sylvestris*, the highest resistance values were observed in Luesia and Aliaga-Villarroya de los Pinares (Fig. 6), and temporal differences pointed to a higher resistance to the 2012 drought as compared to the 2005 drought in Napal and Corbalán (Table S9). Overall, recovery had an inverse pattern than resistance being higher in the driest sites for *A. ovalis* (particularly for the 2005 drought in Aliaga-Villarroya de los Pinares), and in Corbalán for *P. sylvestris* (Fig. 6). Recovery varied between time in the two species (Table S9) but without a clear pattern. Regarding resilience, the response of *A. ovalis* to the 2005 drought was significantly higher in Napal than in Aliaga-Villarroya de los Pinares and Corbalán, and the lowest values were found in Corbalán (Fig. 6). However, the resilience to the 2012 drought displayed a different pattern, with Napal displaying the lowest values and Luesia the highest. Accordingly, the resilience values were lower in Napal for the year 2012 than for the year 2005 (Table S9). In *P. sylvestris*, the resilience to the 2005 drought was higher in Napal than in Aliaga-Villarroya de los Pinares, while in 2012 the resilience was higher in Luesia than in the rest of the sites being the lowest in Corbalán (Fig. 6; Table S7).

When comparing between species, the resistance to the 2005 and 2012 droughts was higher for *A. ovalis* than for *P. sylvestris* in all sites expect in Aliaga-Villarroya de los Pinares where a reverse pattern was found (Fig. S6; Table S10). In addition, differences in resistance between the two species in the 2012 drought were not significant in Luesia (Table S10). The recovery to the 2005 and 2012 droughts was higher for *P. sylvestris* than for *A. ovalis* in all sites excluding again Aliaga-Villarroya de los Pinares (Fig. S6; Table S10). However, these differences were not significant in Luesia during the 2005 drought. Resilience displayed different results in the 2005 and 2012 droughts. In 2005, the resilience was significantly higher for *A. ovalis* than for *P. sylvestris* in all sites except Corbalán (Table S10). In 2012, the resilience was higher for *P. sylvestris* than for *A. ovalis* in Napal and Luesia, while it was higher for *A. ovalis* than for *P. sylvestris* in Corbalán.

3.3. Modeling growth rates of trees and shrubs

Statistics showed that the model fits were reliable in all sites and species (Fig. 7), with higher correlations between measured and fitted series of RWI in the case of *P. sylvestris* (Table 2).

The VS-model fits in the period 1980–2020 (Table 2) and in the two dry years (2005, 2012) showed that growth was mainly limited by low soil moisture levels in August and September both in *A. ovalis* and *P. sylvestris* (Figs. 7, S3 and S4). In 2012, growth rates were very limited

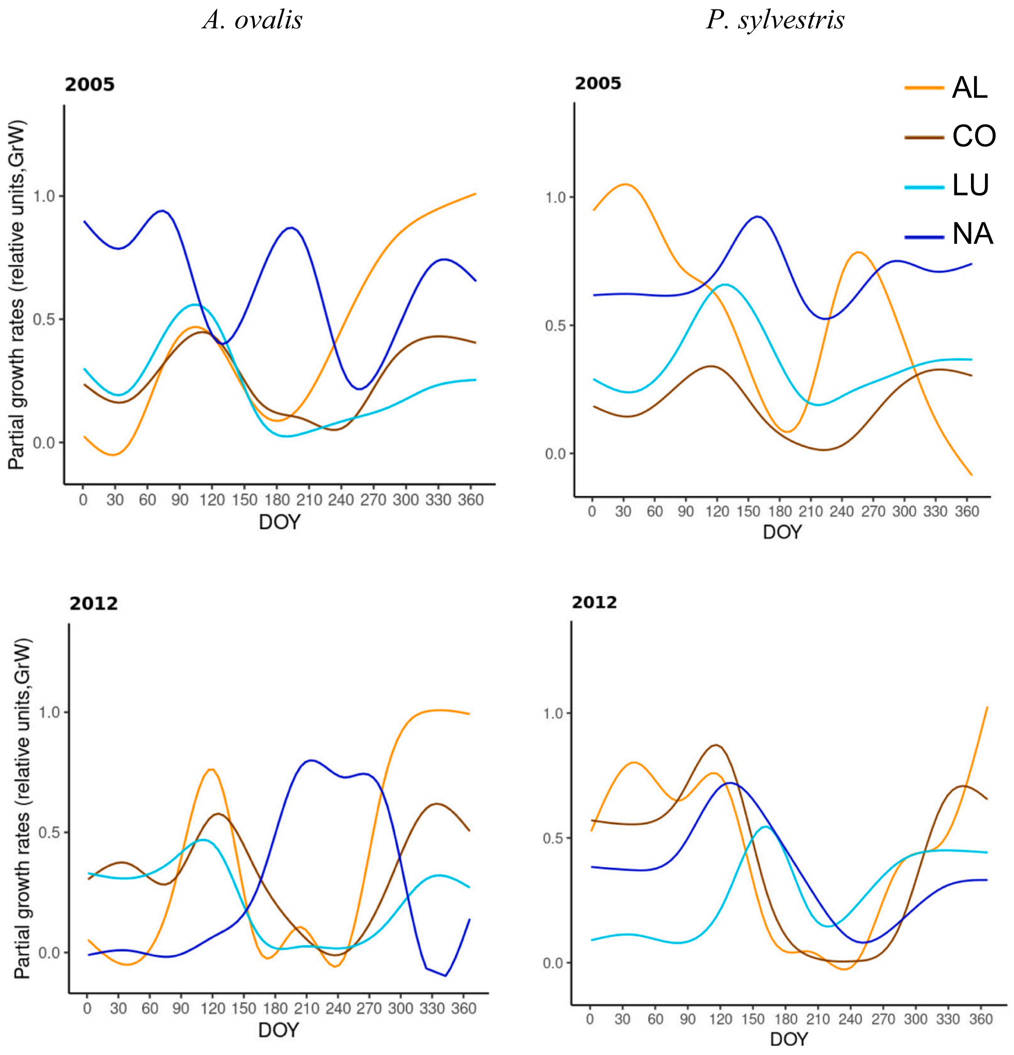

Fig. 7. Monthly partial growth rates of *A. ovalis* and *P. sylvestris* due to soil moisture (GrW) predicted by the VS- model in the two driest years (2005, 2012). Letters indicate study sites where the two species were sampled (AL, Aliaga-Villarroya de los Pinares; CO, Corbalán; LU, Luesia; NA – Napal).

Table 2

Coherence statistics of the indexed ring-width series based on the VS model and considering the complete (1980–2020), calibration (1980–2000) and verification (2001−2020) periods. Statistics are Pearson correlation coefficient (*r*), Gleichläufigkeit (Glk) and root-mean-square error (RMSE).

Site	Species	Timespan	Complete period 1980–2020			Calibration period (1980–2000)			Verification period (2001–2020)		
			r	Glk (%)	RMSE	r	Glk (%)	RMSE	r	Glk (%)	RMSE
Corbalán	*A. ovalis*	1980–2020	0.58	58	0.204	0.47	48	0.218	0.51	65	0.250
	P. sylvestris	1980–2020	0.83	83	0.251	0.80	67	0.241	0.92	95	0.262
Luesia	*A. ovalis*	1980–2020	0.41	63	0.239	0.43	76	0.245	0.33	45	0.243
	P. sylvestris	1980–2020	0.56	61	0.211	0.58	71	0.245	0.40	50	0.280
Napal	*A. ovalis*	1982–2020	0.45	58	0.256	0.30	58	0.288	0.54	55	0.246
	P. sylvestris	1980–2020	0.74	70	0.137	0.70	61	0.122	0.63	65	0.157
Aliaga-Villarroya de los Pinares	*A. ovalis*	1980–2020	0.53	76	0.203	0.56	52	0.219	0.85	75	0.178
	P. sylvestris	1980–2020	0.60	68	0.203	0.61	62	0.210	0.52	70	0.337

by low soil moistures levels during summer in the two dry sites (Aliaga-Villarroya de los Pinares, Corbalán).

4. Discussion

The occurrence of drought leaves an imprint in the radial growth of tree and accompanying shrub species along temperature and precipitation gradients as demonstrated for *A. ovalis* in this study. This shrub forms annual growth rings that can be identified, cross dated and measured (Figs. 2 and 3). Previous studies demonstrated that the phenology of this shrub species is constrained by water scarcity during summer in Mediterranean regions (Milla et al., 2005). Our results align with these studies and point to the importance of summer drought as a factor reducing the radial growth of this species particularly in drier and more continental sites (Figs. 4–7). As expected, the growth synchrony was higher in the case of *P. sylvestris* than in the case of *A. ovalis*. These results can be strongly contingent on the growth form because we compared a low-stature, multistemmed shrub vs. a tall, unistemmed tree (Götmark et al., 2016). However, this fact did not impair the ability to detect the impact of drought on *A. ovalis* growth (Fig. 6). The process-based VS model confirmed the dependency of *A. ovalis* growth on summer water availability, particularly in arid sites and during dry years (Fig. 7). In the driest sites, the low competition capacity of the winter deciduous *A. ovalis* in comparison with other evergreen shrubs and trees (Milla et al., 2005) can make its growth more dependent on precipitation seasonality than in wetter sites such as Napal and Luesia. However, caution is required when interpreting results since we do not have detailed information on the microsite conditions surrounding each sampled individual and the root system of the shrub species. Thus, further research is required to elucidate why drought reduced growth mainly in the two dry sites.

Our results concur with previous studies on the strong dependency of *P. sylvestris* growth on water availability (Martínez-Vilalta et al., 2009; Camarero et al., 2015b; Pretzsch et al., 2023). Besides, we found stronger growth reductions due to drought in arid sites which is consistent with some studies (e.g. Camarero et al., 2021a). However, climate-growth couplings did not show a stronger dependency of growth on drought in dry sites as could be expected giving that in the wet Napal site growth depended on summer precipitation too. These discrepancies could be attributed to site factors (e.g., soil type, topography) or to population- and individual-level factors that modulate growth responses to drought (e.g. Martínez-Vilalta et al., 2012; Serra-Maluquer et al., 2018). In the Napal site, greater soil nutrient availability can affect growth patterns modifying interspecific competition and thus enhancing the dependency of growth on water availability (Martínez-Vilalta et al., 2012; Bose et al., 2020). Alternatively, microsite conditions related with the presence of rocky outcrops can reduce soil water availability. Unfortunately, we do not have data on stand density, competition intensity or local soil conditions in the different sites which would have been of great utility to elucidate why the growth *of P. sylvestris* is so dependent on water availability in the wet Napal site. However, both short-term responses to drought events, regression models and results of the VS-model concur on the greater dependency of tree growth on drought in the driest Corbalán site. This is in line with our previous results that have revealed the occurrence of drought-induced mortality events in *P. sylvestris* as a consequence of climate change in that site (Camarero et al., 2015).

The results obtained for *A. ovalis* partially aligned with those obtained for *P. sylvestris* but with some differences. Overall, the inter-series correlations were higher for *P. sylvestris* than for *A. ovalis*. It is expected that the growth of shrubs will rely on microsite conditions more strongly than the growth of trees (Gazol and Camarero, 2012) due to the shorter stature of shrubs, the presence of multiple stems with narrower rings and lower conductive area (Treml et al., 2019) and a greater proportion of shallow fine roots (Yang et al., 2020). Besides, trees will be more exposed to changes in air temperature because they have longer vertical trunks and meristems and canopies more exposed to free air conditions (Körner, 2012; Fajardo et al., 2019). In general terms, the radial-growth rate (ring width) of *A. ovalis* does not vary in the same order of magnitude in which the growth of *P. sylvestris* does (Fig. 2; Table 1; Table S3). The two species have ample distribution gradients ranging from Northeastern to southwestern Eurasia (Martínez-Vilalta et al., 2009; Milla et al., 2005, 2010) but *A. ovalis* has a great capacity to thrive in Mediterranean environments, subjected to summer drought, while *P. sylvestris* extends more to boreal forests. Besides, the growth of *A. ovalis* is more limited by drought in the two dry sites studied as indicated by the correlation between RWI and SPEI (Fig. 5), the resilience indices (Fig. 6) and VS-model results (Fig. 7). Thus, the differences in growth variation between sites detected in the case of *P. sylvestris*, which were less apparent in the case of *A. ovalis*, will be caused by the different growth patterns of trees and shrubs (e.g. Götmark et al., 2016). In general, shrubs present stepper growth trajectories than trees meaning that they will be growing "as much as they can" irrespectively of site conditions blurring the differences in growth between sites. Trees like *P. sylvestris* forming conifer wood, mainly composed of tracheids, maintain a single trunk to support its entire canopy and connect it with roots through the stem sapwood. In contrast, shrubs like *A. ovalis* forming diffuse and semi-ring porous wood with different xylem cell types have multiple thin stems that can be renewed faster and substitute the main stem if xylem embolism occurs (Götmark et al., 2016; Treml et al., 2019). In addition, the shrub has more parenchyma tissue, thus having higher concentrations of non-structural carbohydrates in the wood which can be used as osmolytes during dry periods (Plavcová and Jansen, 2015; Morris et al., 2016). The interaction with other species is a factor that can also modulate the growth of both trees and shrubs in the studied sites but unfortunately, we lack these data.

Despite growth rates did not vary considerably between some sites, the growth response to drought of *A. ovalis* did, confirming that the growth of this species is negatively impacted by drought, at least in two of the studied sites (Fig. 4). We expected that the growth of *P. sylvestris* to be more tightly related to air temperature variations than the growth of *A. ovalis*, but our results do not show a clear pattern in this respect. Besides, a stronger dependency of *A. ovalis* growth on spring-summer precipitation would have been expected based on the dependency of shrub growth on microsite conditions (Gazol and Camarero, 2012; Yang et al., 2020). It has been suggested that the success of winter deciduous shrubs like *A. ovalis* in Mediterranean environments rely on their capacity to grow in spring avoiding the summer drought stress (Milla et al., 2005), which might explain the negative impacts of elevated temperatures during spring. Nevertheless, these results confirm that both elevated temperatures and water scarcity limit the radial growth of trees and shrubs.

We found stronger relationship between growth and the SPEI drought index in the dry sites (Figs. 4 and 5) and a stronger impact of the 2005 and 2012 droughts in these sites (Fig. 6), despite the studied shrubs were able to recover pre-drought growth levels. In the case of *P. sylvestris*, the relationship between growth and SPEI was also significant in Napal (Fig. 4). We speculate that the growth of *A. ovalis* will be more responsive to the drought index in these sites because of two reasons. First, since shrubs have fine roots and strongly depend on microsite conditions coupled to surface microclimate (Gazol and Camarero, 2012; Yang et al., 2020) their growth will be more limited in these two dry sites. Second, in Aliaga-Villarroya de los Pinares and Corbalán *A. ovalis* individuals were sampled in the understory of open, mixed stands which might increase the competition for soil water (Milla et al., 2005). Conversely, *A. ovalis* in Napal and Luesia were sampled in treeless sites which probably have different soil conditions. Testing these hypotheses will require a different sampling strategy characterizing microsite conditions and testing for the root exploring capacity of the species and accounting for any competition for light with overstory trees. Nevertheless, these limitations do not contradict our conclusions showing that the growth of *A. ovalis* is limited by drought in dry sites.

Mediterranean woody species tend to reduce their cambial activity during the summer drought as an adaptation to water scarcity (Camarero et al., 2010). In the case of trees and shrubs, this results in a bimodal growth pattern with two growth peaks in spring and autumn (e.g., Campelo et al., 2021; Valeriano et al., 2023b). The bimodal growth pattern is less frequently observed in temperate-boreal species such as *P. sylvestris* even when they grow in dry, continental sites (Camarero et al., 2010; Valeriano et al., 2023b). The VS-model has proven its ability to properly replicate bimodal growth patterns of both, trees and shrubs, and so the question that emerges here is whether *A. ovalis* is able to present a bimodal growth. The results suggest that the capacity to growth bimodally is facultative for this species (Fig. S3). In the driest sites, the growth of the two species occurs earlier and in the case of Aliaga-Villarroya de los Pinares a slightly bimodal pattern is observed. In the more temperate wet sites (Napal and Luesia), the growth of the two species extends during the early summer, particularly in the case of *A. ovalis*. These modeling results should be further checked using dendrometers (e.g., Dobbert et al., 2022) or through xylogenesis monitoring (e.g., Li et al., 2016).

5. Conclusions

Climate change is expected to increase the duration and intensity of drought, impairing tree and shrub growth and reducing the productivity of forests and scrublands. In such aridification scenario, trees could be replaced by more drought-tolerant shrubs leading to a transition from forests to woodlands or scrublands. Knowledge on how shrub species respond to drought in sites with contrasting climate conditions is fundamental to fill in this research gap. In this respect, species distributed along wide environmental and climatic gradients are important to track climate change impacts on vegetation. Giving its wide environmental gradient, from treeless sites at high elevation to sclerophyllous seasonally dry forests and open woodlands, *A. ovalis* has a strong potential to track changes in climate through the analysis of its annual growth rings. This study demonstrates the dendrochronological potential of *A. ovalis*, a widely distributed shrub species which often coexists with major tree species such as *P. sylvestris* and oaks. Monitoring the growth of shrub species at inter- and intra-annual scales is fundamental to understand the role they will play in a potentially warmer and drier future world where shrublands may expand and encroach as former pastures and croplands are abandoned.

CRediT authorship contribution statement

Antonio Gazol: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Cristina Valeriano:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **Michele Colangelo:** Writing – review & editing, Methodology, Data curation. **Ricardo Ibáñez:** Writing – review & editing, Data curation. **Mercedes Valerio:** Writing – review & editing, Data curation. **Álvaro Rubio-Cuadrado:** Formal analysis, Writing – review & editing. **J. Julio Camarero:** Writing – review & editing, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.170539.

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