



# Disentangling the role of sex dimorphism and forest structure as drivers of growth and wood density in expanding *Juniperus thurifera* L. woodlands

Raquel Alfaro-Sánchez<sup>1</sup> · Josep Maria Espelta<sup>2</sup> · Fernando Valladares<sup>3</sup> · Belén Acuña-Míguez<sup>3</sup> · Irene Martín-Forés<sup>4</sup>

Received: 17 February 2021 / Accepted: 23 August 2021 / Published online: 1 October 2021  
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## Abstract

**Key message** The dioecious tree species *Juniperus thurifera* L. is undergoing a spontaneous process of forest expansion in southwest Europe. We investigated how growth, climate sensitivity, and wood density varied simultaneously between sexes and among stages of expansion while accounting for the variability of forest structure. We found few sex-based differences but detected lower wood density, greater growth rates, and higher sensitivity to drought in expanding fronts compared to long-existing forests.

**Context** *Juniperus thurifera* L. (Spanish juniper) is a dioecious tree species undergoing a natural process of forest expansion in southwest Europe.

**Aims** To assess how radial growth and wood density are simultaneously shaped by sex-based differences, the stage of forest expansion (long-existing forests, transition zones, and expanding fronts), variability in forest structure, and climate (in the case of radial growth).

**Methods** We measured forest structure characteristics, tree rings, and wood density in 17 plots dominated by Spanish juniper in three stages of forest expansion in central Spain. We used linear mixed models (LMMs) to explore the main drivers of variability in radial growth and wood density and sex- and stage-based differences in climate-growth sensitivity.

**Results** Rather than by sex, growth and wood density were mainly shaped by the stage of forest expansion, forest structure variables that characterize these stages, and climate variables (in the case of growth).

**Conclusion** Sexual dimorphism had a minimal effect in growth and wood density in expanding Spanish juniper woodlands. Expanding fronts could be benefiting from land-use legacies in the abandoned fields they are colonizing, as reflected in higher growth rates and lower wood density, especially during years with less summer drought stress. However, this pattern could be reversed in the event of an increase in drought episodes.

**Keywords** Dioecy · *Juniperus thurifera* L. · Tree rings · Forest expansion · Spontaneous tree establishment · Abandoned fields · Mediterranean region

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Handling Editor: Shuguang (Leo) Liu

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This article is part of the topical collection on *Establishment of second-growth forests in human landscapes: ecological mechanisms and genetic consequences*

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**Contribution of the co-authors** Conceptualization: Irene Martín-Forés, Raquel Alfaro-Sánchez; Methodology: Raquel Alfaro-Sánchez, Irene Martín-Forés; Formal analysis and investigation: Raquel Alfaro-Sánchez; Writing—original draft preparation: Raquel Alfaro-Sánchez; Writing—review and editing: Josep Maria Espelta, Belén Acuña-Míguez, Irene Martín-Forés; Funding acquisition: Fernando Valladares; Supervision: Irene Martín-Forés

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Extended author information available on the last page of the article

## 1 Introduction

In recent decades, southwest Europe has experienced a significant expansion of Mediterranean and temperate tree species that differ in their tolerance to harsh environmental conditions: *Quercus robur* L., *Quercus ilex* L., *Fagus sylvatica* L., and *Juniperus thurifera* L. (Gimeno et al. 2012c; Bañnou et al. 2013; Vilà-Cabrera et al. 2017; Valdés-Correcher et al. 2019; Acuña-Míguez et al. 2020; Martín-Forés et al. 2020). European forests have undergone natural expansion—primarily into former cultivated areas—as a consequence of a rural exodus and the abandonment of traditional agricultural practices (Keenan 2015; Palmero-Iniesta et al. 2020; Hampe

et al. 2020). The vegetation dynamics of abandoned fields is driven by soil characteristics, climate conditions, and propagule availability (Tasser et al. 2007). Land-use legacies from previous agricultural practices including greater nutrient content (De Schrijver et al. 2011) or more decomposer activity (Freschet et al. 2014) facilitate the establishment of trees and shrubs during the initial period after colonization and give rise to increased tree growth (Lambin and Meyfroidt 2011; Gerstner et al. 2014). Recently expanding forests in Europe have reported greater growth rates than long-existing forests—even after accounting for the effects of age and competition—but lower wood density (Pretzsch et al. 2018; Alfaro-Sánchez et al. 2019, 2020). A reduction in wood density implies a greater number and surface area of conductive vessels that can modify the growth-climate sensitivity of trees (Greenwood et al. 2017). However, expanding forests of broadleaf species such as *F. sylvatica* have lower wood density but no significant differences in growth-climate sensitivity when compared to long-existing forests, probably because of the better growth conditions present in the former croplands they are colonizing (Alfaro-Sánchez et al. 2019). Yet, little is known about the response in growth, wood density, or climate sensitivity in expanding tree species of other functional types such as the evergreen Mediterranean conifer *J. thurifera* (but see Gimeno et al. 2012c).

The *J. thurifera* (Spanish juniper) is a dioecious species of tree that is endemic to North Africa and the Iberian Peninsula (Blanco and Castro 1997), recognized under the European Habitats Directive. It is drought-tolerant and under continental climates tends to grow in low densities (Olano et al. 2008). It is well adapted to rocky, poorly developed soils (Gauquelin et al. 1999) and has been shown to increase in secondary growth under harsh climatic conditions (Granda et al. 2014). The Spanish juniper is currently undergoing wide-ranging expansion and densification processes in certain areas of central Spain (Blanco and Castro 1997; Thompson 2005), whereas in other areas, it is facing competition from other fast-growing tree species including pines and oaks (Olano et al. 2012). Since the middle of the nineteenth century, the expansion of Spanish juniper woodlands has been facilitated by the progressive abandonment of the traditional management of wood-pasture systems and the existence of a diverse dispersal community that ensures seed availability and the frugality of the species (Thompson 2005; Escribano-Avila et al. 2012). The expansion of Spanish juniper woodlands in central Spain has created a mosaic of forest patches ranging from long-existing stands to expanding fronts. Most of these expanding fronts are composed of young juniper trees, and their performance and survival under current and future climate hazards remain unknown.

Sexual dimorphism in secondary (non-reproductive) sexual characteristics (e.g., growth, vigor, and physiology) has been

reported in many dioecious trees, including Spanish juniper (Gauquelin et al. 2002; Montesinos et al. 2006; Rozas et al. 2009; Juvany and Munné-Bosch 2015). Previous studies of Spanish juniper woodlands differ regarding the presence of sexual dimorphism in radial growth and climate-growth sensitivity: differences between sexes were found for these traits by Montesinos et al. (2006), Rozas et al. (2009), Olano et al. (2015), and DeSoto et al. (2016), but no evidence was found by Gimeno et al. (2012c). In fact, as a response to environmental heterogeneity, in dioecious plants, sex-based variation in non-reproductive traits may be more limited than intraspecific variation (e.g., Anderson et al. 2014). Thereby, the inclusion of forest structure variables as covariates in experimental design may improve our understanding of the trade-offs between growth and reproduction (Obeso 2002; McKown et al. 2017).

In this study, we assessed whether or not radial growth and wood density in juniper woodlands undergoing a natural process of forest expansion in southwest Europe are simultaneously influenced by (i) sex-based differences, (ii) the stage of forest expansion, and (iii) the variables of forest structure that characterize each stage (e.g., tree density, age, and size). We also explored sex- and stage-based differences with regard to climate-growth sensitivity. We studied a unique mosaic of patches of Spanish juniper in central Spain that, to the best of our knowledge, contains the largest number of Spanish juniper trees in this hotspot for this species (90% of its world distribution is located in Spain, Blanco and Castro 1997). In these patches, a mix of young and mature junipers grow along a gradient of forest expansion, from low-density areas in expanding fronts to relatively dense areas in long-existing stands. We hypothesized that sex-based differences in growth would increase with cambial age due to the increase with age of reproductive costs in females (Montesinos et al. 2012). Given the findings of previous studies on the effect of land-use legacies on growth, wood density, and climate-growth sensitivity (Alfaro-Sánchez et al. 2019), we expected greater growth, lower wood density, and higher climate sensitivity in both female and male junipers in the expanding fronts that are colonizing former croplands. Overall, our results should help understand how variation in forest structure—in this case, mainly derived from the processes of forest expansion into abandoned fields—can influence the expression of secondary differences between sexes in Spanish juniper woodlands, which ultimately will help their future preservation.

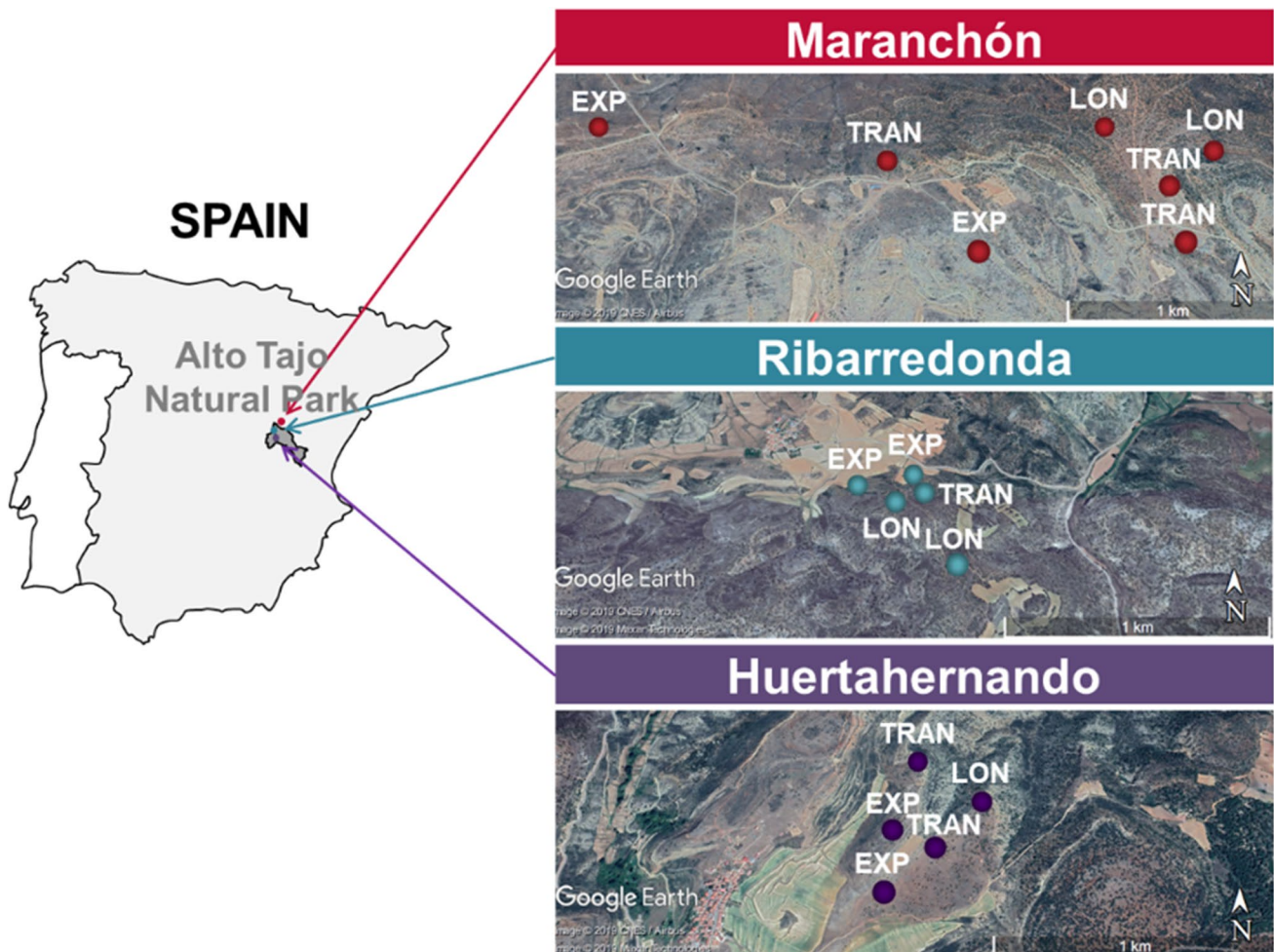
## 2 Methods

### 2.1 Study area

This study was conducted in central Spain in the Alto Tajo Natural Park and surrounding areas (Fig. 1). The climate of

this area is continental Mediterranean, characterized by hot dry summers and cold winters. Mean annual temperature and precipitation were 10.7 °C and 462 mm for the period 1950–2017, respectively (KNMI Climate Explorer; <http://climexp.knmi.nl/>). We selected three sites with unmanaged and well-preserved juniper woodlands, in which the Spanish juniper is the dominant tree species. Maranchón is the northernmost site, followed by Ribarredonda and then Huertahernando to the south (Fig. 1). The maximum distance between sites was 30 km along an elevation gradient of 1000–1300 m a.s.l. Seventeen plots were established at these three sites along a gradient of forest expansion: seven plots in Maranchón and five plots in both Ribarredonda and Huertahernando (Fig. 1). The gradient of forest expansion was separated into three stages, namely, long-existing forests, expanding fronts, and transition zones. The stages were identified by previous studies of the area based on the comparison of land-cover maps dating back

to the 1950s (Escribano-Avila et al. 2012; Gimeno et al. 2012c; Vilellas et al. 2020; Acuña-Míguez et al. 2020). We defined long-existing forests as patches containing cores of well-preserved juniper woodlands that existed in 1956. The expanding fronts correspond to areas of recent colonization characterized by scattered trees located on former agricultural land. The transition zones were intermediate forests between these two extremes of gradient. All three forest stages were represented at all three sites (Fig. 1). It is important to note that the three age categories were defined by the land-use age and not by the age of trees in the stand, as in previous studies (Başnou et al. 2013, Alfaro-Sánchez et al. 2019). Therefore, long-existing juniper patches in the area do not necessarily have a tree age structure that is characteristic of old-growth forests and may even have been disturbed by thinning or fires recently, so young trees are also present in these patches.



**Fig. 1** Location of the three sampling sites (Maranchón, Ribarredonda, and Huertahernando) in central Spain in the Alto Tajo Natural Park and surrounding areas. The gradient of forest expansion is indi-

cated for each plot (EXP, expanding front; TRAN, transition zone; LON, long-existing forest)

## 2.2 Field sampling

Exhaustive field sampling was conducted in autumn 2017. In total, we georeferenced 816 juniper trees in the study plots. Due to the differences in tree density among forest stages, plot areas were flexible to be able to sample a minimum of 35 adult trees per plot (Table 1). We visually identified the sex of all the selected individuals when they had male flowers or female cones and considered these trees to be reproductive individuals. If the tree did not have flowers or cones, we scored it as a tree of unknown sex. The 451 trees identified as reproductive at the time of sampling had a minimum size threshold of trunk diameter at breast height of  $\geq 3$  cm and total height of  $> 1.40$  m. Above this size threshold, we found that only 5.5% of trees were of unknown sex.

We determined the mean tree density per plot and measured the quadratic diameter (QD, calculated as the square root of the sum of square diameter at breast height of each stem of a tree; Stewart and Salazar 1992), the maximum tree height (measured with Haglöf Vertex IV hypsometer), and the average crown diameter calculated as the mean of the projection of two perpendicular axes passing through the axis of the trunk (measured with a Haglöf DME distance measurer).

## 2.3 Wood density and tree growth measurements

We only measured the wood density and tree growth of the 451 reproductive trees. We extracted two increment cores 50 cm from ground height using a Pressler increment borer (0.5 cm; Haglöf, Långsele, Sweden). One of these two cores was used to estimate wood density ( $\text{g cm}^{-3}$ ), following Williamson and Wiemann (2010), which is calculated as the dry weight of the full core (including heartwood and softwood) divided by its saturated volume (see also Alfaro-Sánchez

et al. 2019, 2020). We used the second cores to count and measure annual ring widths. They were air-dried, glued onto wooden mounts, and polished using sandpaper of progressively finer grain until tree rings were visible. The cores were dated with a stereomicroscope and scanned at 2400 d.p.i. We measured ring widths to an accuracy of 0.001 mm using the CooRecorder v9.3 software (Cybis Elektronik 2018). The dataset is available in Alfaro-Sánchez et al. 2020. The cross-dating of individual series was checked using the CooRecorder and COFECHA programs (Holmes 1983). For subsequent climate-growth analyses, individual tree ring width series were detrended with cubic smoothing splines of 10 years to remove non-climatic growth trends related to the increase in tree age and size (Cook and Kairiukstis 1990). A comparison between detrended methods is shown in Figs. 6 and 7.

## 2.4 Climate sensitivity

Sums of the monthly mean temperatures and precipitation were accessed for the period 1950–2017 from the homogenized and quality-checked E-OBS v.17.0 dataset (Haylock et al. 2008) in the KNMI Climate Explorer (<http://climate.knmi.nl/>). Our study sites are spatially located in two different E-OBS v.17.0 grid cells, Maranchón in one and Ribarredonda and Huertahernando in another. Given the proximity of the sites, we averaged the climate data from these two grid cells at  $0.25^\circ$  spatial resolution for use in subsequent analyses. We calculated the drought index SPEI (standardized precipitation-evapotranspiration) using the R package SPEI (Vicente-Serrano et al. 2010) with a time scale of 3 months, based on temperature and precipitation data from E-OBS v.17.0. Lower values of SPEI correspond to greater drought stress.

**Table 1** Plot and tree characteristics at different sites and stages along the forest expansion gradient

Site (lat., long.)	Gradient	Plots	n	Plot area (ha)		Sex		Tree density (trees $\text{ha}^{-1}$ )		Tree age*		QD (cm)		Height (m)		Crown diameter (m)		Number of stems	
				Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Maranchón (41.06, -2.20)	Long	2	59	0.58	0.17	0.6	0.5	115	14	50	19	24	15	6	1.9	5.5	2	2.4	1.8
	Transition	3	86	0.84	0.32	0.6	0.5	71	29	33	13	15	9	4.1	1.2	4.2	1.4	2.4	1.7
	Expanding	1	30	1.35		0.7	0.5	32		26	8	11	5	3.8	0.7	3.8	1	2	1.1
Ribarredonda (40.87, -2.30)	Long	2	56	0.42	0.03	0.6	0.5	125	9	46	14	21	10	5.7	1.4	4.9	1.7	2.4	1.9
	Transition	1	28	0.35		0.7	0.4	123		26	10	12	8	4.6	1.5	3.6	1.8	1.5	1.1
	Expanding	2	48	0.83	0.2	0.8	0.4	49	8	28	12	12	7	4.4	1.2	3.8	1.3	1.6	1.1
Huertahernando (40.83, -2.28)	Long	1	29	0.6		0.6	0.5	89		33	11	23	10	5.5	1.1	6	1.4	3	2
	Transition	2	58	1	0.5	0.6	0.5	68	34	30	14	18	9	4.9	1.3	5	1.5	2.5	1.5
	Expanding	2	57	1.8	0.05	0.6	0.5	22	1	23	7	14	7	4.1	1.1	4.4	1.5	1.7	1.1

QD: quadratic mean diameter; sex: female = 0, male = 1.

\*Tree age is estimated as the number of rings measured per core. The total tree age of trees is expected to be older.

To assess the effect of climate on growth, we ran linear regression models (LMs) at tree level between detrended ring width series and climate variables. The considered climate variables were monthly and seasonal (combination of several consecutive months) temperatures and SPEI-3 from September of the previous growing season to September of the year in which the ring was formed. We calculated the percentage of trees with significant slopes for each of the climate variables considered in the LMs to identify the month or season with the highest temperature-growth and drought-growth sensitivity, that is, the average February–April temperatures and August SPEI-3 (see “Results” section). We used these two climate variables as explanatory variables in the linear mixed effects models (LMMs) in the subsequent analyses of climate-growth sensitivity (see the following sections).

## 2.5 Statistical analyses

We used ANOVAs to test for differences in tree density and the proportion of sexes in stages of forest expansion and at sites (significance level was set at  $p < 0.05$ ). We used LMMs and generalized linear mixed effects models (GLMMs) to assess how tree characteristics varied between sexes and among stages of forest expansion and sites. Specifically, LMMs were used to model the following dependent variables: tree age, QD, height, and crown diameter; a generalized linear mixed effects model (GLMM) with a Poisson regression was used to model the number of stems. For all models (LMMs and GLMM), the explanatory variables were sex, stages of forest expansion, and site. Plot was included as a random effect. We used Tukey–Kramer post-hoc analysis for multiple comparisons in the R package *lsmeans* (Lenth 2016) to identify specific differences in tree age, QD, height, crown diameter, and number of stems among the three stages of forest expansion and at sites and between sexes for each stage and site.

We used LMMs to assess how wood density and annual growth varies between sexes, among stages of forest expansion, and is associated with forest structure. Specifically, for the wood density LMM, the explanatory variables were sex, stage of forest expansion, site, QD, number of stems (*nstems*), tree density (TD), and tree age. To determine if wood density varied between sexes or among stages in terms of tree age, we included in the model the interactions between tree age with sex and stages of forest expansion. Plot was included as a random effect. For the growth LMM, the dependent variable, annual growth, was transformed with a natural logarithm to conform to normality. The explanatory variables were sex, stage of forest expansion, site, QD, number of stems, tree density, cambial age, February–April temperature (T), and August SPEI-3 (SPEI-3). To determine if growth varied between sexes or among stages

with age, we included the interactions between cambial age with sex and stages of forest expansion. Cambial age is the age of the sampled cores, where the first year corresponds to the first tree ring outside the pith. To determine if climate-growth sensitivity varied between sexes and among stages, we included the interactions between February–April temperature and August SPEI-3 with sex and stages. To allow for comparisons among stages of forest expansion, annual growth was restricted to the first 35 years of life of the trees, the maximum period of time in which the three stages overlapped with a minimum of five trees at each site (see Fig. 8). Tree individuals nested in plot was included as a random effect to compensate for the repeated measures taken from an individual tree. A first-order autocorrelation structure (AR1) was also included in the growth LMM to control for the temporal autocorrelation of growth measures.

In both the wood density and growth models, the explanatory variables were standardized to eliminate differences in scale measurements. Crown diameter, tree height, and QD were highly correlated, and so to avoid collinearity, we only included QD in the models. We compared alternative full-saturated models including linear or spline adjustments (up to two degrees of freedom) for each continuous predictor and selected the adjustment used in the model with the lowest AIC. We then checked for collinearity within the predictor variables included in the two selected full-saturated models (including linear or spline adjustments for the continuous variables) using variance inflation factors (VIF) with the performance R package (Lüdecke et al. 2020); we found VIF scores  $\leq 10$ , which indicates a lack of collinearity (Kock and Lynn 2012). A full model for wood density (WD) would look like this in R syntax (considering linear adjustments for the continuous variables, Eq. 1):

$$\begin{aligned} \text{lme}(\text{WD} \sim \text{Sex} + \text{Stage} + \text{Site} + \text{QD} \\ + \text{nstems} + \text{TD} + \text{Age} + \text{Age} \times \text{Sex} \\ + \text{Age} \times \text{Stage}, \text{random} = \sim 1|\text{Plot}, \\ \text{data} = \text{dataset}, \text{method} = \text{'ML'}) \end{aligned} \quad (1)$$

A full model for log-transformed growth ( $\log[\text{Growth}]$ ) would look like this in R syntax (considering linear adjustments for the continuous variables, Eq. 2):

$$\begin{aligned} \text{lme}(\log[\text{Growth}] \sim \text{Sex} + \text{Stage} + \text{Site} + \text{QD} \\ + \text{nstems} + \text{TD} + \text{Cambial age} + \text{T} + \text{SPEI} \\ - 3 + \text{Cambial age} \times \text{Sex} + \text{Cambial age} \times \\ \text{Stage} + \text{T} \times \text{Sex} + \text{T} \times \text{Stage} + \text{SPEI} \\ - 3 \times \text{Sex} + \text{SPEI} - 3 \times \text{Stage}, \\ \text{random} = \sim 1|\text{Plot}/\text{Tree}, \\ \text{correlation} = \text{corCAR1}(\text{form} = \sim 1|\text{Plot}/\text{Tree}), \\ \text{data} = \text{dataset}, \text{method} = \text{'ML'}) \end{aligned} \quad (2)$$

Next, the models were reduced to those with the lowest Akaike Information Criterion (AIC) (the best or most parsimonious models) using the dredge function from the *MuMIn* R package (Barton 2019). The method was set to maximum likelihood (ML) during the fixed effect model selection phase, although the final models are presented using restricted maximum likelihood (REML) (Kuznetsova et al. 2017). Model fits were checked visually to ensure that they conformed to model assumptions. We calculated marginal (i.e., the proportion of variance explained by fixed effects) and conditional (i.e., the proportion of variance explained by fixed and random effects)  $r^2$  with the *sjPlot* R package (Lüdtke 2021). All statistical analyses were performed using R version 3.5.1 (R Core Team 2019).

### 3 Results

Tree density increased gradually from the sparse expanding fronts (28 trees  $\text{ha}^{-1}$ ) to the relatively dense (for juniper woodland) long-existing forests (116 trees  $\text{ha}^{-1}$ ). The transition zone showed no significant differences in tree density (83 trees  $\text{ha}^{-1}$ ) with either the expanding fronts or the long-existing forests (Fig. 2a). No significant differences were found in tree density among sites (Fig. 9a).

The proportion of male trees doubled that of female trees in the three stages of forest expansion and at all three sites, i.e., ~60% of trees were male and ~30% females (Fig. 2b, 9b). The highest proportion of unknown sex trees (9%) was detected in the expanding front (Fig. 2b) and at Ribarredonda (Fig. 9b), probably due to a higher proportion of younger trees (Fig. 10a, f).

Female trees were significantly older and taller and had greater QDs, more stems per tree, and larger crown diameters than male trees for each stage of forest expansion and site (Fig. 10). The long-existing forests had significantly older and taller trees, greater QDs, and larger crown diameters than the trees in the transition zone and the expanding front (Fig. 10a, c–e, Table 1; Acuña-Míguez et al. 2020). The long-existing forests also had significantly more stems

per tree than the expanding fronts; the transition zone showed no significant differences when compared to the other two stages (Fig. 10b, Table 1). We found no significant differences among sites for the variables tree age, number of stems, QDs, or height, although larger crown diameters were found in Huertahernando, the southernmost site (Fig. 10f–h, Table 1).

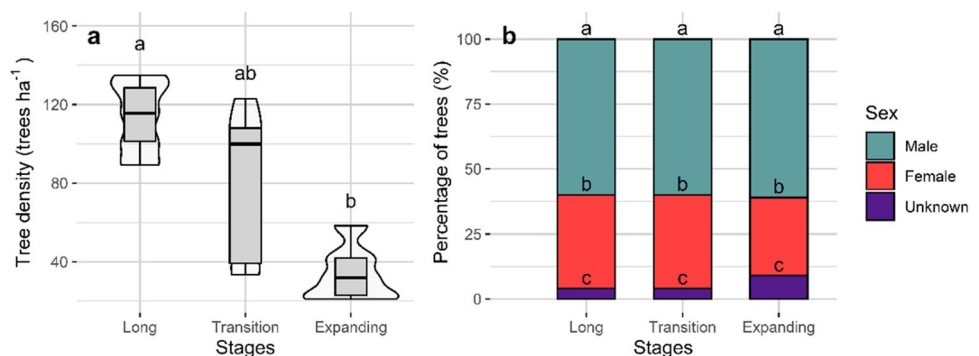
#### 3.1 Wood density patterns

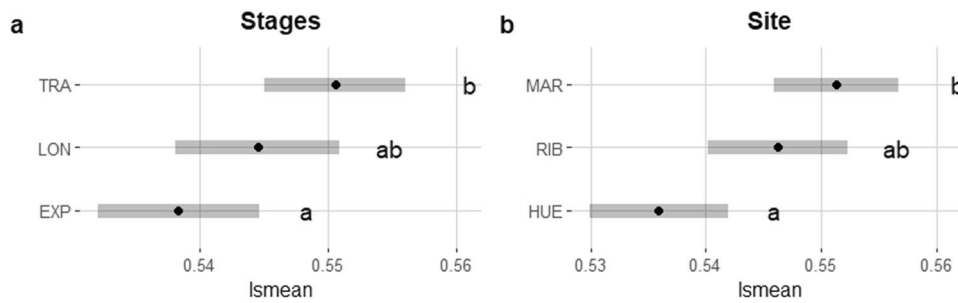
Wood density increased with tree age, decreased with QD, and varied among stages of forest expansion and sites. Post-hoc analysis confirmed significantly lower wood density in the expanding front and at the southernmost site (Huertahernando) compared to the transition zone and the northernmost site (Maranchón), respectively. The long-existing forests and Ribarredonda showed no significant differences in wood density compared to the other two stages and sites, respectively (Table 2, Fig. 3).

**Table 2** Wood density LMM coefficients. The marginal and conditional  $r^2$  are also shown. The level site: Maranchón and the level stage: expanding is included in the intercept. SE standard error. Plot was included as a random effect in the model, but the within-group variance (or residual variance,  $\sigma^2$ ) and the between-group variance (or random intercept variance,  $\tau_{00}$  Plot) were effectively 0

Predictors	Estimates	SE	p
(Intercept)	0.545	0.004	<0.001
Quadratic diameter	-0.003	0.002	0.097
Age	0.010	0.002	<0.001
Site [Ribarredonda]	-0.005	0.004	0.218
Site [Huertahernando]	-0.015	0.004	<0.001
Stage [Transition]	0.012	0.004	0.003
Stage [Long]	0.006	0.005	0.202
Marginal $r^2$ /conditional $r^2$	0.14/0.14		

**Fig. 2** Variations in tree density (violin and boxplots) for each stage of forest expansion (a). Sex percentage for each stage of forest expansion (b). All sampled juniper trees were considered ( $n=816$ ). The significant differences among stages of forest expansion (a) and between sexes at each stage of forest expansion (b) are denoted by small letters





**Fig. 3** Post-hoc differences among stages of forest expansion (a) and sites (b) derived from the wood density LMM. Black circles indicate the least square (LS) mean. Error bars indicate the 95% confidence

interval of the LS mean. EXP, expanding front; TRAN, transition zone; LON, long-existing forest; MAR, Maranchón; RIB, Ribarronda; HUE, Huertahernando

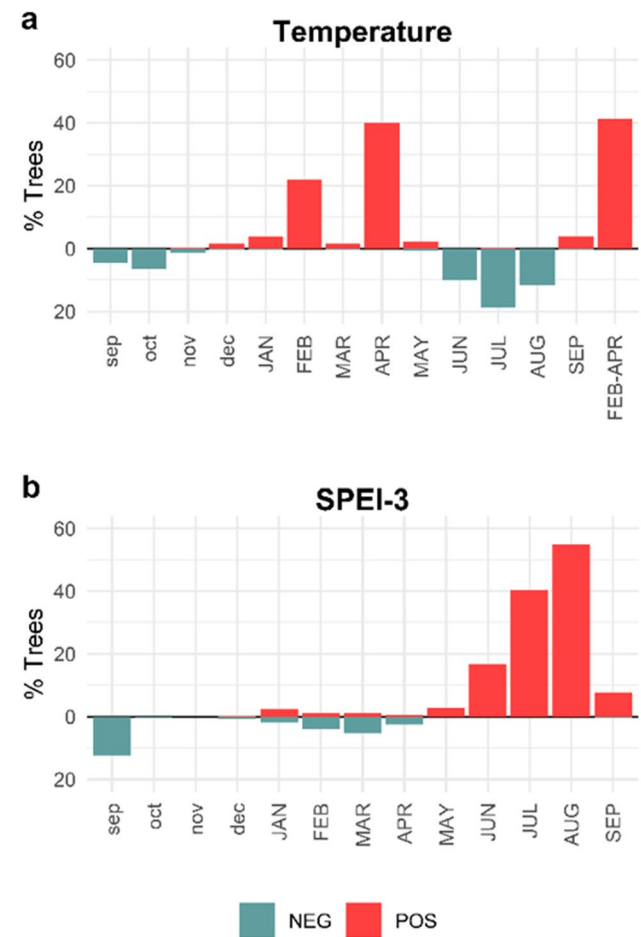
### 3.2 Climate-growth sensitivity and annual growth patterns

We found a higher percentage of trees showing a positive response in tree ring growth in years with high February–April temperatures (~41% of trees) and August SPEI-3 (~52% of trees; Fig. 4).

Growth in trees increased with warmer temperatures, under low drought stress, and with greater QD and cambial age during approximately the first 20 years of life but showed a slightly negative trend during the final 15 years of the study period. Growth decreased with tree density and the number of stems per tree. We found greater growth in Spanish junipers in the expanding front than in the transition zone and the long-existing forests, particularly after the first 20 years of life of the trees. In the expanding front, Spanish junipers also showed higher growth under low drought stress conditions compared to the trees growing in the other two stages. We found a minimal difference in climate-growth sensitivity between sexes. Males showed higher growth sensitivity to early spring temperatures (February–April) than females; i.e., males grew more during years with warmer early spring temperatures. Females showed higher growth sensitivity to summer drought; that is, females grew more during years with less drought stress. Sex-based differences were almost indiscernible when we plotted the model predictions (Table 3, Fig. 5). Climate variables, QD, and the interaction between cambial age and stages of forest expansion were the best explanatory variables for the growth LMM (Table 3, Fig. 5a, d).

## 4 Discussion

In this study, we investigated how radial growth and wood density were influenced by sex, the stage of forest expansion, and variability in forest structure. We also explored sex-based and stage-based differences in climate-growth sensitivity. The stage of forest expansion and the variability



**Fig. 4** Percentage of trees showing positive (POS, red bars) or negative (NEG, blue bars) responses in growth to monthly and seasonal temperature and SPEI-3 variables. The positive or negative slopes ( $p < 0.05$ ) obtained for each individual tree in linear regression models between detrended growth and climate variables

in forest structure found among stages—i.e., tree density, age, and tree diameter—had a much greater effect on growth and wood density of junipers than sex. Specifically, trees

**Table 3** Growth LMM coefficients. Marginal and conditional  $r^2$  are also given. The level stage: expanding is included in the intercept. *SE* standard error.  $\sigma^2$  is the residual variance.  $\tau_{00}$  Tree and  $\tau_{00}$  Plot are the between-group variance for the random effects tree and plot, respectively

Predictors	Estimates	SE	p
(Intercept)	-0.341	0.118	<b>0.004</b>
QD [1st degree]	1.205	0.147	<b>&lt;0.001</b>
QD [2nd degree]	0.475	0.222	<b>0.033</b>
Number of stems [1st degree]	-0.584	0.11	<b>&lt;0.001</b>
Number of stems [2nd degree]	-0.058	0.196	0.768
Tree density	-0.113	0.066	0.112
Cambial age [1st degree]	1.879	0.103	<b>&lt;0.001</b>
Cambial age [2nd degree]	0.417	0.087	<b>&lt;0.001</b>
FEB-APR T	0.072	0.005	<b>&lt;0.001</b>
AUG SPEI-3	0.108	0.006	<b>&lt;0.001</b>
Sex [male]	0.006	0.037	0.867
Gradient [transition]	0.133	0.133	0.338
Gradient [long]	0.39	0.177	<b>0.048</b>
FEB-APR T $\times$ sex [male]	0.013	0.006	<b>0.027</b>
AUG SPEI-3 $\times$ sex [male]	-0.011	0.005	<b>0.047</b>
AUG SPEI-3 $\times$ gradient [transition]	-0.014	0.006	<b>0.026</b>
AUG SPEI-3 $\times$ gradient [long]	-0.034	0.006	<b>&lt;0.001</b>
Cambial age [1st degree] $\times$ gradient [transition]	-0.515	0.138	<b>&lt;0.001</b>
Cambial age [2nd degree] $\times$ gradient [transition]	-0.396	0.108	<b>&lt;0.001</b>
Cambial age [1st degree] $\times$ gradient [long]	-1.363	0.143	<b>&lt;0.001</b>
Cambial age [2nd degree] $\times$ gradient [long]	-0.472	0.102	<b>&lt;0.001</b>
<b>Random effects</b>			
$\sigma^2$	0.25		
$\tau_{00}$ Tree	0.15		
$\tau_{00}$ Plot	0.27		
Marginal $r^2$ /conditional $r^2$	0.22/0.43		

in the expanding fronts had higher growth rates and lower wood density than junipers in the transition zone and long-existing forests. The positive response in growth found in the expanding fronts increased more during summers with low drought stress than in the other two stages.

#### 4.1 Sex-based differences in expanding juniper woodlands

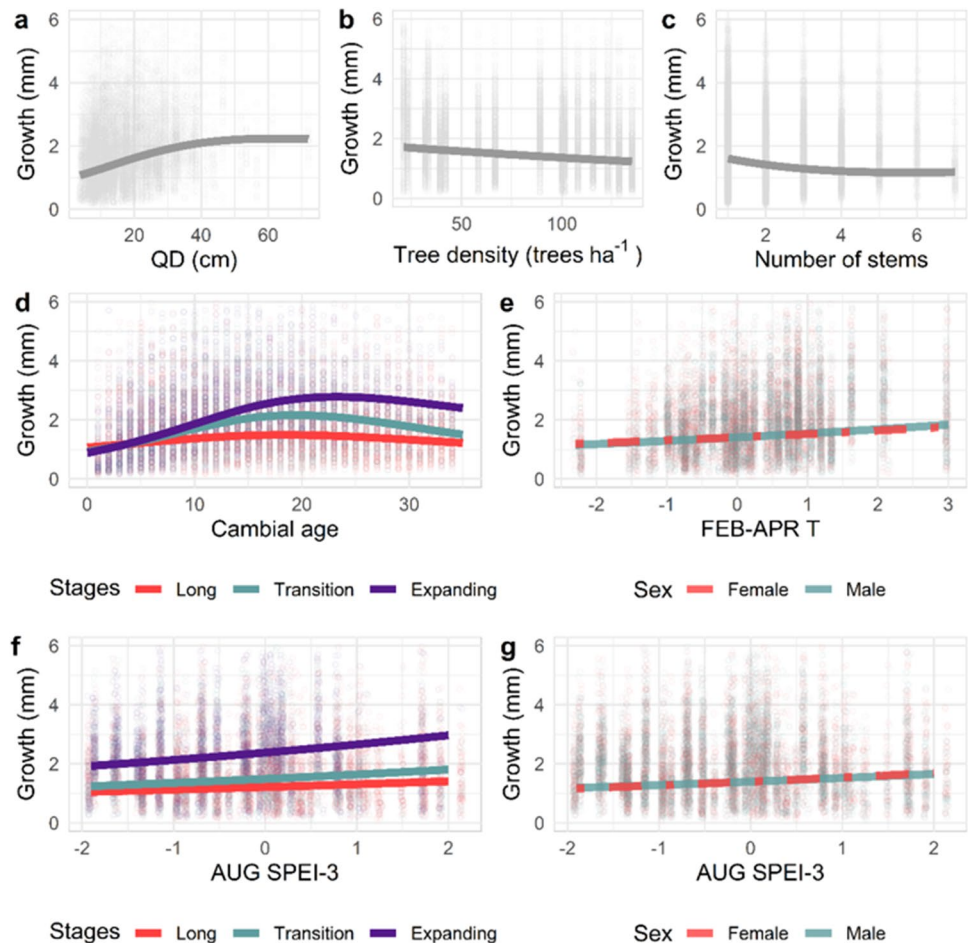
It is important to know whether sex effects on growth and density exist in Spanish juniper stands to improve our understanding of compensatory mechanisms (or trade-offs) between growth and reproduction. A higher proportion of male trees were found in all three stages of forest expansion and at all three sites, suggesting that Spanish juniper stands in central Spain are male-biased. Similar results have been found in other studies conducted in juniper stands in central Spain (Gimeno et al. 2012c), Morocco, and the Pyrenees (Gauquelin et al. 2002). In young populations, these results can be explained simply because males begin to flower earlier than females and consequently can be identified more readily (Gauquelin et al. 2002). However, male-biased sex ratios are also commonly found in more stressful

environments (Ortiz et al. 2002; Barrett et al. 2010) and have been associated with the greater cost of reproduction for females trees (Vasilias and Aarssen 1992; Montesinos et al. 2012). Compensatory mechanisms for the higher reproductive cost in females such as greater photosynthetic capacity or water-use efficiency (WUE; Dawson and Bliss 1989; Olano et al. 2015; Rozas et al. 2009) have been identified as the most likely explanation for this paradox (Tozawa et al. 2009). Nevertheless, no evidence of sex-related differences in WUE was found in a previous study conducted at our study sites (Acuña-Míguez et al. 2020).

Females outperformed males in height, QD, number of stems, crown diameter, and age, irrespectively of the stage and site considered. Females invested more resources in vegetative height growth than males (Gauquelin et al. 2002) as their larger canopies, consisting of a greater number of stems, allow them to bear a large number of cones that may enhance their reproductive capacity. Our results showed minimal sex-based differences in wood density and growth. Specifically, we found that males may grow slightly more than females during years with warmer early spring temperatures, whereas females may grow more than males during years with low summer drought stress. However,



**Fig. 5** Growth LMM predictions as a function of QD (**a**), tree density (**b**), and the number of stems per tree (**c**). Growth LMM predictions for the three stages of forest expansion during the first 35 years of life of the trees (cambial age) (**d**) and for August SPEI-3 (**f**). Growth LMM predictions for female and male individuals in terms of February–April temperatures (**e**) and August SPEI-3 (**g**). Individual growth values are shown with circles. Note that the lower values of SPEI correspond to greater drought stress



when plotting the predictions of our models, sex-based differences were almost indiscernible (Fig. 5e, g). Hence, we suggest taking into account tree size or other relative growth response variables in forest structure in sex dimorphism models for a better understanding of the impact of sex on the performance of dioecious species (Obeso 2002).

Previous studies reporting sex-based differences in Spanish juniper radial growth and climate-growth sensitivity have reached divergent conclusions regarding which sex performs best in each of these traits. For instance, some authors report greater growth in males than in females (Gauquelin et al. 2002; Montesinos et al. 2006), whereas other studies found greater growth and higher summer precipitation-sensitivity in females (Rozas et al. 2009). Sex-based differences with regard to climate may be site-dependent (Olano et al. 2015; DeSoto et al. 2016), with females growing more than males under less restrictive environmental conditions, or age-dependent (Rozas et al. 2009) as young females are more sensitive to drought conditions. Given the great reproductive effort of Spanish juniper females (Montesinos et al. 2012), we hypothesized that sexual dimorphism in secondary growth in Spanish junipers should occur from early stages onwards. By contrast, the interaction between sex

and cambial age was not selected in the most parsimonious growth model, suggesting that there are no significant differences in annual growth rates before or after the trees become reproductive. During early stages, negligible differences in reproductive resource investment is evident for the lack of sex-based differences that we found (McKown et al. 2017). The Spanish junipers in our study system, although reproductive, are relatively young. Thus, we cannot rule out the possibility that sex-related differences in secondary growth may be modified during ontogeny due to physiological adjustments (Rozas et al. 2009).

#### 4.2 Main drivers of growth and wood density in expanding juniper woodlands

Less trait divergence has been reported in dioecious species adapting to new environmental conditions (Arbuthnott et al. 2014), which is consistent with the expansion that the Spanish juniper woodlands are currently undergoing in central Spain. Rather than sex, the main drivers of radial growth and wood density were the specific stage of forest expansion (and the variables of forest structure that characterize each stage) and climate (in the case of growth). We found

greater growth rates at the expanding front, followed by the transition zone and the long-existing forest (differences that became evident at approximately 10 years of age, Fig. 5d). Growth decreased with tree age, higher tree density (Rozas et al. 2009; Gimeno et al. 2012c), and the number of stems per tree. The Spanish juniper is a multi-stemmed species, and we show here that annual growth increased in trees with fewer stems. In unmanaged stands, long-existing forests tend to have more stems because, given the lack of logging or browsing by livestock, older trees have more stems. A reduction in growth in multi-stemmed individuals has been observed in other resprouting species and is attributed to the preferential investment of resources in height growth owing to the competition for light among stems (see Espelta et al. 2003). Favorable climatic conditions, i.e., warm spring temperatures and wet summers, enhance annual growth in Spanish junipers (Rozas et al. 2009; Gimeno et al. 2012a). Relatively high temperatures at the beginning of the growing season stimulate earlier cambium reactivation and so enhance growth (Begum et al., 2008). Despite the excellent adaptation in Mediterranean tree species to drought, constraints in water availability during the growing season can result in markedly less growth that lasts for several years (e.g., Anderegg et al. 2015; Gazol et al. 2018). Therefore, growth in Spanish junipers could be severely reduced by the increase in the frequency and severity of drought episodes projected for southwest Europe, particularly in the highly sensitive expanding fronts.

As hypothesized, the expanding fronts had greater positive responses in growth during years with greater water availability than the other stages of forest expansion (Gimeno et al. 2012c). Similar results have been found for other tree species developing on former agricultural land (Alfaro-Sánchez et al. 2019). We suggest that growth is mediated by nutrient limitations (Forrester 2015) deriving from the tree density and land-use legacies found at each of the stages of forest expansion. Indeed, the expanding fronts had lower tree densities, followed by the transition zone and the long-existing forests. Furthermore, Gimeno et al. (2012c) found no clear nucleation in some of the expanding fronts studied here but did detect clumped patterns in the long-existing forests. The clumping patterns, mostly attributable to perching and nursing effects in adult trees, could have increased competition for resources in junipers growing in these relatively dense long-existing patches. By contrast, the lower tree density in the expanding front ( $\sim 28$  trees  $\text{ha}^{-1}$ ) has the effect of reducing intraspecific competition and facilitating greater exposure to light, which is reflected in higher growth rates. Increased or stable growth at increased intrinsic water use efficiency (WUE) has been reported in recent decades in juniper woodlands elsewhere (Granda et al. 2014). Previous studies analyzing the spontaneous establishment of secondary forests have reported

greater WUE than in long-existing forests owing to changes in certain functional attributes (e.g., higher leaf mass per area) and greater nitrogen availability stemming from the former agricultural use (Guerrieri et al. 2021). Indeed, in our study area, Acuña-Míguez et al. (2020) found increased WUE in the expanding fronts that was mainly related to their lower vegetation cover and younger age. As such, our results agree with the general pattern that trees growing under low competitive stress have higher growth rates, greater WUE, and a better response in growth to high water availability (e.g., Linares et al. 2009; Sánchez-Salguero et al. 2015). Rozas et al. (2009) showed that growth-climate sensitivity in Spanish junipers is higher in earlier life stages. Here, we accounted for a possible age effect when comparing sexes (females are significantly older than males) and among stages of forest expansion (the expanding fronts and transition zone were significantly younger than the long-existing forests) by restricting our analyses to the first 35 years of cambial age. Thus, we can rule out any possibility that sex- and stage-based differences in the growth response to climate variability are caused by an age effect.

Tree and cambial age also affect wood density (Franceschini et al. 2013). Specifically, our results showed a decrease in mean wood density with tree age. Tree ring density chronologies show that larger rings are associated with a decrease in mean wood density (Lundgren 2004). As such, years with high water availability increased tree ring growth and decreased mean ring density (Franceschini et al. 2013), particularly in younger trees. The expanding fronts had less wood density than the transition zone and the long-existing forests, even after accounting for age effects. Greater densities are thought to be less vulnerable to cavitation (Hacke et al. 2001). However, the rapid growth of expanding forests enables the development of large vessels that could increase the risk of cavitation during periods of continuous drought (Lambers et al. 2008).

### 4.3 Land-use legacies

Expanding juniper woodlands are mainly colonizing adjacent former agricultural land that was abandoned in recent decades as a result of the rural exodus towards urban nuclei. Spontaneous tree establishment in abandoned fields in the Mediterranean region has proved to benefit from increased soil nitrogen levels deriving from their previous agricultural use (Nadal-Romero et al. 2018; Guerrieri et al. 2021). Recently expanding forests have been reported to enhance growth rates but lower wood density in comparison with long-existing forests, even after accounting for age and competition effects (Alfaro-Sánchez et al. 2019). Similarly, the expanding fronts of Spanish juniper are probably benefiting from land-use legacies inherited from the former croplands (De Schrijver et al. 2011; Vilà-Cabrera et al. 2017; Alfaro-Sánchez et al. 2019), as is confirmed by the greater survival rate of saplings

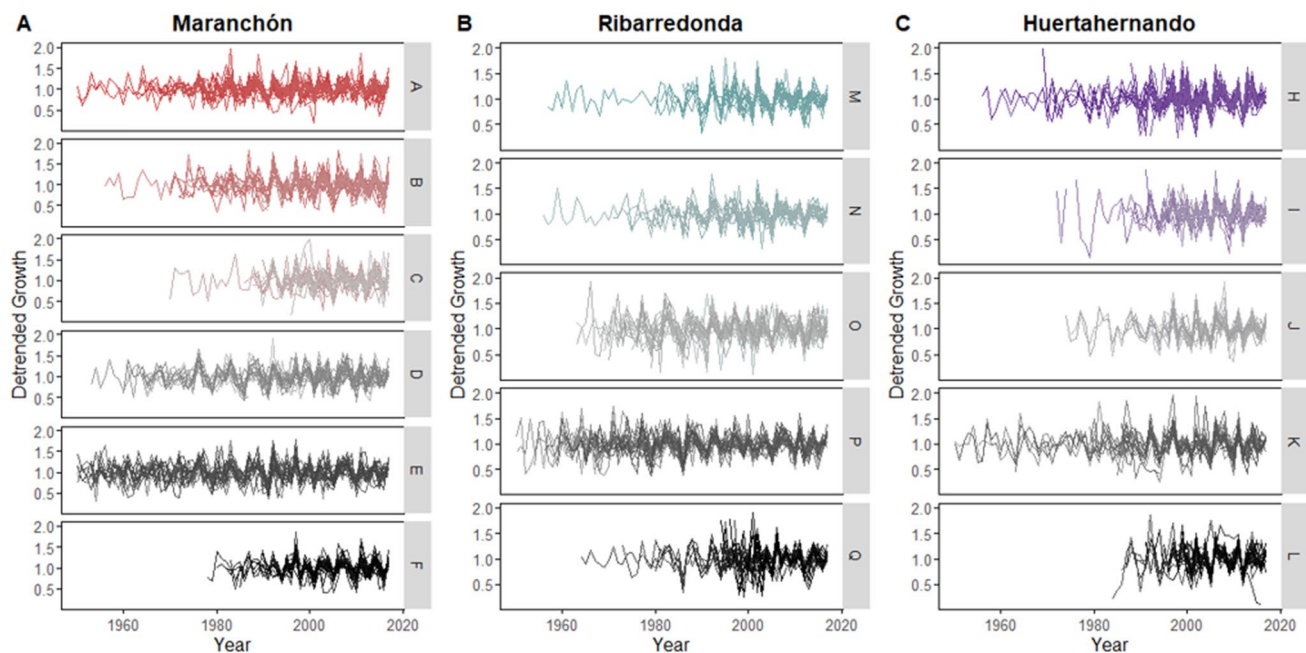
(Gimeno et al. 2012b), higher WUE (Granda et al. 2014; Acuña-Míguez et al. 2020), and the greater growth rates and lower wood density values reported at the expanding fronts in this study. Greater vigor and survival rates in the expanding fronts of Spanish junipers have been related to environmental differences between expanding and long-existing forests (Gimeno et al. 2012b), i.e., better soil water-retention capacity in former agricultural fields due to plowing (Flinn and Marks 2007). However, our study lacked soil nutrient content information for each of the stages of forest expansion. Further studies should assess differences in nitrogen content among stages of forest expansion in Spanish junipers to help understand the specific drivers of the reported stage-based differences in growth, wood density, and climate sensitivity.

## 5 Conclusions

In this study, we assessed the simultaneous effect of sex, forest expansion stage, and forest structural characteristics on radial growth and wood density and explored sex- and stage-based differences in climate-growth sensitivity. We found that sex had only a minimal effect on the first stages of growth in Spanish junipers (the first 35 years of cambial age) and showed that radial growth, wood density, and climate sensitivity varied among stages of forest expansion, mainly due to the different structural characteristics of the forests found in each of the stages. By restricting our analyses to the first 35 years

of cambial age, we ruled out the possibility that stage-based differences in growth and climatic sensitivity are caused by an age effect. Instead, we suggest that expanding fronts of Spanish juniper are benefitting from a combination of lower intraspecific competition found in the expanding patches and land-use legacies stemming from the abandoned fields they colonize, as is shown by higher growth rates and lower tree densities. Our results also reveal that the different intraspecific competition found in the stages of forest expansion mediate tree growth response to climate variability under adverse weather conditions. As such, the greater intraspecific competition in long-existing forests (which, as reported in other studies, show clumping patterns and lower WUE) is causing a lower positive response in growth during years with low drought stress compared to the other two stages. Assessing how growth, wood density, and climate-growth sensitivity varied among three stages of forest expansion—i.e., the long-existing forests, expanding fronts, and transitions zones—will improve our understanding of the dynamics of Spanish junipers undergoing a natural process of forest expansion. It will also ultimately help in their future preservation and, in particular, prevent risks associated with any increase in the severity and number of drought episodes in the Mediterranean region.

## Appendix



**Fig. 6** Detrending growth at individual level using cubic smoothing splines of 10 years for the three studied sites and a negative exponential method

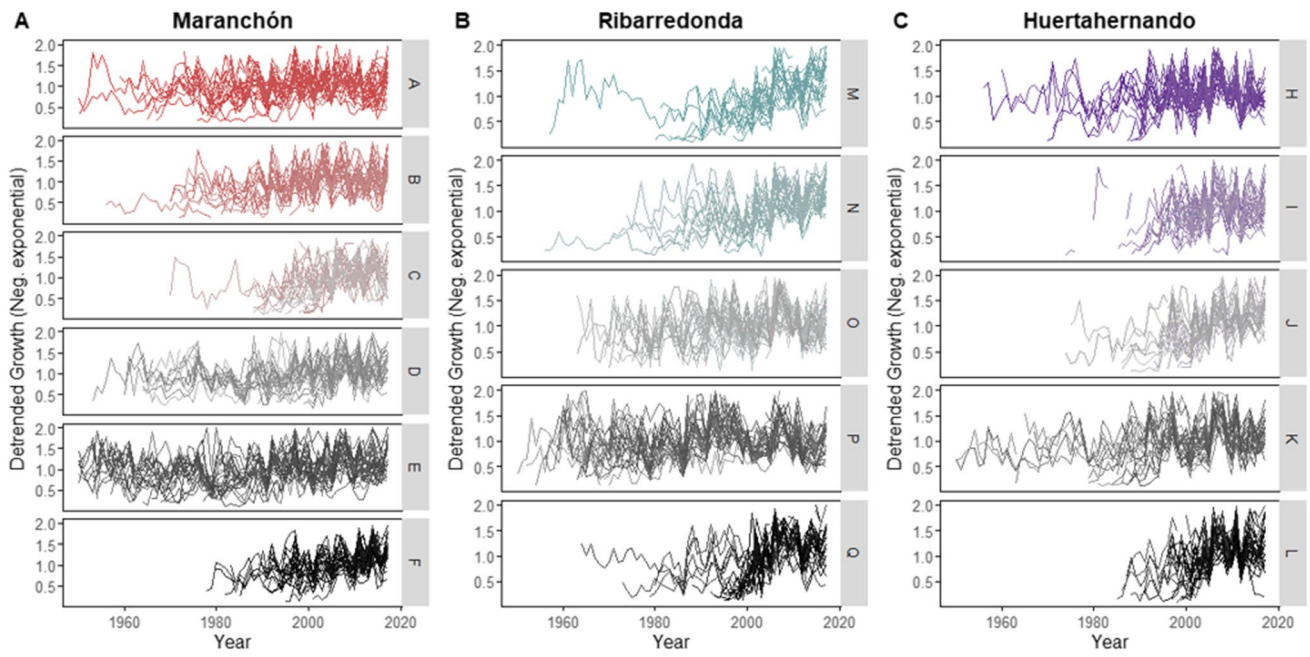
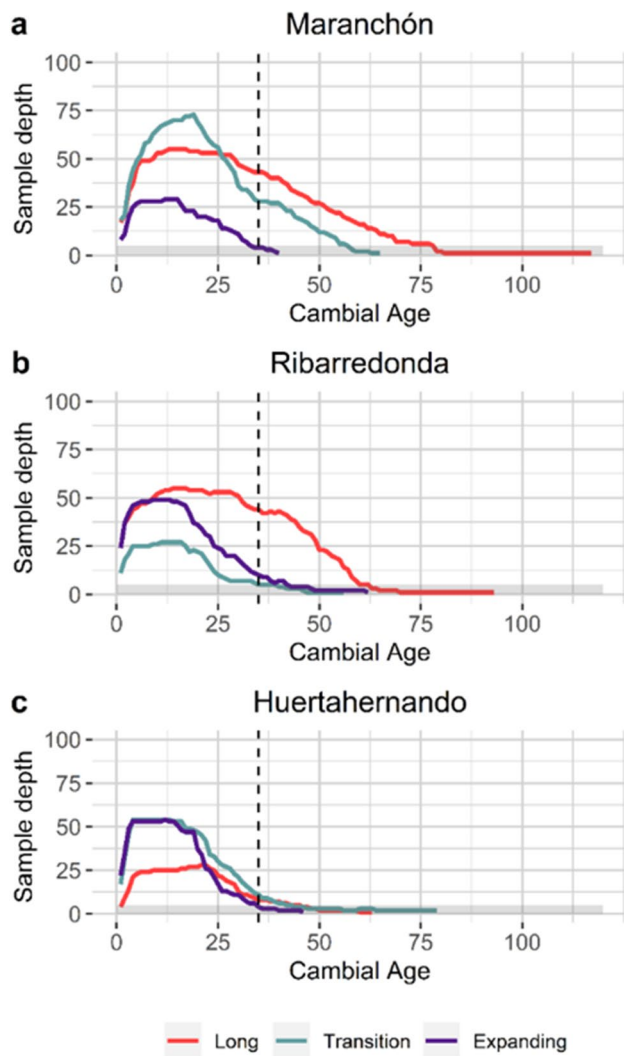
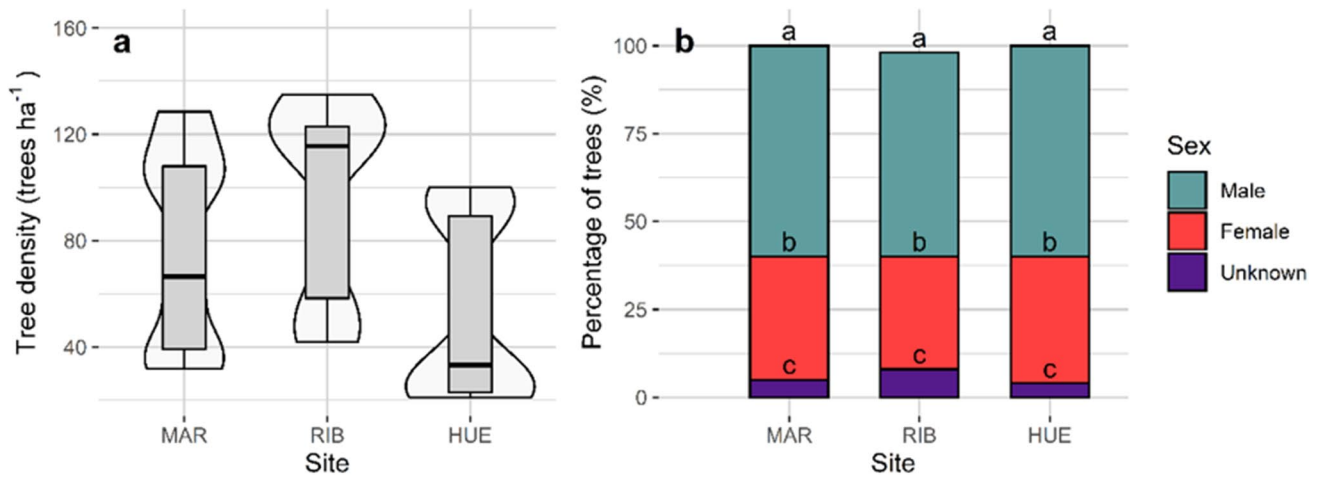


Fig. 7 Detrending growth at individual level using the negative exponential method for the three studied sites

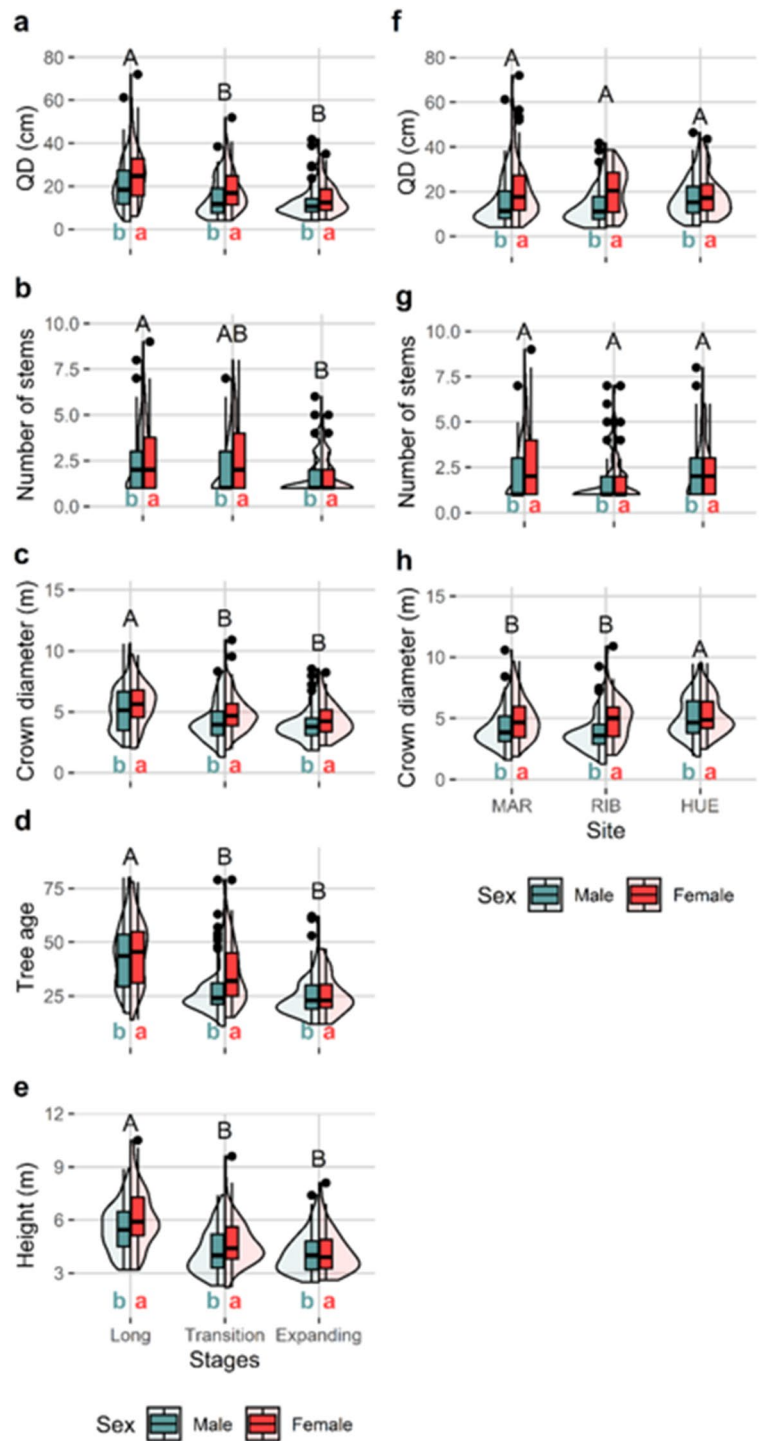


**Fig. 8** Sample depth for the three stages of forest expansion and site. The dashed line indicates the 35 years of cambial age. The gray area indicates a sample depth of 5 trees



**Fig. 9** Tree density variations (violin and boxplots) for each site (a). Percentage of trees per sex for each site (b); all sampled juniper trees were considered ( $n=816$ ). Significant differences between sexes at each site (b) are denoted by small letters

**Fig. 10** Violins and boxplots displaying differences in reproductive trees ( $n=451$ ) among stages of forest expansion and at sites for the following variables: tree age (a, f), number of stems per tree (b, g), quadratic diameter (QD, c, h), height (d, i), and crown diameter (e, j). The capital letters indicate significant differences among stages of forest expansion or at sites, while the lowercase letters indicate significant differences between sexes obtained in post-hoc tests from LMMs (Table 4)



**Table 4** LMM coefficients for the following dependent variables: tree age, number of stems per tree, quadratic mean diameter (QD), height, and crown diameter using only reproductive trees ( $n = 451$ ). The variable QD is log-transformed. The marginal and conditional  $r^2$  is also provided (delta for number of stems). The levels sex: female; site: Maranchón, and gradient: long-existing are included in the intercept

Predictors	QD [log]			Number of stems			Crown diameter			Tree age			Height		
	Estimates	SE	p	Estimates	SE	p	Estimates	SE	p	Estimates	SE	p	Estimates	SE	p
(Intercept)	3.08	0.10	< 0.001	2.90	0.27	< 0.001	5.54	0.23	< 0.001	45.64	2.90	< 0.001	5.99	0.24	< 0.001
Gradient [transition]	-0.39	0.11	< 0.001	0.88	0.09	0.179	-0.99	0.24	< 0.001	-13.15	3.81	0.001	-1.29	0.30	< 0.001
Gradient [expanding]	-0.53	0.11	< 0.001	0.71	0.08	0.002	-1.38	0.26	< 0.001	-18.34	3.99	< 0.001	-1.50	0.32	< 0.001
Sex [male]	-0.22	0.05	< 0.001	0.85	0.06	0.012	-0.51	0.15	0.001	-2.83	1.17	0.015	-0.42	0.13	0.001
Site [Ribaredonda]	-0.06	0.11	0.564	0.81	0.09	0.050	-0.27	0.25	0.277						
Site [Huertahernando]	0.18	0.11	0.101	1.04	0.10	0.696	0.84	0.24	< 0.001						
<b>Random effects</b>															
$\sigma^2$	0.28			0.38			2.33			131.82			1.56		
$\tau_{00}$ Plot	0.02			0.01			0.07			34.92			0.20		
Marginal $r^2$ /conditional $r^2$	0.18/0.24			0.09/0.11			0.18/0.21			0.26/0.42			0.22/0.30		

**Acknowledgements** We are especially grateful for the help, advice, and support provided by David López-Quiroga, José Miguel Olano, Adrián Escudero, Pablo Álvarez, Esteban Manrique, Eduardo Serna and Miguel Díaz. We are also thankful to José Antonio Lozano, director of the Alto Tajo Natural Park, for facilitating the research at the park.

**Funding** This study was funded by the grants SPONFOREST (BiodiversA3-2015–58), PCIN-2016–055 (financed by the Spanish Research Agency (AEI) and the Spanish Ministry of Economy, Industry and Competitiveness (MINECO)), COMEDIAS (MINECO, CGL2017-83170-R), and REMEDINAL TE (Ref. TE-CM. S2018/EMT-4338, 2019–2023-Comunidad de Madrid).

**Data availability** The dataset used in the current study will be available on Figshare after a 1-month embargo period in this link: <https://doi.org/10.6084/m9.figshare.14806683.v1>.

The provisional link to download the data during the embargo period is <https://figshare.com/s/d42a29f95da711d586a5>.

**Declarations**

**Consent for publication** All authors gave their informed consent to this publication and its content.

**Conflict of interest** The authors declare no competing interests.

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## Authors and Affiliations

Raquel Alfaro-Sánchez<sup>1</sup>  · Josep Maria Espelta<sup>2</sup> · Fernando Valladares<sup>3</sup> · Belén Acuña-Míguez<sup>3</sup> · Irene Martín-Forés<sup>4</sup>

✉ Raquel Alfaro-Sánchez  
r.alfarosanchez@gmail.com

Josep Maria Espelta  
josep.espelta@uab.cat

Fernando Valladares  
valladares@ccma.csic.es

Belén Acuña-Míguez  
belacumig@gmail.com

Irene Martín-Forés  
imfores@pdi.ucm.es

<sup>1</sup> Department of Biology, Wilfrid Laurier University, 75  
University Avenue W, Waterloo, ON N2L 3C5, Canada

<sup>2</sup> Centre de Recerca Ecològica i Aplicacions Forestals,  
CREAF, Bellaterra (Cerdanyola de Vallès), 08193 Catalonia,  
Spain

<sup>3</sup> Departament of Biogeography and Global Change, National  
Museum of Natural Sciences, Spanish Council for Scientific  
Research, CSIC, C/Serrano, 115dpdo, 28006 Madrid, Spain

<sup>4</sup> School of Biological Sciences, The University of Adelaide,  
Adelaide, South Australia 5005, Australia