



# Evaluating tree-to-tree competition during stand development in a relict Scots pine forest: how much does climate matter?

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Received: 29 March 2020 / Accepted: 19 February 2021  
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## Abstract

**Key message** Competitive interactions change over time and their influence on tree growth is intensified during drought events in marginal Scots pine populations.

**Abstract** Competition is a key factor driving forest dynamics and stand structure during the course of stand development. Although the role of neighbourhood competition on stand dynamics has received increasing attention, the response of competition to environmental fluctuations and stand development remains poorly explored. We evaluated changes in competition during stand development in a dry-edge Scots pine relict population located in Central Spain. Typically, tree-to-tree interactions have been investigated through static competition measurements, which usually lack the temporal variation associated to natural forest development and environmental conditions. Here, we assessed how individual and neighbourhood components of competition evolved along a 35-year period, and we related competition dynamics to population structure and drought levels. On six plots, 508 trees were mapped and diameters at breast height (DBH) were measured. Two increment cores were taken from target trees to derive basal area increment (BAI), and neighbourhood was reconstructed back to 1980. Results provide insights into inter-annual variability in competition effects and their role on tree radial growth depending on climatic conditions. From the year 2005 onwards, both individual and neighbourhood components of competition showed a decoupled pattern over time. This effect was particularly pronounced during the extreme drought in 2012, in which the individual component decreased, whereas the neighbourhood component increased. In addition, climatic variability modulated the competition effects during stand development. This approach of evaluating competition dynamics proves to be promising for studying forest stand development and the influence of climate impacts on tree populations subjected to xeric conditions.

**Keywords** Competition effects · Dendroecology · Drought stress · *Pinus sylvestris* · Stand development · Tree radial growth

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Communicated by Vospernik.

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## Introduction

Competition is a key biotic factor driving stand dynamics (Oliver and Larson 1996; Kunstler et al. 2011) through its influences on light, soil water and nutrients interception (Coomes and Allen 2007; Das et al. 2008). A number of studies have pointed out the effect of competition on tree radial growth (Stadt et al. 2007; Looney et al. 2016; Buechling et al. 2017), as well as its variation along environmental gradients (Cotillas et al. 2009; Linares et al. 2010; Gómez-Aparicio et al. 2011). Different competition indices have often been applied; these indices either used distance-independent metrics at the stand level (Biging and Dobbertin 1995) or distance-dependent indices taking the spatial distribution of trees into account (Canham et al. 2006; McTague and Weiskittel 2016; Tatsumi et al. 2016). Most of these studies have investigated spatial interactions among individual trees using static approaches (Brooker and Callaghan 1998; Coomes and Allen 2007), which lack a temporal component and may be inadequate to represent competitive dynamics over time (Burton 1993; De Luis et al. 1998).

Population dynamics are subjected to their own endogenous demographic processes, which intrinsically vary over time. For instance, increasing tree size and density in a population imply an increase in space filling that may intensify competitive interactions among neighbouring individuals (Yoda et al. 1963; Jump et al. 2017). Furthermore, temporal fluctuations in the environment can modify the interactions between neighbouring tree individuals (Biondi 1996; Travis et al. 2005), thereby affecting their competitive ability (Weber et al. 2008; Sánchez-Salguero et al. 2015; Aakala et al. 2018). Understanding how competition evolves over time is therefore essential to evaluate how forest functioning might be compromised under changing environmental conditions.

The degree to which the outcome of competition is either symmetric or asymmetric plays a fundamental role for plant population structure (Pacala and Weiner 1991; Keddy 2001). When light is a limiting resource, tree-to-tree competition often shows size asymmetry, with larger trees having a competitive advantage over smaller trees. In contrast, symmetric competition has been related to limiting below-ground resources (Schwinning and Weiner 1998) since root competition may not be associated with tree size (Berntson and Wayne 2000). Size-asymmetric competition may become increasingly symmetric at later stages of stand development (Masaki et al. 2006; Pothier 2017), possibly as a result of decreasing soil water availability (Pretzsch and Dieler 2010). Thus, competitive effects can be decomposed into two main aspects: i.e. (i) the size of target trees, and (ii) the influences from

neighbouring trees. Quantifying the relative contribution of each component over the course of stand development is therefore crucial to properly assess the importance of competition under climatic fluctuations.

Tree species compete intensively for light, but also for soil water in drought-prone Mediterranean forests (Zavala et al. 2000) where ongoing climate change is already affecting ecosystem functioning negatively by reducing productivity and increasing mortality (Schröter et al. 2005; Doblas-Miranda et al. 2017). Intraspecific competition has been particularly observed when the abiotic stress gradient is driven by water resources (Maestre et al. 2009). Increased aridity may promote more intense tree-to-tree competitive interactions than in other, non-water limited areas (Zavala and Bravo de la Parra 2005), particularly in tree populations subjected to xeric conditions (Hampe and Petit 2005; Sánchez-Salguero et al. 2015). One of the most drought-vulnerable species in Mediterranean forests is Scots pine (*Pinus sylvestris* L.) (Martínez-Vilalta et al. 2008; Camarero et al. 2015a, b). Scots pine is a widely distributed conifer with its southwestern limit of distribution on the Iberian Peninsula (Barbero et al. 1998), where natural populations are highly fragmented (Ruiz-Labourdette et al. 2012). Further, interactions between climate, stand structure and competition have also been reported for Scots pine (Gómez-Aparicio et al. 2011; Primicia et al. 2016; Marqués et al. 2018), with more negative effects observed in dryer areas (Vilà-Cabrera et al. 2011; González de Andrés et al. 2017), as well as drought- (Camarero et al. 2015b) and competition-induced mortality (Ruiz-Benito et al. 2013).

In this study, we use a tree-ring width dataset of Scots pine stands sampled in Central Spain with the aim to evaluate the role of competition as a driver of population dynamics over a 35-year period that exhibits a warming trend and includes several intense drought episodes. We analyse the abovementioned two aspects of competition: the individual component of competition, associated with target tree size, and the neighbourhood component of competition, relative to the effect exerted by neighbouring trees. The focus of the study is on the temporal variation of competition effects. Specifically, we address the following questions: (i) What is the effect of target tree size (individual component) and neighbouring trees (neighbourhood component) on tree growth through time? and (ii) To what extent does climatic variability modulate such components of competition in a dry-edge Scots pine population? We hypothesize that competition will be strongly tied to structure dynamics in the sense that increasing space filling would lead to progressively stronger competitive interactions among individuals. Additionally, competition will be modulated in time by climatic variability (droughts in this case), although with different intensities over each of the components of competition (target tree size, neighbouring effects). These research

questions will help us to better understand how competitive interactions vary over time and are altered by climate fluctuations.

## Materials and methods

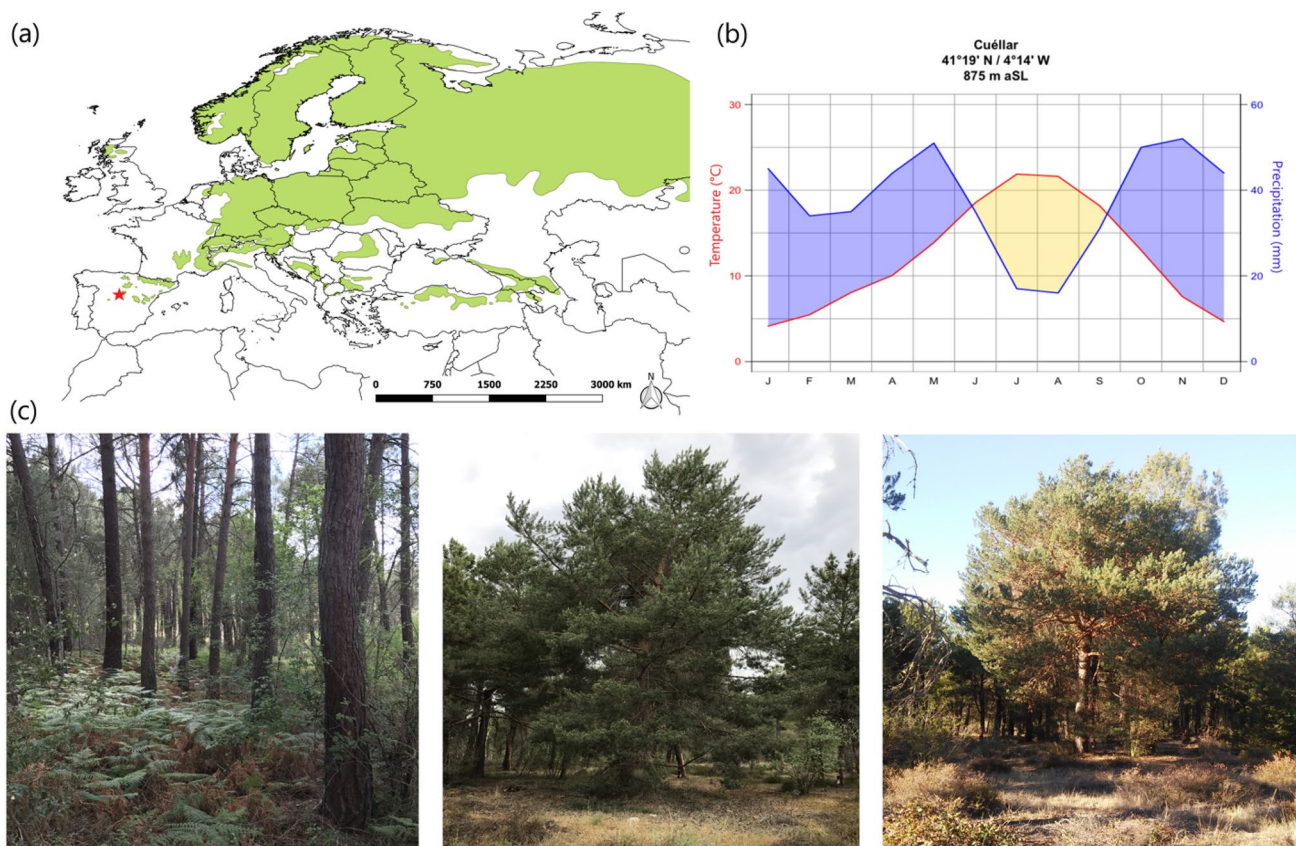
### Study area and species

The study was carried out in a managed pine forest located in the central-northern part of the Iberian Peninsula at an elevation of 875 m a.s.l. ( $4^{\circ}14' \text{ W}$ ,  $41^{\circ}19' \text{ N}$ ; Fig. 1). The dominant species is maritime pine (*Pinus pinaster* Ait.), followed by Scots pine, although black pine (*Pinus nigra* Arnold), and several shrub species [*Helichrysum stoechas* (L.) Moench or *Thymus mastichina* L.] are also present in the area. Scots pine is located at the lower altitudinal and latitudinal limit of the trees species distribution where water availability becomes the main constraint of forest growth (dry-edge, Hampe and Petit 2005), forming relict and scattered populations. As documented in the historical forest management archives, the Scots pine population established naturally after the last clear-cut in the 1960s and no further

management interventions have been carried out since. Likewise, neither has individual natural mortality been registered in the archives nor observed in the field. Together, this represents a unique opportunity to study stand development and to reconstruct spatial neighbourhood changes in a dry-edge population of Scots pine. Climate in the area is continental Mediterranean, with cold winters and warm dry summers (Peel et al. 2007). Mean annual temperature is  $12^{\circ}\text{C}$  and annual total precipitation ranges from 430 to 450 mm. This forest occupies inland dunes with sandy soils displaying low nutrient content and very low water retention capacity (Gómez-Sanz and Garcia-Viñas 2011).

### Climate records

Mean annual temperature and annual total precipitation records were obtained from the nearest meteorological stations (National Agency for Meteorology in Spain, AEMET): Valladolid ( $4^{\circ} 43' \text{ W}$ ,  $41^{\circ} 39' \text{ N}$ , 690 m; located 51 km northwards) and Segovia ( $4^{\circ} 07' \text{ W}$ ,  $40^{\circ} 57' \text{ N}$ , 1002 m; located 50 km southwards). We computed the associated climatic aridity index (AI) defined in terms of the ratio between precipitation and evapotranspiration (UNEP 1992), as follows:



**Fig. 1** a Geographical situation of the study area and distribution of Scots pine in Europe. b Climograph illustrating the climatic conditions at the study area. c Illustrative views of the Scots pine populations in three of the study sites. Species distributions are provided by EUFORGEN



$$AI = \frac{P}{PET} \quad (1)$$

where P is the annual total precipitation and PET is the potential evapotranspiration which was calculated following Thornthwaite (1948). Note that following this formulation, the aridity index increases with higher precipitation and lower PET (for more humid conditions), so it should be interpreted as water balance (Fig. 2a). Total annual precipitation and annual temperature were computed from September of the previous year to August of the present year so as to adapt climatic records to the most influential period for tree growth in this area (Madrigo-González et al. 2018). This climatic drought index is a good indicator of the soil water availability in the study area because of the high permeability of these sandy soils.

We focussed our study on two extreme drought events occurred in 2005 and 2012 (AI=0.43 and 0.45, respectively), that had different characteristics. The 2005 drought was characterized by unusually low values of spring–summer precipitation that induced widespread growth decline and triggered forest dieback across many Iberian forests (Peñuelas et al. 2011; Carnicer et al. 2014; Madrigo-González et al. 2018). The 2012 drought was initiated by very warm and dry conditions during the previous winter and the early growing season, and it also caused canopy dieback and tree mortality (Camarero et al. 2015b).

## Dendrochronological methods and growth assessments

Field sampling was done during 2016–2017. We established six circular sampling plots with a 25 m radius distributed across the Scots pine forest (see Supplementary Information, Appendix S1). As a prerequisite, a minimum number of 10 Scots pine target trees per sampling plot was needed. To quantify neighbourhood, we selected a fixed radius of 10 m from the target tree following previous studies applied in conifer forests (Stadt et al. 2007; He and Duncan 2000; Fraver et al. 2014), and Scots pine forests in particular (Pukala and Kolström 1987; García-Abril et al. 2007; González

de Andrés et al. 2017). To assure that the influence of neighbouring trees is properly caught, the core sampling area was defined within an inner 15 m radius, leaving a measured buffer area for the external part of the circle up to the 25 m radius in each plot. We measured target trees in the core sampling area (15 m radius) and neighbouring trees in each plot (25 m radius). Target trees were those whose growth was analysed as a response variable, whereas neighbouring trees were considered to have a competitive effect on target trees. As for the target trees we focussed on Scots pine; maritime pine and black pine were also included in the neighbourhood analysis, but not as target individuals. The centre of each sampling plot was mapped using a GPS with a resolution of  $\pm 4$  m. Within each plot, the distance ( $d$ ) and the azimuth ( $a$ ) from the plot centre to each tree were measured with a rangefinder device ( $\pm 1$  m) and a protractor placed on a tripod following the clockwise direction. The spatial position ( $x$ – $y$  coordinates) of every tree in the plot was calculated using the trigonometric functions:  $x = \sin(a) * d$  and  $y = \cos(a) * d$ . Diameter at breast height (DBH) was measured for each tree in the 25 m plot using a girth tape. Tree bark thickness was also measured using a bark gauge. Then, two cores were sampled per target tree, perpendicular to the maximum slope and in opposite directions, at 1.3 m using a Pressler increment borer. In total, 88 trees were sampled for a total of 176 increment cores (see Table 1).

The cores were prepared following standard dendrochronological methods (Fritts 2001). Wood samples were air-dried, glued on wooden supports and polished on a sanding machine until tree rings were clearly visible. Tree-ring widths were visually cross-dated following the marker year method and measured to the nearest 0.01 mm using a binocular microscope and a LINTAB measuring device (Rinntech, Heidelberg, Germany) linked to a computer. Cross-dating of tree-ring sequences was checked using the programme COFECHA (Holmes 1983) (see Supporting Information, Appendix S2). To estimate tree age at 1.3 m, pith-offset estimates were calculated by fitting a geometric pith locator to the innermost measured rings (Applequist 1958). For the oldest trees, tree age at 1.3 m was estimated by counting the

**Table 1** Characteristics of the Scots pine trees sampled (values are means  $\pm$  SD) in the six study plots. DBH is the diameter at breast height (measured at 1.3 m)

Plot	No. trees (no. cores)	Basal area target trees ( $\text{m}^2 \text{ha}^{-1}$ )	Basal area all trees ( $\text{m}^2 \text{ha}^{-1}$ )	DBH (cm)	Age at 1.3 m (years)
1	31 (61)	14.82	31.37	33.0 $\pm$ 5.0	49 $\pm$ 6
2	10 (21)	10.27	34.42	45.0 $\pm$ 14.4	56 $\pm$ 9
3	10 (20)	6.07	50.05	38.7 $\pm$ 4.8	42 $\pm$ 4
4	12 (25)	8.11	32.61	40.0 $\pm$ 9.8	47 $\pm$ 7
5	13 (24)	9.99	40.33	43.6 $\pm$ 4.6	58 $\pm$ 7
6	12 (24)	5.86	17.68	33.7 $\pm$ 9.6	32 $\pm$ 7

rings in the core of living trees and adding the estimated length of core missing up to the predicted pith.

To quantify growth, tree-ring width series were converted into basal area increment (BAI) which provides a biologically meaningful variable as BAI shows trends which are typically linear and less dependent on tree age and size than tree-ring width (Biondi and Qeadan 2008). We used the following formula and assumed a circular shape of the stems:

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

where  $r_t$  and  $r_{t-1}$  are the stem radial increments at the end and the beginning of a given annual ring increment corresponding to rings formed in  $t$  and  $t-1$  years, respectively.

### Effects of competition on tree growth

We reconstructed diameters at 1.3 m for all trees to calculate values prior to the sampling date. We focussed our analysis on the period 1980–2015 to reduce uncertainties of the DBH reconstruction and competition calculation back in time. Annual diameter increments for target trees were estimated by multiplying the ring width measurements from the cores by two. Diameter increments of cored trees were fitted against time using Generalized Additive Mixed models (GAMMs, Wood 2017). Based on the adjusted model and the DBH measurements taken in 2015, annual diameter increments of non-cored trees were reconstructed back to 1980. Finally, we added bark thickness and calculated the diameter for each tree and each year during the period 1980–2015. The variance explained by the GAMMs ranged between 0.216 and 0.644.

We described the effects of competition in terms of growth per year ( $t$ ) using a simple density and distance-dependent function predicting growth increases with target tree size and growth declines towards zero with rising neighbourhood size in relation to their proximity to the target tree:

$$\text{Growth}_t = \frac{\text{BA}_i^\alpha}{\sum_{j=1}^n \left( \frac{\text{BA}_j}{d_{ij}} \right)^\beta} \quad (3)$$

where the individual component of competition (numerator) was the basal area of the target tree  $i$  and the neighbourhood component of competition (denominator) was the basal area of the neighbour tree  $j$  divided by the distance between  $i$  and  $j$  and summed over all  $j$  neighbouring trees within a radius of 10 m from the target tree  $i$ , as the maximum search distance evaluated.

### Statistical analysis

Firstly, we estimated the parameters  $\alpha$  and  $\beta$  for each year using maximum likelihood methods (Canham et al. 2004).

This non-linear mixed effect model (Eq. 3) assumes that the ability of trees to capture light and nutrients depends on the total basal area of the target and neighbouring trees. The non-linear model was fitted using the stochastic approximation expectation maximisation (SAEM) algorithm (Comets et al. 2017), which estimates the population parameters per each year and includes a random intercept term associated with non-independent sampling (i.e., plot identity). The target tree size ( $\alpha$ ) and the neighbourhood ( $\beta$ ) components of competition were estimated over the study period 1980–2015. Neighbourhood was established with a fixed radius of 10 m from each target tree, and parameters estimation was repeated with a smaller fixed radius of 6 m to ensure support for our conclusions (see Appendix S3).

Secondly, we fitted linear mixed-effects models to assess the effect of climate on the individual and neighbourhood components of competition (i.e., parameters  $\alpha$  and  $\beta$ ) for the period 1980–2015. To control for the long-term linear trend associated with tree size development in the neighbourhood, the stand basal area (SBA) was included in the models. The general structure of the models can be summarized as:

$$Y_t = Xa_t + Zb + \varepsilon_t \quad (4)$$

where  $Y_t$  represents the  $\alpha$  and  $\beta$  components from the non-linear model per year  $t$ ,  $a$  is the vector of fixed effects (i.e., AI and SBA for each year),  $b$  is the vector of random effects, (i.e., plot identity),  $X$  and  $Z$  are regression matrices of fixed and random effects, respectively, and  $\varepsilon_t$  is the within-group error vector. A first-order autocorrelation structure was included in the models. The predictor variables (AI and SBA) were standardized (i.e. the mean was subtracted from the variable, and the resulting value was divided by the variable's standard deviation). We performed a moving window analysis with a 15-year window to explore when and how the effect of climate had more importance on competition dynamics (Ives et al. 2010). A sensitivity analysis was conducted to test the importance of the length of the moving window (10 to 15 and 20 years) and the results are included in Appendix S4. Residuals of the models were checked for normality and homoscedasticity. Fixed effects selection was based on Akaike Information Criterion corrected for small sample size (AICc). For each time window, we selected the model with the lowest AICc as being the most parsimonious model (Burnham and Anderson 2002). We considered the models with substantial support to be those in which the difference in AICc between the full model and the model without AI was negative and smaller than  $-4$ .

The abovementioned analyses were performed using the R statistical software version 3.4.3 (R Core Team 2018). Tree-ring data were processed via the *dplR* package (Bunn et al. 2018). Generalized additive mixed models were computed using the *mgcv* package (Wood 2017). Competition

effects were modelled with the *saemix* package in R (Comets et al. 2017). Linear mixed-effects models were conducted using *nlme* (Pinheiro et al. 2018).

## Results

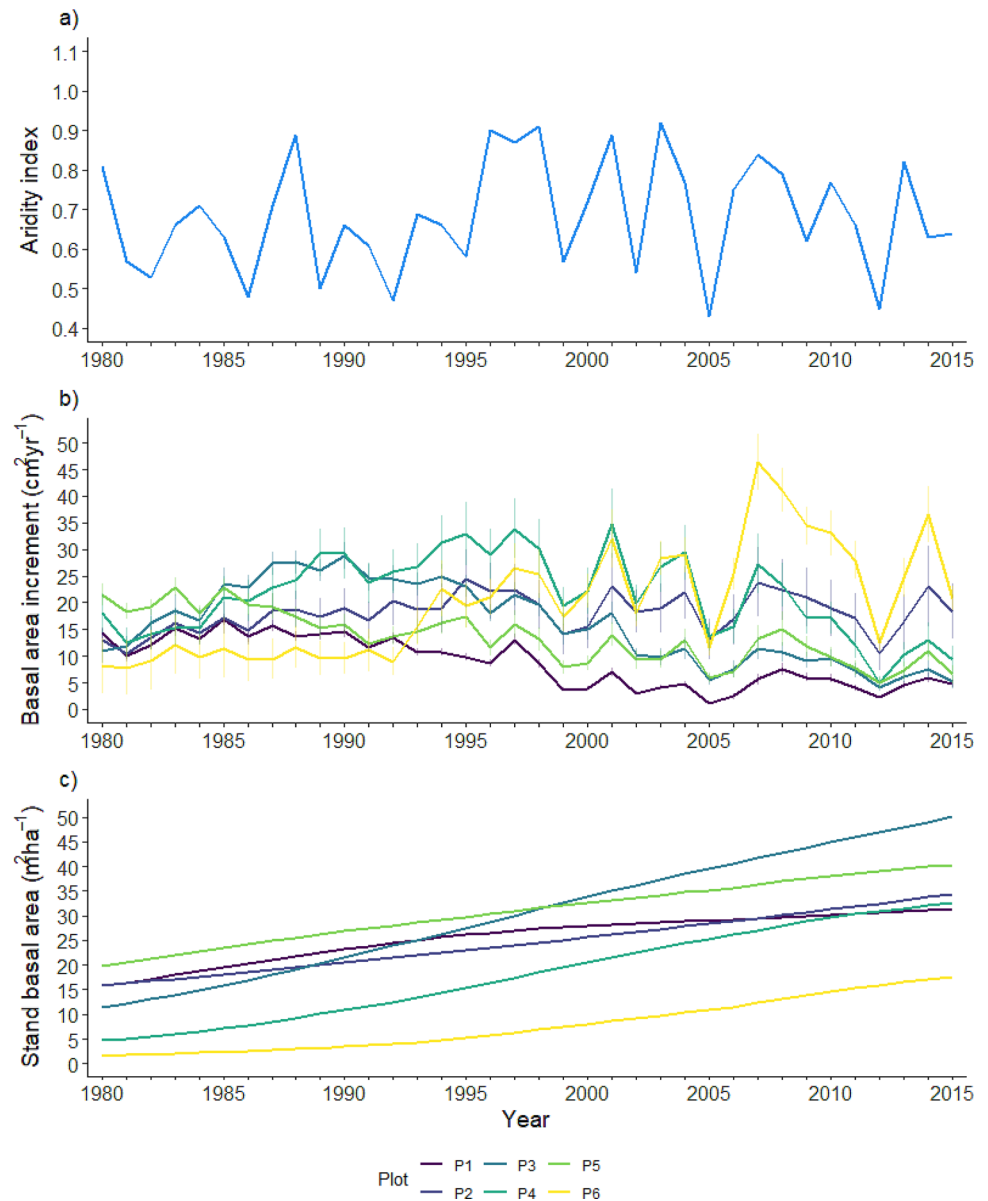
### Growth patterns

Tree growth showed similar patterns across all plots (Fig. 2b), with BAI decreasing strongly during the dry years 1986, 1992, 2005 and 2012. Scots pine showed an increase in BAI until the early 1990s when BAI stabilized at values of 10–30 cm<sup>2</sup> year<sup>-1</sup> (Fig. 2b). At plot 6, Scots pine individuals were the youngest such that BAI stabilized only in

the late 1990s. The lowest values of BAI were found at plot 1 (8.79 ± 6.31 cm<sup>2</sup> year<sup>-1</sup>), while the highest values corresponded to plot 3 (21.23 ± 9.57 cm<sup>2</sup> year<sup>-1</sup>). Mean DBH of sampled trees ranged from 33.0 to 45.0 cm, and age at 1.3 m varied from 32 to 58 years (see Table 1), confirming the stand establishment of the Scots pine population after the last clear-cutting in the 1960s.

Stand basal area reached the highest values at plot 3 (50.05 m<sup>2</sup> ha<sup>-1</sup>), where stand density was also highest (140 trees ha<sup>-1</sup>; see Appendix S1). The lowest values found at plot 6 (17.68 m<sup>2</sup> ha<sup>-1</sup>) corresponded to the youngest individuals (Fig. 2c). Growth of the Scots pine trees was positively correlated with target tree size (Appendix S5a), and negatively correlated with total basal area of all neighbouring trees located within the area around a target stem (Appendix S5b).

**Fig. 2** **a** Climatic patterns in the study area illustrated by the aridity index (AI, higher values indicate higher water balance) over 1980–2015. **b** Basal area increment (BAI, cm<sup>2</sup> year<sup>-1</sup>) of Scots pine target trees and **c** stand basal area (SBA, m<sup>2</sup> ha<sup>-1</sup>) of all trees in the six study plots for the same period



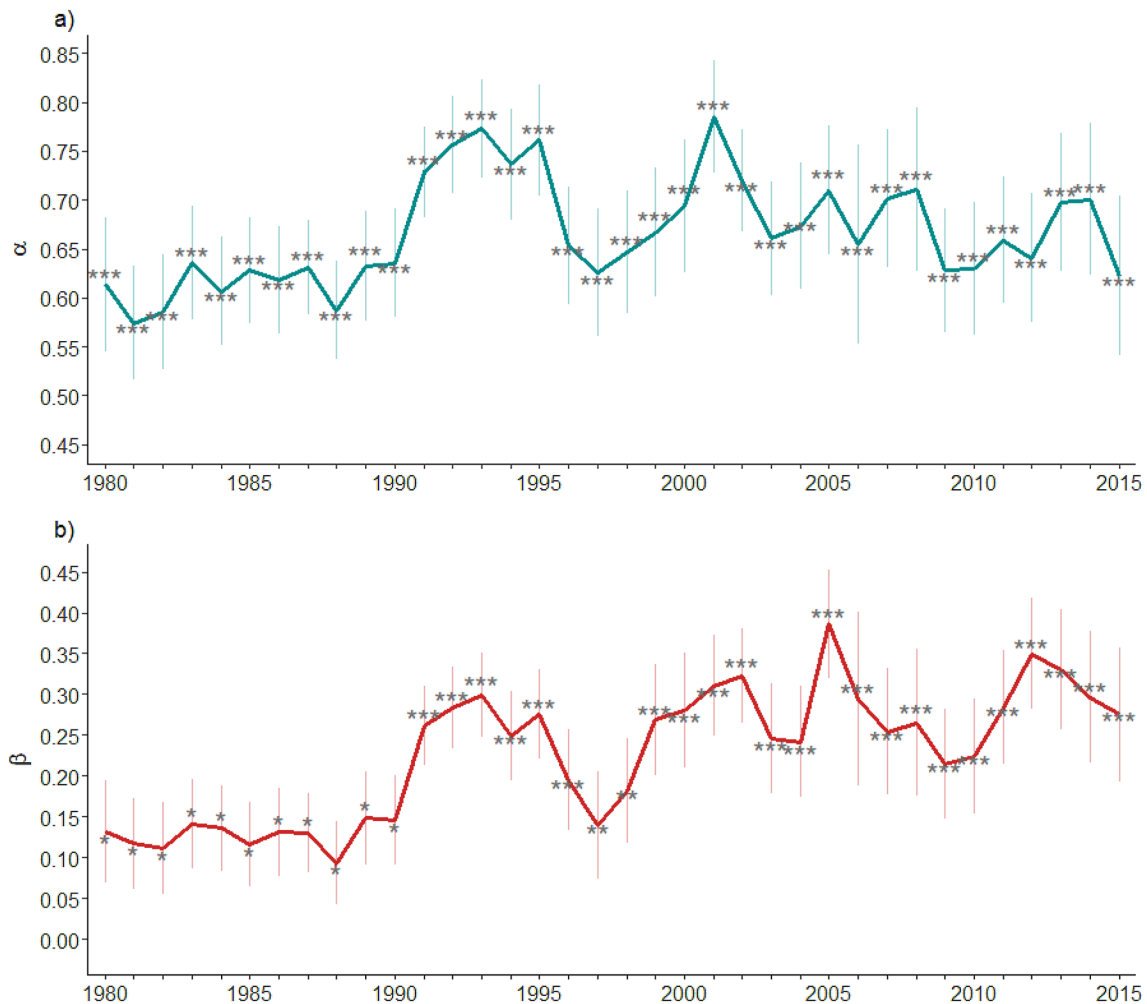
## Competition effects on tree growth

The individual component ( $\alpha$ ) was significantly positive all over the study period 1980–2015, with higher values indicating stronger opposing effects of basal area of target trees on neighbours' negative influence (Fig. 3a). The  $\alpha$  estimated for Scots pine during the study period varied from 0.57 to 0.78. The parameter  $\alpha$  showed an increasing tendency up to 1995, when the parameter stabilized, before it tended to decrease by the end of the period. From 1980 to 1995, the lowest  $\alpha$  values were observed in 1981 and 1988, whereas after 1995, the lowest  $\alpha$  values were reached in 2009, 2010, 2012 and 2015 and the highest in 2001.

The parameter controlling the effects of neighbourhood basal area on target tree growth ( $\beta$ ) showed a consistent positive trend for the study period 1980–2015, with higher

values indicating a stronger negative influence of the neighbourhood on tree growth (Fig. 3b). The  $\beta$  estimated for Scots pine varied from 0.09 to 0.38. However,  $\beta$  was only slightly significant until 1990, and since then the neighbourhood competition showed a significant effect over the period. The highest significant  $\beta$  values were found in 2002, 2005 and 2012 whereas the lowest  $\beta$  values were found in 1988, 1997 and 2009.

Comparison of parameters  $\alpha$  and  $\beta$  as estimated by considering the neighbourhood with a fixed radius of 10 m vs. 6 m are shown in Appendix S3. Pearson correlations yielded values of 0.90 for the target component ( $\alpha$ ) and 0.96 for the neighbourhood component ( $\beta$ ) of competition for both fixed radius analyses. Along the study period, parameters did not show differences between the neighbourhood radius considered as shown by the overlapping errors, with the exception



**Fig. 3** Parameter estimations for both **a** the target size ( $\alpha$ ) and **b** the neighbourhood ( $\beta$ ) components of competition over the study period 1980–2015. Neighbourhood is established with a fixed radius of 10 m from each target tree. Line charts are the means of the parameters and

error bars are the standard errors (SE) of the parameter estimates. Parameters significance is annotated for each year as follows: ns ( $p > 0.05$ ), \* ( $p < 0.05$ ), \*\* ( $p < 0.01$ ), \*\*\* ( $p < 0.001$ )

of years 1991–1993, where differences were consistent in both parameters  $\alpha$  and  $\beta$ .

### Influence of climate on competition components

The moving window analysis identified the time periods for which the aridity index had an influence on competition dynamics (Table 2). The AI affected the individual component of competition ( $\alpha$ ) in the 1980s and 1990s (1983–1998), and to a lesser extent to the early 2000s. During this period of time AI had a negative effect on the individual component. The neighbourhood component ( $\beta$ ) was mainly affected by AI from 1991 to 2015. Particularly, the effect was stronger when a dry year was included in the time window, specifically 1992, 1994–1995, 2005 and 2012. Along the entire period, the neighbourhood component of competition decreased under wetter and cooler conditions

**Table 2** Model comparison for both target tree size and neighbourhood components of competition ( $\alpha$  and  $\beta$ ) based on Akaike Information Criterion corrected for small sample size (AICc) for moving window analysis of 15 years

Time window	Individual component ( $\alpha$ )		Neighbourhood component ( $\beta$ )	
	AI	$\Delta$ AICc	AI	$\Delta$ AICc
1980–1994	0.005	9.928	–0.002	11.685
1981–1995	–0.001	11.943	–0.004	10.149
1982–1996	–0.014	2.487	–0.014	–1.332
1983–1997	<b>–0.017</b>	<b>–5.625</b>	<b>–0.015</b>	<b>–6.888</b>
1984–1998	–0.016	–1.735	–0.014	–0.566
1985–1999	–0.011	3.647	–0.015	–3.998
1986–2000	–0.010	5.610	–0.013	–0.001
1987–2001	–0.009	7.290	–0.013	–1.244
1988–2002	–0.005	10.217	–0.012	–2.050
1989–2003	0.000	11.473	–0.011	1.696
1990–2004	–0.003	10.959	–0.010	2.276
1991–2005	–0.013	5.333	<b>–0.038</b>	<b>–32.068</b>
1992–2006	–0.017	0.828	<b>–0.039</b>	<b>–36.425</b>
1993–2007	–0.016	3.075	<b>–0.041</b>	<b>–37.243</b>
1994–2008	–0.014	4.662	<b>–0.042</b>	<b>–38.151</b>
1995–2009	–0.011	7.459	<b>–0.035</b>	<b>–20.105</b>
1996–2010	–0.002	10.767	<b>–0.031</b>	<b>–16.142</b>
1997–2011	–0.001	10.925	<b>–0.031</b>	<b>–15.620</b>
1998–2012	0.002	10.981	<b>–0.030</b>	<b>–16.929</b>
1999–2013	0.005	10.151	<b>–0.026</b>	<b>–9.649</b>
2000–2014	0.002	10.884	<b>–0.030</b>	<b>–8.793</b>
2001–2015	0.001	10.713	<b>–0.034</b>	<b>–7.227</b>

The  $\Delta$ AICc was estimated as the difference between the full model with stand basal area (SBA) and aridity index (AI) as main effects and the model without AI. Models with significant effects are determined by more negative values of  $\Delta$ AICc and are given in bold

(negative effect of AI on  $\beta$ ). Interestingly, a sensitivity analysis conducted on these estimates supported the idea that the influence of aridity on neighbourhood effects was mostly determined in time-windows with marked fluctuations of the AI. Correlations between AI variability (SD) and  $\Delta$ AICc resulted in  $r = -0.62$  ( $p < 0.001$ ).

### Discussion

In this study, we evaluated individual and neighbourhood components of competition over time, as well as their influence on tree growth according to climate conditions, with an emphasis on drought effects. Our results indicate that competitive effects change over time, and support an intensification of competitive influences on tree growth in dry years and, in particular, during the 2005 and 2012 dry spells. The contribution associated with mean target tree size showed an increasing trend during early successional stages as a consequence of the population increase, and tended to decrease towards the end of the period. The competition related to neighbourhood size revealed a progressive linear increase across time, with higher values occurring in dry years. We also identified the time period during which the aridity index mostly influenced competition dynamics. In particular, we found a significant negative effect on neighbourhood competition, which illustrates the modulating role of climatic variability on stand dynamics over time. Nonetheless, the influence of climate controlling the neighbourhood component of competition was evident in periods with high fluctuations in the AI, which denotes a major role of climate extremes driving tree-to-tree competition.

During the 1980s, the individual component of competition was more important than the neighbourhood component as trees established in the stand and occupied the available space. This finding is consistent with general patterns described in literature where tree growth of young individuals was found to increase rapidly because of growing space of individual trees (Long et al. 2004; Benedict and Frelich 2008). At this early stage of stand development, competing understory vegetation can also exert a control on tree growth, as shown by Zhang et al. (2013) for a ponderosa pine forest plantation in Northern California. A decreasing relative effect of the individual component of competition and an increasing neighbourhood competition by the end of the period also suggests that competitive interactions intensify with increasing tree size. The continuous tree size development modulates growth (Stephenson et al. 2014), stand productivity (Coomes et al. 2014), and within-population interactions (Le Roux et al. 2013). Competition effects have been seen to increase faster in denser stands (García-Abril et al. 2007; Sohn et al. 2016; Del Río et al. 2017), and intensified due to lower water availability (Marqués et al.



2018). Stand development implies an increasing stand basal area and stand density leading to forest encroachment, and a reduction on space availability that may lead to an intensification in tree-to-tree interactions (Aldea et al. 2017).

In fact, we found that the neighbourhood component of competition exerted an increasing negative influence on radial growth of Scots pine trees (Jäghagen and Albrektson 1996), with significant effects since 1991. Strong impacts of neighbourhood competition on Scots pine growth may be explained by the high susceptibility of this species to competition for light (Jucker et al. 2014). The strong negative relationship between stand density and mean tree size in a population over time refers to the so-called self-thinning (Yoda et al. 1963). It has been reported that small trees are more affected by light competition than taller trees (Weiner 1990; Coomes and Allen 2007). Noteworthy, shade and drought have been shown to have interactive effects on plant performance (Holmgren et al. 1997; Sack 2004). Under drier conditions, taller trees may offer partial shade to smaller trees, reducing evapotranspiration and thus maintaining soil moisture availability (Joffre and Rambal 1993). Larger pine stems, by contrast, may also experience increasing vulnerability to drought (Hember et al. 2017), reflecting rising hydraulic and respiration costs with increasing tree height (Ryan et al. 2006). In addition, taller trees are subject to greater wind stress, resulting in reduced leaf area (Oliver and Larson 1996). Increased aridity may intensify neighbourhood competition over the target tree size effect, such that competition may become more symmetric, i.e., larger individuals may not compensate for the negative effect of neighbourhood competition effects (Stoll et al. 1994). Similar results were suggested by Masaki et al. (2006), who showed that the degree of size-asymmetrical competition decreases with stand age. Pretzsch and Dieler (2010) also predicted that increased stress limits the monopolization of resources from large trees, and thus reduces self-thinning of smaller trees. Pothier (2017) reached similar conclusions using a different analytical approach, suggesting these results are supported by a growing body of evidence. In this study, from 2005 onwards, both components of competition were uncoupled through time. This effect was particularly pronounced during the extreme drought of 2012, in which the individual component of competition decreased whereas the neighbourhood component increased. This finding is in line with results from other drought-limited forests, where competition has also been seen to become inverse size-asymmetric, thereby impacting larger trees disproportionately (Biondi 1996). In the future, self-thinning processes could even be anticipated and occur at early stages of population development if droughts were to become more frequent and/or severe, with a direct rise in mortality rates (Ruiz-Benito et al. 2013).

In principle, our findings are in line with general effects of changes in light and space availability on forest dynamics (Oliver and Larson 1996; Callaway and Walker 1997). In Mediterranean climates, however, water availability can modify species responses to light competition (Zavala and Bravo de la Parra 2005; Vilà-Cabrera et al. 2014). Our results suggest that the aridity index had a negative effect on the neighbourhood component of competition from the middle towards the end of the study period. These effects of water balance on the neighbourhood component of competition were consistent with the limiting role that water plays in the Mediterranean ecosystems. Also, sensitivity to competition increased with rising temperatures for Mediterranean forests, which could be linked to a higher transpiration demand and an increase in water scarcity. These results agree with the prediction that climate warming would increase competition for water in Mediterranean forests (Cotillas et al. 2009; Linares et al. 2010). Surprisingly, the aridity index showed a relatively small, but negative effect on the individual component of competition when analysing the time window 1983–1997, probably due to the early stage of the population at that time.

Our findings also agree with previous studies stating that competition may negatively interact with those climate conditions affecting tree growth (Piutti and Cescatti 1997; Fernández-de-Uña et al. 2015; Bottero et al. 2017; Andrews et al. 2020). Scots pine was found to be subject to higher competition in dry years by Weber et al. (2008) when studying competitive dynamics of pines and oaks over time in Valais (Switzerland). Other studies also found tree growth and competition effects to be highly dependent on local climatic conditions (Gómez-Aparicio et al. 2011; Sánchez-Salguero et al. 2015; Madrigal-González et al. 2016). In that sense, drought constraints on growth are particularly important in the southernmost dry limits of the tree species distribution (Hampe and Petit 2005; Sánchez-Salguero et al. 2016). Strong competition may exacerbate water shortage and therefore influence vulnerability of forests to recurrent drought events (McDowell et al. 2008). Climate conditions controlling the neighbourhood component of competition were more evident in periods with very high fluctuations in the aridity index, which denotes a major influence of climate variability affecting competition as compared to regular climatic fluctuations.

Previous field studies on competition in forest communities were conducted mainly by studying either mature trees at a given time (Ledo et al. 2014; Buechling et al. 2017) or juvenile trees over a short time period (Davis et al. 1999; Caldeira et al. 2014; Benavides et al. 2016). Our study shows evidence of tree-to-tree competition effects in a dry-edge population and its temporal variability. Although our findings are based on radial growth measurements and partial tree size reconstructions along a temporal gradient

in a natural environmental rather than on experiments, the observed growth patterns indeed allow us to suggest potential mechanisms associated with the two components of competition in the studied system. We found that competitive interactions in the context of stand development were dynamic, as was shown by the oscillations in the components of competition trends. The resulting neighbourhood component of competition was influenced significantly by higher climatic fluctuations. Our results therefore constitute relevant new information, which furthers our understanding of how tree competition interactions and stand structure will influence stand dynamics under more severe drought episodes in a context of climate change. Future research should complement our findings with other proxies of tree functioning related to water-use efficiency, such as carbon isotope discrimination in tree rings (e.g. González de Andrés et al. 2017).

## Conclusions

Our study confirmed the expectation that competition effects vary over time and that their influence on tree growth is intensified during drought events in marginal Scots pine populations. We found a significant, positive effect of the individual component of competition which decreased by the end of the period, and a significant negative effect of neighbourhood competition after the population establishment which increased progressively with time. We also found significant evidence that climate modulated the competition effects during stand development, with the aridity index negatively affecting neighbouring tree size. Our study is one of the first attempts to examine the variation of competition effects over time considering climate variability in a dry-edge Scots pine population. Our results therefore provide key insights into inter-annual variability in competition effects depending on population dynamics and climatic conditions, and also highlight the complexity of competitive interactions in drought-prone forest ecosystems. The findings presented here are also relevant to better understand interactions among biotic and climatic mechanisms driving tree populations subjected to seasonal droughts, with the goal of preserving their functioning under future climatic changes.

## Author contribution statement

JMG conceived the study and designed the methodology; JMG, CSG and LM collected the data; JMG, LM and JJC conducted the lab work; LM conducted the statistical analysis and led the writing of the manuscript; JJC and MAZ devised conceptual ideas and provided project support;

JABC and MS added substantial edits to the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00468-021-02109-8>.

**Acknowledgments** We thank Daniel Gómez and Patricia González-Díaz for their support during field work. L. Marqués acknowledges funding from University of Alcalá for a mobility grant at the Institute for Environmental Sciences (University of Geneva), and thanks all members of the C-CIA group for their helpful advices. L. Marqués was supported by a FPI grant from the University of Alcalá. We acknowledge funding provided by projects VULPINECLIM (Spanish Ministry of Economy and Competitiveness, MINECO, Spain; CGL-2013-44553-R) and FUNDIVER (MINECO, Spain; CGL2015-69186-C2-1-R and CGL2015-69186-C2-2-R projects).

**Funding** Open Access funding provided by ETH Zürich.

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