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Drought modifies tree competitiveness in an oak-beech temperate forest

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Abstract

Over recent decades, forest management in Europe has increasingly moved towards the emulation of natural dynamics. Natural dynamics in beech-oak forests leads to the formation of monospecific beech stands, the oak usually being excluded or restricted to sites with poor growing conditions. However, beech is more vulnerable than oak to drought and high temperatures. In this study, we examine whether climate change could attenuate the dominance of beech and improve the competitive capacity of oak in an old-growth temperate forest located in the “Picos de Europa” National Park, northern Spain. We used a dendroecological approach to reconstruct the competitive capacity of beech and oak and developed a projection for the 21st century based on forecasted climate conditions under three different emission scenarios. Beech is the dominant tree species in the studied forest, where the disturbance regime has favored the replacement of oak by beech. In general oaks are older than beeches and most of the small trees are beeches. Our results show that this substitution process may weaken due to the vulnerability of beech to warmer and drier conditions. Climate change will benefit oak growth over beech over the course of the 21st century, as was observed in the late 20th century. However, the natural gap dynamic benefits beech due to its greater shade-tolerance. Therefore, if the resilience of the ecosystem is to be increased, management strategies favoring oak regeneration are necessary given the better adaptation of oak to climate change.

Keywords: dendroecology, projection, *Fagus sylvatica*, *Quercus petraea*, successional dynamics, succession, species dynamics, competitive advantage.

1-Introduction

Climate extremes such as droughts can reduce the productivity of temperate forests (Frelich *et al.*, 2015) by leading to a decrease in radial growth or by triggering dieback episodes, often preceding mortality events or the replacement of one species by a more competitive or drought-tolerant tree species (Suárez *et al.*, 2004; van Mantgem *et al.*, 2009; Pederson *et al.*, 2014; Martin *et al.*, 2015; Sangüesa-Barreda *et al.*, 2015). Researchers and managers are interested in identifying and promoting mechanisms to enhance the resilience of these forests so as to make them less vulnerable to climate extremes such as severe droughts. Detailed studies of long-term relationships between coexisting tree species may provide useful information to improve the resilience of such temperate forests under a scenario of regional warming and local drying.

Species mixing may improve resource use efficiency, tree growth and stand productivity due to niche complementarity and facilitation between coexisting tree species (Richards *et al.*, 2010). Several studies have shown that the negative effect of extreme drought on tree growth is often lower in mixed than in pure stands (Lebourgeois *et al.*, 2013; Pretzsch *et al.*, 2013; Mölder and Leuschner, 2014; Gazol and Camarero, 2016). However, this is not always the case (Grossiord *et al.*, 2014; Forrester *et al.*, 2016) and mixing may favor certain species more than others (González de Andres *et al.*, 2017).

In recent decades, management of temperate beech-oak forests in Europe has moved towards emulating natural dynamics to increase the adaptability and resilience of these stands (Brang *et al.*, 2014). However, the dynamics in beech-oak forests often lead to the formation of monospecific beech stands, with oak usually being excluded or restricted to sites with poor growing conditions (Rozas, 2001b; Petritan *et al.*, 2017). Beech is more shade-tolerant, has a greater production of seeds (Harmer, 1994) and is

more competitive than oak (Gazol and Ibáñez, 2010; del Río *et al.*, 2014), especially under gap-dominated disturbance regimes (Petrigan *et al.*, 2013), which predominate in temperate forests (McCarthy, 2001). In addition, oak has difficulty regenerating (Pérez-Ramos, 2014) and as a result, a decline in the abundance of oak has been observed over recent decades in several European countries (Thomas *et al.*, 2002). However, beech is more vulnerable to drought (Aranda *et al.*, 2000, 2005; Piovesan *et al.*, 2008) and high temperatures than oak (Dorado-Liñán *et al.*, 2017). This greater vulnerability to drought could reverse the dominance of beech and increase the competitive capacity of oak in mixed beech-oak forests under warmer, drier climate conditions.

The competitive capacity of individual trees can vary considerably over time (Weber *et al.*, 2008; Sánchez-Salguero *et al.*, 2015). In this study we use dendroecology to reconstruct the competitive capacity of beech (*Fagus sylvatica* L.; hereafter beech) and oak (*Quercus petraea* (Matt.) Liebl.; hereafter oak) in a mixed, old-growth temperate forest located in the “Picos de Europa” National Park, northwestern Spain. We then develop a projection of this competitive capacity over the course of the 21st century based on the forecasted climate conditions under three different emission and climate scenarios (IPCC, 2014). The study area is located in the transition between the Mediterranean and the temperate bioregions and thus is subject to episodic summer droughts. We hypothesize that the forecasted rise in temperatures and decrease in precipitation will benefit oak growth over beech, attenuating the current greater competitiveness of beech. Our specific objectives are: (1) to study the forest history and dynamics through age and size structures; (2) to determine the factors that influenced radial growth in beech and oak; (3) to analyze the influence of climatic factors on the competitive capacity of beech and oak.

2-Materials and methods

2.1-Study area

The study site is located in the “Picos de Europa” National Park (Oseja de Sajambre, León, northwestern Spain). The climate is temperate oceanic with average temperatures of 8 °C and annual precipitation of 1250 mm (data from Riaño station, AEMET, 42° 58' N, 05° 01' W, 1048 m a.s.l.; located at 20 km from the study site). The soils are Mollic Leptosols (FAO, 2015). This area represents one of the southernmost distribution limits of European beech and sessile oak in Western Europe (**Appendix, Fig. A.1**). In the study area beech is the most abundant and widespread species throughout the studied forest (see **Table 1**), with a sparse presence of oaks. Both tree species are deciduous and form conspicuous annual rings. Oak forms ring-porous wood, whereas beech forms diffuse-porous wood. Natural dynamics prevail in this well-preserved forest situated in a protected area and no logging has taken place over the last century. Over this time the forest use has been limited to cattle grazing and occasional firewood extraction.

2.2-Field sampling

We performed the field survey during 2014 and 2015 consisting of 98 sampling plots systematically distributed on a square grid of 250 m x 250 m, occupying an area of 800 ha between coordinates 43° 08' 59'' – 43° 10' 29'' N, 4° 58' 48'' – 5° 02' 40'' W. The altitude ranges from 900 to 1600 m with a mean elevation of the sampling sites of 1283 m. In each plot a pair of stereoscopic hemispherical images was captured using ForeStereo to characterize the stand. The image segmentation and tree matching was carried out using the methods described in Sánchez-González *et al.* (2016). The matching process provides information on cross-sectional diameters along the detected stems, which are used to fit linear taper equations and individual tree diameter at breast

height and volume (Rodríguez-García *et al.*, 2014). The instrument bias (non-detection due to image resolution) and occlusions effect is corrected, setting a maximum plot radius of 8 m to estimate stand basal area (BA), stand tree density (N), stand mean diameter at breast height (DBH_{stand}) and diametric distribution (Sánchez-González *et al.*, 2016). The ForeStereo estimates show high correlations with field measurements of BA and N in high forests without a shrub layer, as is the case of the studied forest, but show limitations in very dense forest with a large proportion of small sized trees or a dense shrub layer. In addition, a dominant tree of each species was randomly selected in each plot and its diameter at breast height (DBH_{cored}) was measured with a calliper. Two cores were extracted from the selected dominant trees using a Pressler increment borer at a height of 1.3 m and always perpendicular to the maximum slope. In total we sampled 90 beeches and 31 oaks. Topographical variables (altitude, slope and aspect) for each plot were obtained from a Digital Terrain Model with a spatial resolution of 25 m (PNOA, Instituto Geográfico Nacional, Spain).

2.3-Climate data

Due to the lack of long, complete series of data from meteorological stations situated in the study area, we used monthly data for precipitation and mean temperature from the 0.5°-gridded Climatic Research Unit (CRU) dataset (Harris *et al.*, 2014). CRU climate data are homogeneous and quality-controlled and data from 1901 onwards are available. We obtained the CRU climate data for the period 1901-2013 from the 0.5° grid with coordinates 42.5°-43.0° N and 5.0°-5.5° W. Local (Riaño station, AEMET) and CRU climate data revealed an increase in temperatures, particularly from the 1990s onwards, together with a decrease in precipitation during the 20th century (**Appendix, Fig. B.1**).

We considered the climate projections for monthly precipitation and mean temperature during the 21st century produced by the Coordinated Regional Climate Downscaling Experiment (CORDEX) (Jacob *et al.*, 2014) for the same 0.5° grid as that for which the CRU climate data was obtained. We considered three ‘representative concentration pathways’ (RCPs), which are climate projections consistent with a wide range of possible climate scenarios (0.3–4.8 °C global warming by the year 2099) according to anthropogenic greenhouse gas emissions (IPCC, 2014). We used data for the scenarios RCP 2.6, RCP 4.5 and RCP 8.5. The RCP 2.6 scenario represents a situation an increase in warming ranging between 0.3 and 1.7 °C during 21st century. Under the RCP 4.5 scenario temperature increases between 0.9 and 2.6 °C, whereas under the RCP 8.5 scenario warming ranges between 1.4 and 4.8 °C (van Vuuren *et al.*, 2011).

2.4-Dendrochronological data

Cores were mounted on wooden supports and carefully sanded until the tree rings were clearly visible. Tree rings were visually cross-dated. The ring widths were then measured to the nearest 0.01 mm using the semi-automatic Lintab device with the TSAP-Win software (Rinntech, Heidelberg, Germany). Cross-dating was further verified with the COFECHA program (Holmes, 1997).

We calculated mean growth series for each individual and these tree-ring widths were subsequently transformed into basal area increments (BAI) as this variable is better than tree-ring width for capturing growth trends (Biondi and Qeadan, 2008). The BAI was calculated as follows:

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

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

The age was estimated for the sampled dominant beech and oak trees in accordance with Rozas (2003), this method is further explained in **Appendix C**.

2.5-Stand structural features

To characterize the different structure types present in the studied zone, we first separated the data from the plots in which only beech was present from the data corresponding to the rest of plots. For each structure type, we then attempted to identify common patterns of diameter distribution using hierarchical Ward cluster analysis based on Euclidean distances (Ward, 1963). The input data for the analysis was the matrix of densities by diameter class, distinguishing between beech and oak. We used diameter classes of 10 cm from 7.5 cm (minimum measurement made by ForeStereo) to 57.5 cm. From 57.5 cm upwards we used a single diameter class due to the lower densities of trees of this size. We used Silhouette graphs to obtain the optimal number of clusters (Rousseeuw, 1987).

To infer the long-term canopy coverage patterns and to provide quantitative information on tree origin, the trees in which radial growth records reach the pith (37% of the sampled trees) were classified into two groups (Rentch *et al.*, 2003; Hart *et al.*, 2012): gap origin and understory origin. To classify the sampled trees into these groups, we compared the average radial growth for years 1 through 20 with the average growth for years 21 through 40 (McCarthy and Bailey, 1996). If the average for the first 20-year interval exceeded the average for the second 20-year interval, then the tree was classified as having originated in a forest canopy gap. If the average growth for the first 20-year interval was below that for the second 20-year interval, then the tree was

classified as being of understory origin (Lorimer *et al.*, 1988; McCarthy and Bailey, 1996; Hart *et al.*, 2012). To confirm these quantitative classifications, the BAI data was graphically analyzed.

2.6-Factors influencing beech and oak growth

We used linear mixed-effects models to evaluate long-term BAI trends of beech and oak with the following variables as predictors or fixed factors: diameter at breast height of the cored tree in 2015 (DBH_{cored} , which represents tree size and growth potential); age of cored trees at the year of each annual radial growth (AGE) (which represents the growth trend with ageing); variables that characterize the physiographic variability within the study area: altitude, aspect, calculated as cosine of the maximum slope direction (1 indicates north, and 0 corresponds to south), and slope; structure type (from Ward cluster analysis); and variables characterizing the inter-annual climatic variability: annual mean temperature and total precipitation. To find the best model we tested different time intervals for the climate variables, although the maximum length of the interval was restricted from February to June, since this is the period when most radial growth occurs (cf. Pérez-de-Lis *et al.*, 2017). To test any CO_2 -related fertilization effect we also included annual mean CO_2 values and annual mean rates of increase in CO_2 since 1959 as explanatory variables (data from Mauna Loa (Hawaii, USA) observatory <ftp://aftp.cmdl.noaa.gov/products/trends/co2/>). Only tree identity was considered as a random component of the models. Continuous variables were standardized. We only considered the 1959–2013 period because CO_2 data are only available for that period.

We adjusted a linear mixed-effects model with random intercept and fixed slope:

$$y_{ij} = \alpha + a_j + \beta z_{ij} + \varepsilon_{ij} \quad (2)$$

where y_{ij} represents $\log(\text{BAI}+1)$ for year i and tree j , α is the general intercept, a_j is the random intercept (tree identity), β is the vector of general slopes, z_{ij} is the vector of fixed effects and ε_{ij} is the error with a first-order temporal autocorrelation [AR(1)] structure. We used the log-transformation of BAI because it had a Gamma distribution. The distribution was tested using the Kolmogorov-Smirnov test.

To identify the best-supported model we constructed all possible combinations of alternative models from the full model considering main and random effects and the interactions between the fixed effects. As the restricted maximum likelihood method (REML) estimates an unbiased variance but does not allow models to be compared by minimizing the Akaike Information Criterion (AIC), we first adjusted all possible models using the Maximum Likelihood method (ML), then selected the best model by minimizing AIC and finally adjusted it again using the restricted maximum likelihood method (REML) (Zuur *et al.*, 2009). The existence of multicollinearity among explanatory variables was evaluated by calculating the variance inflation factor (VIF). VIF values greater than 10 mean that there is high collinearity among variables (Dormann *et al.*, 2013). The percentage of variance explained by the model was obtained in accordance with Nakagawa and Schielzeth (2013). These authors proposed a method adapted to mixed-effects models to estimate the total variance explained by the model (conditional pseudo- R^2) and the variance explained only by the fixed effects (marginal pseudo- R^2).

2.7-Retrospective analyses of species competitive dynamics

Using BAI data for the cored trees, we derived a retrospective competitive ability index of beech and oak over time. The index calculation was based on the assumption that for trees of the same species, higher BAI growth values imply higher competitive ability

(Weber *et al.*, 2008). Trees from the same stand usually show a common climate signal in their tree-ring width series (Fritts, 2001) and differences in BAI patterns or trends are due to the distinct microclimates, distinct responses to the same climate and to the competitive stress with neighbors (Weber *et al.*, 2008). We were interested in extracting the specific (non-common) signals of growth patterns to analyze the differences in relation to climate. By sampling dominant trees it is possible to eliminate part of the growth signal due to competition with neighbors because of the asymmetric nature of competition (Schröder and von Gadow, 1999; Stadt *et al.*, 2007; del Río *et al.*, 2014; Maleki *et al.*, 2015) as well as to eliminate part of the noise produced by the disturbances of the forest dynamics (Vašíčková *et al.*, 2016).

The BAI patterns for beech and oak were compared by calculating interval trends (Schweingruber, 1988; Schweingruber *et al.*, 1990). An interval is a link between two adjacent years. An interval trend value shows the percentage of intervals with the same trend within a given period. In order to obtain this, firstly the BAI series of all beeches and oaks was smoothed, calculating it for 10-year moving intervals, since we are interested in the long-term BAI trends. Secondly, the number of ascending increments of BAI between consecutive years was summarized for each species. This was then transformed to percentages for species (i.e. percentage of beeches or oaks with ascending increments of BAI for each interval) to give a percentage series of competitive ability over time. To calculate the competitive advantage series of oak over beech (CA_{oak}), the percentage series of competitive ability for beech was subtracted from the percentage series of competitive ability for oak. In the resulting competitive advantage series, positive values indicate competitive advantage for oak, whereas negative values indicate competitive advantage for beech (Weber *et al.*, 2008). We reconstructed growth releases as a proxy of forest disturbances (this methodology is

explained in **Appendix D**), and used only BAI data from the tenth year following the first release to avoid the inclusion of BAI data from when the cored trees had not yet reached the canopy.

We also constructed partial oak competitive advantage series using only the data from the clusters M2 and M3, but not from cluster M1 because of the small quantity and young age of the beeches. The Pearson correlations between CA_{oak} and the partial oak competitive advantage series were analyzed.

To reveal the relationships between climate and CA_{oak} , series were built for monthly temperature and precipitation, averaged in 10-year moving intervals. A regression was fitted between CA_{oak} (response variable) and the monthly series of climate variables (predictor variables) from October of the previous year to November of the growth year considering that: (i) climate during the previous year affects growth during the following year (Rozas, 2001a), and (ii) the growing season can last until November (Pérez-de-Lis *et al.*, 2017). Due to this potentially long growing season, we also grouped monthly climatic data into seasons to better reflect the relationships between competitive advantage and climate. The regression was fitted for the period 1901-2013 because climate data previous to this period is not available for this area. To identify the best-supported model we constructed all possible combinations and selected the model with the lowest AIC. The model assumptions were checked (normality, no multicollinearity and homoscedasticity).

2.8-Projecting competitive advantage of tree species as a function of climate forecasts

We projected CA_{oak} for the 21st century, using the previously mentioned regression model (in section 2.7). The predictor variable was the expected CORDEX values for the 21st century, according to the emission scenarios RCP 2.6, RCP 4.5 y RCP 8.5,

smoothing it through 10-year-moving averages. The projected values of the competitive advantage for the year 2013 (first year of the series) were matched to the value of the previous retrospective analysis in this year. Finally a linear regression competitive advantage-year was fitted for each climate scenario.

3-Results

3.1-Characterization of the forest structure

We differentiated two clusters for pure beech plots: without abundant small sized trees (P1) and with abundance of small sized trees (P2). Three clusters were distinguished for the rest of the plots, which were mostly mixed stands: one with abundant small sized oaks (M1), another with abundant small sized beeches (M2) and one with scarce small sized oaks and beeches (M3) (see **Table 1** and **Fig. 1**). While young beeches are present in most of the forest, the presence of young oaks is restricted to those stands established after the 1940s (**Appendix, Fig. E.1**). In all clusters with oaks, the age of the oaks is greater than that of the coexisting beeches (**Appendix, Fig. F.1**). Considering all the clusters together; M1, M2 and M3, oak presented significantly greater ($t = 3.01$, $P = 0.004$) age (202 years on average) than beech (121 years).

The forest is uneven-aged, with an abundance of trees of all diameter classes (**Fig. 1**). Beech is the most abundant species (**Table 1** and **Appendix, Fig. E.1**), but it is also the only species with a recent decrease in BAI for the period 1994-2013. In recent years, beeches have increased their growth in plots with abundant small sized oaks (cluster M1) but their growth has reduced in most of the rest of the studied area (**Table 1**). Oak has retracted in the study area over the last few centuries, with only a scattering of trees remaining in the forest (**Appendix, Fig. E.1**) and the only places where it is spreading are the abandoned lowland farming and grazing areas (the average altitudes

for oak and beech in the studied area are 1161 and 1302 m, respectively). However, unlike beech, the BAI for oak shows no trend over recent years except in plots with abundant small sized beeches (cluster M2) (**Table 1**). About 70% of cored trees of more than 200 years of age are oaks, with 342 and 487 years of age being the greatest ages observed for beech and oak, respectively.

Table 1. Summary of structure and growth data for beech and oak. Values are means (for basal area increment, BAI) and medians (for the rest of variables) with standard deviations in parentheses. Asterisks indicate significant differences (Wilcoxon's signed-rank test for paired samples) between both BAI periods considered. Significance levels: $*P < 0.05$, $**P < 0.01$ and $***P < 0.001$, respectively. Note that N, BA and DBH_{stand} are stand variables obtained from ForeStereo for all trees measured in the plot while DBH_{cored} is a variable of the cored trees.

Cluster	Species	No. plots	N (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)	DBH _{stand} (cm)	DBH _{cored} (cm)	BAI period 1974-1993 (cm ² year ⁻¹)	BAI period 1994-2013 (cm ² year ⁻¹)
P1	Beech	30	209 (103)	18 (21)	30 (11)	42 (16)	15.9 (12.2)	12.8 (11.6)***
P2		37	679 (267)	50 (19)	26 (4)	39 (8)	12.8 (8.9)	11.8 (9.9)***
M1	Beech	5	213 (90)	6 (7)	21 (7)	18 (6)	3.4 (2.8)	5.6 (3.8)***
	Oak	10	246 (163)	19 (9)	22 (14)	50 (14)	27.2 (9.3)	27.0 (11.1)
M2	Beech	9	488 (280)	36 (16)	25 (5)	34 (10)	7.2 (3.3)	6.3 (3.3)***
	Oak	9	104 (64)	19 (22)	56 (17)	57 (7)	12.6 (8.4)	13.7 (8.9)**
M3	Beech	9	159 (70)	9 (8)	30 (15)	40 (12)	17.8 (14.5)	18.1 (13.4)
	Oak	12	92 (50)	12 (22)	36 (27)	75 (18)	31.8 (16.9)	30.9 (15.3)
All	Beech	90	379 (334)	34 (23)	27 (9)	38 (13)	13.4 (10.9)	12.0 (10.8)***
	Oak	31	106 (135)	18 (20)	36 (23)	62 (18)	24.0 (15.2)	23.9 (14.4)

Figure 1. Size distribution (DBH_{stand}) of the clusters shown for the two studied species.

Note that the y-axis scale varies between graphs.

The establishment of the currently dominant oaks occurred steadily over time whereas most of the dominant beeches date from between 1840 and 1880 (**Fig. 2**).

Figure 2. Establishment history of cored beeches and oaks (shown for 20-year age classes) presented according to size (DBH_{stand}) clusters.

Most of the dominant cored beeches (63%) were classified as being of understory origin (37% of gap origin) whereas most of the oaks (80%) were of gap origin (20% with understory origin). In the mixed stands the percentage of beeches with gap origin was higher (57%) than in pure stands (26%).

3.2-Factors influencing beech and oak growth

The coefficients of the variables of the most parsimonious BAI model for each species are shown in **Table 2**. The effects of the interactions are shown in **Fig. 3 and 4**. Taking into account the two selected models, the most important predictors of tree growth were: DBH_{cored}, AGE, annual mean rates of increase of CO₂, mean temperature from February to May, total precipitation from February to June, altitude and the interactions between the latter three variables. The most important variable of the beech growth model was DBH_{cored}, whereas in the oak model the most important predictors were DBH_{cored} and AGE, which produced opposite effects on BAI. Altitude was inversely related to the BAI of oak but its effect on beech growth is variable, depending on the climatic conditions (**Fig. 3 and 4**). Climatic variables are more important predictors of BAI in the case of beech than in oak. The CO₂ concentration was directly related to beech BAI. Temperatures seem to benefit growth whenever they are accompanied by wet conditions, whilst low levels of precipitation and warm temperatures associated with dry conditions lead to reduced growth. The percentage of BAI variance explained by the fixed and random effects (conditional pseudo-R²) was 72% and 70% for the beech and oak model respectively, and the fixed effects explained (marginal pseudo-R²) 62% and 58% of variance for the same species. In both models the VIF was lower than 3.

Table 2. Coefficients (standard errors in parentheses) for the best linear mixed-effects models of basal area increment for beech and oak, considering the 1959–2013 period. Significance levels: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$, respectively. Predictors have been standardized previously to fit the models. Temperature is the average from February to May, and precipitation is the total rainfall from February to June. Carbon dioxide is the annual mean rates of increase in CO₂. “X” indicates interactions.

	Beech	Oak
Intercept	2.360*** (0.029)	2.981*** (0.045)
DBH _{cored}	0.589*** (0.028)	0.310*** (0.049)
AGE	-0.092*** (0.025)	-0.286*** (0.061)
Temperature	0.039*** (0.007)	0.038*** (0.007)
Precipitation	0.047*** (0.005)	0.014* (0.006)
Altitude	-0.049 (0.032)	-0.173** (0.059)
Carbon dioxide	0.042*** (0.006)	—
Temperature X Precipitation	0.123*** (0.005)	0.032*** (0.005)
Temperature X Altitude	-0.022*** (0.006)	—
Precipitation X Altitude	0.016** (0.005)	-0.045*** (0.006)
Temperature X Precipitation X Altitude	0.044*** (0.005)	—

Figure 3. Effects of the interactions between climate variables and altitude on beech radial growth (log-transformed BAI data). The predictors are standardized. Temperature

is the average from February to May, and precipitation is the total rainfall from February to June. Shaded bands indicate the confidence intervals. Positions of the data along x axis are denoted by tick marks.

Figure 4. Effects of the interactions between temperature and precipitation (a) and between temperature and altitude (b) on oak radial growth (log-transformed BAI data). The predictors are standardized. Temperature is the average from February to May, and precipitation is the total rainfall from February to June. Shaded bands indicate the confidence intervals. Positions of the data along x axis are denoted by tick marks.

3.3-Retrospective analyses of species competitive dynamics

During the 20th century, there were alternating periods of competitive advantage for one or other of the two studied species (**Fig. 5**), with 46% of the years being favorable for oak growth and 54% of the years favorable for beech growth. From the 1960s onwards the percentage of years favorable for oak has risen to 64%. The Pearson correlations between CA_{oak} and the partial oak competitive advantage series for the clusters M2 and M3 were 0.793 ($P < 0.001$) and 0.565 ($P < 0.001$), respectively; thus, the general evolution of the competitive advantage is maintained in each cluster.

Figure 5. Reconstructed oak competitive advantage (CA_{oak}) from 1901 to 2013.

For the oak competitive advantage model (adjusted $R^2 = 0.257$), the variables selected are the temperatures of the winter previous to the growth period and late spring and summer precipitations of the growth period (**Table 3**). According to this model warmer winter temperatures and higher precipitations in August-September increase the competitive advantage of oak over beech, while wet conditions in June-July increase the competitive advantage of beech over oak. Although January and February temperatures are only marginally significant in the model, the Pearson correlation with CA_{oak} is significant ($r = 0.299$, $P = 0.002$).

Table 3. Regression calculated between the competitive advantage of oak and the climatic variables. VIF is the variance inflation factor.

	Coefficients	Standardized coefficients	P	VIF
Constant	-75.29		0.019	
Temperature January to February	8.43	0.15	0.090	1.13
Precipitation June to July	-0.29	-0.21	0.019	1.12
Precipitation August to September	0.60	0.37	0.000	1.06

3.4-Projecting competitive ability of tree species as a function of climate forecasts

The projections forecast an increase in the competitive advantage of oak under the three emission scenarios (**Fig. 6**). According to these projections, oak will be favored by climate warming, although the slope of the regression line of each emission scenario is lower than 5% in two out of three cases. The rates of increase of the CA_{oak} for the twenty-first century are 17.3%, 4.7% and 1.6% for the RCP 2.6, RCP 4.5 and RCP 8.5 scenarios, respectively. The models showed R^2 of 0.58 ($P < 0.001$), 0.16 ($P < 0.001$) and 0.06 ($P = 0.019$), for the RCP 2.6, RCP 4.5 and RCP 8.5 scenarios, respectively. The low effect of the latter climate scenario on the CA_{oak} predictions is related to the trade-off between the rise in winter temperatures and the forecasted reduction in late spring and early summer precipitations, which would benefit oak, and to the reduction in August-September precipitations, which would benefit the competitive ability of beech.

Figure 6. Projection of the competitive advantage of oak (CA_{oak}) over beech over the course of the 21st century for three emission and climatic scenarios (RCP 2.6, RCP 4.5 and RCP 8.5). Simple linear regressions were fitted for each scenario.

4-Discussion

4.1-Forest history and dynamics and growth trends

The dynamics in the studied mixed beech-oak forest, located at the south-western distribution limit of both species in Europe, is similar to other old-growth forests in other parts of the continent, in which the disturbance regime has favored the replacement of oak by beech (Rozas, 2001b; Rohner *et al.*, 2012; Petritan *et al.*, 2017).

In general the oaks are older than beeches (**Fig. 2 and Appendix, Fig. F.1**) and are heterogeneously distributed in form of scattered trees or forming small patches. The presence of young oaks is mainly circumscribed to the forest patches where trees established themselves after the 1940s (**Appendix, Fig. E.1**). Conversely, beeches are

spread throughout the area, forming mainly pure stands that comprise more than half of the study forest (**Table 1 and Appendix, Fig. E.1**). The presence of young beeches is common in most of the studied forest. In a great part of that forest, both tree species presented basal area values which are characteristic of old-growth forests (Hart *et al.*, 2012; Petritan *et al.*, 2015). Therefore the replacement of oak by beech has reached an advanced stage. However, this process of substitution may have taken place slowly. Beech has been both widespread and abundant in the region since at least 3000 cal. years BP (López-Merino *et al.*, 2008) and in more recent times has been dominant over oak since the 19th century at least (Miñano y Bedoya, 1829; Engineers Corps, 1859). Most of the currently dominant beeches date from between 1840 and 1880 (**Fig. 2**). As in other mixed temperate Spanish forests (Gea-Izquierdo *et al.*, 2014; Dorado-Liñán *et al.*, 2017), during those decades there were social and economic changes that led to a reduction in grazing, and especially in transhumant cattle raising (García Sanz, 1978), which would have resulted in a reduction in logging intensity and an increase in regeneration in formerly grazed forests, such as the forest studied here (Miñano y Bedoya, 1829). The low proportion of beeches established before 1840 may be due to the lower sprouting capacity of beech in comparison to oak, which reduces the ability of the species to withstand grazing in the early stages of growth. The subsequent increase in the proportion of beeches also points to a small-gap disturbance regime typical of temperate forests (McCarthy, 2001). Small-gap dynamics may favor the establishment of a shade-tolerant species like beech (Niinemets and Valladares, 2006; Rozenbergar *et al.*, 2007), whereas the limited availability of radiation may hinder the regeneration of oak (Petritan *et al.*, 2013). Due to the reduction in logging intensity since the early 20th century, the natural dynamics of the forest would relegate the oaks to the areas in which the forest is expanding.

4.2-Factors influencing beech and oak growth

Growth (BAI) for beech and oak is mainly determined by tree size (DBH_{cored}), cambial age and the interactions between altitude, spring temperature and precipitation. As reported in previous studies (Cescatti and Piutti, 1998; Diaconu *et al.*, 2015; Monserud and Sterba, 1996), most of the growth variance was explained by tree size (**Table 2**). AGE effect reflects the BAI decrease produced when trees enter the senescent phase (Piovesan *et al.*, 2008; Kint *et al.*, 2012). Growth reached a peak when high temperatures and precipitations occurred simultaneously (**Fig. 3 and 4**). The overall positive effect of temperature on growth indicates that growth in the study area is limited by low temperatures, as occurs in some cold-temperate regions (Toïgo *et al.*, 2015; Lévesque *et al.*, 2016). However, in years with low spring precipitation, high temperatures may increase drought stress and hence decrease growth (Rozas, 2001a; Kint *et al.*, 2012). The growth of beech was also related to CO_2 values, indicating a potential fertilization effect, as occurs in areas where growth is limited by low temperatures (Keenan *et al.*, 2013; Camarero *et al.*, 2015; Madrigal *et al.*, 2015).

Beech showed a more pronounced sensitivity to climatic variables than oak, as observed in other studies (Kint *et al.*, 2012; Toïgo *et al.*, 2015; Dorado-Liñán *et al.*, 2017), which may indicate a better adaptation of oak to adverse climatic conditions including drought (Aranda *et al.*, 2000; Rubio-Cuadrado *et al.*, 2018).

4.3-Alternating beech-oak competitive ability dynamics

Growth trends may result from different interacting factors, abiotic factors such as climate and biotic factors such as tree age or social status, which operate at different spatial scales from patch to stand or biome, and also depend on forest management and

disturbances (Dittmar *et al.*, 2003; Boisvenue and Running, 2006). We only used growth data from dominant trees, which are assumed to have been subjected to similar climate conditions and are less affected by forest dynamics.

Periods with a competitive advantage for one or other of the studied species alternate over the interval considered (**Fig. 5**). However, while years in which beech has a competitive advantage predominate in the first half of the 20th century, since the 1960s there has been an increase in the number of years in which oak has a competitive advantage. The growth series show a decline in beech but oak growth remains constant (**Table 1**). This different behavior of the two species is in accordance with the findings of other studies reporting a growth decline for beech since the 1960s associated with climate warming (Dittmar *et al.*, 2006; Piovesan *et al.*, 2008; Bontemps *et al.*, 2010; Braun *et al.*, 2010; Kint *et al.*, 2012; Dorado-Liñán *et al.*, 2017) and a growth increase for oak during the 20th century (Becker *et al.*, 1994; Bergès *et al.*, 2000; Kint *et al.*, 2012; Dorado-Liñán *et al.*, 2017).

High temperatures at the beginning of the year increase the competitive advantage of oak (**Table 3**). Oak produces earlywood prior to budburst whereas beech growth starts later; just after budburst with a maximal growth rate when the leaves are mature (Michelot *et al.*, 2012). Close to the study area, the radial growth of the oaks usually starts in February (Pérez-de-Lis *et al.*, 2017), while the beginning of the beech growth period varies from March to April (Čufar *et al.*, 2008; Martínez del Castillo *et al.*, 2016). In addition, we found a positive effect of temperature on oak growth (**Table 2**). Hence, a rise in temperature during the first months of the year could extend the growing period, thus increasing the growth rates of oak (Michelot *et al.*, 2012).

The competitive advantage of beech is directly related to precipitation in late spring and early summer. This agrees with observations in temperate European forests

where beech growth is very sensitive to water-limitation and drought stress in the period between budburst and late July (Dittmar *et al.*, 2003; Piovesan *et al.*, 2008; Kint *et al.*, 2012) (see also **Table 2**). However, high precipitation in August and September improves the competitive advantage of oak, possibly due to the extension of the growth period, which can continue until late autumn (Pérez-de-Lis *et al.*, 2017). The higher sensitivity of beech to hydraulic failure (Aranda *et al.*, 2005) limits its growth in late summer and therefore this species probably benefits less from the rainfall that occurs at this time of the year in comparison to oak.

4.4-Projecting competitive ability of tree species as a function of climate forecasts

The three climate scenarios considered predicted an increase in temperatures and a decrease in rainfall. An increase in the winter temperatures and a reduction in June and July rainfall would give a competitive advantage to oak whereas a reduction in August and September precipitation would give a competitive advantage to beech (**Table 3**). In the study area as in other mixed temperate forests (Kint *et al.*, 2012), these climate forecasts point to increasing competitive advantage for oak over the course of the 21st century (**Fig. 6**). However, warmer and drier scenarios were not associated with greater increases in the competitive advantage of oak due to the trade-off between climate variables. Our results only reflect growth projections, and other factors affecting forest dynamics (regeneration rates, tolerance to competition, mortality rates, disturbance regime) should also be taken into account in future research since these factors have an important influence on the persistence of coexisting tree species in temperate forests.

5-Conclusions and management implications

The replacement of oak by beech is a slow process due to the longevity of both tree species and their niche complementary under certain circumstances. Natural dynamics will restrict oaks to zones of forest expansion or to disturbance-related gaps in mixed forests, eliminating them from the rest of the forest patches dominated by the shade-tolerant beech. This process may be attenuated because of the vulnerability of beech to the forecasted warmer and drier conditions, which that would have a lesser effect on oak. In fact, according to our results, oaks have displayed greater adaptability than beech to the site conditions since the 1960s. In addition, the projected climate changes including warmer and drier conditions will benefit oak growth over beech over the course of the 21st century. Therefore, the ongoing retraction of oak may bring about a loss of ecosystem resilience due to the poorer adaptation of beech to warmer, drier conditions. The forecasted competitive advantage of oak will lead to the dominance of this species in scattered, favorable sites such as gaps, rocky outcrops or on the margin of beech-dominated patches. Management strategies aimed at maintaining a mixed stand with presence of both beech and oak should be considered as a means to better adapt to the forecasted climate change.

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