



Drought modifies tree competitiveness in an oak-beech temperate forest

Álvaro Rubio-Cuadrado^{a,*}, J. Julio Camarero^b, Miren del Río^{c,d}, Mariola Sánchez-González^c, Ricardo Ruiz-Peinado^{c,d}, Andrés Bravo-Oviedo^{c,d,e}, Luis Gil^a, Fernando Montes^c

^a Departamento de Sistemas y Recursos Naturales, Escuela Técnica Superior de Ingeniería de Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid. Ciudad Universitaria s/n, 28040 Madrid, Spain

^b Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, 50080 Zaragoza, Spain

^c INIA, Forest Research Centre, Department of Silviculture and Forest Management, Crta. La Coruña km 7.5, 28040 Madrid, Spain

^d iuFOR, Sustainable Forest Management Research Institute University of Valladolid & INIA, Spain

^e Department of Biogeography and Global Change, National Museum of Natural Sciences, Spanish National Research Council (MNCN, CSIC), Spain



ARTICLE INFO

Keywords:

Dendroecology
Projection
Fagus sylvatica
Quercus petraea
Successional dynamics
Succession
Species dynamics
Competitive advantage

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.

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 (Petritan et al., 2013), which predominate in

* Corresponding author.

E-mail address: alvaro.rubio.cuadrado@upm.es (Á. Rubio-Cuadrado).

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 (IUSS Working Group WRB, 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.

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	Beech	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)***
M1	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)***
M2	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)
M3	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)***
All	Oak	31	106 (135)	18 (20)	36 (23)	62 (18)	24.0 (15.2)	23.9 (14.4)

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.foreco.2018.06.035>.

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 × 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 CO₂-related fertilization effect we also included annual mean CO₂ values and annual mean rates of increase in CO₂ 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 CO₂ 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 $\log(BAI + 1)$ 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-R²) and the variance explained only by the fixed effects (marginal pseudo-R²).

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.

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).

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 Figs. 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 CO_2 , 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 (Figs. 3 and 4). Climatic variables are more important predictors of BAI in the case of beech than in oak. The CO_2 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- R^2) was 72% and 70% for the beech and oak model

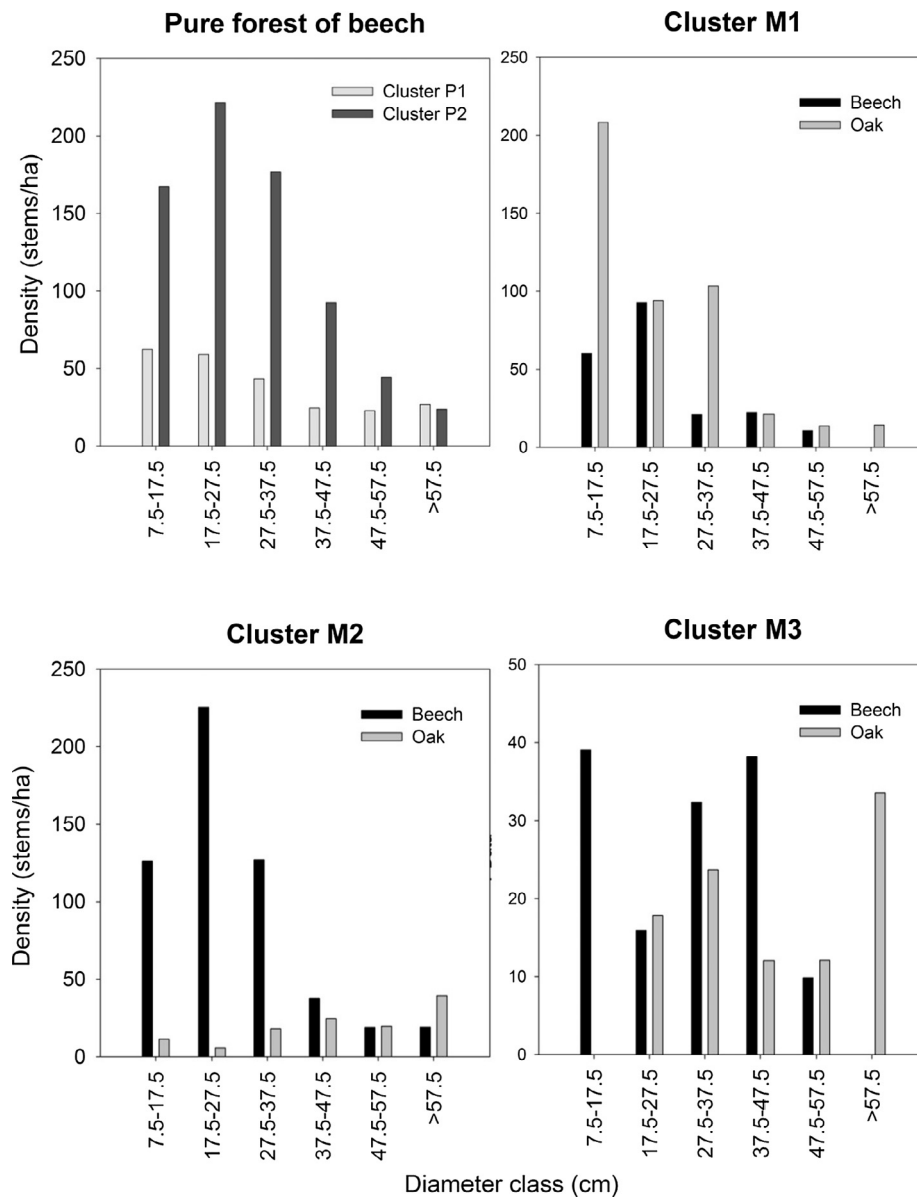


Fig. 1. Size distribution (DBH_{stand}) of the clusters shown for the two studied species. Note that the y-axis scale varies between graphs.

respectively, and the fixed effects explained (marginal pseudo- R^2) 62% and 58% of variance for the same species. In both models the VIF was lower than 3.

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.

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 ($r = 0.299$, $P = 0.002$).

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

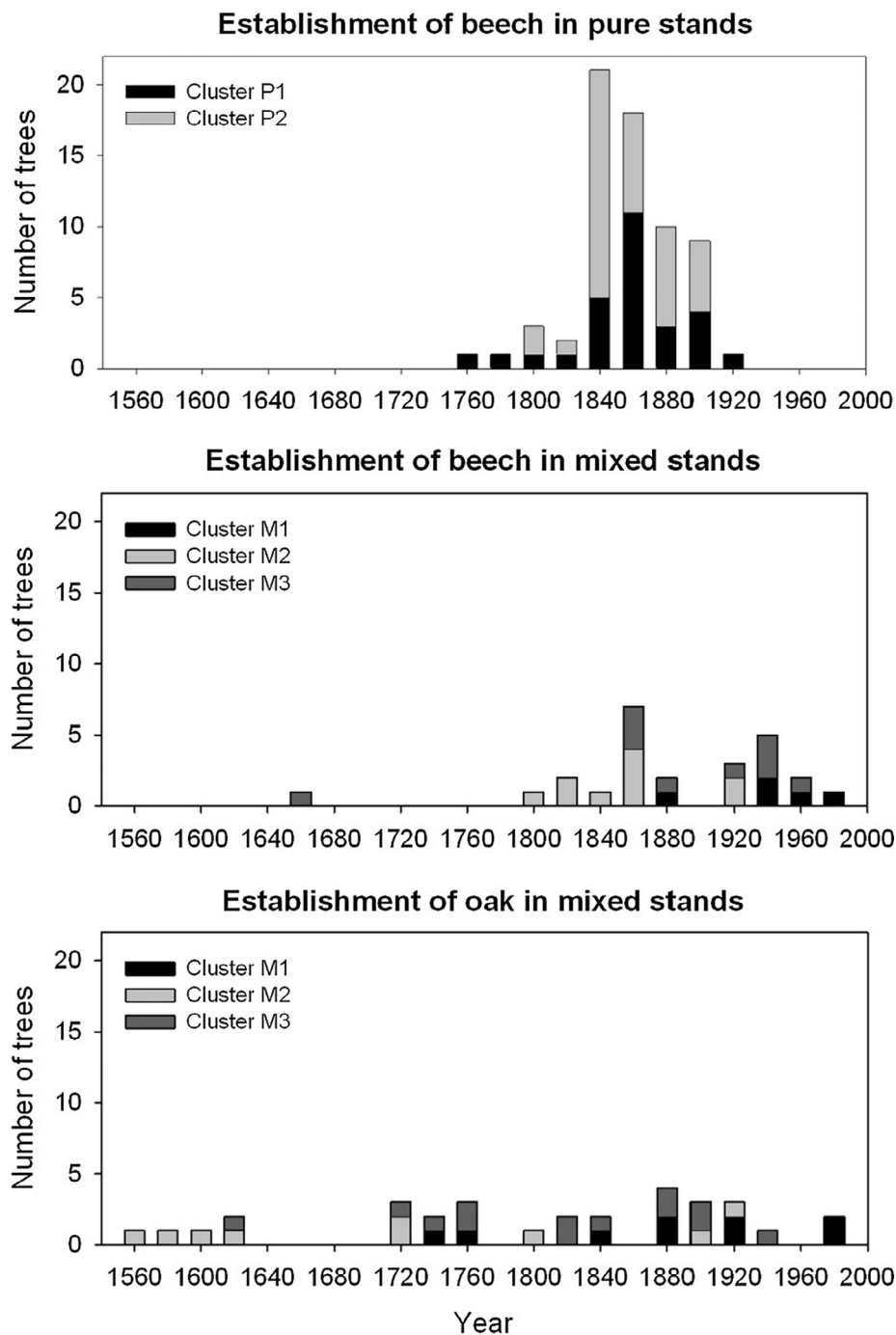


Fig. 2. Establishment history of cored beeches and oaks (shown for 20-year age classes) presented according to size (DBH_{stand}) clusters.

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.

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.

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)	–

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 (Petrutan 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 (Figs. 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 CO₂ 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

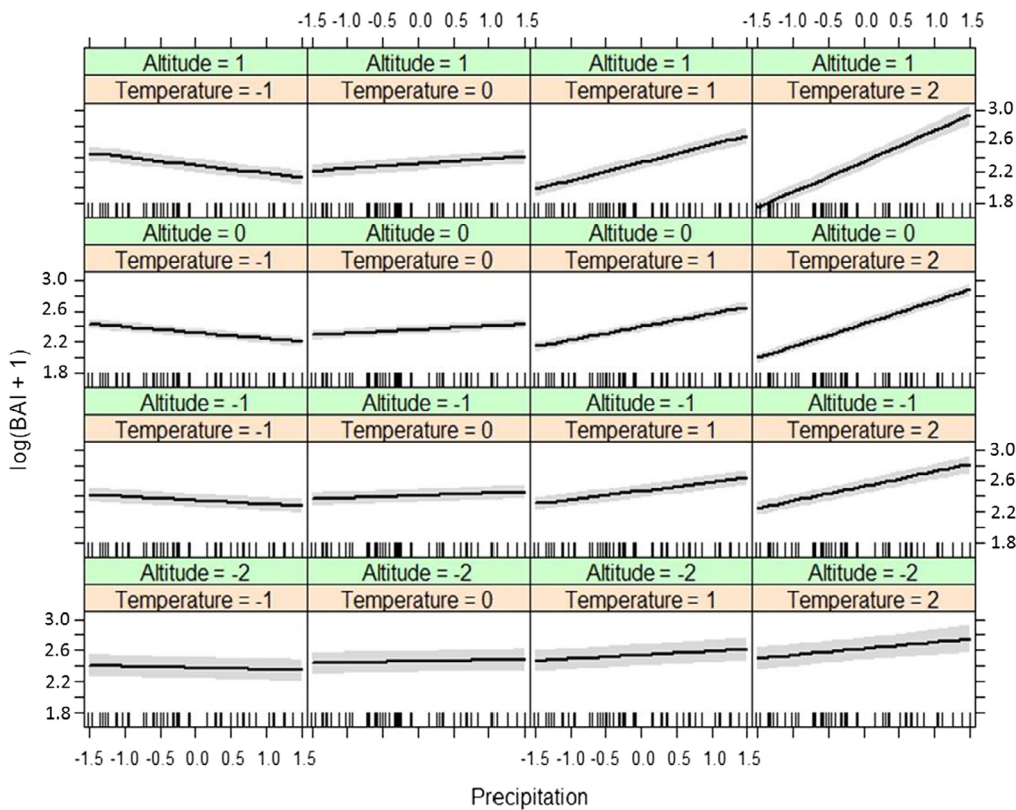


Fig. 3. Effects of the interactions between climate variables and altitude on beech radial growth (log-transformed BAI data). The predictors are standardized. Temperature is the average from February to May, and precipitation is the total rainfall from February to June. Shaded bands indicate the confidence intervals. Positions of the data along x axis are denoted by tick marks.

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

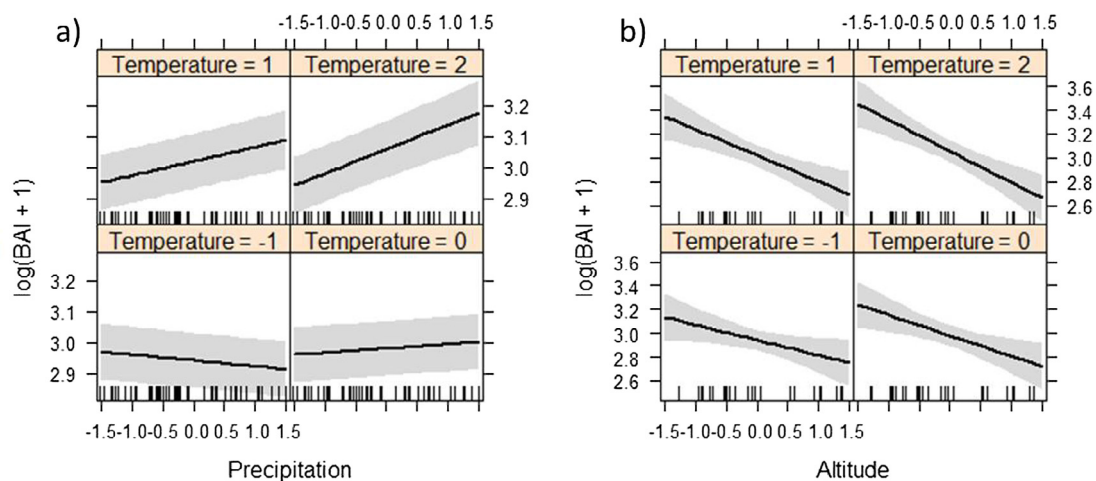


Fig. 4. Effects of the interactions between temperature and precipitation (a) and between temperature and altitude (b) on oak radial growth (log-transformed BAI data). The predictors are standardized. Temperature is the average from February to May, and precipitation is the total rainfall from February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

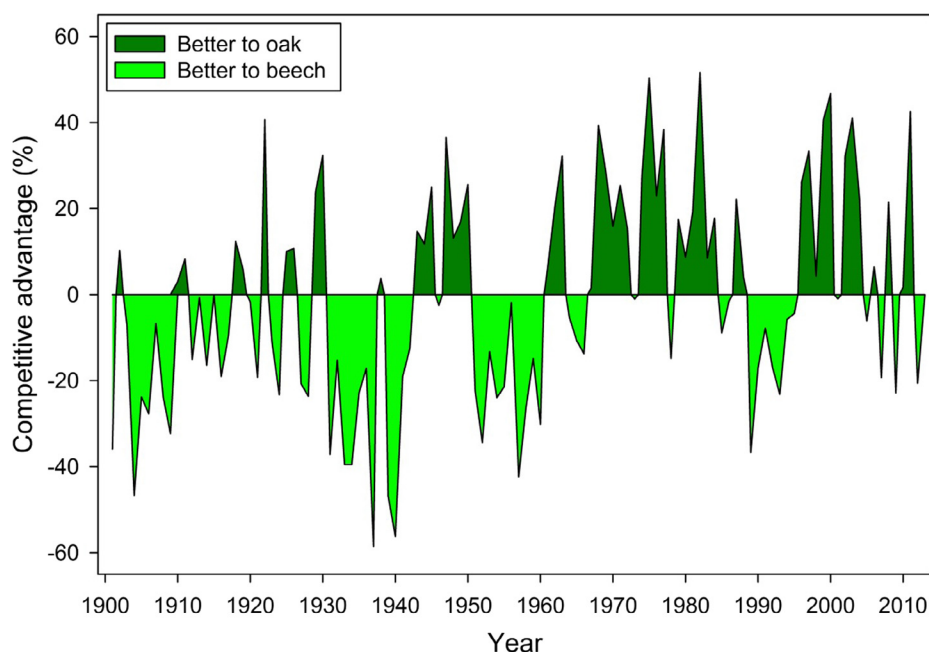


Fig. 5. Reconstructed oak competitive advantage (CA_{oak}) from 1901 to 2013.

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

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.

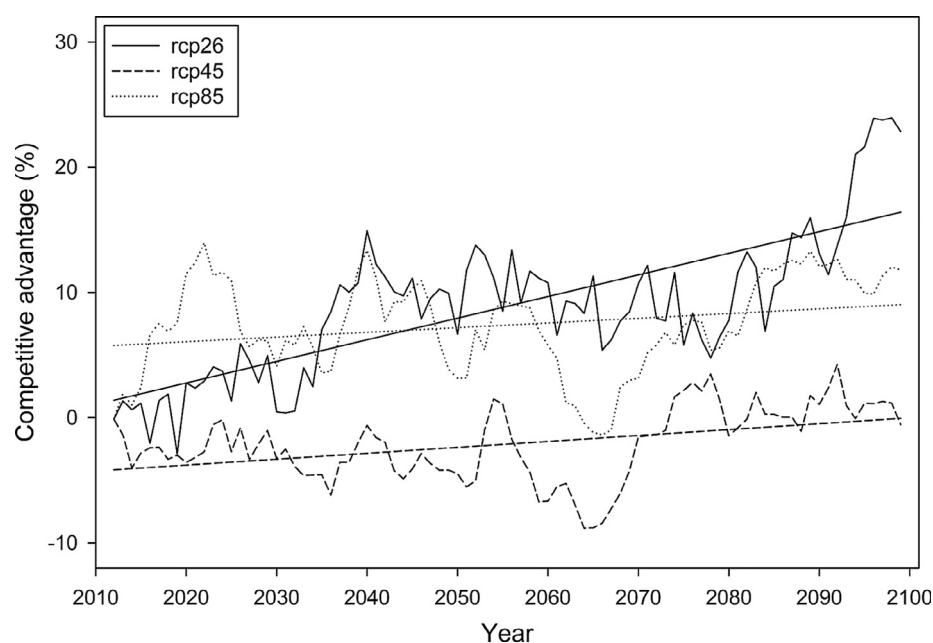


Fig. 6. Projection of the competitive advantage of oak (CA_{oak}) over beech over the course of the 21st century for three emission and climatic scenarios (RCP 2.6, RCP 4.5 and RCP 8.5). Simple linear regressions were fitted for each scenario.

6. Conflict of interest

None.

Acknowledgments

This project has been funded by the National Parks Autonomous Agency of the Spanish Ministry of Agriculture, Fisheries, Food and Environment through the project 979S/2013, by the Autonomous Community of Madrid through the project P2013/MAE-2760, by the project AGL2016-76769-C2-1-R of the Spanish Ministry of Economy, Industry and Competitiveness and through a PhD fellowship of the Spanish Ministry of Education, Culture and Sports. JJC acknowledges the support of the project “Fundiver” (CGL2015-69186-C2-1-R, Spanish Ministry of Economy).

References

- Aranda, I., Gil, L., Pardos, J.A., 2000. Water relations and gas exchange in *Fagus sylvatica* L. and *Quercus petraea* (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. *Trees-Struct. Funct.* 14, 344–352. <http://dx.doi.org/10.1007/s004680050229>.
- Aranda, I., Gil, L., Pardos, J.A., 2005. Seasonal changes in apparent hydraulic conductance and their implications for water use of European beech (*Fagus sylvatica* L.) and sessile oak *Quercus petraea* (Matt.) Liebl in South Europe. *Plant. Ecol.* 179, 155–167. <http://dx.doi.org/10.1007/s11258-004-7007-1>.
- Becker, M., Nieminen, T.M., Geremia, F., 1994. Short-term variations and long-term changes in oak productivity in northeastern France. The role of climate and atmospheric CO₂. *Ann. Sci. Forest* 51, 477–492. <http://prodinra.inra.fr/record/112992>.
- Bergès, L., Dupouey, J.L., Franc, A., 2000. Long-term changes in wood density and radial growth of *Quercus petraea* Liebl. in northern France since the middle of the nineteenth century. *Trees-Struct. Funct.* 14, 398–408. <http://dx.doi.org/10.1007/s004680000055>.
- Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Res.* 64, 81–96. <http://dx.doi.org/10.3959/2008-6.1>.
- Boisvenue, C., Running, S.W., 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Glob. Change Biol.* 12, 862–882. <http://dx.doi.org/10.1111/j.1365-2486.2006.01134.x>.
- Bontemps, J.D., Herve, J.C., Dhote, J.F., 2010. Dominant radial and height growth reveal comparable historical variations for common beech in north-eastern France. *Forest Ecol. Manage.* 259, 1455–1463. <http://dx.doi.org/10.1016/j.foreco.2010.01.019>.
- Braun, S., Thomas, V.F.D., Quiring, R., Flueckiger, W., 2010. Does nitrogen deposition increase forest production? The role of phosphorus. *Environ. Pollut.* 158, 2043–2052. <http://dx.doi.org/10.1016/j.envpol.2009.11.030>.
- Brang, P., Spathelf, P., Larsen, J.B., Bauhus, J., Bončina, A., Chauvin, C., Drössler, L., García-Güemes, C., Heiri, C., Kerr, G., Lexer, M.J., Mason, B., Mohren, F., Mühlthaler, U., Nocentini, S., Svoboda, M., 2014. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. *Forestry* 87, 492–503. <http://dx.doi.org/10.1093/forestry/cpu018>.
- Camarero, J.J., Gazol, A., Tardif, J.C., Conciatori, F., 2015. Attributing forest responses to global-change drivers: limited evidence of a CO₂-fertilization effect in Iberian pine growth. *J. Biogeogr.* 42, 2220–2233. <http://dx.doi.org/10.1111/jbi.12590>.
- Cescatti, A., Piutti, E., 1998. Silvicultural alternatives, competition regime and sensitivity to climate in a European beech forest. *Forest Ecol. Manage.* 102, 213–223. [http://dx.doi.org/10.1016/S0378-1127\(97\)00163-1](http://dx.doi.org/10.1016/S0378-1127(97)00163-1).
- Čufar, K., Prislan, P., Gricar, J., 2008. Cambial activity and wood formation in beech (*Fagus sylvatica*) during the 2006 growth season. *Wood Res-Slovakia* 53, 1–12.
- del Río, M., Schütze, G., Pretzsch, H., 2014. Temporal variation of competition and facilitation in mixed species forests in Central Europe. *Plant Biol.* 16, 166–176. <http://dx.doi.org/10.1111/plb.12029>.
- Diaconu, D., Kahle, H.P., Spiecker, H., 2015. Tree- and stand-level thinning effects on growth of European beech (*Fagus sylvatica* L.) on a northeast- and a southwest-facing slope in southwest Germany. *Forests* 6, 3256–3277. <http://dx.doi.org/10.3390/f6093256>.
- Dittmar, C., Fricke, W., Elling, W., 2006. Impact of late frost events on radial growth of common beech (*Fagus sylvatica* L.) in Southern Germany. *Eur. J. For. Res.* 125, 249–259. <http://dx.doi.org/10.1007/s10342-005-0098-y>.
- Dittmar, C., Zech, W., Elling, W., 2003. Growth variations of common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe – a dendroecological study. *Forest Ecol. Manage.* 173, 63–78. [http://dx.doi.org/10.1016/S0378-1127\(01\)00816-7](http://dx.doi.org/10.1016/S0378-1127(01)00816-7).
- Dorado-Liñán, I., Cañellas, I., Valbuena-Carabaña, M., Gil, L., Gea-Izquierdo, G., 2017. Coexistence in the mediterranean-temperate transitional border: multi-century dynamics of a mixed old-growth forest under global change. *Dendrochronologia* 44, 48–57. <http://dx.doi.org/10.1016/j.dendro.2017.03.007>.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Márquez, J.R.G., Gruber, B., Laforest, B., Leitao, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46. <http://dx.doi.org/10.1111/j.1600-0587.2012.07348.x>.
- Corps, Engineers, 1859. *Clasificación General de los Montes Públicos*. Imprenta nacional, Madrid, Spain.
- Forrester, D.I., Bonal, D., Dawud, S., Gessler, A., Granier, A., Pollastrini, M., Grossiord, C., 2016. Drought responses by individual tree species are not often correlated with tree species diversity in European forests. *J. Appl. Ecol.* 53, 1725–1734. <http://dx.doi.org/10.1111/1365-2664.12745>.
- Frelich, L.E., Montgomery, R.A., Oleksyn, J., 2015. Northern temperate forests. In: Peh, K.S.H., Corlett, R.T., Bergeron, Y. (Eds.), *Routledge Handbook of Forest Ecology*. Routledge, London, United Kingdom.
- Fritts, H.C., 2001. *Tree Rings and Climate*. The Blackburn Press, New Jersey, USA.
- García Sanz, Á., 1978. La agonía de la Mesta y el hundimiento de las exportaciones laneras: un capítulo de la crisis económica del antiguo régimen en España. *Agric. Soc.* 6, 283–356.
- Gazol, A., Camarero, J.J., 2016. Functional diversity enhances silver fir growth resilience to an extreme drought. *J. Ecol.* 104, 1063–1075. <http://dx.doi.org/10.1111/1365-2745.12575>.
- Gazol, A., Ibáñez, R., 2010. Scale-specific determinants of a mixed beech and oak seedling-sapling bank under different environmental and biotic conditions. *Plant Ecol.* 211, 37–48. <http://dx.doi.org/10.1007/s11258-010-9770-5>.
- Gea-Izquierdo, G., Viguera, B., Cabrera, M., Canellas, I., 2014. Drought induced decline could portend widespread pine mortality at the xeric ecotone in managed Mediterranean pine-oak woodlands. *Forest Ecol. Manage.* 320, 70–82. <http://dx.doi.org/10.1016/j.foreco.2014.02.025>.
- González de Andrés, E., Camarero, J.J., Blanco, J.A., Imbert, J.B., Lo, Y.H., Sangüesa-Barreda, G., Castillo, F.J., 2018. Tree-to-tree competition in mixed European beech–Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions. *J. Ecol.* 106, 59–75. <http://dx.doi.org/10.1111/1365-2745.12813>.
- Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruehlheide, H., Čeko, E., Forrester, D.I., Dawud, S.M., Finér, L., Pollastrini, M., Scherer-Lorenzen, M., Valladares, F., Bonal, D., Gessler, A., 2014. Tree diversity does not always improve resistance of forest ecosystems to drought. *Proc. Natl. Acad. Sci. USA* 111, 14812–14815. <http://dx.doi.org/10.1073/pnas.1411970111>.
- Harmer, R., 1994. Natural regeneration of broadleaved trees in Britain. 2. Seed production and predation. *Forestry* 67, 275–286.
- Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H., 2014. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *Int. J. Climatol.* 34, 623–642. <http://dx.doi.org/10.1002/joc.3711>.
- Hart, J.L., Clark, S.L., Torreano, S.J., Buchanan, M.L., 2012. Composition, structure, and dendroecology of an old-growth *Quercus* forest on the tablelands of the Cumberland Plateau, USA. *Forest Ecol. Manage.* 266, 11–24. <http://dx.doi.org/10.1016/j.foreco.2011.11.001>.
- Holmes, R.L., 1997. The Dendrochronology Program Library. Version 2.1 users manual. The International Tree Ring Data Bank Program. Laboratory of Tree-Ring Res. University of Arizona, Tucson, USA.
- IPCC, 2014. Long-term climate change: projections, commitments and irreversibility. *Climate change 2013 – The physical science basis: working group I contribution to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge, United Kingdom.
- IUSS Working Group WRB, 2015. World Reference Base for Soil Resources 2014, update 2015. International soil classification system for naming soils and creating legends for soil maps. *World Soil Resources Reports* N° 106. FAO, Rome, Italy.
- Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O.B., Bouwer, L.M., Braun, A., Colette, A., Déqué, M., Georgievski, G., Georgopoulou, E., Gobiet, A., Menut, L., Nikulin, G., Haensler, A., Hempelmann, N., Jones, C., Keuler, K., Kovats, S., Kröner, N., Kotlarski, S., Kriegsmann, A., Martin, E., van Meijgaard, E., Moseley, C., Pfeifer, S., Preuschmann, S., Radermacher, C., Radtke, K., Rechid, D., Rousevlev, M., Samuelsson, P., Somot, S., Soussana, J.F., Teichmann, C., Valentini, R., Vautard, R., Weber, B., Yiou, P., 2014. EURO-CORDEX: new high-resolution climate change projections for European impact research. *Reg. Environ. Change* 14, 563–578. <http://dx.doi.org/10.1007/s10113-013-0499-2>.
- Keenan, T.F., Hollinger, D.Y., Bohrer, G., Dragoni, D., Munger, J.W., Schmid, H.P., Richardson, A.D., 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature* 499, 324–327. <http://dx.doi.org/10.1038/nature12291>.
- Kint, V., Aertsens, W., Campioli, M., Vansteenkiste, D., Delcloc, A., Muys, B., 2012. Radial growth change of temperate tree species in response to altered regional climate and air quality in the period 1901–2008. *Clim. Change* 115, 343–363. <http://dx.doi.org/10.1007/s10584-012-0465-x>.
- Lebourgeois, F., Gómez, N., Pinto, P., Mérian, P., 2013. Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *Forest Ecol. Manage.* 303, 61–71. <http://dx.doi.org/10.1016/j.foreco.2013.04.003>.
- Lévesque, M., Walthert, L., Weber, P., 2016. Soil nutrients influence growth response of temperate tree species to drought. *J. Ecol.* 104, 377–387. <http://dx.doi.org/10.1111/1365-2745.12519>.
- López-Merino, L., López-Sáez, J.A., Ruiz-Zapata, M.B., Gil-García, M.J., 2008. Reconstructing the history of beech (*Fagus sylvatica* L.) in the north-western Iberian Range (Spain): from Late-Glacial refugia to the Holocene anthropic-induced forests. *Rev. Palaeobot. Palynol.* 152, 58–65. <http://dx.doi.org/10.1016/j.revpalbo.2008.04.003>.
- Lorimer, C.G., Frelich, L.E., Nordheim, E.V., 1988. Estimating gap origin probabilities for canopy trees. *Ecology* 69, 778–785. <http://dx.doi.org/10.2307/1941026>.
- Madrigal, J., Hantson, S., Yue, C., Poulter, B., Ciais, P., Zavala, M.A., 2015. Long-term wood production in water-limited forests: evaluating potential CO₂ fertilization along

- with historical confounding factors. *Ecosystems* 18, 1043–1055. <http://dx.doi.org/10.1007/s10021-015-9882-9>.
- Maleki, K., Kiviste, A., Korjus, H., 2015. Analysis of individual tree competition effect on diameter growth of silver birch in Estonia. *For. Syst.* 24, e023. <http://dx.doi.org/10.5424/fs/2015242-05742>.
- Martin, P.A., Newton, A.C., Cantarello, E., Evans, P., 2015. Stand dieback and collapse in a temperate forest and its impact on forest structure and biodiversity. *Forest Ecol. Manage.* 358, 130–138. <http://dx.doi.org/10.1016/j.foreco.2015.08.033>.
- Martínez del Castillo, E., Longares, L.A., Gricar, J., Prislán, P., Gil-Pelegrin, E., Čufar, K., de Luis, M., 2016. Living on the edge: contrasted wood-formation dynamics in *Fagus sylvatica* and *Pinus sylvestris* under Mediterranean conditions. *Front. Plant Sci.* 7, 370. <http://dx.doi.org/10.3389/fpls.2016.00370>.
- McCarthy, B.C., Bailey, D.R., 1996. Composition, structure, and disturbance history of Crabtree Woods: an old-growth forest of western Maryland. *Bull. Torrey Bot. Club* 123, 350–365. <http://dx.doi.org/10.2307/2996783>.
- McCarthy, J., 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environ. Rev.* 9, 1–59. <http://dx.doi.org/10.1139/a00-012>.
- Michelot, A., Simard, S., Rathgeber, C., Dufrene, E., Damesin, C., 2012. Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree Physiol.* 32, 1033–1045. <http://dx.doi.org/10.1093/treephys/tps052>.
- Miñano y Bedoya, S., 1829. *Diccionario geográfico-estadístico de España y Portugal*. Imprenta de Pierart-Peralta, Madrid.
- Mölder, I., Leuschner, C., 2014. European beech grows better and is less drought sensitive in mixed than in pure stands: tree neighbourhood effects on radial increment. *Trees-Struct. Funct.* 28, 777–792. <http://dx.doi.org/10.1007/s00468-014-0991-4>.
- Monserud, R.A., Sterba, H., 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. *Forest Ecol. Manage.* 80, 57–80. [http://dx.doi.org/10.1016/0378-1127\(95\)03638-5](http://dx.doi.org/10.1016/0378-1127(95)03638-5).
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142. <http://dx.doi.org/10.1111/j.2041-210X.2012.00261.x>.
- Niinemets, U., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547. [http://dx.doi.org/10.1890/0012-9615\(2006\)076\[0521:TTSDAW\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2).
- Pederson, N., Dyer, J.M., McEwan, R.W., Hessel, A.E., Mock, C.J., Orwig, D.A., Rieder, H.E., Cook, B.L., 2014. The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecol. Monogr.* 84, 599–620. <http://dx.doi.org/10.1890/13-1025.1>.
- Pérez-de-Lis, G., Olano, J.M., Rozas, V., Rossi, S., Vázquez-Ruiz, R.A., García-González, I., 2017. Environmental conditions and vascular cambium regulate carbon allocation to xylem growth in deciduous oaks. *Funct. Ecol.* 31, 592–603. <http://dx.doi.org/10.1111/1365-2435.12789>.
- Pérez-Ramos, I.M., 2014. The miracle of regenerating in *Quercus* species. How will be oak forests in future? *Ecosistemas* 23, 13–17. <http://dx.doi.org/10.7818/ECOS.2014.23-2.03>.
- Petritan, A.M., Bouriaud, O., Frank, D.C., Petritan, I.C., 2017. Dendroecological reconstruction of disturbance history of an old-growth mixed sessile oak-beech forest. *J. Veg. Sci.* 28, 117–127. <http://dx.doi.org/10.1111/jvs.12460>.
- Petritan, A.M., Nuske, R.S., Petritan, I.C., Tudose, N.C., 2013. Gap disturbance patterns in an old-growth sessile oak (*Quercus petraea* L.)-European beech (*Fagus sylvatica* L.) forest remnant in the Carpathian Mountains, Romania. *Forest Ecol. Manage.* 308, 67–75. <http://dx.doi.org/10.1016/j.foreco.2013.07.045>.
- Petritan, I.C., Commarmot, B., Hobi, M.L., Petritan, A.M., Bigler, C., Abrudan, I.V., Rigling, A., 2015. Structural patterns of beech and silver fir suggest stability and resilience of the virgin forest Sinca in the Southern Carpathians, Romania. *Forest Ecol. Manage.* 356, 184–195. <http://dx.doi.org/10.1016/j.foreco.2015.07.015>.
- Piovesan, G., Biondi, F., Di Filippo, A., Alessandrini, A., Maugeri, M., 2008. Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Glob. Change Biol.* 14, 1265–1281. <http://dx.doi.org/10.1111/j.1365-2486.2008.01570.x>.
- Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biol.* 15, 483–495. <http://dx.doi.org/10.1111/j.1438-8677.2012.00670.x>.
- Rentch, J.S., Fajvan, M.A., Hicks, R.R., 2003. Oak establishment and canopy accession strategies in five old-growth stands in the central hardwood forest region. *Forest Ecol. Manage.* 184, 285–297. [http://dx.doi.org/10.1016/S0378-1127\(03\)00155-5](http://dx.doi.org/10.1016/S0378-1127(03)00155-5).
- Richards, A.E., Forrester, D.I., Bauhus, J., Scherer-Lorenzen, M., 2010. The influence of mixed tree plantations on the nutrition of individual species: a review. *Tree Physiol.* 30, 1192–1208. <http://dx.doi.org/10.1093/treephys/tpq035>.
- Rodríguez-García, C., Montes, F., Ruiz, F., Cañellas, I., Pita, P., 2014. Stem mapping and estimating standing volume from stereoscopic hemispherical images. *Eur. J. For. Res.* 133, 895–904. <http://dx.doi.org/10.1007/s10342-014-0806-6>.
- Rohner, B., Bigler, C., Wunder, J., Brang, P., Bugmann, H., 2012. Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech. *J. Veg. Sci.* 23, 892–905. <http://dx.doi.org/10.1111/j.1654-1103.2012.01408.x>.
- Rousseeuw, P.J., 1987. Silhouettes – a graphical aid to the interpretation and validation of cluster-analysis. *J. Comput. Appl. Math.* 20, 53–65. [http://dx.doi.org/10.1016/0377-0427\(87\)90125-7](http://dx.doi.org/10.1016/0377-0427(87)90125-7).
- Rozas, V., 2001a. Detecting the impact of climate and disturbances on tree-rings of *Fagus sylvatica* L. and *Quercus robur* L. in a lowland forest in Cantabria, Northern Spain. *Ann. For. Sci.* 58, 237–251. <http://dx.doi.org/10.1051/forest:2001123>.
- Rozas, V., 2001b. Dinámica forestal y tendencias sucesionales en un bosque maduro de roble y haya de la zona central de la Cornisa Cantábrica. *Ecología* 15, 179–211. <http://hdl.handle.net/10261/46626>.
- Rozas, V., 2003. Tree age estimates in *Fagus sylvatica* and *Quercus robur*: testing previous and improved methods. *Plant Ecol.* 167, 193–212. <http://dx.doi.org/10.1023/A:1023969822044>.
- Rozenberger, D., Mikac, S., Anic, I., Diaci, J., 2007. Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech-fir forest reserves in South East Europe. *Forestry* 80, 431–443. <http://dx.doi.org/10.1093/forestry/cpm037>.
- Rubio-Cuadrado, A., Camarero, J.J., del Río, M., Sánchez-González, M., Ruiz-Peinado, R., Bravo-Oviedo, A., Gil, L., Montes, F., 2018. Long-term impacts of drought on growth and forest dynamics in a temperate beech-oak-birch forest. *Agr. Forest Meteorol.* 259, 48–59. <http://dx.doi.org/10.1016/j.agrformet.2018.04.015>.
- Sánchez-González, M., Cabrera, M., Herrera, P.J., Vallejo, R., Cañellas, I., Montes, F., 2016. Basal area and diameter distribution estimation using stereoscopic hemispherical images. *Photogramm. Eng. Rem. S* 82, 605–616. [http://dx.doi.org/10.1016/S0099-1112\(16\)30098-2](http://dx.doi.org/10.1016/S0099-1112(16)30098-2).
- Sánchez-Salguero, R., Linares, J.C., Camarero, J.J., Madrigal-González, J., Hevia, A., Sánchez-Miranda, A., Ballesteros-Cánovas, J., Alfaro-Sánchez, R., García-Cervigón, A.I., Bigler, C., Rigling, A., 2015. Disentangling the effects of competition and climate on individual tree growth: a retrospective and dynamic approach in Scots pine. *Forest Ecol. Manage.* 358, 12–25. <http://dx.doi.org/10.1016/j.foreco.2015.08.034>.
- Sangüesa-Barreda, G., Camarero, J.J., Oliva, J., Montes, F., Gazol, A., 2015. Past logging, drought and pathogens interact and contribute to forest dieback. *Agr. Forest Meteorol.* 208, 85–94. <http://dx.doi.org/10.1016/j.agrformet.2015.04.011>.
- Schröder, J., von Gadow, K., 1999. Testing a new competition index for maritime pine in northwestern Spain. *Can. J. Forest Res.* 29, 280–283. <http://dx.doi.org/10.1139/x98-199>.
- Schweingruber, F., 1988. *Tree Rings: Basics and Applications of Dendrochronology*. Kluwer Academic, Dordrecht, The Netherlands.
- Schweingruber, F., Eckstein, D., Serre-Bachet, F., Bräker, O.U., 1990. Identification, presentation and interpretation of event years and pointer years in dendrochronology. *Dendrochronologia* 8, 9–38. <https://www.dora.lib4ri.ch/wsl/islandora/object/wsl:2189>.
- Stadt, K.J., Huston, C., Coates, K.D., Feng, Z., Dale, M.R.T., Lieffers, V.J., 2007. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. *Ann. For. Sci.* 64, 477–490. <http://dx.doi.org/10.1051/forest:2007025>.
- Suárez, M.L., Ghermandi, L., Kitzberger, T., 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. *J. Ecol.* 92, 954–966. <http://dx.doi.org/10.1111/j.1365-2745.2004.00941.x>.
- Toigo, M., Vallet, P., Perot, T., Bontemps, J.D., Piedallu, C., Courbaud, B., 2015. Overyielding in mixed forests decreases with site productivity. *J. Ecol.* 103, 502–512. <http://dx.doi.org/10.1111/1365-2745.12353>.
- Thomas, F.M., Blank, R., Hartmann, G., 2002. Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. *Forest Pathol.* 32, 277–307. <http://dx.doi.org/10.1046/j.1439-0329.2002.00291.x>.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323, 521–524. <http://dx.doi.org/10.1126/science.1165000>.
- van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S.K., 2011. The representative concentration pathways: an overview. *Clim. Change* 109, 5–31. <http://dx.doi.org/10.1007/s10584-011-0148-z>.
- Vašíčková, I., Šamonil, P., Fuentes Ubilla, A.E., Král, K., Daněk, P., Adam, D., 2016. The true response of *Fagus sylvatica* L. to disturbances: a basis for the empirical inference of release criteria for temperate forests. *Forest Ecol. Manage.* 374, 174–185. <http://dx.doi.org/10.1016/j.foreco.2016.04.055>.
- Ward, J.H., 1963. Hierarchical grouping to optimize an objective function. *J. Am. Stat. Assoc.* 58, 236–244. <http://dx.doi.org/10.1080/01621459.1963.10500845>.
- Weber, P., Bugmann, H., Fonti, P., Rigling, A., 2008. Using a retrospective dynamic competition index to reconstruct forest succession. *Forest Ecol. Manage.* 254, 96–106. <http://dx.doi.org/10.1016/j.foreco.2007.07.031>.
- Zuur, A., Ieno, E., Walker, N., Saveliev, A., Smith, G., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer-Verlag, New York, NY, USA.