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Geographically Structured Growth decline of Rear-Edge Iberian *Fagus sylvatica* Forests After the 1980s Shift Toward a Warmer Climate

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ABSTRACT

Warming-related growth decrease on southern *Fagus sylvatica* forests has been observed in different regions; however, whether it is a generalized fact or not remains unclear. Here we investigate the geographical pattern on growth response of the southwestern European beech forests to the warming climate shift which started in the 1980s. We sampled 15 beech forests (215 trees) across four climatically contrasting regions (Mediterranean, Pyrenean, low- and high-elevation Atlantic areas) near the southern distribution limit of the species in the Iberian Peninsula. Dendrochronological analyses were carried out to evaluate the growth of European beech since the 1950s. Growth responses quantified as pointer years, abrupt growth changes and long-term growth trends were compared between periods (before and after the 1980s climate shift), geographical regions and tree sizes. Analyses of the studied variables indicated a growth decrease in basal area increment after the climate shift in three of the four studied regions. Pyrenean stands were not negatively influenced by the climate shift, although an increase in the frequency of negative abrupt growth changes was also found there. Growth after the climate shift presented divergent patterns depending on the geographical region. Although Mediterranean and Atlantic stands presented different indicators of constrained growth, Pyrenean stands showed rising long-term growth trends. Such results suggest that regional characteristics differentially determine the growth response of the southern European beech forests to recent warming periods. Iberian beech forests located at the Pyrenees would benefit from forecasted warming conditions, whereas Atlantic and Mediterranean forests would be more prone to suffer warming-related growth decline.

Key words: climate warming; dendroecology; growth decline; tree rings; climate shift; beech; Iberian Peninsula.

HIGHLIGHTS

- Growth decrease in southwestern beech forests after 1980s climate shift.
- Growth decrease is geographically structured through northeast Iberian Peninsula.
- Mediterranean and Atlantic stands presented more growth constrains than Pyrenean ones.

INTRODUCTION

Tree populations growing in the southernmost distribution limits of the species range (xeric rear edges) face harsh climate conditions, which can compromise their performance and growth (Gazol and others 2015; Sánchez-Salguero and others 2017). Future climate projections forecast warmer climate and an increase of extreme weather events such as droughts and/or heat waves (IPCC 2014), which could trigger local extinctions and/or range shifts of the most vulnerable rear-edge tree populations (Chen and others 2011). Warming-related growth decline and forest dieback triggered by dry spells are a major concern for scientists and managers (Allen and others 2010, 2015), and its influence on forest dynamics and possible retractions of rear-edge tree populations is still under debate (Sánchez-Salguero and others 2017).

European beech (*Fagus sylvatica* L.) is a drought-sensitive tree species widely distributed across Europe (Köchner and others 2009; Zimmermann and others 2015) which displays productivity and growth reduction (Lendzoin and Leuschner 2008; Thiel and others 2014), and leaf and root trait alteration as a consequence of drought (Knutzen and others 2015). Increase in temperature and water shortage affects beech radial growth across the entire continent, indicating a widespread vulnerability to future warming climate (Hacket-Pain and others 2016). Special attention must be paid at drought-prone rear-edge forests in continental areas such as the Iberian Peninsula, where warm and dry summers constrain beech performance (Gutiérrez 1988; Rozas and others 2015; Dorado-Liñán and others 2017). In the last four decades, a warming trend has been observed in the Iberian Peninsula; particularly, a rapid rise in temperatures has occurred since the 1980s followed by successive severe droughts in the 1990s, 2000s and 2010s (Gonzalez-Hidalgo and others 2015). Such abrupt warming occurred in the transition from the 1970s to the 1980s, and it was partly linked to changes in the winter atmospheric circulation over the northern Atlantic Ocean (Hurrell 1996) and impacted ecosystems worldwide by accelerating climate warming (Reid and others 2016). This climate shift has led to warmer and more arid conditions on several European regions, generating harsher climatic conditions for beech forests. For instance, Jump and others (2006) found a warming-related growth decline in low-elevation beech stands in the Montseny Mountains (NE Spain) due to warming conditions after the 1980s. In a previous study in the same forest, water shortage was suggested as the main constrain of tree growth, indicating that an increase in evapotranspiration could seriously compromise future forest productivity (Gutiérrez 1988). Comparable episodes of warming-induced growth decline have been found at rear-edge stands from Italy (Piovesan and others 2008) and Hungary (Garamszegi and Kern 2014). In the core of its distribution range, beech populations growing at lower altitudes in dry areas have also experienced marked growth declines (Zimmermann and others 2015; Dulamsuren and others 2016; Knutzen and others 2017). Nevertheless, increased climate sensitivity has been also found in mesic stands, while stands from dry sites were not so responsive, suggesting local adaptation to water shortage and extreme conditions in populations from dry sites (Weber and others 2013; Cavin and Jump 2017). Similarly, rising growth trends or absence of a warming-triggered growth decline has been reported for recent decades in other European beech rear-edge forests (Tegel and others 2014; Cavin and Jump 2017; Hacket-Pain and Friend 2017).

The occurrence of warming- and drought-related growth decreases could be modulated by different intrinsic factors (McDowell and others 2008; Galván and others 2012). For instance, tree size has been suggested as a key factor of the resistance to extreme drought events, with larger trees more susceptible to such events than small ones (Bennett and others 2015). In addition, trees of the same species but different size can respond differently to climate (Rozas 2015). Warming- and drought-related growth decline could thus be a consequence of the combined effect of extrinsic (climatic) and intrinsic (size) factors influencing tree growth (Colangelo and others 2017). Therefore, considering individual characteristics as tree size might help to better depict the causes of warming and drought effects on beech radial growth.

Here we study the stem secondary growth of fifteen Iberian beech forests during the period 1950–2008. Our study region covers a large area and includes a wide climatic gradient, from dry

Mediterranean to wet Atlantic sites, encompassing the major climatic conditions where beech grows at southwestern Europe. Our aim is to quantify the effect of the 1980s climate shift on radial growth of the studied beech forests. We use a dendrochronological approach, considering tree-ring width as a reliable proxy of tree growth rate and vitality. We evaluate growth variability at different time scales, from short (year to year) to long-term growth changes (30-year periods), to investigate the possible warming- and drought-related effects on tree growth. Furthermore, we also evaluate the effect of tree size (stem diameter at breast height) on the response of trees to a climate shift toward warmer and more arid conditions. Our specific aims are to determine: (1) whether there has been a negative effect on growth of Iberian beech populations caused by the 1980s climate shift; (2) whether there is any biogeographical pattern in the response of these beech populations to climate warming; (3) whether tree size partially modulates the growth response of beech to the 1980s climate shift. We hypothesize that, after the 1980s climate shift, forests from xeric sites will present more growth constraints than those in mesic sites. We expect that Iberian beech forests growth responses to warming climate would vary among regions and would depend on tree size.

MATERIALS AND METHODS

Study Sites and Data Sampling

Our study was conducted in the northeast Iberian Peninsula, which represents the southwestern distribution limit of European beech (Figure 1). We sampled 15 forests across a marked climatic gradient, with mean annual temperatures ranging from 6.7 to 15.7 °C and mean annual precipitation ranging from 579 to 1208 mm (CRU TS 4.01 climate data from 1950 to 2008) (Harris and Jones 2017) (Figure 2, Supplementary materials Figure S1). During the growing season (May–September), the mean temperature and precipitation vary considerably depending on the sampled region (Rozas and others 2015). For instance, stands in the Mediterranean and Atlantic areas have higher temperatures (16 °C) than stands found in the Pyrenees (12 °C). In terms of growing season precipitation, Atlantic and Pyrenean stands present higher values than Mediterranean stands, with mean values of 446, 497 and 378 mm, respectively. A different range of altitudes was also present on the sampled stands, going from 300 m to 1530 m a. s. l. More detailed characteristics of each plot are described in Table 1.

Climate Variables and Climatic Areas

Monthly temperature and precipitation series from 1901 to 2010 at 0.5° resolution were downloaded from CRU TS 4.01 dataset (Harris and Jones 2017). Next, mean annual temperature (MAT) and mean annual precipitation (MAP) series for the period 1950–2008 were calculated (Figure 2). To assess the aridity of each site, we calculated De Martonne's aridity index (hereafter, AI), which is calculated as the ratio of mean annual precipitation and mean annual temperature plus 10 (Tuhkanen 1980). High values of AI indicate wet conditions and low values indicate arid conditions. To estimate drought severity at each site, time series from 1950 to 2008 of the Standardized Precipitation and Evapotranspiration Index (hereafter, SPEI) at 0.5° resolution (Vicente-Serrano and others 2010) were downloaded (Figure 2). We used March to August
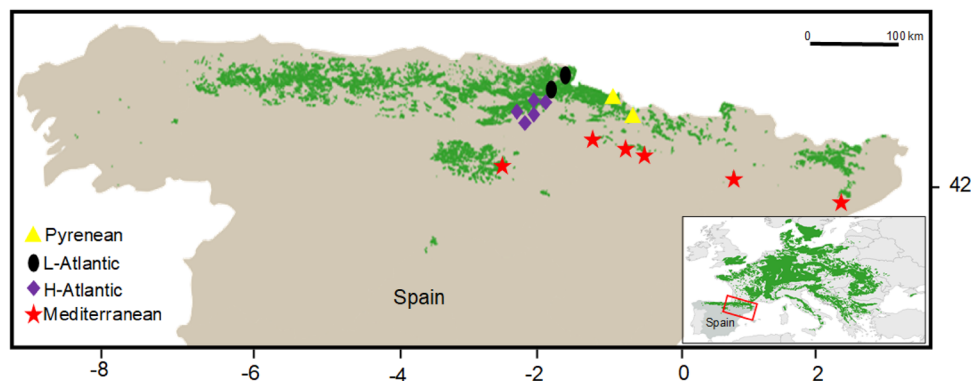

Figure 1. Beech (*Fagus sylvatica*) distribution in Europe (right down inset) and northern Spain showing the four biogeographical forest groups: Pyrenean (yellow triangles), low-elevation Atlantic (black circles), high-elevation Atlantic (purple rhombus) and Mediterranean (red stars) (Color figure online).
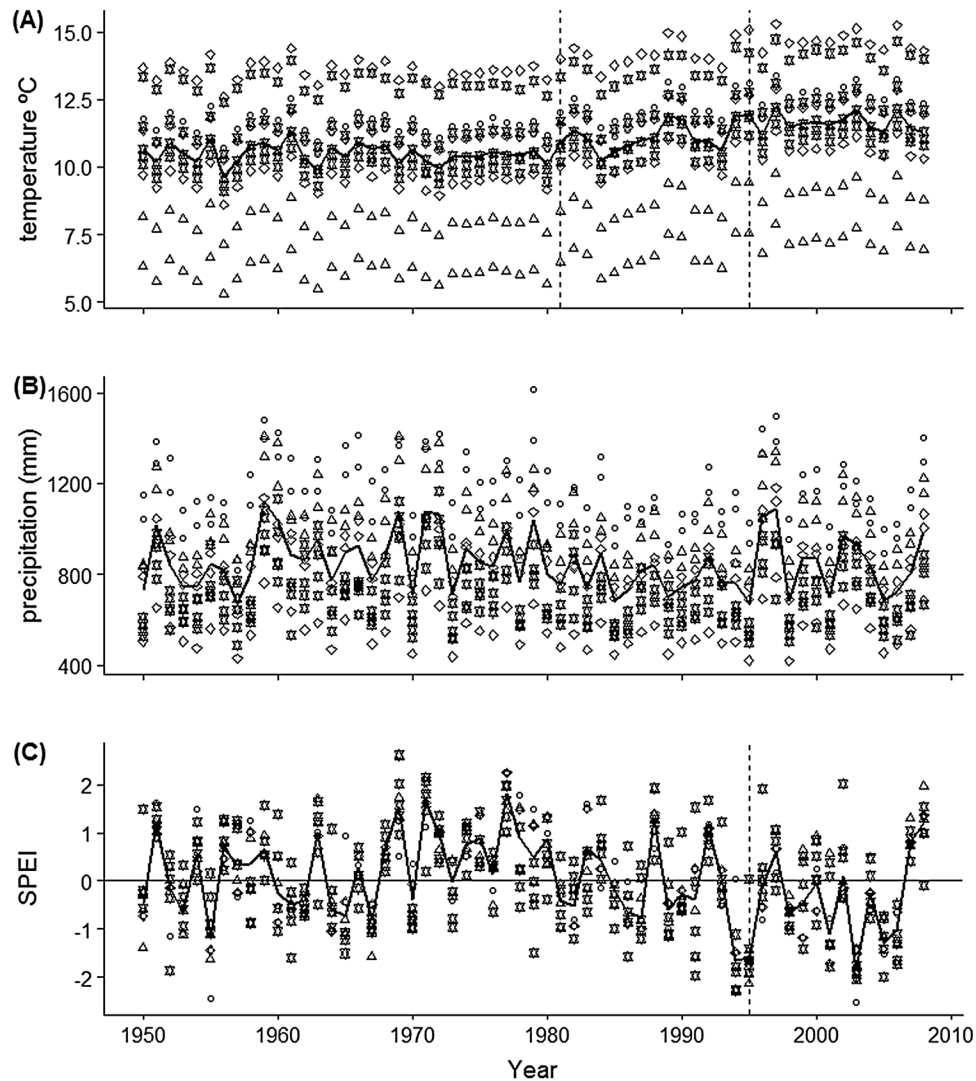
Figure 2. (**A**) Temperature, (**B**) precipitation and (**C**) Standardized Precipitation and Evapotranspiration Index (SPEI) on the area during 1950–2008 period. Bold lines represent mean values. Points represent single site values. Vertical dashed lines represent the detected shifts on the mean temperature and SPEI series. Symbols indicate the biogeographical area: Mediterranean (stars), Pyrenean (triangles), low-(circles) and high-elevation Atlantic (rhombus).

SPEI to cover the main growth season of beech. We evaluated mean annual precipitation, mean annual temperature and SPEI along the studied period in order to detect possible climate shifts. We looked for shifts in climate variables using the function *breakpoints* from the *strucchange* (Zeileis and others 2003) package in R (R core team 2017). This function detects breakpoints that mark separation between segments of time series. Series are divided in segments of constant mean values; thus, years between segments, which we call breakpoint, are years where an increase or decrease of mean values occurs. Furthermore, we calculated trends of spring–summer mean values of temperature and precipitation to evaluate changes on the climate

variables during the growing season (Supplementary materials Figure S2).

In order to find groups of stands with similar climatic conditions, we performed a hierarchical cluster analyses based on the Euclidean distance of the climate variables (MAT, MAP and AI for the 1950–2008 period) including the site elevation. These analyses resulted in four different groups that would be used in all the analyses (Supplementary materials Table S1, Figure S3): two stands with low temperatures, high precipitation and situated at high elevation, the Pyrenean stands; six stands situated at high elevations, with warm temperature and low precipitation, the Mediterranean stands; finally, two groups characterized by

Table 1. Characteristics of the Study Beech Forests

Site name (code)	MAT (°C)	MAP (mm)	Elevation (m a.s.l.)	Biogeographical region	AI	Mean DBH ± SE (cm)	Mean Age at 1.3 m ± SE (years)
Aisa (AIS)	6.5	1054	1105	PYR	173	19 ± 2	78 ± 5
Bertiz (BER)	11.6	1111	300	L-ATL	106	20 ± 1	126 ± 3
Diustes (DIU)	10.7	658	1320	MED	71	15 ± 1	90 ± 2
Eraso (ERA)	12.0	1208	600	L-ATL	110	16 ± 1	103 ± 4
Gamueta (GAM)	8.4	972	1400	PYR	126	25 ± 2	179 ± 24
Izki (IZK)	10	889	800	H-ATL	99	15 ± 1	94 ± 4
Lokiz (LOK)	11.6	845	984	H-ATL	83	14 ± 1	120 ± 7
Luesia (LUE)	11.7	691	1250	MED	69	16 ± 1	77 ± 3
Monrepos (MRE)	10.9	744	1290	MED	78	14 ± 1	95 ± 5
Montsec (MSC)	10.3	802	1340	MED	88	16 ± 1	90 ± 5
Montseny (MNY)	13.5	702	1530	MED	62	12 ± 2	111 ± 6
Opakua (OPK)	10.0	889	975	H-ATL	99	19 ± 1	133 ± 9
Peiró (PEI)	10.89	744	1350	MED	78	19 ± 2	96 ± 10
Urbasa (URB)	11.58	845	920	H-ATL	83	30 ± 1	148 ± 5
Arutz (ART)	13.9	556	1000	H-ATL	50	16 ± 1	94 ± 5

Values shown as mean ± SE. Forests were grouped into four biogeographical regions based on climate data (mean annual temperature—MAT, and mean annual precipitation—MAP, De Martonne Aridity Index—AI) and elevation: Low-elevation Atlantic (L-ATL), high-elevation Atlantic (H-ATL), Pyrenean (PYR) and Mediterranean (MED) forests. DBH is the diameter measured at breast height (1.3 m).

high precipitation and temperatures, one with two stands located at low elevation and one formed by four stands located at high elevation, the low- and high-Atlantic stands, respectively.

Tree Radial Growth Data

At each stand from 6 to 26 trees (20 in Pyrenean bioregion, 61 in Mediterranean bioregion and 31 and 103 in low- and high-Atlantic bioregions, respectively) were cored at 1.3 m height using Pressler increment borers (Table 2). These cores were air-dried in the laboratory and mounted on wooden supports for further processing. The samples were sanded with progressively finer sandpaper until tree rings were clearly visible. Ring widths were measured at 0.01 mm resolution using measuring device systems (Lintab, F. RinnTech, Germany; Velmex Inc., USA). Visual cross-dating was performed and checked with the program CO-FECHA (Holmes 1983). Tree-ring widths were transformed to basal area increments (BAI_t) (Figure 3), which allows removing the geometrical constraint of adding a volume of wood to a stem of increasing radius (Biondi and Qeadan 2008), using the following formula:

$$BAI_t = \pi * \left(R_t^2 - R_{t-1}^2 \right)$$

where R_t is the radius of the ring formation year and R_{t-1} is the radius of the year preceding the ring formation. BAI_t was used to compute different analyses of tree growth variability and determine

the 1980s climate shift effects on the studied beech stands. We calculated standardized BAI values by dividing the raw BAI values by the mean BAI value.

Tree-ring width data were detrended to calculate mean series of ring width indices for each site so as to assess the quality of each site chronology. In short, individual horizontal series were fitted using the mean of the series to obtain dimensionless ring width indices. We calculated several dendrochronological statistics based on these chronologies (Table 2). Specifically, we calculated the first-order autocorrelation of ring width data and the mean sensitivity, mean inter-series correlation and expressed population signal (EPS) of ring width indices. Such statistics were calculated on data from 1950 until present. These analyses were carried out using the *dplR* package (Bunn and others 2018).

To quantify short-term tree growth response to drought, we calculated the number of years with extreme low growth at individual level (hereafter, individual pointer years), from 1950 to 2008. Individual pointer year analyses reflect growth variability at inter-annual scales and may be associated to extreme climate events, such as droughts and frosts (compare Schweingruber and others 1990). To detect individual pointer years, we used the function *pointer.norm* of the package *pointRes* (van der Maaten-Theunissen and others 2015). Individual pointer years were calculated using normalized growth deviations in a 5 years length

Table 2. Main Statistics of the Tree-Ring Width Data Considered from 1950 to the Present

Site name	Biogeographical region	No. trees/ No. cores	Mean BAI (mm² year⁻¹)		First-order autocorrelation	Mean sensitivity	Mean inter-series correlation	EPS
			1950–1979	1980–2008				
Aisa	PYR	7/14	402	442	0.72	0.22	0.59	0.93
Bertiz	L-ATL	17/32	1241	1018	0.58	0.29	0.62	0.95
Diustes	MED	7/14	1063	786	0.79	0.23	0.78	0.96
Eraso	L-ATL	14/14	801	1231	0.64	0.31	0.39	0.82
Gamueta	PYR	13/23	514	1498	0.47	0.36	0.61	0.95
Izki	H-ATL	20/39	2979	2387	0.73	0.27	0.76	0.97
Lokiz	H-ATL	22/22	841	956	0.63	0.28	0.57	0.92
Luesia	MED	9/18	900	982	0.82	0.22	0.83	0.98
Monrepos	MED	11/22	748	1688	0.75	0.22	0.63	0.97
Montsec	MED	15/18	723	643	0.65	0.22	0.64	0.95
Montseny	MED	13/31	1406	1542	0.70	0.23	0.53	0.87
Opakua	H-ATL	26/32	1101	1223	0.53	0.31	0.63	0.95
Peiró	MED	6/12	1590	1398	0.67	0.24	0.66	0.92
Urbasa	H-ATL	19/38	2969	2436	0.57	0.31	0.73	0.97
Arutz	H-ATL	16/16	884	1324	0.63	0.24	0.48	0.84
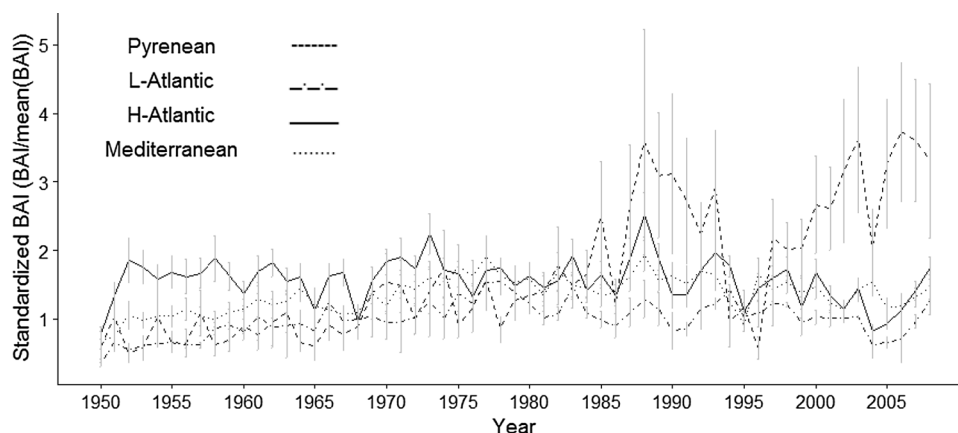
Figure 3. Mean series of standardized basal area increment (basal area increment/mean basal area increment) of the Pyrenean, high- (H-) and low-elevation (L-) Atlantic and Mediterranean forests. Values are mean ± SE.

window, with a greater than 0.5 threshold on the so-called Cropper values (Cropper 1979). As we were interested in warming- and drought-related growth decline, we analyzed the individual negative pointer years only. Furthermore, we also defined regional pointer years as those years in which more than 50% of the trees per biogeographical region presented an individual pointer year. With these metrics, we expect to see whether climate shift has changed the pattern of extreme short-term low growth episodes.

To quantify midterm tree growth response to drought, we analyzed abrupt growth changes resulting in longer periods of low growth. This was accomplished using the function *breakpoints* from the package *strucchange* (Zeileis and others 2003). We set that minimum distance between breakpoints cannot be shorter than 10% length of the tree-ring series, in order to avoid changes in shorter BAI trends. Therefore, a year with an abrupt growth change indicates a growth deviation that last at least for more than 6, giving an intermediate timescale effect compared with the one offered by pointer years. As in the case of pointer years, we only analyzed negative abrupt growth changes. Finally, we also evaluated long-term growth trends, calculated as the slope of the linear regression between BAI raw data series and calendar years in two different periods (1950–1979 and 1980–2008). These long-term growth trends indi-

cate whether, in overall, growth is increasing or decreasing before and after the 1980s climate shift (Camarero and others 2018).

Statistical Analyses

To evaluate differences between tree growth before and after the climate shift, we used the following linear mixed model:

$$\begin{aligned}
Y_{ij} = \alpha_{ij} &+ \beta_1 * \text{period}_i + \beta_2 * \text{DBH}_{ij} \\
&+ \beta_3 * \text{biogeography}_j \\
&+ \beta_4 * (\text{period}_i * \text{DBH}_{ij} \\
&+ \beta_5 * \left(\text{period}_i * \text{biogeography}_j\right) \\
&+ \beta_6 * \left(\text{DBH}_{ij} * \text{biogeography}_j\right) + \varepsilon_{ij}
\end{aligned}$$

where Y_{ij} represents the growth variable, either negative individual pointer years, negative abrupt growth changes or long-term growth trends. The sub-index i represents the stand level, and the sub-index j represents the tree level; α_{ij} represents the random effect for each tree j nested in each stand i; β_1 to β_6 are the coefficients for every fixed effect and their interactions; ϵ_{ij} is the error term for each tree j nested in each stand i. The fixed effects are: period, a factor with two levels, that is, before (1950–1979) or after (1980–2008) the climate shift; biogeography, a factor with four levels determined by the aforementioned cluster analyses (Mediterranean, low- and high-elevation Atlantic and Pyrenean) and diameter at breast height (DBH). Three different models were considered, one per each of the different tree growth variables (negative individual pointer years, negative abrupt growth changes and long-term growth trends). First, we evaluated the individual pointer years, using the total number of individual negative pointer years per tree as a response variable. Second, we analyzed the individual tree growth trends along each period. Finally, to evaluate the abrupt growth changes, we reduced the variability to stand level by calculating the percentage of trees in each stand that suffered an abrupt growth change, thus in this latter model DBH was also calculated at stand level and not at individual level, as well as the random effect that represented only the variability at stand level. The percentage of abrupt growth changes was log-transformed to achieve normality.

The models were fitted using the *nlme* package (Pinheiro and others 2017). When a significant influence of factors and interactions was found, post hoc comparisons between levels of factors and interactions were done using the package *emmeans*

(Lenth 2018). All statistical analyses were performed in the R environment (R Core Team 2017).

RESULTS

Climate Shift

We detected a significant climate shift on the mean annual temperature series of the studied stands (Figure 2a, Supplementary materials Figure S2). Specifically, two changes were observed on the temperature data, one in 1981 and another one in 1994 (Figure 2a), indicating the 1980s temperature increase and the 1990s warming hiatus. However, no changes were detected in the precipitation series along the studied period (Figure 2b), but a negative shift in August SPEI was detected in 1994 for most of the studied regions (Figure 2c).

Pointer Year Analyses

Fewer individual pointer years were found after the 1980s climate shift than before (Table 3), a pattern independent of the biogeographical region (Table 4). A change in the effect of DBH on the number of pointer years was found after the climate shift (marginally significant interaction period * dbh, Table 4), changing from negative in 1950–1979 (mean ± SE = − 0.03 ± 0.02) to positive in 1980–2008 (0.01 ± 0.02).

Considering regional pointer years (years were > 50% of trees in a region showed an individual pointer year), we found that at Mediterranean and Atlantic forests, the number of regional pointer years increased after the 1980s climate shift (Figure 4). Contrarily, the number of regional pointer years decreased at Pyrenean stands (Figure 4). When analyzing the four regions altogether, no differences were found between regional pointer years before and after the 1980s ($p = 0.15$).

Abrupt Growth Changes

Abrupt growth changes varied among the two analyzed periods (Table 3), with a higher percentage of trees experiencing abrupt growth changes after the 1980s climate shift (Table 3, Figure 4). Such effect was independent of the biogeographical region or tree size (Table 4, Figure 4).

Long-Term Growth Trends

We found overall positive growth trends before the climate shift that turned negative after the 1980s (Table 3, Figure 5). Such change was related to the biogeographical region (Table 4). Negative post-

Table 3. Comparisons Between Values (mean ± SE) of the Studied Tree Growth Variables (Individual Pointer Years, Abrupt Growth Changes, Negative Long-term Growth Trends) for the Periods 1950–1979 and 1980–2008, that is, Before and After the 1980s Climate Shift

Variables	Period	
	1950–1979	1980–2008
Individual pointer years (No. pointer year tree/period)	8.73 ± 0.18	8.15 ± 0.18
Abrupt growth changes (% trees showing abrupt growth changes/site)	0.15 ± 0.04	0.37 ± 0.04
Long-term growth trends (regression coefficient BAI ∼ calendar year, mm^2 year^{-1})	18.2 ± 4.18	− 3.56 ± 4.18

All values showed highly significant (p = 0.001) differences between the two compared periods. BAI stands out for basal area increment.

Table 4. Results of the Linear Mixed-effects Models (ANOVA table) Testing the Different Growth Variables (Individual Pointer Years, Abrupt Growth Changes, Long-term Growth Trends) as a Function of Period, Biogeographical Region (Pyrenees, Atlantic Low-Elevation, Atlantic High-Elevation and Mediterranean), Tree Size (DBH, Diameter Measured at Breast Height) and Their Interactions

	Pointer years	Abrupt growth changes	Long-term growth trends
Period (Pre- or post-1980 shift)	**0.01**	**0.0005**	**< 0.0001**
Biogeographical region	0.37	0.23	0.33
DBH	0.33	0.33	0.37
Period * Biogeography	0.24	0.27	**0.0003**
Period * DBH	**0.05**	0.09	0.08
Biogeography * DBH	0.88	0.39	0.32

Bold characters highlight significant (p < 0.05) variables.

shift trends were found in forests from Mediterranean and Atlantic areas (Figure 5). Contrarily, positive growth trends were observed in Pyrenean forests (Figure 5). There was no effect of tree size on the long-term growth trends at any of the studied periods (Table 4).

DISCUSSION

Understanding the temporal and spatial growth variability among contrasting biogeographical regions in response to recent climate shifts is fundamental to assess long-term changes in forest productivity, growth and adaptability of tree species to forecasted climate warming (Sánchez-Salguero and others 2017). Our results present a marked growth reduction after the 1980s climate shift in most beech stands investigated within southwest Europe, near the species' rear-edge. We also found a marked increase in the occurrence of negative abrupt growth changes across all biogeographical regions and a generalized decrease in long-term growth trends in many regions. Thus, although the number of individual pointer years per tree did not increase during the second studied period, all the other parameters pointed out a

growth decline after the 1980s climate shift. Notably, the Pyrenean stands, which are located at higher elevation and present the low temperature and high precipitation values, were the only forests showing a long-term growth enhancement. These results agree with previous studies observing warming-related growth decreases in southern and xeric edges of beech distribution (Gutiérrez 1988; Jump and others 2006; Piovesan and others 2008; Zimmerman and others 2015; Dulamsuren and others 2016; Knutzen and others 2017; but see Tegel and others 2014; Hacket-Pain and Friend 2016; Cavin and Jump 2017). However, the comparison between regions allowed us to disentangle that regional climate variability modulates warming-induced growth reductions.

Although there was no increase in individual pointer years after the climate shift, a different effect of tree size (DBH) between periods was observed (Table 4). Before the 1980s, larger trees presented a lower number of pointer years, which changed after the climate shift. This change suggests that under warming periods, larger trees experience harsher conditions making them more vulnerable to drought-related growth decline and potential damage (Benett and others 2015). This
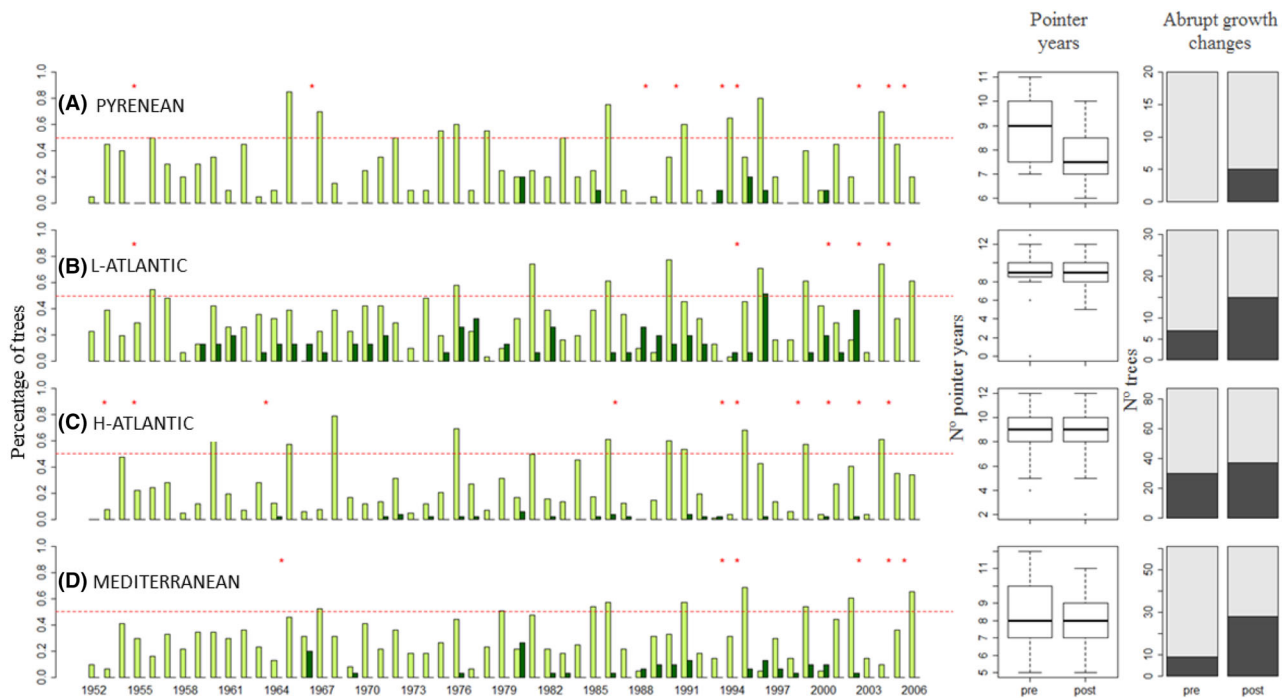
Figure 4. Percentage of individual pointer years per region (olive-green bars) and percentage of abrupt growth changes (dark-green bars), boxplots of number of individual pointer years detected before and after the 1980s climate shift and percentage of abrupt growth changes before and after the shift for (**A**) Pyrenean (PYR), (**B**) low-elevation Atlantic (L-ATL), (**C**) high-elevation Atlantic (H-ATL), and (**D**) Mediterranean (MED) stands. Red stars mark the dry years with Standardized Precipitation and Evapotranspiration Index values lower than − 1 (Color figure online).
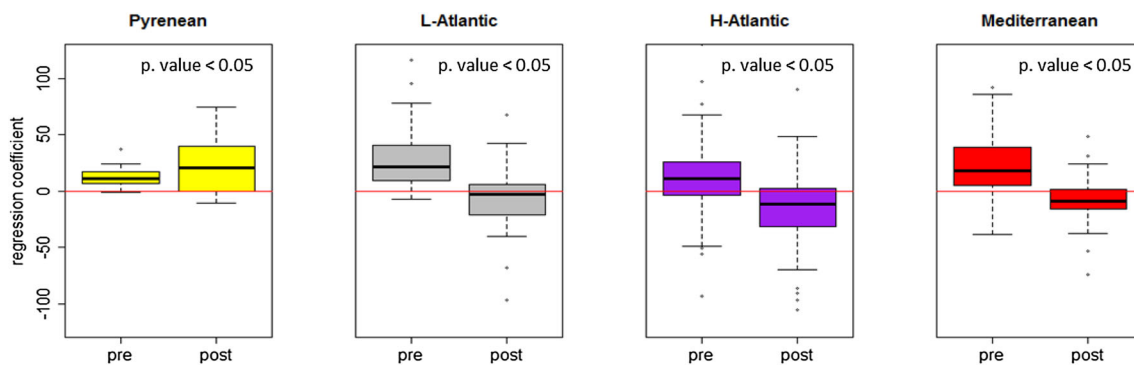
Figure 5. Boxplots of long-term growth trends of basal area increment for the periods before (pre, 1950–1979) and after (post, 1980–2008) the 1980s climate shift. Values represent the coefficients of linear regressions among basal area increment and calendar year calculated for the four biogeographical groups: Pyrenean (yellow), low-elevation Atlantic (L-Atlantic, gray), high-elevation Atlantic (H-Atlantic, purple) and Mediterranean (red) and forests (Color figure online).

size-related effect could be explained by physiological constraints related to the higher xylem tension that suffer the hydraulic systems of larger trees (Ryan and others 2006). However, the reverse pattern has also been observed and attributed to a higher hydraulic capacitance due to more sapwood volume in larger trees (Colangelo and others 2017). Moreover, the frequency of individual pointer years differed among periods in some of the bio-

geographical regions. Regional pointer years (> 50% of trees in a region) increased in three out of the four regions, as they did in temperate beech populations of central Europe (Zimmerman and others 2015; Knutzen and others 2017). Such increase on the number of regional pointer years indicates that, even if the number of individual pointer years is similar between periods, their distribution along the periods is different. Individual

pointer years before the 1980s shift were more homogeneously distributed (that is, more years with equal number of trees showing pointer years) and more heterogeneously distributed after the shift (that is, some years with many trees having a pointer year and other years with almost no tree having pointer years, that is, extreme growth responses) (Supplementary materials Figure S4). This could be explained by an increase of growth sensitivity to drought caused by an increase of dry spells as climate warms, thus reducing radial growth rates (van der Werf and others 2007). The fact that the hottest and most extreme droughts of the study period occurred after 1980s supports this hypothesis (Figure 4). Pyrenean forests were the only ones where the number of regional pointer years did not increase. The Pyrenean region is relatively cooler than the other regions; moreover, it also registers high precipitation; thus, droughts there are expected to be less intense, with lower impacts on those forests (Greenwood and others 2017; Gazol and others 2018). Therefore, the climatic conditions of the Pyrenees may benefit beech stands growth and provide them topographic refuges against the climate warming. Other climate extremes (for example, frosts) could explain this biogeographical differentiation. Because Pyrenean forests are located in the coldest conditions, they might be also more prone to suffer early-spring or late-autumn frost damage resulting in narrow rings (Príncipe and others 2017). As Pyrenean stands has equal number of regional pointer years before and after 1980s shift and extreme droughts occurred mostly after 1980s, our results suggest that contrary to the other regions, frost could be limiting growth more than drought on these stands.

The percentage of abrupt growth changes per forest (that is, percentage of trees displaying abrupt growth reductions lasting for more than 6 years) increased after the 1980s, probably as a consequence of the higher number of extreme droughts observed after the 1980s climate shift (Camarero and others 2015). For instance, Vanoni and others (2016) found that higher drought intensity increased the probability to suffer an abrupt growth change. In this case, a similar pattern is shown for the four biogeographical regions, including the Pyrenean stands. Here frost events may not play a relevant role as it was the case in pointer years, as beech can recover quickly from late frosts (Príncipe and others 2017).

The long-term growth trends indicate that tree growth had an increasing tendency before 1980s climate shift, but this changed in the subsequent decades. Consequently, during the 1980–2008 period a decreasing growth trend was observed in all regions with the exception, again, of Pyrenean forests (Figure 4). These results seem to indicate a growth constraint after the climate shift and match with previous studies reporting a growth decline after 1980s for beech in the southern distribution limit of the species (Jump and others 2006; Piovesan and others 2008; but see Tegel and others 2014; Cavin and Jump 2017) and also in central Europe (Zimmerman and others 2015; Dulamsuren and others 2016). However, Pyrenean forests did not show any growth decrease, in terms of long-term growth trends, after the climate shift. These mountain forests present a climate that can buffer the stressing conditions of the warming observed after the climate shift. As summer temperatures strongly limit beech growth at high elevation (Dittmar and others 2003), the warming trend could be positively influencing beech growth in the Pyrenean stands, as observed in high-elevation beech forests in central Europe (Dulamsuren and others 2016). Moreover, the abrupt topography of the Pyrenees generates a wide range of microclimatic conditions, which can alter climate-growth relationships (Adams and others 2014), resulting in a possible range of environments where beech can find more appropriate conditions (for example, lower atmospheric water vapor demand and evapotranspiration, higher soil moisture). Such effects of topography and elevation would be also expected in Mediterranean sites with similar elevation as Pyrenean forest. Nevertheless, precipitation is usually lower in the Mediterranean area, mainly summer, and even if these forests are located at high elevation, negative long-term growth trends were observed. Our results suggest a divergent response in the studied beech forests near the southern distribution limit of the specie. Such divergence is in accordance with the idea that vegetation chronic stress caused by increased drought frequency is higher in drier sites at the Iberian Peninsula (Carnicer and others 2011). Alternatively, legacies of historical forest management, such as removing big and fast-growing individuals through selective logging or former coppicing in some stands (Camarero and others 2011), could have caused reduced growth rates. This explanation does not seem plausible on our results since most sampled forests had similar ages (Table 1).

The decreases of tree growth after the climate shift could be caused by multiple reasons. Drought stress suffered by consecutive drought episodes can promote higher defoliation rates (Carnicer and others 2011), and as a consequence lower photo-

synthetic carbon gain and a reduction in radial growth and forest productivity (Gazol and others 2018). Increasing temperatures and drought stress may also limit water consumption and enhance water-use efficiency, as seen in declining silver fir populations of the Pyrenees, promoting a long-term growth reduction (Linares and Camarero 2012). Moreover, warming temperatures and drought stress may promote carbon starvation and hydraulic failure, which can compromise tree performance and cause die-off episodes (Adams and others 2009; McDowell and others 2008; Camarero and others 2015; Adams and others 2017). As explained above, the most severe droughts in the study area (for example, 1986, 1994, 2005) occurred after the climate shift, and it is well known that trees can have legacy effects after droughts lasting several years (Anderegg and others 2015; Peltier and others 2016; Gazol and others 2017, 2018) that, together with an increase in the time of recovery (Schwalm and others 2017), could compromise the long-term growth of some beech forests in a nearby future. Even if we did not study tree mortality, we focused on how tree growth can be constrained under a period of high temperatures. Low growth or productivity can be a signal of impending tree death, even several years before the mortality episode occurs (Camarero and others 2015; Rogers and others 2018); thus, our results anticipate the vulnerability of the studied forests if the temperature increase persists. Lastly, our findings are relevant to better understand how warmer and drier climate conditions will impact similar temperate mesic forests dominated by deciduous tree species. These impacts will vary as a function of climatic conditions acting at different spatial scales, and the negative effects of droughts on trees could be buffered in topographic refuges with favorable conditions.

In conclusion, we show that after the 1980s climate shift a divergent response was observed on the studied beech forests near the species' rear edges. Mediterranean and Atlantic beech stands showed negative growth trends and growth limitations after the 1980s shift, but Pyrenean stands presented a long-term growth enhancement. These biogeographical differences indicate that regional climate characteristics can buffer, at some extent, the negative effects of warmer and drier conditions on beech forests near their southern distribution limits in Europe. Our results suggest a high vulnerability of beech forests in the northeast Iberian Peninsula out of the Pyrenean stands, which agrees with the forecasted beech retraction in the area (Benito-Garzón and others 2008). Therefore, under the projected warming scenario, the future distribution range of beech in the northeast Iberian Peninsula would be likely restricted to cold and wet mountainous areas acting as climatic refuges.

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