Alfaro Sánchez, Raquel; Jump, Alistair S.; Pino, Joan; [et al.]. «Land use legacies drive higher growth, lower wood density and enhanced climatic sensitivity in recently established forests». Agricultural and Forest Meteorology, Vol. 276-277 (October 2019), art. 107630. DOI 10.1016/j.agrformet.2019.107630

Title

Land use legacies drive higher growth, lower wood density and enhanced climatic sensitivity in recently established forests

List of authors:

Raquel Alfaro Sánchez[1], Alistair S. Jump[1,2], Joan Pino[1,3], Oihane Díez-Nogales[3], Josep Maria Espelta[1, 3]

Institutional affiliations:

[1] CREAF, Centre de Recerca Ecològica i Aplicacions Forestals E08193 Bellaterra (Cerdanyola de Vallès), Catalonia, Spain

[2] Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, FK9 4LA, UK

[3] Universitat Autònoma de Barcelona, E08193 Bellaterra (Cerdanyola del Vallès), Catalonia, Spain

Corresponding author: Raquel Alfaro Sánchez (r.alfarosanchez@gmail.com). CREAF, Centre de Recerca Ecològica i Aplicacions Forestals E08193 Bellaterra (Cerdanyola de Vallès), Catalonia, Spain. Tlf: +34 935814850

Declarations of interest: none

Abstract

Europe is undergoing significant forest expansion due to the abandonment of rural areas driven by economic and demographic changes. Recently established forests provide key ecosystem services such as habitat provision and increased carbon stocks. However, we lack understanding of whether past land use might alter their resilience to climate change compared with long-established forests. Forests established in former agricultural areas may benefit from land use legacies resulting in higher fertility, yet such a benefit might turn into a disadvantage if it involves changes in functional attributes that lower their ability to cope with negative climatic events (e.g. droughts). Here we examined whether recently (post 1956) and long-established (pre 1956) beech forests in Catalonia (NE Spain) differ in their growth patterns, wood density, sensitivity to climate and response to extreme climatic events. Our results indicate higher growth (32%) and lower wood density (3%) in trees from recently established forests, even when controlling for tree age and competition. In addition, recently established forests showed a higher sensitivity to Standardised Precipitation-Evapotranspiration Index (SPEI), precipitation and temperature and to extreme negative and positive climatic events. In particularly wet years, recently established forests show twice the number of positive pointer years than long-established forests. Compensatory growth during positive years in recently established forests, may be driving the similar or even higher recovery and resilience detected after drought episodes. Nevertheless, the higher climatic sensitivity of the recently established forests, together with their greater growth and lower wood density indicates that they may be particularly vulnerable to future droughts. Such enhanced vulnerability might question their ability to contribute to carbon sequestration in the long term and emphasises the need to account for land use legacies to better predict future forest function as climate changes.

Keywords

Forest expansion; land-use history; *Fagus sylvatica*; low latitude distribution; dendroecology; extreme climatic events

1. Introduction

The last decade (from 2008 to 2017) was the world's warmest, with global average temperatures increasing at approximately 0.2ºC per decade above pre-industrial levels (EEA, 2017). In Europe, temperatures have risen above the global average and climate models project further increases in temperature exceeding global average projections over the 21st Century (EEA, 2017). In Southern Europe, the strongest warming and decrease of precipitation is projected to occur in summer, together with more frequent extreme heat waves and heavy precipitation events by 2100 (EEA, 2017). Mitigation actions are vital to limit global warming of 1.5°C above pre-industrial levels over the next decades (Masson-Delmotte et al., 2018). Land use and land-use change is considered a critical feature of almost all mitigation pathways for the next decades (Masson-Delmotte et al., 2018). For instance, the terrestrial carbon sink since the 1990s, only from world's re-growing forests, equalled 24% of cumulative fossil carbon emissions (Pan et al., 2011). However, it is uncertain whether this accelerated trajectory of C sink will be sustained in the future.

In temperate forests, the increasing carbon sink detected during recent years has been attributed to a transition recovery from past land use and natural disturbances (Thom et al., 2018). Thus, in Europe the recent forest expansion is taking place mainly on former agricultural lands as a consequence of the widespread abandonment of rural landscapes (Keenan, 2015). New forests established in former agricultural lands can show enhanced tree growth due to the legacies of the previous land-use (Gerstner et al., 2014; Lambin and Meyfroidt, 2011; Leuschner et al., 2014). In comparison to forests with a continuous land-use history, former agricultural soils tend to be deeper, more basic, have higher N and P content and mineralization rates (Compton and Boone, 2000; Fraterrigo et al., 2005), include a larger biomass of bacteria (Fichtner et al., 2014) and a greater general decomposer activity (Freschet et al., 2014). Ultimately, these characteristics may result in a positive and accelerated feedback between the belowground and the aerial component leading to higher growth and productivity, e.g. 35% greater plant biomass (Freschet et al., 2014) or 25% higher growth (Vilà-Cabrera et al., 2017). On the other hand, the initial advantage of higher growth might become a disadvantage if it is accompanied by changes in functional traits. Changes in functional traits can constrain the ability of trees to face unfavourable climatic conditions, such as a reduction in wood density (i.e. greater number and area of conductive vessels) and in water use efficiency. Indeed, lower wood density is associated with higher susceptibility to drought and mortality responses (Greenwood et al., 2017). Lower wood density also involves less resistance to wind forces (Anten and Schieving, 2010; Putz et al., 1983), pathogen attacks (Augspurger, 1984), cavitation (because it's associated with larger vessel diameter; Lambers et al., 2008) and implies less carbon storage for a given stock of standing volume (Zeller et al., 2017). For example, Pretzsch et al., (2018) reported faster stand and tree growth since 1870 in Europe for several dominant tree species. However, this faster growth rate was associated with 8-12% decrease in wood density, particularly on fertile sites (Pretzsch et al., 2018). Similarly, nitrogen fertilization experiments have demonstrated a reduction in wood density with enhanced nitrogen supplies for tree species (e.g. Cao et al., 2008; Mäkinen et al., 2002). These examples imply that the effects of land use legacies in trees growing in recently established forests may result in differences in functional attributes in comparison to more continuously forested areas, potentially involving a different sensitivity to climate, and particularly to extreme climatic events (e.g. drought episodes). Up to now, differences in the response of forests to adverse climatic events has been mostly analysed from the perspective of the previous climatic conditions experienced ('climate legacy effects', Lloret and

Kitzberger, 2018). Thus, it has been often reported that populations living in more favourable climatic conditions would be more affected by adverse events than conspecifics that had experienced harsher climates (Lloret and Kitzberger, 2018). In fact, climatic legacies could contribute to explain why populations living in climatically marginal areas of a species distribution can be more resistant to negative climatic events than those in the core (see Cavin and Jump, 2017). Very few studies have addressed the potential interactions among land use legacies and climate sensitivity (but see Mausolf et al., 2018), although it is well known that soil nutrients and physical soil properties can influence the growth sensitivity of temperate tree species (Lévesque et al., 2016).

We sought to determine whether recently established beech (*Fagus sylvatica* L.) forests present differences in growth, wood density and climatic sensitivity, especially when subject to extreme events, when compared to forests with a continuous land-use history. Beech is one of the most abundant and extensively distributed broadleaf trees in Europe (Ellenberg et al., 2010). This species is highly vulnerable to drought and consequently it is expected to retreat from its current southern distribution limit (Zimmermann et al., 2015). In fact, some studies have shown a decline in beech growth in marginal distributional areas (Jump et al., 2007, 2006; Piovesan et al., 2008), accompanied by the replacement by other more drought tolerant tree species (Peñuelas et al., 2007; Zimmermann et al., 2015). In addition, tree populations within the species' range can be affected differently by regional extreme events due to variation of local climatic conditions or past history (Hampe and Petit, 2005). Populations at the southern edge of distribution of *F. sylvatica* can be found in Northern Spain, where it occupies 8667 km^2 according to the Spanish Forest Inventory with almost 22% of the forest surface established after 1950 (Vilà-Cabrera et al., 2017). Interestingly, this forest expansion is occurring in a region where ongoing changes in climatic conditions are predicted to result in its decline, raising the question of whether recently established forests will cope with climate change in a similar way to long-established forests. Consequently, these Southern *Fagus sylvatica* populations provide an important opportunity to determine the response of growth and functional traits of recently established forests to extreme climatic events. We hypothesise that 1) recently established forests should show higher annual growth due to improved soil conditions resulting from former agricultural or pasture land-use. 2) higher growth will be accompanied by the production of lower density wood and 3) will result in a higher sensitivity to climate and a poorer performance under extreme climatic events that exacerbate limiting factors for the species, such as droughts. Ultimately, our results will improve our understanding of whether beech forests established in former agricultural areas will help the maintain of this species at low latitudes of its geographical distribution. Alternatively, under harsher climatic scenarios, the positive effect of forests growing in former agricultural areas could be transient, even predisposing such forests to faster future decline.

2. Methods

2.1 Study area and sampling design

This research was conducted in Catalonia, NE Spain, where *Fagus sylvatica* forests occur at the south western (rear-edge) of this species distribution in Europe (Hultén and Fries, 1986). In this area, detailed cartography of land use changes is available for the second half of the twentieth century (Fig. 1).

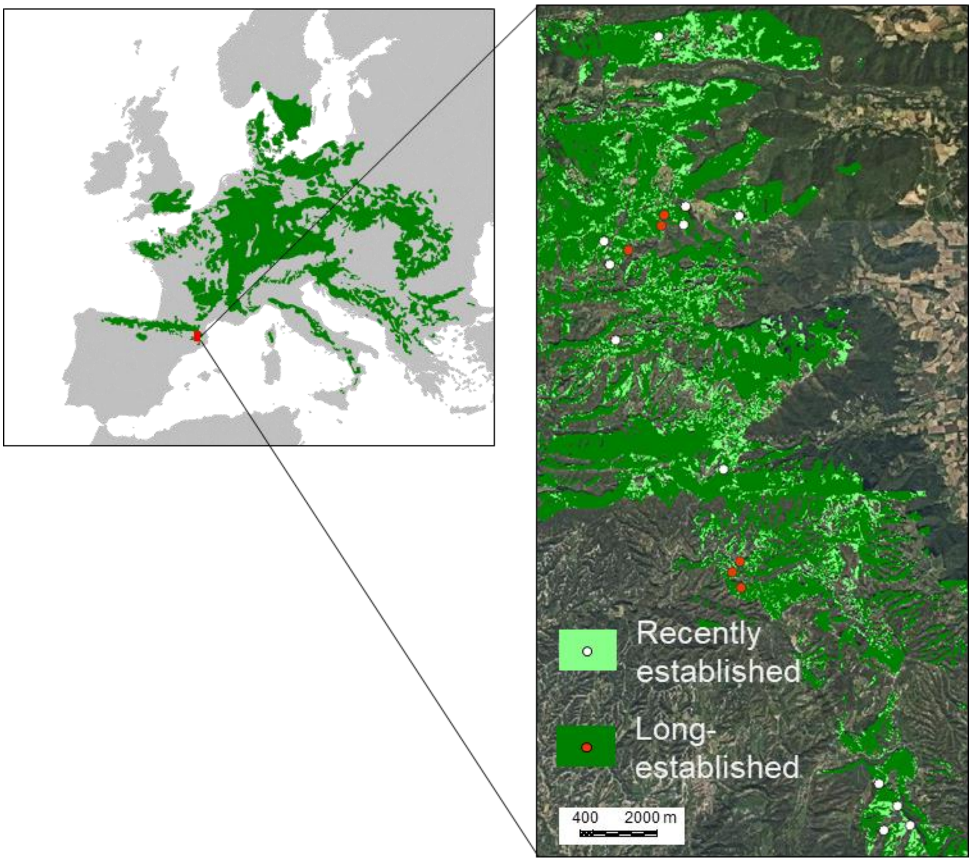


Figure 1. Natural distribution area of *Fagus sylvatica* distribution in Europe according to EUFORGEN (Pott, 2000; left panel) and location of the recently (light green) and long-established (dark green) beech forests in the study region (right panel). White and red circles in the right panel indicate the location of the studied recently and long-established forest patches, respectively (see Fig. S1 for details of patch selection).

Land-use change was identified by combining two land cover maps (http://www.creaf.uab.cat/mcsc) obtained through photo-interpretation of 1956-1957 and 2005 orthoimages (Başnou et al., 2013). Current forest patches established in cropland/pastures abandoned after 1956 were considered as ‘recently established forests’, while forests that already existed in 1956, entailing a longer forest history, were classified as ‘long-established forests’. Notice that these two categories were not defined by the stand age, but by the age of the land use (see for similar criteria Mausolf et al., 2018). In fact, the two forest types could have a similar stand age and physiognomy if long-established forests had been disturbed (e.g. logged) around the 50s (Fig. S1). After field validation of the orthoimage photointerpretation, we selected six patches of long-established forest and twelve patches of recently established forests in similar topographic conditions. Maximum distance among patches was 45 km across an elevation gradient from 831 to 1452 m asl (Fig. 1). From November 2017 to February 2018, 30 trees were randomly selected and geolocated per patch (511 trees were included in the final analyses after discarding 29 trees with unreadable cores). Since one of the main differences between trees growing in recently *vs.* long-established forests could be their nutritional status owing to the positive land use legacies of previous cropland/pastures (i.e. natural or artificial manuring; see Fraterrigo et al., 2005; Mausolf et al., 2018), we previously analysed N content and $\delta^{15}N$ in a random sample of 10 fully sun-exposed leaves per tree as a proxy of nutrient availability (Aerts and Chapin, 1999). The measurement of $\delta^{15}N$ can provide evidence of the N source used by plants, with more positive values expected in trees growing in former agricultural soils as a consequence of past manuring or cattle raising (Treasure et al., 2016). After drying to constant weight at 60º, all leaves per tree were pooled and ground and N and $\delta^{15}N$ were analysed at the UC Davis Stable Isotope Facility (Univ. California, Davis, USA). ANOVA tests were applied to test for differences in N and $\delta^{15}N$ between type of forests.

2.2 Tree growth and wood density measurements

Two increment cores were extracted per tree using a Pressler increment borer (46 mm) at 50 cm above the ground level, to enable a more accurate estimation of tree age. Cores were labelled and brought to the laboratory for subsequent analyses of tree-ring width and wood density. Owing to the time-consuming nature of the analytical process, we only determined wood density in a random sub-sample of 284 trees corresponding to 5 recently and 5 long-established forest patches. Wood density (g cm^{-3}) was calculated using one of the two cores per tree as the dry weight of the core divided by its volume, following Williamson and Wiemann (2010). Cores were first oven dried for at least two hours at a temperature of 102ºC and weighed to obtain the dry weight. Then, volume was obtained by Archimedes' principle which is a reliable measurement for irregularly shaped samples (Archimedes, 2009).

Once wood density was measured, cores were air dried, mounted on wood supports, and sanded until rings were clearly visible with a stereomicroscope. For the dendrochronological analyses, we used 935 cores from 511 trees from the 6 recently and 12 long-established forest patches. The two cores from the same tree were visually crossdated with a stereomicroscope, scanned at 1600 d.p.i and ring widths measured to an accuracy of 0.001 mm using the software CooRecorder v9.3 (Cybis Elektronik, 2018). Cross-dating of individual series was checked using CooRecorder and COFECHA programs (Holmes, 1983). Whenever the pith was not reached in the core, we estimated the distance from the innermost measured ring to the pith of the tree with the software CooRecorder. Cambial age was also adjusted by adding the number of rings to the pith estimated with CooRecorder, when none of the cores from a tree reached the pith. Finally tree-ring width series were converted to basal area increment (BAI) measurements (mm^{2} year^{-1}) using the R package 'dplR' (Bunn, 2008). For climate-growth analyses, tree-ring width series were individually detrended with cubic smoothing splines of 30 years to remove non-climatic growth trends related to the increase in tree age and size (Cook and Kairiukstis, 1990). All tree-level indexed ring-width series within recently or long-established forests were averaged to form a chronology per type of forest by using a bi-weight robust mean. Average interseries correlation and mean sensitivity were determined for each chronology with 'dplR'.

2.3 Forest structure and competition indices

In order to assess whether differences in competition in recently *vs.* long-established forests influenced growth patterns, we calculated competition indices in a subsample of 140 focal trees (69 and 71 for recently and long-established forests, respectively). This sampling included a minimum of three focal trees per patch from a range of ages between 45 and 61 years. This range of ages was selected to avoid biases in subsequent analyses due to tree age differences found between the two forest types (Fig. S2).

Neighbouring trees to the focal *F. sylvatica* individuals, including other tree species (e.g. *Buxus sempervirens* L., *Quercus humilis* Mill., *Corylus avellana* L. and *Juniperus communis* L.*)* were counted in circular subplots of 8 m of radius. Diameter at breast height (DBH) of all trees (including the focal tree) larger than 5 cm DBH was measured to calculate the basal area. To calculate the competition indices, we used a modification of the index by Rozas and Fernández Prieto (2000), based on Lorimer (1983) and defined as:

$$CI = \sum_{j=1}^{n} \frac{BA_j}{BA_i}$$

Where CI is the competition index, BA_i is the basal area of the focal tree *i*, and BA_j is the basal area of neighbouring trees *j*. In addition, tree density (trees ha^{-1}) and basal area (m^2 ha^{-1}) was determined for each of the 18 forest patches. ANOVA tests were applied to test for differences in tree density, basal area and mean DBH and mean raw ring width between type of forests.

2.4 Climate data

We used monthly mean temperature and precipitation sum for the period 1950–2016 from the homogenized and quality-checked E-OBS v.17.0 dataset available on a 0.25º grid (Haylock et al., 2008) from the KNMI Climate Explorer (http://climexp.knmi.nl/). To assess drought severity at each location, the Standardised Precipitation-Evapotranspiration Index (SPEI) was calculated using the R package 'SPEI' (Vicente-Serrano et al., 2010) for a time scale of 1 month based on input data from E-OBS v.17.0.

Our study plots are spatially distributed across four different E-OBS v.17.0 grid cells and total annual precipitation and mean annual temperature range from 734 to 810 and 10.8 to 12ºC, respectively. We averaged the climate data from these four grid cells of 0.25º spatial resolution for subsequent analyses of climate sensitivity of study trees. We then used the R package 'treeclim' (Zang and Biondi, 2015) to run *Pearson* correlation analyses between monthly SPEI, precipitation and temperature data (averaged for the four grid cells of climate data for the period 1950-2016) and the mean tree-ring chronologies built for recently and long-established forests for the maximum overlapping period (Table S1). A bootstrapping procedure was used to test for significant correlations at $P < 0.05$ (Zang and Biondi, 2015).

These climate-growth analyses revealed that *F. sylvatica* forests showed the highest response in growth during the months of June and July (see section 3). Consequently, we focused on averaged June-July climate data for subsequent analyses of climate sensitivity. To determine if climate variability is increasing over time in the study area, we employed thirty-one years running variation for June-July SPEI, precipitation and temperature data for the period 1950-2016. We also ran linear regression models to determine if there is a significant rate of increase or decrease of

June-July precipitation and temperature from 1950 to 2016 in the study area (significance level was set at $P<0.05$).

2.5 Events and pointer years

Event years are defined as abrupt growth changes in individual tree-ring samples (Schweingruber et al., 1990). To identify event years, we used the normalization in a moving window method following Cropper (1979) and Schweingruber et al. (1990). Annual ring width values for each individual tree were transformed into Cropper values (Cropper, 1979) by using a 3 year window. A 13-year weighted low-pass filter (Fritts, 1976) was applied to tree-ring series prior to the calculation of event and pointer years. This filter improves the detection of event and pointer years in complacent series, and has little effect in sensitive series (Cropper, 1979). At the tree level, we identified a negative (positive) event year when there is a significant decrease (increase) in growth in the Cropper values.

A pointer year occurs when a higher proportion of tree-ring series from a group show the same trend in a specific year (Schweingruber et al., 1990). The threshold in the proportion of tree-ring series to identify a particular year as a pointer year is species and site dependent. For instance, for coniferous trees a threshold value of 75% is often set (e.g. Alfaro-Sánchez et al., 2018), whereas for deciduous trees, such as our target species, *Fagus sylvatica*, lower threshold values are often considered to obtain a reasonable number of pointer years, e.g Cavin and Jump (2017). Here, we set a threshold value of 50% following Cavin and Jump (2017). Then, negative and positive pointer years were identified when $\geq$ 50% of the tree-ring series within a patch presented an abrupt change in growth in a particular year; i.e. negative and positive event years.

Pointer years can be associated with climatic and non-climatic events, such as droughts or wildfires, respectively. Here we linked pointer years to extreme climatic events, including extremely dry, wet, warm and cold years defined as the 90th or 10th percentile values of the June-July SPEI, precipitation and temperature time series. The period from 1970 to 2010 was used for the identification of pointer years. This period covered a representative number of trees per patch and type of forest (after applying the 13-year low pass filter that truncates the tree-ring time series by 6 years at both ends). Subsequently, pointer years were compared to June-July SPEI, precipitation and temperature values, and classed as climatic-linked pointer years when the negative (positive) pointer year fell below the 10th or 90th percentiles (above the 90th or 10th percentiles) of the June-July precipitation or temperature climate time series during that year, respectively.

2.6 Resilience components

The resilience components were calculated at the patch level for the climate-linked pointer years with the R package ‘pointRes’ (van der Maaten-Theunissen et al., 2015) following Lloret et al. (2011). The resilience components evaluated the recovery, resistance and resilience of tree growth, here detrended growth values. To calculate the resilience components, we considered a time window of 3 years before and after the climate-linked pointer years. Therefore, the resistance index was calculated as the ratio between the growth during the climate-linked pointer year and the averaged growth of the 3 previous years. The recovery index was calculated as the ratio between the averaged growth during the 3 years following the climate-linked pointer year and the growth during that pointer year. Finally, the resilience index was calculated as the ratio between the averaged growth during the 3 years following the climate-linked pointer year and the averaged growth during the 3 years before the pointer year. ANOVA tests were applied to test for differences in the resilience components between type of forests.

2.7 Climate sensitivity, wood density and growth models

The effects of forest type on the climate sensitivity of trees, wood density and growth (BAI) were tested using Linear Mixed Effects Models (LMEMs; (Zuur, 2009). Two LMEMs were performed for every response variable. The first one included all trees sampled and the second one controlled any tree age effect by considering the range of ages well represented in both recently and long-established forests, i.e. trees from 45 to 61 years (Fig. S2), hereafter referred to as 'the comparable age subset'. Hence, we focused on the results obtained using the comparable age subset and placed the analysis carried out with all the sampled trees in the *Supplementary material*.

In order to study climate sensitivity, we used as the independent variable for the LMEMs the slope coefficients obtained in linear regression models between detrended ring-width series and June-July SPEI values at the tree level (the climatic variable showing the highest correlation with tree growth in our study sites).

In the slope and wood density statistical models (LMEM or LM), the predictor variables were: forest type, tree age, tree density obtained at the patch level (for all sampled trees) or CI (for the comparable age subset between 45 and 61 years), tree elevation (the elevation at which each tree is found), mean growth (only for the wood density models) and the second order interactions among the factor type of forest and the remaining variables. The patch was included in all the models as a random effect (LMEM), with the exception of the WD models using the comparable age subset, where the linear model (LM) showed a lower AIC and higher adjusted R^2. The 'lme4' package was used to fit the slope and wood density linear mixed effects models with the function ‘lmer’ (Bates et al., 2015).

The effects of type of forest on growth (BAI) across the first 61 years of the life of the trees (the period of time that trees from both type of forests shared in common) were tested using LMEMs. The initial set of variables tested in the BAI LMEMs included: forest type, tree density at the patch level (for all sampled trees) or CI (for the comparable age subset between 45 and 61 years), June-July SPEI, and individual tree variables such as the year of the tree life (considering only the first 61 years), tree elevation, and the second order interactions among these variables and the factor type of forest. We included the tree code as a random effect to account for the repeated measures across an individual. A first-order autocorrelation structure (AR1) was also included in the LMEMs to control for the temporal autocorrelation of BAI measures. BAI, tree density and CI variables were transformed with a natural logarithm to conform to normality. The influence of age across the first 61 years of the life of the trees on BAI was modelled with a natural cubic spline with a B-spline basis with 5 equally spaced knots. The ‘nlme’ package was used to fit the BAI linear mixed effects models with the function ‘lme’ (Pinheiro et al., 2018). The predictor variables were standardized to eliminate differences in scale measurements.

The best model for each response variable, i.e. slope, wood density and BAI, was chosen in a two-step procedure. First we identified the predictor variables with a significant ecological or biological interest for the response variables by selecting the LMEM or LM with the lowest AIC (Akaike Information Criterion), among sets of alternative models fitted by maximum likelihood (for the LMEMs), and removing all terms that were not significant according to likelihood ratio tests. Then, we tested whether the variable of interest, type of forest, and its interaction with the remaining variables improved the previous selected models in terms of AIC. We followed this procedure to avoid possible collinearity effects of the variable type of forest with other predictor variables such as the tree age. The final LMEMs were fitted using the restricted maximum likelihood (REML) method (Zuur, 2009). We calculated marginal (i.e. the proportion of variance explained by fixed effects) and conditional (i.e. the proportion of variance explained by fixed and random effects) R^2 for the LMEMs with the ‘MuMIn’ R package (Barton, 2018).

3. Results

Mean tree age was significantly higher in long-established than in recently established forests (65.2 ± 1.3 vs. 37.8± 0.6 years, respectively). Yet recently and long-established forests showed similar forest structural characteristics, since no significant differences were found in tree density, DBH and basal area (Table S1a). However, trees in recently established forests have significantly higher N content and more positive leaf δ^{15}N values than long-established forests (2.74 ± 0.03 *vs*. 2.46 ± 0.02 % and -3.14 ± 0.09 *vs*. -5.76 ± 0.08 ‰, respectively, Table S1a).

3.1 Climate sensitivity

Climate-growth *Pearson* correlations indicate that both types of forests are highly sensitive to June-July (summer) conditions. However, recently established forests displayed higher correlation values than long-established ones for the three climate variables analysed: SPEI, precipitation and temperature (Fig. 2). This result is in line with the higher mean sensitivity and higher interseries correlation found in the recently established forests (Table S1b).

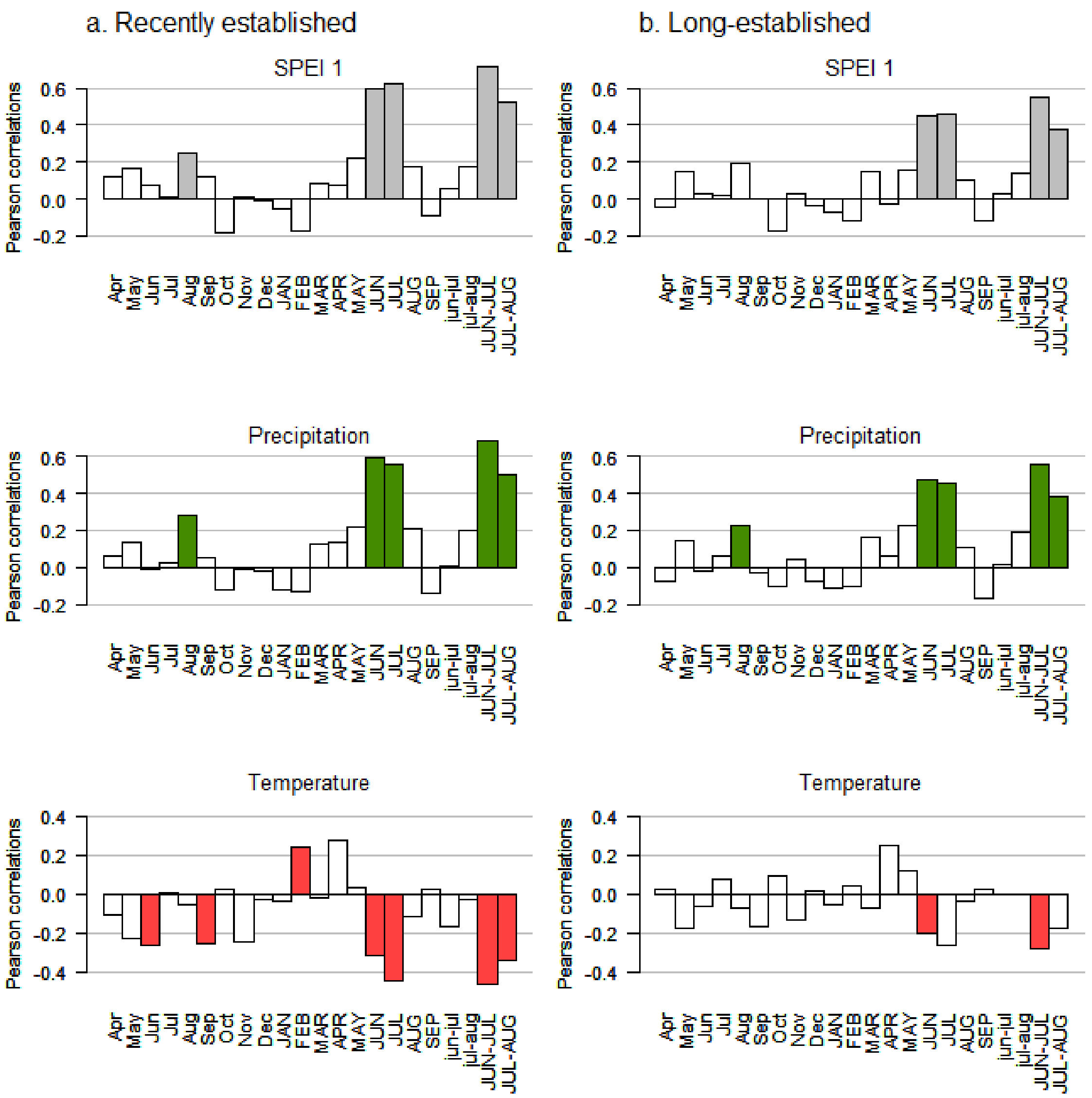


Figure 2. Climate-growth relationships for recently (a) and long-established (b) forests. SPEI, precipitation and temperature variables are considered for the period 1950-2016. Previous and current year months are indicated in lowercase letters and uppercase letters, respectively. The label 'SPEI 1' indicates that SPEI was calculated for a timescale of 1 month, which gave higher correlations than timescales of 3, 6 and 12 months.

The study area has recorded an increase in summer (June-July) SPEI, precipitation and temperature variability through time, and successive extreme wetter and warmer summers since the early 1980s (Fig. S3). A significant increase in summer temperature of 0.18˚C per decade and an increase (although not significant) in summer precipitation of 5.6 mm, has also been recorded for the period 1950-2017 (Fig. 3).

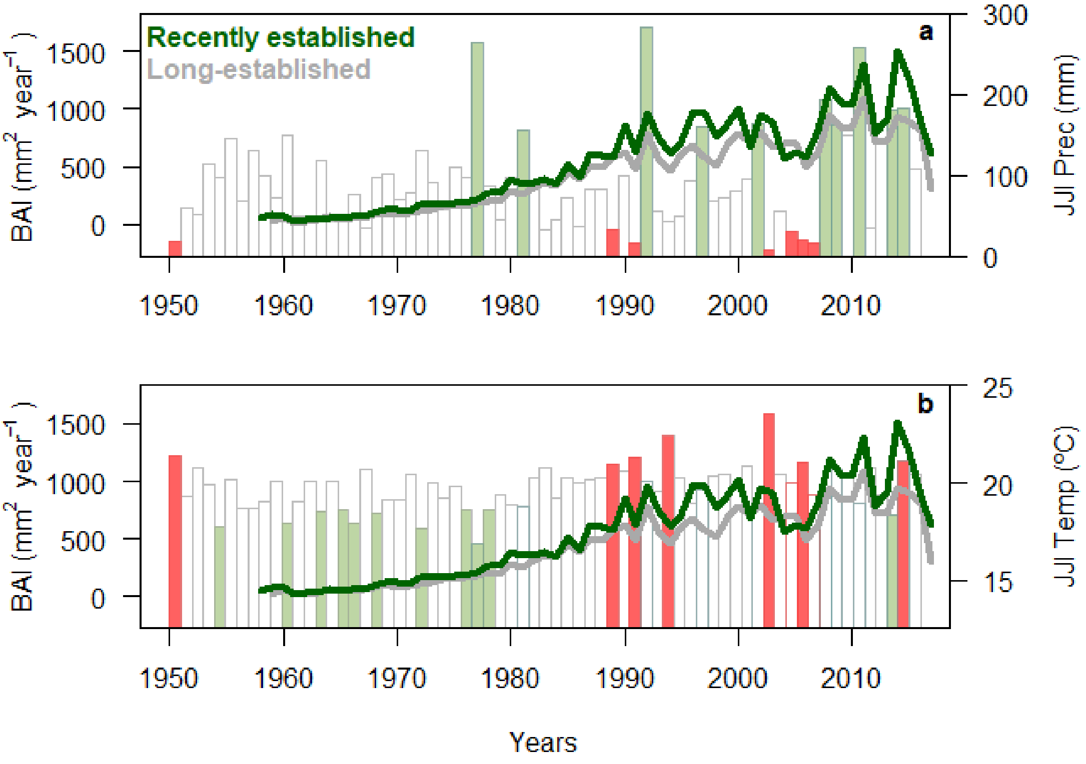


Figure 3. Basal area increment (BAI) chronologies for recently and long-established forests (green and grey lines, respectively) *vs.* June-July precipitation (a) or June-July temperature (b) time series for the period 1950-2016. Only the comparable age subset of trees between 45 and 61 years is considered. Green (pink) bars indicate extremely wet or relatively cool (extremely dry or warm) summers, as those with June-July precipitation and temperatures values above (below) the average plus (minus) 2 times the standard deviation of the June-July climate time series.

For the two types of forests, the drought years 1991 and 2006 (one of the warmest years on record since 1950s) appeared as negative pointer years. Interestingly, the recently established forests presented twice the number of positive pointer years (i.e.

years with a significant response to exceptional precipitation) compared to long-established forests (Fig. 4).

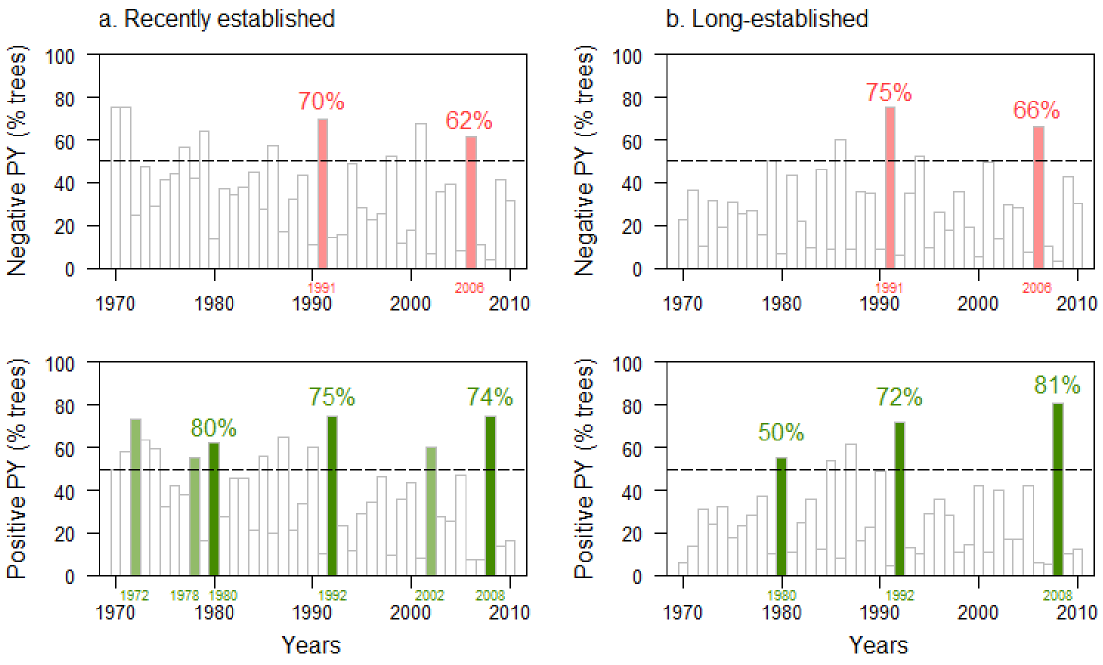


Figure 4. Climatic-linked negative (upper panels) and positive (lower panels) pointer years for recently (a) and long-established forests (b). Red (green) bars denote negative (positive) pointer years where more than 50% of the trees responded with a significant decreased in growth. Positive pointer years in recent forests but absent in long-established ones are indicated in light green.

In response to these pointer years, recently established forests presented significant higher recovery, resistance and resilience values only for the negative pointer year of 1991 (recovery and resilience, Fig. 5).

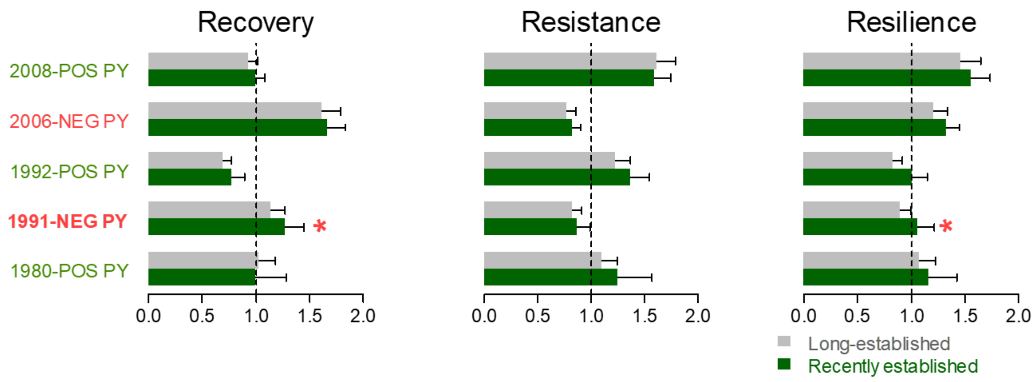


Figure 5. Mean ± SE recovery, resistance and resilience values for the negative (red characters) or positive (green characters) pointer years identified in both, recently (dark green bars) and long-established (grey bars) forests (see Fig. 4). Asterisks denote significant differences among type of forests.

The higher climatic sensitivity of recently established forests was also confirmed by the significantly higher slope coefficient, obtained in linear regression models between detrended ring-width series and June-July SPEI, both when using all sampled trees (Table S2, Fig. S3a) or the comparable age subset between 45 and 61 years (Table 1, Fig. 6a). In addition, climate sensitivity of growth increased with tree age in both type of forests, when using the comparable age subset (Table 1).

Table 1. LMEM and LM results for the effects of type of forest (recently or long-established), tree age and tree density on the slope and wood density (WD) variables, respectively. The slope coefficient was obtained in linear regression models between detrended ring-width series and June-July SPEI. Only the comparable age subset between 45 and 61 years is considered. Tree age and tree density were scaled in the models. The R^2_{adj} and R^2 due to fixed (R^2_{m}) and due to fixed and random effects (R^2 c) is also provided. Significance of the p values is indicated by: ***P<0.001; **P<0.01 or *P<0.05. The level type of forest: *recently established* is included in the intercept. n.a. not applied

	Slope				WD			
Fixed effects	Estimate	SE	t value	p value	Estimate	SE	t value	p value
(Intercept)	-0.010	0.06	-0.17	0.862	0.506	0.016	30.88	<0.001***
Type of forest: *Long-established*	-0.044	0.020	-2.21	<0.05*	0.014	0.003	4.46	<0.001***
Tree age	0.0027	0.0011	2.46	<0.05*	0.0010	0.0003	3.04	<0.01**
Tree density	n.a.				-0.0036	0.0015	-2.46	<0.05*
Random effects	Std. Dev							
Patch	0.03							
Residual	0.06							
R^2_m / R^2_{adj}	0.10				0.32			
R^2 c	0.31							

3.2 Wood density

The LMEM and LM results revealed a significant difference in wood density between type of forests, i.e, higher wood density (3%) in long-established forests (Fig. 6b, Table 1) and a negative effect of tree density, both when using all sampled trees or the comparable age subset (Table S2,1). Tree age also exhibited a positive effect on WD when the comparable age subset was analysed, i.e. wood density increases with tree age (Table 1).

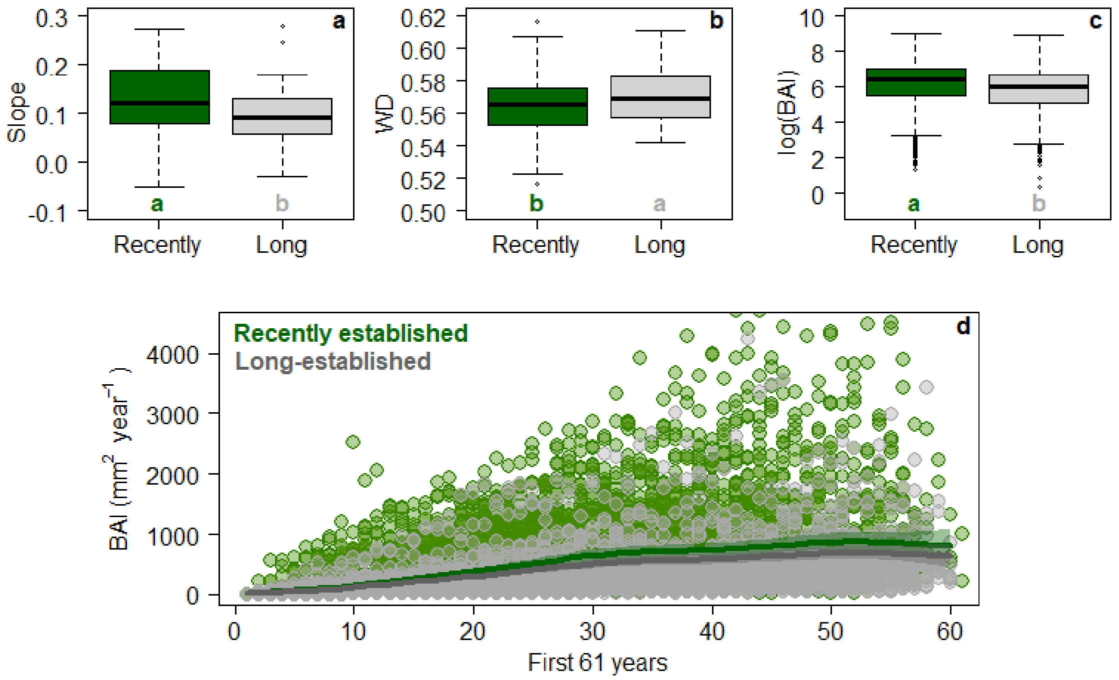


Figure 6. Boxplots displaying slope coefficients obtained in linear regression models between detrended growth values and June-July SPEI (a), wood density (WD, g cm^{-3}; b) and log-transformed BAI (c) differences between type of forest (recently or long-established). Lowercase coloured letters indicate significant differences found between type of forests (See Tables 1-2). Basal area increment (BAI) predictions across the first 61 years of the life of the trees for recently (green line) and long-established (grey line) forests (d). The observed BAI values are indicated with green and grey circles, for recently and long-established forests, respectively. Only the comparable age subset between 45 and 61 years is considered.

3.3 Tree growth

Recently established forests displayed significant higher mean raw ring width (32%) than the long-established forests (Table S1b) and LMEMs indicated that during the first 61 years of the trees' lifetime (i.e. the time period covered by both recently or long-established forests), trees growing in recently established forests also presented higher growth (BAI) rates, when using all the sampled trees (Table S3) and even when comparing a similar range of ages (Table 2, Fig. 6c-d).

Table 2. Results of basal area increment (BAI) using the comparable age subset, from 45 to 61 years. Age is the year of the life of the tree. The R^2 due to fixed (R^2_m) and due to fixed and random effects (R^2c) of each selected model is also provided. Significance of the p values is indicated by: ***P<0.001; **P<0.01 or **P<0.05.

BAI				
Fixed effects	Estimate	SE	t value	p value
(Intercept)	4.52	0.17	26.3	<0.001***
Age (0-10)	2.77	0.12	22.5	<0.001***
Age (10-20)	3.41	0.14	24.5	<0.001***
Age (20-30)	3.38	0.13	25.5	<0.001***
Age (30-40)	3.06	0.12	25.0	<0.001***
Age (40-50)	5.33	0.24	22.3	<0.001***
Age (50-60)	2.34	0.15	15.3	<0.001***
Type of forest: *Long-established*	-0.24	0.09	-2.8	<0.01**
Competition index (CI)	-0.47	0.05	-10.2	<0.001***
Jun-July SPEI	0.103	0.004	23.5	<0.001***
Random effects	Std. Dev			
Tree	0.39			
Residual	0.69			
R^2_m	0.57			
R^2c	0.67			

Both LMEM BAI models presented a high explained variation; i.e. the LMEM using all the range of ages explained 41% of the variation (Table S3) whereas the model that accounted only for the trees between 45 and 61 years explained 57% of the variation (Table 2). Favourable June-July SPEI conditions exerted a positive influence on both growth LMEMs (Table 2; Table S3).

The LMEM that included all range of ages showed that tree elevation also exerted a positive influence on growth for both types of forests. Growth in the long-established forests was also less sensitive to climatic conditions, as reflected by the negative interaction between type of forest and June-July SPEI conditions (Table S3).

For the LMEM that used the comparable age subset, between 45 and 61 years, we additionally included as a predictor variable a competition index calculated at the individual level for that selection of trees. This competition index was significant in the LMEM, showing a negative effect of tree competition on growth in both types of forests (Table 2).

4. Discussion

This study stresses that recently established forests are more sensitive to climate. To the best of our knowledge, our study is the first to highlight the importance that positive climatic events may have in buffering the negative effects of drought episodes. In addition, we noticed that the particular distribution of negative and positive climatic extreme events can be crucial for forecasting the effects of climate change on forests, particularly when conclusions about vulnerability are inferred only from resilience components (*sensu* Lloret et al. 2011) across large geographical gradients.

In agreement with our first hypothesis, recently established beech forests grew more than long-established ones even when controlling for tree age, i.e. running the analyses with the common subset of trees aged between 45 and 61 years (Fig. 3, 6). For this subset of trees, our analyses indicate that the recently established forests grew some 32% (in terms of mean raw ring width) more than long-established forests. Lower tree competition during tree establishment might be invoked as a potential cause benefiting trees growing in recently established forests. However, several pieces of evidence cast doubts on this effect. First, no significant differences were found in patch structure among the two types of forests, either in tree density or in basal area (Table S1). Furthermore, competition at the individual level (CI) was included in the models and although, as expected, it negatively affected tree growth (e.g. Zeller et al., 2017), no significant interaction between CI index and the type of forest was observed. Second, during the first years after establishment, growth was very similar in the two forest types (i.e. see the period 1960-1970 in Fig. 3) and this trend persisted until some unusual wet years occurred in the late 70s. In fact, recently established beech forests only start demonstrating a clear advantage in their growth in recent decades when negative, but also the majority of positive-climatic extreme years have occurred (from the 90s onwards, see Fig. 3a).

These results, coupled with the higher N content observed in tree leaves in recently established forests, suggest that legacies from a former agricultural or pastoral use might be the main factor favouring a faster growth of trees in recently established forests (see also Mausolf et al., 2018). Interestingly, the fact that differences in tree growth between forest types become particularly high during wet years, is in line with the paramount importance of water availability for nutrient uptake in Mediterranean mountain ecosystems (Matías et al., 2011; He and Dijkstra, 2014). Thus, it is during wetter years when the advantage of recently established forests, established in more fertile soil, can be maximized. Furthermore, we cannot discard that due to this higher soil fertility, recently established forests are obtaining an additional benefit in comparison to long-established ones, from the overall positive physiological effects of warming (see Fig. 3b), extension of the vegetative season and rising atmospheric CO_2, reported for European forests during recent decades (Churkina et al., 2010; Pretzsch et al., 2018).

Our second hypothesis was also confirmed with trees in recently established forests showing a reduction in wood density of c.a. 3%, even after restricting the analysis to the common 45-61 age class. This result is likely associated with the higher growth detected in these recently established forests, which is also in line with previous studies for beech in Central Europe (Pretzsch et al., 2018). However, a less pronounced reduction in wood density was found in our study area, 3%, compared to the reduction of 11% found by Pretzsch et al. (2018), possibly because of the different methodologies used for wood density determination or in tree age (older trees in Pretzsch et al., 2018). Reduced wood density implies a higher vulnerability to drought-induced cavitation (Hacke et al., 2001) for the recently established forests, since low wood density is often associated with wider vessels (Eilmann et al., 2014), that are more prone to suffer cavitation at negative xylem pressures during drought episodes (Anderegg et al., 2015; Hacke et al., 2001; Jump et al., 2017). Due to the decrease in mechanical stability, lower wood density is also associated with less resistance to other disturbances such as wind (Anten and Schieving, 2010) and pathogens (Augspurger, 1984), i.e., reduced stiffness and strength (weaker wood in Pretzsch and Rais, 2016) and it implies less C accumulation for similar tree volume (Zeller et al., 2017).

In our research, wood density also increased with tree age and decreased with tree density. This positive relationship between wood density and tree age has been previously reported (Diaconu et al., 2016) and attributed to the duraminization (or heartwood formation) process, i.e. the chemical maturation of wood that increases the density of the tree-rings over time (Bontemps et al., 2013).

In addition to differences in wood density, attention should be paid to the consequences of a potential oversizing of canopies in trees growing in recently established forests during their larger growth response in wetter years (Fig. 3a) for their future vulnerability to increasing drought. A strong and positive relationship has been reported between tree growth, mediated by favourable environmental conditions, and canopy development and productivity (Fernández-Martínez et al., 2015), but also the more negative effects that drought may have for larger trees for example due to the higher evaporative demand of their larger crowns (Bennett et al., 2015; Jump et al., 2017).

Both forest types showed a drought sensitive response of growth, i.e, positive correlations with summer precipitation and SPEI and negative correlations with summer temperature. This general pattern of climate-growth relationships is in agreement with previous studies covering a latitudinal gradient in Western Europe that included our study area located at the climatic margin of the species (Cavin and Jump, 2017). However, climate-growth correlations and the slope coefficients between detrended growth series and June-July SPEI values confirmed our third hypothesis that recently established forests were more sensitive than long-established forests to climate (summer conditions). As for other tree species, intraspecific differences in climate sensitivity in beech have been reported to stem from genotypic differentiation or phenotypic plasticity (Nielsen and Jørgensen, 2003; Rose et al., 2009). Preliminary results suggests the lack of genetic differences among recently and long-established beech forest in our study area (M. Mayol, unpublished results), as might be expected from the moderate geographical scale covered and the wind-pollination habit of this species (see Leonardi and Menozzi, 1996). Aside from genotypic differences, past climate legacies (Lloret and Kitzberger, 2018) or land use legacies (von Oheimb et al., 2014) have also been identified as important influences on the current sensitivity of tree species to climate. Historical climate legacies have been one of the most invoked causes to explain the greater vulnerability to extreme events of climatic-core populations in comparison to climatic-marginal ones (Clark et al., 2016; Jump et al., 2017; Rose et al., 2009), although the geographical and temporal scale of our study does not support this explanation. Rather, our results suggest the combination of higher growth and lower wood density in recently established forests to be responsible of their higher sensitivity to climate. This finding is in agreement with previous studies that have stressed the role that land use legacies play in determining differences in tree sensitivity to climate (Mausolf et al., 2018; von Oheimb et al., 2014). As for our study area, Mausolf et al. (2018) also observed that recently established Central European beech forests were more sensitive to climatic variations than forest with a continuous land use history. Ultimately, this higher sensitivity to climate of trees established in richer soils from former agricultural areas agrees with the findings of Lévesque et al., (2016) who detected higher growth sensitivity in beech trees growing on richer soils in a study that followed a gradient of different soil properties in Central Europe.

Despite the observed higher climatic sensitivity of recently established beech forests, they showed a similar or even higher recovery, resistance and resilience capacity than long-established forests when challenged with drought events. These results disagree with the findings of Mausolf et al. (2018) for Northern Germany, where the authors detected higher growth reductions under drought and less resistance in recently than in long-established beech forests. Divergences might arise from methodological differences among these studies, such as differences in tree age of recently established forests (100-150 *vs.* 61 yrs, respectively,) or the length of the series used to explore the link between land-use legacies and climate sensitivity (1994-2013 *vs.* 1956-2017, respectively). In addition, other local characteristics (e.g. forestry practices, historic climatic legacies) may lead to divergent results among distant latitudinal points. However, it should also be taken into account that recovery and resilience indices rely on the climatic conditions after the studied event. For instance, we found a recovery value around 1.5 after the drought event of 2006 which can be associated to the extremely rainy years of 2008 and 2009 that fall in the 3 years range of the resilience components calculations (Fig. 3a, 5). The fact that most severe drought events in our study area were followed by extremely wet years (Fig. 3a), and that recently established forests experienced twice the positive pointer years than long-established ones (Fig. 4), may help to explain the divergence in the response of recently established beech forests to drought between Mausolf et al. (2018) and the results presented here.

Indeed, our results strongly suggest that the decrease in growth during negative climatic events is probably overcompensated by a large increase in rainy years, explaining why the recently established forests show a strong response to drought years despite their higher climate sensitivity. Furthermore, the relevance of favourable years diminishing the negative impacts of drought in our marginal-climate beech forests, is in line with the evidence of highly locally variable drought-linked growth decline in this dry range-edge beech populations, particularly for the youngest forests (Cavin and Jump, 2017) or the lack of changes in growth after drought episodes observed for beech forests in the Pyrenees (Gazol et al., 2018).

5. Conclusions

During the 20th Century, Europe has experienced substantial forest expansion because of the widespread abandonment of rural landscapes, a trend expected to continue in the future (Keenan, 2015). These recently established forests are already having a pivotal role in providing ecosystem services such as habitat supply, landscape defragmentation and increased net primary production and terrestrial carbon stocks (Bonan, 2008), while contributing to compensation of fossil carbon emission (Pan et al., 2011, Vilà-Cabrera et al. 2017). Based on our findings, the greater growth of recently established forests resulting from agricultural and pastoral land abandonment can contribute significantly to these services. However, previous studies highlighted the role of enhanced growth during climatically more favourable periods in substantially elevating risk of dieback during subsequent drought (Jump et al., 2017), and the greater drought vulnerability of trees with lower wood density (Greenwood et al., 2017). Therefore, greater growth in combination with changes in functional traits (i.e. lower wood density) and their higher sensitivity to climate pose significant risks of vulnerability of recently established forests when coupled with the projections of a strong decrease of summer precipitation by 2100 across southern Europe (EEA, 2017). With the projected increase in aridity for our study region during the next decades, there is a significant risk that these recently established forests might be more negatively impacted by future drought than forests with more continuous land-use history. Therefore, the ability of recently established forests to contribute to carbon sequestration and other ecosystem services in the long term could be threatened. Given these risks, better understanding of the function and dynamics of forests established following land abandonment is essential to better predict their response to the climates of the future.

Acknowledgements

We thank Marta Ramírez for assistance in the field and laboratory work. This study was supported by the FORASSEMBLY (CGL2015-70558-P), NEWFORLAND (RTI2018-099397-C22) and SPONFOREST (APCIN_2016_0174) projects. R.A.S. is supported by the postdoctoral grant Juan de la Cierva-Formación-FJCI-2015-26848, from the Spanish Ministry of Economy, Industry and Competitiveness.

References

Aerts, R., Chapin, F.S., 1999. The Mineral Nutrition of Wild Plants Revisited: A Re-evaluation of Processes and Patterns, in: Fitter, A.H., Raffaelli, D.G. (Eds.), Advances in Ecological Research. Academic Press, pp. 1–67. https://doi.org/10.1016/S0065-2504(08)60016-1

Alfaro-Sánchez, R., Camarero, J.J., Sánchez-Salguero, R., Trouet, V., Heras, J. de L., 2018. How do Droughts and Wildfires Alter Seasonal Radial Growth in Mediterranean Aleppo Pine Forests? Tree-Ring Res. 74, 1–14. https://doi.org/10.3959/1536-1098-74.1.1

Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Ogle, K., Shaw, J.D., Shevliakova, E., Williams, A.P., Wolf, A., Ziaco, E., Pacala, S., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349, 528–532. https://doi.org/10.1126/science.aab1833

Anten, N.P.R., Schieving, F., 2010. The Role of Wood Mass Density and Mechanical Constraints in the Economy of Tree Architecture. Am. Nat. 175, 250–260. https://doi.org/10.1086/649581

Archimedes, 2009. PREFACE, in: Heath, T.L.E. (Ed.), The Works of Archimedes: Edited in Modern Notation with Introductory Chapters, Cambridge Library Collection - Mathematics. Cambridge University Press, pp. v–x. https://doi.org/10.1017/CBO9780511695124.001

Augspurger, C.K., 1984. Seedling Survival of Tropical Tree Species: Interactions of Dispersal Distance, Light-Gaps, and Pathogens. Ecology 65, 1705–1712. https://doi.org/10.2307/1937766

Barton, K., 2018. MuMIn: Multi-Model Inference.

Başnou, C., Álvarez, E., Bagaria, G., Guardiola, M., Isern, R., Vicente, P., Pino, J., 2013. Spatial Patterns of Land Use Changes Across a Mediterranean

Metropolitan Landscape: Implications for Biodiversity Management. Environ. Manage. 52, 971–980. https://doi.org/10.1007/s00267-013-0150-5

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01

Bennett, A.C., McDowell, N.G., Allen, C.D., Anderson-Teixeira, K.J., 2015. Larger trees suffer most during drought in forests worldwide. Nat. Plants 1, 15139. https://doi.org/10.1038/nplants.2015.139

Bonan, G.B., 2008. Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. Science 320, 1444–1449. https://doi.org/10.1126/science.1155121

Bontemps, J.-D., Gelhaye, P., Nepveu, G., Hervé, J.-C., 2013. When tree rings behave like foam: moderate historical decrease in the mean ring density of common beech paralleling a strong historical growth increase. Ann. For. Sci. 70, 329–343. https://doi.org/10.1007/s13595-013-0263-2

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124. https://doi.org/10.1016/j.dendro.2008.01.002

Cao, T., Valsta, L., Härkönen, S., Saranpää, P., Mäkelä, A., 2008. Effects of thinning and fertilization on wood properties and economic returns for Norway spruce. For. Ecol. Manag. 256, 1280–1289. https://doi.org/10.1016/j.foreco.2008.06.025

Cavin, L., Jump, A.S., 2017. Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. Glob. Change Biol. 23, 362–379. https://doi.org/10.1111/gcb.13366

Churkina, G., Zaehle, S., Hughes, J., Viovy, N., Chen, Y., Jung, M., Heumann, B.W., Ramankutty, N., Heimann, M., Jones, C., 2010. Interactions between nitrogen deposition, land cover conversion, and climate change determine the contemporary carbon balance of Europe. Biogeosciences 7, 2749–2764. https://doi.org/10.5194/bg-7-2749-2010

Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C., D'Amato, A.W., Davis, F.W., Hersh, M.H., Ibanez, I., Jackson, S.T., Matthews, S., Pederson, N., Peters, M., Schwartz, M.W., Waring, K.M., Zimmermann, N.E., 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Glob. Change Biol. 22, 2329–2352. https://doi.org/10.1111/gcb.13160

Compton, J.E., Boone, R.D., 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology 81, 2314–2330. https://doi.org/10.1890/0012-9658(2000)081[2314:LTIOAO]2.0.CO;2

Cook, E.R., Kairiukstis, L.A. (Eds.), 1990. Methods of Dendrochronology. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-94-015-7879-0

Cropper, J.P., 1979. Tree-ring skeleton plotting by computer. Tree-Ring Bull. 13.

Cybis Elektronik, 2018. CDendro and CooRecorder.

Diaconu, D., Wassenberg, M., Spiecker, H., 2016. Variability of European beech wood density as influenced by interactions between tree-ring growth and aspect. For. Ecosyst. 3. https://doi.org/10.1186/s40663-016-0065-8

EEA, 2017. Climate change. impacts and vulnerability in Europe 2016: an indicator-based report. European Environment Agency.

Eilmann, B., Sterck, F., Wegner, L., de Vries, S.M.G., von Arx, G., Mohren, G.M.J., den Ouden, J., Sass-Klaassen, U., 2014. Wood structural differences between northern and southern beech provenances growing at a moderate site. Tree Physiol. 34, 882–893. https://doi.org/10.1093/treephys/tpu069

Ellenberg, H., 1913-1997 (viaf)22201609, Leuschner, C., Dierschke, H., 2010. Vegetation Mitteleuropas mit den Alpen : in Ökologischer, dynamischer and historischer Sicht, 6., vollständig neu bearbeitete und stark erweiterte Auflage. ed. Stuttgart : Ulmer.

Fernández-Martínez, M., Garbulsky, M., Peñuelas, J., Peguero, G., Espelta, J.M., 2015. Temporal trends in the enhanced vegetation index and spring weather predict seed production in Mediterranean oaks. Plant Ecol. 216, 1061–1072. https://doi.org/10.1007/s11258-015-0489-1

Fichtner, A., von Oheimb, G., Härdtle, W., Wilken, C., Gutknecht, J.L.M., 2014. Effects of anthropogenic disturbances on soil microbial communities in oak forests persist for more than 100 years. Soil Biol. Biochem. 70, 79–87. https://doi.org/10.1016/j.soilbio.2013.12.015

Fraterrigo, J.M., Turner, M.G., Pearson, S.M., Dixon, P., 2005. Effects of past land use on spatial heterogeneity of soil nutrients in southern Appalachian forests. Ecol. Monogr. 75, 215–230. https://doi.org/10.1890/03-0475

Freschet, G.T., Östlund, L., Kichenin, E., Wardle, D.A., 2014. Aboveground and belowground legacies of native Sami land use on boreal forest in northern Sweden 100 years after abandonment. Ecology 95, 963–977. https://doi.org/10.1890/13-0824.1

Fritts, H.C., 1976. Tree Rings and Climate, Academic Press. ed. Elsevier, London.

Gazol, A., Camarero, J.J., Vicente-Serrano, S.M., Sánchez-Salguero, R., Gutiérrez, E., de Luis, M., Sangüesa-Barreda, G., Novak, K., Rozas, V., Tíscar, P.A., Linares, J.C., Martín-Hernández, N., Martínez del Castillo, E., Ribas, M., García-González, I., Silla, F., Camisón, A., Génova, M., Olano, J.M., Longares, L.A., Hevia, A., Tomás-Burguera, M., Galván, J.D., 2018. Forest resilience to drought varies across biomes. Glob. Change Biol. 24, 2143–2158. https://doi.org/10.1111/gcb.14082

Gerstner, K., Dormann, C.F., Stein, A., Manceur, A.M., Seppelt, R., 2014. Effects of land use on plant diversity - A global meta-analysis. J. Appl. Ecol. 51, 1690–1700. https://doi.org/10.1111/1365-2664.12329

Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C.D., Fensham, R., Laughlin, D.C., Kattge, J., Bönisch, G., Kraft, N.J.B., Jump, A.S., 2017. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. Ecol. Lett. 20, 539–553. https://doi.org/10.1111/ele.12748

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D., McCulloh, K.A., 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126, 457–461. https://doi.org/10.1007/s004420100628

Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters: Rear edges and climate change. Ecol. Lett. 8, 461–467. https://doi.org/10.1111/j.1461-0248.2005.00739.x

Haylock, M.R., Hofstra, N., Klein Tank, A.M.G., Klok, E.J., Jones, P.D., New, M., 2008. A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. J. Geophys. Res. 113. https://doi.org/10.1029/2008JD010201

He, M., Dijkstra, F.A., 2014. Drought effect on plant nitrogen and phosphorus: a meta-analysis. New Phytol. 204, 924–931. https://doi.org/10.1111/nph.12952

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43, 69–78.

Hultén, E., Fries, M., 1986. Atlas of North European vascular plants : north of the Tropic of Cancer. Königstein, Federal Republic of Germany : Koeltz Scientific Books.

Jump, A.S., Hunt, J.M., Peñuelas, J., 2007. Climate relationships of growth and establishment across the altitudinal range of Fagus sylvatica in the Montseny Mountains, northeast Spain. Ecoscience 14, 507–518. https://doi.org/10.2980/1195-6860(2007)14[507:CROGAE]2.0.CO;2

Jump, A.S., Hunt, J.M., Peñuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of Fagus sylvatica. Glob. Change Biol. 12, 2163–2174. https://doi.org/10.1111/j.1365-2486.2006.01250.x

Jump, A.S., Ruiz-Benito, P., Greenwood, S., Allen, C.D., Kitzberger, T., Fensham, R., Martínez-Vilalta, J., Lloret, F., 2017. Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. Glob. Change Biol. 23, 3742–3757. https://doi.org/10.1111/gcb.13636

Keenan, R.J., 2015. Climate change impacts and adaptation in forest management: a review. Ann. For. Sci. 72, 145–167. https://doi.org/10.1007/s13595-014-0446-5

Lambers, H., Chapin, F.S., Pons, T.L., 2008. Plant physiological ecology, 2nd ed. ed. Springer, New York.

Lambin, E.F., Meyfroidt, P., 2011. Global land use change, economic globalization, and the looming land scarcity. Proc. Natl. Acad. Sci. 108, 3465–3472. https://doi.org/10.1073/pnas.1100480108

Leonardi, S., Menozzi, P., 1996. Spatial structure of genetic variability in natural stands of Fagus sylvatica L. (beech) in Italy. Heredity 77, 359–368. https://doi.org/10.1038/hdy.1996.154

Leuschner, C., Wulf, M., Bäuchler, P., Hertel, D., 2014. Forest Continuity as a Key Determinant of Soil Carbon and Nutrient Storage in Beech Forests on Sandy Soils in Northern Germany. Ecosystems 17, 497–511. https://doi.org/10.1007/s10021-013-9738-0

Lévesque, M., Walthert, L., Weber, P., 2016. Soil nutrients influence growth response of temperate tree species to drought. J. Ecol. 104, 377–387. https://doi.org/10.1111/1365-2745.12519

Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120, 1909–1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x

Lloret, F., Kitzberger, T., 2018. Historical and event-based bioclimatic suitability predicts regional forest vulnerability to compound effects of severe drought and bark beetle infestation. Glob. Change Biol. 24, 1952–1964. https://doi.org/10.1111/gcb.14039

Lorimer, C.G., 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manag. 6, 343–360. https://doi.org/10.1016/0378-1127(83)90042-7

Mäkinen, H., Saranpää, P., Linder, S., 2002. Wood-density variation of Norway spruce in relation to nutrient optimization and fibre dimensions. Can. J. For. Res. 32, 185–194. https://doi.org/10.1139/x01-186

Masson-Delmotte, V., Roberts, D., Skea, J., Moufouma-Okia, W., Péan, C., Pidcock, R, Connors, S, Matthews, J. B. R, Chen, Y, Zhou, X, Gomis, M.I, Lonnoy, E, Maycock, T, Tignor, M, Waterfield, T (Eds.), 2018. IPCC, 2018: Global warming of 1.5°C. S.l.

Matías, L., Castro, J., Zamora, R., 2011. Soil-nutrient availability under a global-change scenario in a Mediterranean mountain ecosystem: SOIL NUTRIENTS UNDER A GLOBAL CHANGE SCENARIO. Glob. Change Biol. 17, 1646–1657. https://doi.org/10.1111/j.1365-2486.2010.02338.x

Mausolf, K., Härdtle, W., Jansen, K., Delory, B.M., Hertel, D., Leuschner, C., Temperton, V.M., von Oheimb, G., Fichtner, A., 2018. Legacy effects of land-use modulate tree growth responses to climate extremes. Oecologia 187, 825–837. https://doi.org/10.1007/s00442-018-4156-9

Nielsen, C.N., Jørgensen, F.V., 2003. Phenology and diameter increment in seedlings of European beech (Fagus sylvatica L.) as affected by different soil water contents: variation between and within provenances. For. Ecol. Manag. 174, 233–249. https://doi.org/10.1016/S0378-1127(02)00042-7

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A Large and Persistent Carbon Sink in the World’s Forests. Science 333, 988. https://doi.org/10.1126/science.1201609

Peñuelas, J., Ogaya, R., Boada, M., S. Jump, A., 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). Ecography 30, 829–837. https://doi.org/10.1111/j.2007.0906-7590.05247.x

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2018. nlme: Linear and Nonlinear Mixed Effects Models.

Piovesan, G., Biondi, F., Filippo, A.D., 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. https://doi.org/10.1111/j.1365-2486.2008.01570.x

Pott, R., 2000. Palaeoclimate and vegetation - long-term vegetation dynamics in central Europe with particular reference to beech. Phytocoenologia 30, 285–333. https://doi.org/10.1127/phyto/30/2000/285

Pretzsch, H., Biber, P., Schütze, G., Kemmerer, J., Uhl, E., 2018. Wood density reduced while wood volume growth accelerated in Central European forests since 1870. For. Ecol. Manag. 429, 589–616. https://doi.org/10.1016/j.foreco.2018.07.045

Pretzsch, H., Rais, A., 2016. Wood quality in complex forests versus even-aged monocultures: review and perspectives. Wood Sci. Technol. 50, 845–880. https://doi.org/10.1007/s00226-016-0827-z

Putz, F.E., Coley, P.D., Lu, K., Montalvo, A., Aiello, A., 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. Can. J. For. Res. 13, 1011–1020. https://doi.org/10.1139/x83-133

Rose, L., Leuschner, C., Köckemann, B., Buschmann, H., 2009. Are marginal beech (Fagus sylvatica L.) provenances a source for drought tolerant ecotypes? Eur. J. For. Res. 128, 335–343. https://doi.org/10.1007/s10342-009-0268-4

Rozas, V., Fernández Prieto, J.A., 2000. Competition, mortality, and development of spatial patterns in two Cantabrian populations of *Fagus sylvatica* L. (Fagaceae). An. Jardín Botánico Madr. 58. https://doi.org/10.3989/ajbm.2000.v58.i1.144

Schweingruber, F.H., 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.

Thom, D., Rammer, W., Garstenauer, R., Seidl, R., 2018. Legacies of past land use have a stronger effect on forest carbon exchange than future climate change in a temperate forest landscape. Biogeosciences 15, 5699–5713. https://doi.org/10.5194/bg-15-5699-2018

Treasure, E.R., Church, M.J., Gröcke, D.R., 2016. The influence of manuring on stable isotopes (δ13C and δ15N) in Celtic bean (Vicia faba L.): archaeobotanical and palaeodietary implications. Archaeol. Anthropol. Sci. 8, 555–562. https://doi.org/10.1007/s12520-015-0243-6

van der Maaten-Theunissen, M., van der Maaten, E., Bouriaud, O., 2015. pointRes: An R package to analyze pointer years and components of resilience. Dendrochronologia 35, 34–38. https://doi.org/10.1016/j.dendro.2015.05.006

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. J. Clim. 23, 1696–1718. https://doi.org/10.1175/2009JCLI2909.1

Vilà-Cabrera, A., Espelta, J.M., Vayreda, J., Pino, J., 2017. “New Forests” from the Twentieth Century are a Relevant Contribution for C Storage in the Iberian Peninsula. Ecosystems 20, 130–143. https://doi.org/10.1007/s10021-016-0019-6

von Oheimb, G., Härdtle, W., Eckstein, D., Engelke, H.-H., Hehnke, T., Wagner, B., Fichtner, A., 2014. Does Forest Continuity Enhance the Resilience of Trees to Environmental Change? PLoS ONE 9, e113507. https://doi.org/10.1371/journal.pone.0113507

Williamson, G.B., Wiemann, M.C., 2010. Measuring wood specific gravity…Correctly. Am. J. Bot. 97, 519–524. https://doi.org/10.3732/ajb.0900243

Zang, C., Biondi, F., 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography 38, 431–436. https://doi.org/10.1111/ecog.01335

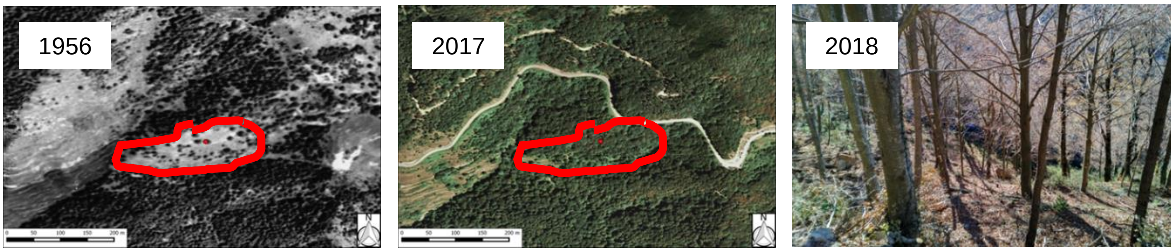
Zeller, L., Ammer, Ch., Annighöfer, P., Biber, P., Marshall, J., Schütze, G., del Río Gaztelurrutia, M., Pretzsch, H., 2017. Tree ring wood density of Scots pine and European beech lower in mixed-species stands compared with monocultures. For. Ecol. Manag. 400, 363–374. https://doi.org/10.1016/j.foreco.2017.06.018

Zimmermann, J., Hauck, M., Dulamsuren, C., Leuschner, C., 2015. Climate Warming-Related Growth Decline Affects Fagus sylvatica, But Not Other Broad-Leaved Tree Species in Central European Mixed Forests. Ecosystems 18, 560–572. https://doi.org/10.1007/s10021-015-9849-x

Zuur, A.F. (Ed.), 2009. Mixed effects models and extensions in ecology with R, Statistics for biology and health. Springer, New York, NY.

Supplementary Figures

a. Recently established forest



b. Long-established forest

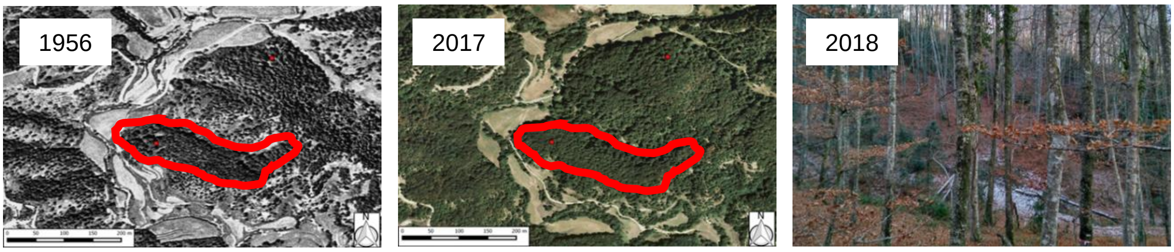


Figure S1. Orthoimages and descriptive pictures from recently and long-established forests in 1956 and 2017-2018.

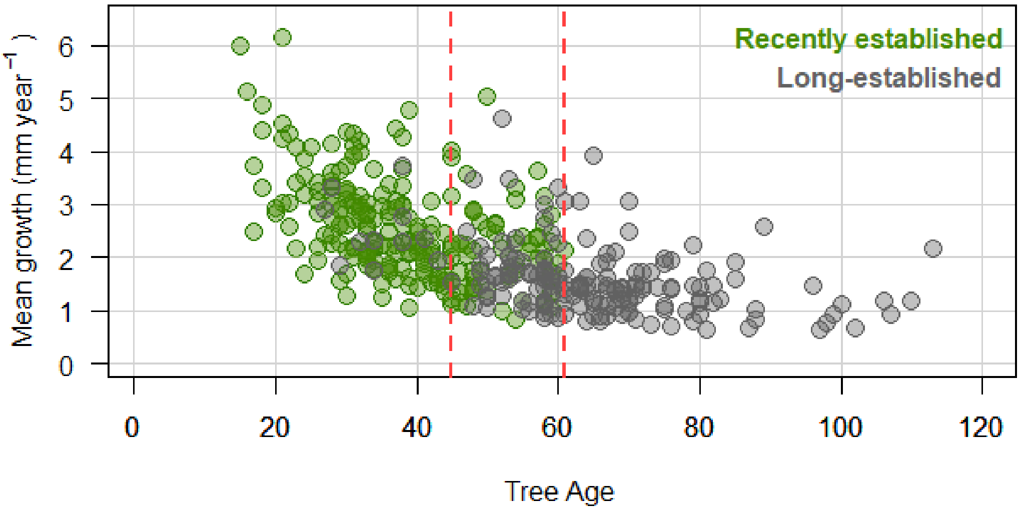


Figure S2. Difference on tree ages in mean growth for both type of forests. Red dashed lines indicate the comparable age subset between 45 and 61 years.

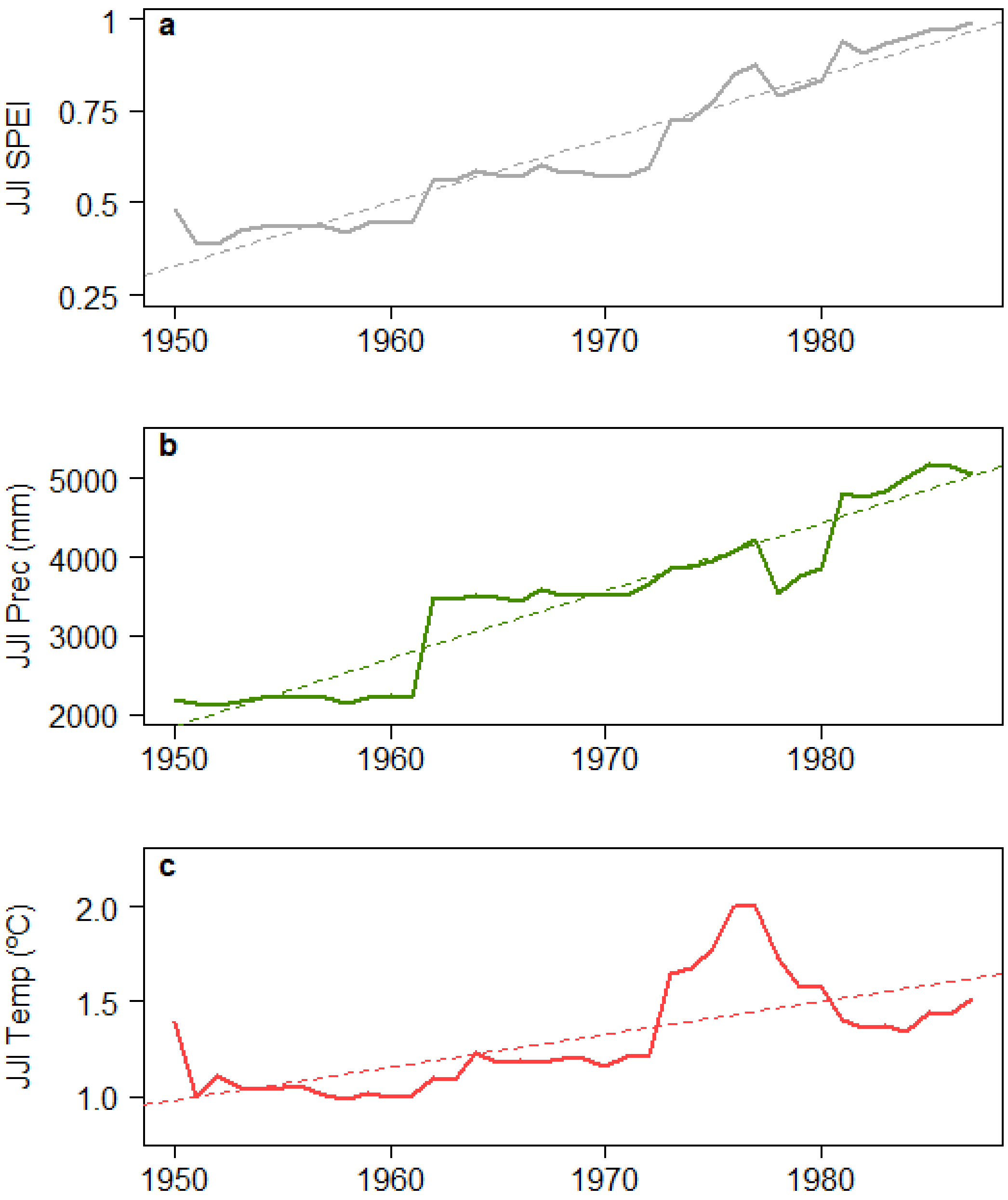


Figure S3. Thirty-one years running variation for June-July SPEI (a) precipitation (b) and temperature (c) derived from E-OBS v.17.0 dataset for the period 1950-2016 and averaged over the four 0.25° spatial resolution grids covering the study region (2.125-2.625 E and 41.125-43.375 N). Dashed lines represent the trend obtained in linear regression models (significant at $P<0.05$ in (a) and (b)).

Supplementary Tables

Table S1. Structural characteristics for recently and long-established forests. Mean ± SE of tree age, tree density, DBH, basal area (BA), leaf nitrogen content and δ^{15}N values (a). Tree-ring statistics for Expressed Population signal (EPS) values above 0.85 for long-established forests, long-established forests younger than 62 years and recently established forests, and mean ± SE raw tree-ring width and basal area increment (BAI, b). Asterisks denote significant differences among type of forests for these variables.

a.

	Tree age (years)		Tree density (trees·ha^{-1})		DBH (cm)		BA (m^2·ha^{-1})		N content (%)		Leaf δ^{15}N (‰)		Elevation (m)
Type of forest	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	range
Long-established	65.2*	1.3	1413	36	19.6	0.5	29.7	0.4	2.46	0.02	-3.14	0.09	831-1333
Recently established	37.8	0.6	1662	56	18.5	0.3	31.3	0.6	2.74	0.03	-5.76	0.08	1027-1452

b.

							Raw ring width (mm)		BAI (mm^2·year^{-1})	
Type of forest	Period	n trees	n cores	EPS	Interseries correlation	Mean sensitivity	mean	SE	mean	SE
Long-established	1917-2017	179	318	0.98	0.47	0.20	1.50	0.010	558	6
Long-established < 62 yrs	1959-2017	84	155	0.97	0.50	0.20	1.78	0.017	645	12
Recently established	1960-2017	332	617	0.99	0.52	0.30	2.35*	0.013	806*	8

Table S2. LMEMs results for the predictive variable slope (obtained from the linear regression models between detrended growth values and June-July SPEI) and wood density (WD) using all range of ages. Tree density was scaled in the models. The R^2 due to fixed ($R^2{}_m$) and due to fixed and random effects (R^2 c) of each selected model is also provided. Significance of the p values is indicated by: ***P<0.001; **P<0.01 or **P<0.05.

	Slope				WD			
Fixed effects	Estimate	SE	t value	p value	Estimate	SE	t value	p value
(Intercept)	0.135	0.010	14.25	<0.001***	0.5528	0.0024	7.10	<0.001***
Type of forest: *Long-established*	-0.045	0.016	-2.75	<0.05*	0.018	0.003	6.96	<0.01**
Tree density	n.a.				-0.0064	0.0017	7.13	<0.01**
Random effects	Std. Dev				Std. Dev			
Patch	0.03				0.004			
Residual	0.06				0.016			
$R^2{}_m$	0.09				0.28			
R^2 c	0.29				0.33			

Table S3. Results of the LMEMs selected to study basal area increment (BAI) using all range of ages. In the models, age is the year of the life of the tree. Type of forest is a categorical variable to distinguish between recently and long-established forests. BAI and tree density variables were log-transformed to conform normality and tree elevation was scaled. The R^2 due to fixed ($R^2{}_m$) and due to fixed and random effects (R^2 c) of each selected model is also provided. Significance of the p values is indicated by: ***P<0.001; **P<0.01 or **P<0.05.

	BAI			
	Estimate	SE	t value	p value
(Intercept)	3.58	0.07	54.5	<0.001***
Age (0-10)	2.86	0.07	42.4	<0.001***
Age (10-20)	3.34	0.08	41.2	<0.001***
Age (20-30)	3.27	0.09	38.1	<0.001***
Age (30-40)	2.94	0.10	29.4	<0.001***
Age (40-50)	5.35	0.15	36.5	<0.001***
Age (50-60)	2.22	0.14	16.1	<0.001***
Type of forest: *Long-established*	-0.46	0.09	-5.0	<0.001***
Tree elevation	0.14	0.04	3.7	<0.001***
Jun-July SPEI	0.127	0.003	39.2	<0.001***
Type of forest: *Long-established* × Jun-July SPEI	-0.030	0.007	-4.5	<0.001***
$R^2{}_m$	0.41			
R^2 c	0.69			