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Contrasting growth forecasts across the geographical range of Scots pine due to altitudinal and latitudinal differences in climatic sensitivity

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Abstract

Ongoing changes in global climate are altering ecological conditions for many species. The consequences of such changes are typically most evident at the edge of a species' geographical distribution, where differences in growth or population dynamics may result in range expansions or contractions. Understanding population responses to different climatic drivers along wide latitudinal and altitudinal gradients is necessary in order to gain a better understanding of plant responses to ongoing increases in global temperature and drought severity. We selected Scots pine (*Pinus sylvestris* L.) as a model species to explore growth responses to climatic variability (seasonal temperature and precipitation) over the last century through dendrochronological methods. We developed linear models based on age, climate and previous growth to forecast growth trends up to year 2100 using climatic predictions. Populations were located at the treeline across a latitudinal gradient covering the northern, central and southernmost populations and across an altitudinal gradient at the southern edge of the distribution (treeline, medium and lower elevations). Radial growth was maximal at medium altitude and treeline of the southernmost populations. Temperature was the main factor controlling growth variability along the gradients, although the timing and strength of climatic variables affecting growth shifted with latitude and altitude. Predictive models forecast a general increase in Scots pine growth at treeline across the latitudinal distribution, with southern populations increasing growth up to year 2050, when it stabilizes. The highest responsiveness appeared at central latitude, and moderate growth increase is projected at the northern limit. Contrastingly, the model forecasted growth declines at lowland-southern populations, suggesting an upslope range displacement over the coming decades. Our results give insight into the geographical responses of tree species to climate change and demonstrate the importance of incorporating biogeographical variability into predictive models for an accurate prediction of species dynamics as climate changes.

Keywords: climate, dendrochronology, distribution, growth, modelling, *Pinus sylvestris*

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Introduction

Distribution limits of plant species are determined by the ecological conditions that allow them to establish permanent populations (Babst *et al.*, 2013). The long-term persistence of many species within their present distribution limits is, therefore, challenged by global warming (Parmesan, 2006; Allen *et al.*, 2015). Indeed, there is increasing evidence of recent changes in climate affecting the ecological performance of plant species worldwide, from phenology, growth or reproductive investment to recruitment rates (Chmielewski & Rotzer, 2001; Peñuelas *et al.*, 2002; Castro *et al.*, 2004; Jump *et al.*, 2006; Walck *et al.*, 2011; Matías & Jump, 2015). Furthermore, these changes are not likely to homogeneously affect species across their geographical ranges, with populations located at the edges of their distributions being especially sensitive to climate alterations (Andreu *et al.*, 2007; Linares & Tíscar, 2011; Candel-Pérez *et al.*, 2012). The evidence of plant responses to climatic drivers and the mechanisms underlying these responses has risen rapidly during the last decades (Camarero & Gutiérrez, 2004; Jump *et al.*, 2006; Kullman, 2007; Benavides *et al.*, 2013; Matías & Jump, 2015). However, there is an urgent need to move beyond reporting changes underway to increase our predictive capacity, enabling us to better estimate the ecological and biogeographical consequences of climate change for species in the future (Steinkamp & Hickler, 2015).

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Climatic factors constraining plant growth in temperate and boreal environments shift along altitudinal and latitudinal gradients, typically moving from water shortage at lower altitudes to low temperature limitation at higher altitudes or latitudes (Babst *et al*., 2013). However, precipitation may constrain growth throughout an altitudinal gradient, as is sometimes the case in Mediterranean mountains (Camarero *et al*., 2015; Sánchez-Salguero *et al*., 2015; Arzac *et al*., 2016). Nonetheless, climate effects on growth are not only subjected to regional climate, but also dependent on local conditions or ontogenetic changes such as changes in tree age and size (Voelker, 2011). For example, older trees are usually more susceptible to drought stress than younger adults are, usually related to hydraulic limitations affecting photosynthesis, water-use efficiency and carbon allocation within the tree (Magnani *et al*., 2000; Martínez-Vilalta & Piñol, 2002; Ryan *et al*., 2006; Knapp & Soulé, 2011). Thus, it is important to explicitly account for factors other than climate such as ontogeny or resource accumulation when predicting the likely consequences of future climate on tree growth. However, species distribution models aimed at predicting future species dynamics usually consider the response of a species to climate as constant through its distribution range (Araújo & Luoto, 2007). Although this may be true for small-ranged species, the high variability of genotypes and climatic conditions make this assumption unrealistic for widely distributed species (Jyske *et al*., 2014; Matías & Jump, 2014; Matías *et al*., 2016). Consequently, detailed information about local responses to past changes in climate and its variation through tree ontogeny is urgently needed to predict future species responses under global climate change (Benavides *et al*., 2013; Mina *et al*., 2016).

Scots pine (*Pinus sylvestris* L.) is one the most abundant tree species of the Holarctic, with a distribution ranging from the Arctic to the Mediterranean (Matías & Jump, 2012). The wide distribution of this species implies a broad range of climatic conditions where it is able to survive, from the severe cold winters of northern Fennoscandia to the Mediterranean climate of southern Spain; and from the wet, oceanic climate of the west coast of Scotland to the dry continental climate of central Europe and Asia (Carlisle & Brown, 1968). Thus, it is logical to expect that different climatic factors are influencing growth across the distribution range of the species (Andreu *et al*., 2007; Kullman, 2007; Candel-Pérez *et al*., 2012; Sánchez-Salguero *et al*., 2015), making this species a valuable study system to evaluate local responses to environmental alterations.

We sought to model future growth trends across the latitudinal and altitudinal distribution of Scots pine under future climates. We quantified radial growth of Scots pine populations across a latitudinal gradient covering the northernmost and southernmost regions of the species' western distribution and across an altitudinal gradient from the treeline to the lower limit at the southernmost range edge of the species. We analysed past growth patterns at range limits across altitudinal and latitudinal gradients and identified the climatic and ontogenetic variables controlling tree growth at range edges. These fundamental data were then used to construct a predictive model to understand likely consequences of forecasted climate on tree growth at the species' range edges.

Materials and methods

Field sites

Scots pine populations were selected at locations along the altitudinal and latitudinal distribution of the species. The altitudinal gradient was located at the southernmost limit of this species in the Sierra de Baza, SE Spain (Table 1). Two different populations were selected (mean size 3.9 ± 0.3 ha) in each of the three altitudinal bands: lowermost limit, medium altitudinal distribution and upper (treeline), covering the whole altitudinal range. For the comparison across the latitudinal distribution range, we selected treeline populations across western Europe (Fig. S1). We used the same populations at the upper limit from the altitudinal range as the southernmost populations and two additional populations at western-central latitude (Cairngorms, UK), and two close to the northern limit of the distribution (Kevo, Finland), making a total of 10 study populations (see Matías & Jump, 2015 for more details). The altitudinal gradient was not replicated in latitude as altitudinal distribution diminishes with increasing latitude, presenting a very narrow altitudinal range at the northern limit of the focal species. To maintain comparability across the study areas, we selected the different populations maintaining orientation, slope and soil type as constant as possible. To minimize human management impacts as far as is practicable, we selected all population within protected areas: Sierra de Baza Natural Park, Cairngorms National Park and Kevo Strict Nature Reserve.

Sampling and width measurements

Between May and July 2012, 30 trees per population were randomly selected for dendrochronological study. Sampling was performed following standard dendrochronological methods (Fritts, 1976). For each sampled tree, two cores were taken using a 4.3 mm increment borer and diameter was recorded at breast height (1.3 m above ground level). Samples were then stored and air-dried in paper straws. The wood core samples were mounted, polished with successively finer grit sandpaper until rings were clearly visible, scanned at 1600 dpi and then measured with an accuracy of 0.001 mm using CooRecorder v7.4 (Larsson, 2003a). We examined samples to detect characteristic rings, and cores were cross-dated per population

Table 1 Main characteristics of the studied populations across latitudinal (northern, 69°47′N; 27°02′E; central, 57°08′N; 3°40′W; southern, 37°22′N; 2°51′W) and altitudinal gradients (treeline, medium, low): climate (TWM, temperature of the warmest month in °C; TCM, temperature of the coldest month in °C; PDM, precipitation of the driest month in mm; mean values for the 1960–211 period), elevation (m a.s.l.), tree density (individuals ha^{-1}), registered period, tree age (estimated at sampling moment from the number of rings measured, in years), diameter at breast height (DBH, in cm) and basal area increment (BAI, in cm^2 yr^{-1}) and growth trends during the last century separated in two periods (1910–1960 and 1961–2011). Values are mean ± SD

		Climate									BAI	Trend	BAI	Trend
Latitude	Altitude	TWM	TCM	PDM	Elevation	Density	Period	Age	DBH	1910–1960	1910–1960	1961–2011	1961–2011
Northern	Treeline	13.0 ± 1.7	−14.5 ± 4.1	19 ± 9	221 ± 13	360 ± 60	1728–2011	177.9 ± 7.7	39.8 ± 1.3	6.4 ± 1.9	0.108	6.4 ± 1.1	0.054
Central	Treeline	13.1 ± 1.2	1.1 ± 2.1	53 ± 29	448 ± 4	426 ± 26	1718–2011	206.6 ± 6.5	47.2 ± 1.3	5.1 ± 0.6	0.020	7.7 ± 1.8	0.111
Southern	Treeline	22.7 ± 1.1	4.4 ± 1.3	5 ± 9	2163 ± 6	290 ± 14	1750–2011	132.5 ± 6.3	47.4 ± 1.3	5.6 ± 1.1	0.021	11.5 ± 3.2	0.189
Southern	Medium				2015 ± 3	372 ± 98	1828–2011	124.6 ± 3.5	51.4 ± 1.7	8.3 ± 1.7	0.018	14.4 ± 2.1	0.079
Southern	Low				1879 ± 2	340 ± 80	1802–2011	126.6 ± 3.5	45.5 ± 1.5	5.3 ± 1.5	0.018	12.2 ± 2.0	0.033

using CDendro v7.4 and cofecha (Holmes, 1983; Larsson, 2003b) and a mean ring width value was calculated per tree and year using the two cores. To control for the geometric trend of decreasing ring width with increasing tree size, the ring width data were converted into increment of basal area (BAI) using the following formula:

$$\mathrm{BAI} = \pi\left(r_t^2 - r_{t-1}^2\right), \tag{1}$$

where r is the tree radius and t is the year of the ring formation. The resulting chronology included 60 trees for the period 1960–2011 and at least 40 trees per site for all the 20th century (Fig. S2).

Climate data

Monthly climatic data series since 1960 were obtained from the nearest meteorological stations for the three latitudinal areas: Kevo Subarctic Research Station (University of Turku), Braemar meteorological station (UK Met Office) and Narvaez meteorological station (Junta de Andalucía; Table S1). In order to reduce the number of variables used for modelling (see below) and to include general climatic trends, monthly data of mean temperatures were seasonally averaged: temperature of the autumn previous to the formation of the current ring (T_{aup}, September$_{(t-1)}$–November$_{(t-1)}$; winter (T_{wi}, December$_{(t-1)}$–February$_{(t)}$); spring (T_{sp}, March$_{(t)}$–May$_{(t)}$); summer (T_{su}, June$_{(t)}$–August$_{(t)}$); and autumn (T_{au}, September$_{(t)}$–November$_{(t)}$). To assign the same weight to all variables in the models, variables were normalized by subtracting the average temperature from each value for the period 1961–1990 and dividing by the standard deviation of the same period. Monthly rainfall was also aggregated into seasonal rainfall in the same way as for temperature values (P_{aup}, P_{wi}, P_{sp}, P_{su} and P_{au}) and standardized by means of the standardized precipitation index (SPI) following McKee *et al.* (1993). SPI shows mean zero and variance of one and represents a Z-score, that is the number of standard deviations above or below the mean of a certain event. The SPI allows the determination of the rarity of a drought or an anomalously wet event at a particular time scale and site (McKee *et al.*, 1993).

Data for the period 1901–2100 were obtained from CRU database (Climate Research Unit, University of East Anglia) for the three latitudinal sites. Forecasted data for the period 2012–2100 are projected according with the ECHAM5 General Circulation Model (Max-Planck Institute für Meteorologie) and A1B scenario from IPCC (2013). This scenario is based on a moderate increase of global population, economy and technology with a balanced use of resources and land-use, being among the most conservative predictions. Seasonal standardized temperature and precipitation indices were calculated for CRU data in the same way as for data from meteorological stations.

The three sites selected for this study across the latitudinal distribution of Scots pine have a strongly contrasted climate. Precipitation has been relatively stable at central and northern latitude sampling sites since 1900, but it has a greater interannual variability at the southern edge of the species (variance ±0.10 at northern, ±0.11 at central and ±0.25 mm at southern latitude, respectively; Fig. 1). Temperature had a stronger variability across sites than precipitation. We detected a colder period during the first half of the 20th century at the three sites, but warmer years have been recorded across the species' range since 1990. The three areas presented a positive trend of rising temperature during the past century, but was more steep during the last 50 years with mean yearly increases of 0.05 °C yr^{-1} for northern latitude for the 1960–2011 period (0.009 °C yr^{-1} for the 1910–1960 period), 0.02 °C yr^{-1} for central latitude (0.008 °C yr^{-1} for the 1910–1960 period) and 0.03 °C yr^{-1} for the southern edge (0.01 °C yr^{-1} for the 1910–1960 period; Fig. S3).

Climate predicted by the ECHAM5 A1B scenario forecast a generalized rise in mean annual temperature for the studied areas (northern 4.2 °C, central 2.4 °C and southern 4.6 °C), a total annual precipitation increase at northern and central latitude (48.6% and 39.2%, respectively) and a reduction at the southern edge (13.6%) when comparing the periods 1961–1990 with 2071–2100.

Data analysis

For modelling the BAI variation across latitudinal and altitudinal gradients, all trees from the same altitude or latitude were pooled together after checking that there were no outliers showing marked discrepancies in growth patterns (maximum $N = 60$ per altitude or latitude). In consequence, all the data shown throughout the text is expressed at site level ($n = 3$ for altitude or latitude). Following the procedure by González-Muñoz *et al.* (2014), for each site (altitudinal or latitudinal band), we first fitted the tree age at the year of ring formation using the most accurate function (linear, polynomial or sigmoidal) and kept the residuals. As radial growth strongly depends on tree age, this method allowed us to obtain an estimate of BAI without ontogenetic effects. After that, linear mixed-effects models were used to identify the effects of 10 climatic variables (T_{aup}, T_{wi}, T_{sp}, T_{su}, T_{au}, P_{aup}, P_{wi}, P_{sp}, P_{su} and P_{au}) on the residuals of the previous function, using climatic variables from meteorological stations for the period 1960–2011 (when instrumental climatic data are available for all sites) as fixed factors and tree as a random factor. Fitted models followed the equation:

$$Y_i = Xa_i + Zb + e_i,$$

where Y_i represents BAI residuals from the age model per year i; a and b are the vectors of fixed (seasonal climatic data) and random effects (tree identity) regression coefficients, respectively; X and Z are regression matrices of fixed and random effects, respectively; and e_i is the within-group error vector (Camarero *et al.*, 2016). Model selection was performed using backward stepwise regression to minimize the Akaike information criterion corrected for sample size (AIC_c). The final model was selected for each site as the one with the lowest number of variables among those with the lowest AIC_c (Burnham & Anderson, 2002). The use of standardized seasonal climatic averages instead of monthly data allowed the creation of more parsimonious models, while maintaining a reliable representation of climatic trends. Finally, first-order autocorrelations were included using a linear regression between the BAI of the previous year (*BAIp*) and the residuals of the climate-growth model. The selected models were run to forecast BAI of each site for the period 1902–2100, using as climatic source CRU data for the period 1902–2011 plus the

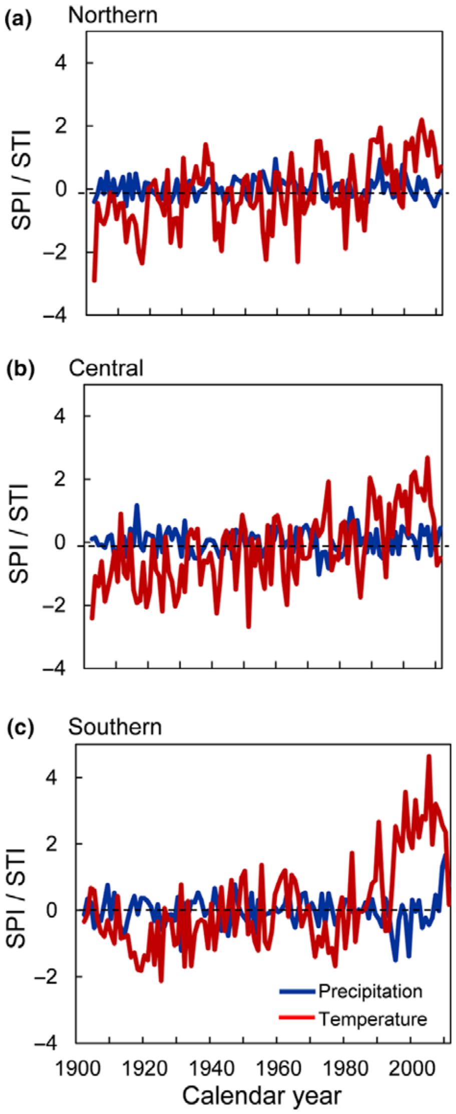

Fig. 1 Yearly variations in temperature and precipitation across the latitudinal gradient (northern: Kevo, Finland; central: Cairngorms, UK; southern: Sierra de Baza, Spain) for the 1902–2011 period. Standardized precipitation index (SPI, blue lines, black in print version) and standardized temperature index (STI, red lines, grey in print version) are normalized by subtracting the average temperature from each value for the period 1961–1990 and dividing by the standard deviation of the same period. Data from 1960 to 2011 obtained from Kevo Subarctic Research Station, Braemar meteorological station and Narvaez meteorological station for northern, central and southern sites, respectively. Data from 1902 to 1959 obtained from CRU (Climate Research Unit, University of East Anglia). [Colour figure can be viewed at wileyonlinelibrary.com]

forecast under the A1B scenario predicted by ECHAM5 for the period 2012–2100, also obtained from CRU. We simulated annual BAI of a group of 1000 individuals per site (either in latitude or in altitude) with initial ages between 5 and 100 years. Accordingly, the individual trees would be a maximum 298 years old at the end of the simulated period. All analyses were performed using the packages 'nlme' and 'mgcv' in R (R Core Team, 2015). Data are shown as mean ± SE throughout the text.

Results

Past growth

Across the latitudinal gradient, we found a contrasting pattern of growth in Scots pine, with BAI at treeline populations decreasing from south to north (Table 1; Fig. S4). All populations showed a positive growth trend during the last 50 years (1960–2011; Fig. S4a), although the slope was highest at the southern edge and lowest at the northern limit (northern: $R^2 = 0.57$, slope = 0.05, $P < 0.0001$; central: $R^2 = 0.81$, slope = 0.11, $P < 0.0001$; south: $R^2 = 0.66$, slope = 0.16, $P < 0.0001$). Across the altitudinal gradient at the southern limit of the distribution, medium-altitude populations presented a higher BAI than those at the high or low limits (treeline: 7.3 ± 0.3^{a} cm^2 yr^{-1}; medium: 9.9 ± 0.3^{b} cm^2 yr^{-1}; low: 7.5 ± 0.4^{a} cm^2 yr^{-1} for the 1900–1990 period; different letters denote significant differences after a post hoc test; Fig. S4). However, growth of lower populations showed a more marked growth decrease in response to especially dry years since the 1990s (such as 1998 and 2005) together with a lower mean BAI than at mid- or high altitude (treeline: 15.0 ± 0.3^{a} cm^2 yr^{-1}; medium: 15.7 ± 0.4^{a} cm^2 yr^{-1}; low: 12.5 ± 0.4^{b} cm^2 yr^{-1} for the 1991–2011 period). Apart from these altitudinal differences, a relatively stable growth trend was evident during the first half of the 20th century, followed by a steep growth increase since the 1950s (Fig. S4). A positive trend appeared during the last 50 years, but the slope of this trend decreased from high to low altitude (treeline: $R^2 = 0.66$, slope = 0.16, $P < 0.0001$; medium: $R^2 = 0.34$, slope = 0.09, $P < 0.0001$; low: $R^2 = 0.12$, slope = 0.05, $P = 0.01$). However, the majority of this growth increase occurred from 1950 to 1990, followed by no trend since then (Fig. S4).

Factors controlling growth

Growth was controlled by different factors across the distribution of Scots pine. The timing and strength of climatic variables affecting growth shifted with latitude and altitude, with earlier and stronger signals in lower sites, and the intensity of the effect of summer variables related to water availability decreasing with latitude (Tables 2 and 3). According to the selected models, temperature is the main factor driving growth at central and northern populations (Table 2). Selected models including climate, age and previous BAI explained between 84% and 88% of growth variability across sites (Fig. 2), with climatic variables as the most important factors (Table 3, Fig. S5).

Across the latitudinal gradient, summer temperature was the main factor positively affecting radial growth in Scots pine at the northern edge, although increased temperature during spring and the previous autumn, and higher precipitation during winter and spring also had a positive effect on growth. At central latitude, all temperature variables except that of summer of the year of ring formation positively affected tree growth. In addition, autumn precipitation also had a positive effect on radial growth. By contrast, precipitation exerted a stronger effect on growth at treeline populations from the southern edge of the species. Precipitation during summer was positively related with growth, whereas it had a negative effect during winter and spring. Additionally, higher winter temperature increased radial growth, and growth was reduced in case that higher temperature occurred during autumn.

Across the altitudinal gradient, temperature of spring and of previous autumn negatively affected tree growth at medium and low elevations. However, the effect of summer temperature differed across the altitudinal gradient, with a positive effect at medium altitude and negative effect at low sites (Table 3). Precipitation had a similar effect across elevations, with a positive effect during summer and negative effect during winter. Although significant, tree age had little effect on tree growth across the species' latitudinal and altitudinal distributions, explaining between 0.2% and 1.6% of the variance (Table 3). However, growth of the previous year explained between 9% and 16% of the variability of radial growth, with a positive relationship in all cases.

Forecasted growth

In response to the changes in climate forecasted by the ECHAM5 A1B scenario, our models predict a growth increase in treeline populations of Scots pine across the latitudinal gradient up to year 2100 (Fig. 3). At the start of the simulations, southern-edge populations present the highest BAI, and BAI is expected to continue rising up to 2060, when growth it becomes more stable ($R^2 = 0.79$, slope = 0.11 cm^2 yr^{-1}, $P < 0.0001$ for the period 2012–2100). Populations at central latitude present the higher responsiveness ($R^2 = 0.95$,

Table 2 Linear mixed models explaining the effect of climate on basal area increment (BAI) after accounting for ontogenetic effects for the different sites across the latitudinal and altitudinal gradients

Latitude	Altitude	Growth model	K	AIC$_c$	ΔAIC$_c$	Wi
Northern	Treeline	**$T_{aup} + T_{sp} + T_{su} + P_{wi} + P_{sp}$**	**7**	**13 280.3**	**0.0**	**55.5**
		$T_{aup} + T_{sp} + T_{su} + P_{wi} + P_{sp} + P_{au}$	8	13 281.6	1.3	29.2
		$T_{aup} + T_{sp} + T_{su} + P_{sp}$	6	13 283.1	2.8	13.5
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + P_{wi} + P_{sp} + P_{au}$	9	13 287.5	7.2	1.5
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + P_{aup} + P_{wi} + P_{sp} + P_{au}$	10	13 291.1	10.8	0.2
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + T_{au} + P_{aup} + P_{wi} + P_{sp} + P_{au}$	11	13 296.4	16.1	0.0
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + T_{au} + P_{aup} + P_{wi} + P_{sp} + P_{su} + P_{au}$	12	13 303.0	22.7	0.0
		Null model	2	13 456.5	176.2	0.0
Central	Treeline	**$T_{aup} + T_{wi} + T_{sp} + T_{au} + P_{au}$**	**7**	**15 232.0**	**0.0**	**47.2**
		$T_{aup} + T_{wi} + T_{sp} + T_{au} + P_{sp} + P_{au}$	8	15 233.1	1.2	26.4
		$T_{aup} + T_{sp} + T_{au} + P_{au}$	6	15 233.6	1.6	20.9
		$T_{aup} + T_{wi} + T_{sp} + T_{au} + P_{wi} + P_{sp} + P_{au}$	9	15 238.9	6.9	1.5
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + T_{au} + P_{wi} + P_{sp} + P_{au}$	10	15 245.1	13.1	0.1
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + T_{au} + P_{aup} + P_{wi} + P_{sp} + P_{au}$	11	15 251.9	19.9	0.0
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + T_{au} + P_{aup} + P_{wi} + P_{sp} + P_{su} + P_{au}$	12	15 258.6	26.6	0.0
		Null model	2	15 611.2	379.3	0.0
Southern	Treeline	**$T_{wi} + T_{au} + P_{wi} + P_{sp} + P_{su}$**	**7**	**17 599.9**	**0.0**	**91.7**
		$T_{wi} + T_{au} + P_{aup} + P_{wi} + P_{sp} + P_{su}$	8	17 605.3	5.4	6.3
		$T_{wi} + P_{wi} + P_{sp} + P_{su}$	6	17 608.3	8.4	1.4
		$T_{wi} + T_{su} + T_{au} + P_{aup} + P_{wi} + P_{sp} + P_{su}$	9	17 610.1	10.1	0.6
		$T_{wi} + T_{su} + T_{au} + P_{aup} + P_{wi} + P_{sp} + P_{su} + P_{au}$	10	17 617.0	17.0	0.0
		$T_{aup} + T_{wi} + T_{su} + T_{au} + P_{aup} + P_{wi} + P_{sp} + P_{su} + P_{au}$	11	17 623.2	23.3	0.0
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + T_{au} + P_{aup} + P_{wi} + P_{sp} + P_{su} + P_{au}$	12	17 628.9	28.9	0.0
		Null model	2	17 740.5	140.6	0.0
Southern	Medium	**$T_{aup} + T_{wi} + T_{sp} + T_{su} + T_{au} + P_{wi} + P_{su}$**	**9**	**17 278.9**	**0.0**	**44.8**
		$T_{aup} + T_{wi} + T_{sp} + T_{au} + P_{wi} + P_{su}$	8	17 279.2	0.3	37.9
		$T_{aup} + T_{wi} + T_{sp} + P_{wi} + P_{su}$	7	17 282.0	3.1	9.4
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + T_{au} + P_{wi} + P_{sp} + P_{su}$	10	17 282.4	3.6	7.5
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + T_{au} + P_{aup} + P_{wi} + P_{sp} + P_{su}$	11	17 289.1	10.2	0.3
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + T_{au} + P_{aup} + P_{wi} + P_{sp} + P_{su} + P_{au}$	12	17 296.5	17.6	0.0
		Null model	2	17 370.7	91.8	0.0
Southern	Low	**$T_{aup} + T_{wi} + T_{sp} + T_{su} + P_{wi} + P_{su}$**	**8**	**17 284.3**	**0.0**	**71.7**
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + P_{aup} + P_{wi} + P_{su}$	9	17 287.6	3.3	14.0
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + P_{aup} + P_{wi} + P_{sp} + P_{su}$	10	17 287.8	3.5	12.5
		$T_{aup} + T_{wi} + T_{sp} + P_{wi} + P_{su}$	7	17 293.1	8.8	0.9
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + P_{aup} + P_{wi} + P_{sp} + P_{su} + P_{au}$	11	17 293.1	8.8	0.9
		$T_{aup} + T_{wi} + T_{sp} + T_{su} + T_{au} + P_{aup} + P_{wi} + P_{sp} + P_{su} + P_{au}$	12	17 299.6	15.3	0.0
		Null model	2	17 649.3	365.0	0.0

Selected models are highlighted in bold. The null model considered the effect of BAI as a constant. The best models were selected on the basis of the Akaike information criteria corrected by sample size (AIC$_c$). K represents the number of variables included in the model plus constant and error terms, ΔAIC$_c$ is the difference in AIC respect the best model, and Wi is the relative probability to be the best model for the observed data. T_{aup}, T_{wi}, T_{sp}, T_{su} and T_{au} are standardized temperatures of previous autumn and winter, spring, summer and autumn of current year, respectively. Similar names for standardized precipitation values (P_{aup}, P_{wi}, P_{sp}, P_{su}, P_{au}).

slope = 0.23 cm^2 yr^{-1}, $P < 0.0001$), with a steep BAI increase from 2040 onwards, and reaching similar values to southern populations by the end of the 21st century. Finally, trees at the northernmost distribution of the species are also expected to increase growth ($R^2 = 0.97$, slope = 0.16 cm^2 yr^{-1}, $P < 0.0001$), but at a lower rate that at central distribution. Across the altitudinal gradient, trees at mid-altitude follow a similar growth trend up to year 2100 as at treeline ($R^2 = 0.60$, slope = 0.08 cm^2 yr^{-1}, $P < 0.0001$). However, trees at the lowest limit follow a completely different pattern, with BAI decreasing after year 2030 ($R^2 = 0.54$, slope = ×0.10 cm^2 yr^{-1}, $P < 0.0001$ for the 2012–2100 period).

Table 3 Regression coefficients of the final full model explaining the basal area increment

Latitude	Altitude	Variable	Value	SE	VE
Northern	Treeline	T_{aup}	0.178	0.039	9.1
		T_{sp}	0.228	0.043	11.7
		T_{su}	0.489	0.049	25.1
		P_{wi}	0.245	0.084	12.6
		P_{sp}	0.269	0.064	13.8
		BAIp	0.686	0.011	15.5
		Age	138.988	3.338	0.3
		Total VE (%)			88.0
Central	Treeline	T_{aup}	0.338	0.035	18.5
		T_{wi}	0.155	0.054	8.5
		T_{sp}	0.351	0.044	19.2
		T_{au}	0.377	0.034	20.6
		P_{au}	0.166	0.047	9.1
		BAIp	0.616	0.011	12.2
		Age	186.532	3.767	0.2
		Total VE (%)			88.3
Southern	Treeline	T_{wi}	0.391	0.063	15.5
		T_{au}	−0.246	0.065	9.8
		P_{wi}	−0.344	0.046	13.7
		P_{sp}	−0.460	0.059	18.3
		P_{su}	0.273	0.054	10.8
		BAIp	0.646	0.011	16.4
		Age	291.521	24.368	1.6
		Total VE (%)			86.0
Southern	Medium	T_{aup}	−0.330	0.072	10.9
		T_{wi}	0.420	0.070	13.8
		T_{sp}	−0.448	0.069	14.8
		T_{su}	0.201	0.080	6.6
		T_{au}	−0.237	0.067	7.8
		P_{wi}	−0.296	0.047	9.7
		P_{su}	0.306	0.058	10.1
		BAIp	0.550	0.012	10.3
		Age	248.602	6.823	1.4
		Total VE (%)			85.3
Southern	Low	T_{aup}	−0.318	0.071	9.7
		T_{wi}	0.485	0.067	14.8
		T_{sp}	−0.763	0.067	23.3
		T_{su}	−0.292	0.076	8.9
		P_{wi}	−0.233	0.043	7.1
		P_{su}	0.357	0.056	10.9
		BAIp	0.523	0.013	9.3
		Age	268.110	5.851	0.3
		Total VE (%)			84.3

Value, standard error (SE) and explained variance (VE, %) are indicated for each variable (see Table 2 for variable names).

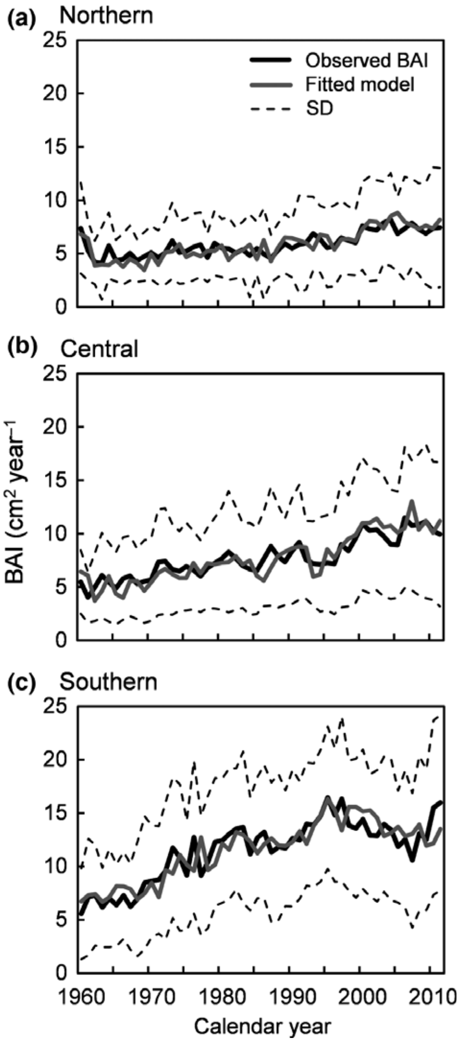

Fig. 2 Mean basal area increment (BAI, black line) ±SD (dashed lines) of Scots pine sites at treeline across its latitudinal distribution gradient during the 1960–2011 period (period with instrumental climate data availability). Grey line represents the predicted growth by the full model based on age, climate and previous BAI.

Discussion

Latitudinal and altitudinal variation in growth

Ecological theory predicts distribution shifts in woody species as the climate warms. Range expansion to higher altitudes and latitudes, as well as increasing population density, is expected following enhanced growth and reproduction at upper elevation and poleward range limits (Harsch *et al.*, 2009). Decreasing growth, as well as declining recruitment, is expected at the rear range edge (Walther *et al.*, 2002; Linares & Tíscar, 2011; Candel-Pérez *et al.*, 2012). Case studies demonstrate that such processes are underway for a wide variety of species (Walther *et al.*, 2002; Harsch *et al.*, 2009), although widespread growth decline and distributional shifts in some range edges are not necessarily as straightforward as theoretical predictions (Cavin & Jump, 2017).

Results presented here show positive growth trends in treeline populations of Scots pine across the

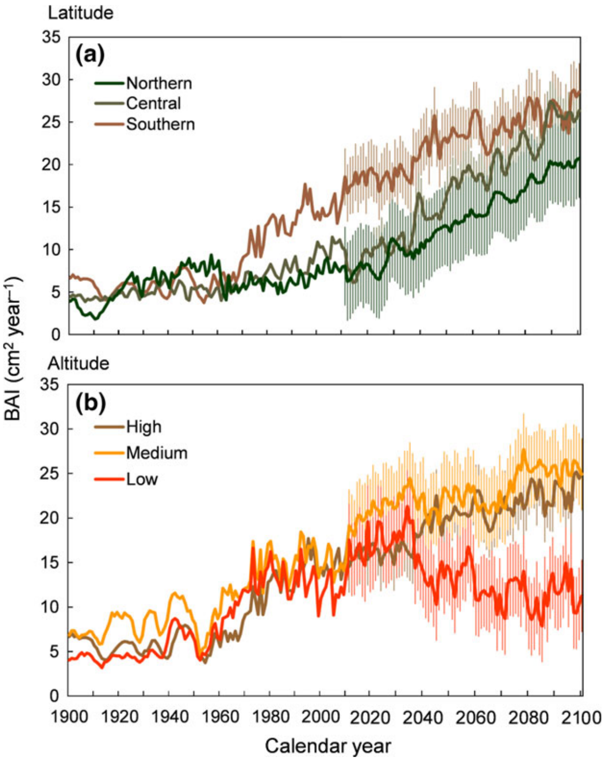

Fig. 3 Mean basal area increment (BAI) per site for the different Scots pine sites across the latitudinal (top panel) and altitudinal (bottom panel) gradients. Values for the 1900–2011 series are the site means of observed individual BAI ($N = 60$), whereas for the 2012–2100 period are the predictions for the full model using climatic data predicted by the General Circulation Models, scenario ECHAM A2 (IPCC 2013). Vertical lines represent ±SD for the model predictions based on the simulation of 1000 trees.

complete latitudinal distribution during the last 50 years (Table 1). Although this trend was consistent, there were important differences in responsiveness (different rates) among sites. Growth increase was highest at the southernmost limit of the species and lowest at the northern edge, which overall agrees with the trend of increasing temperature detected in these areas (Fig. S3; Galván *et al.*, 2015). This generalized growth increase in response to increasing temperature is consistent across the latitudinal gradient as treeline populations usually are not usually water-limited during the growing period. Although long-term changes in temperature alone are not able to explain the geographical growth trends, they can be also explained by the absolute values of temperature, decreasing as latitude increases. This positive growth trend is consistent with the pattern of increased reproductive investment and recruitment already recorded from the same populations (Hofgaard *et al.*, 2013; Matías & Jump, 2015). Together, this evidence points to improved population performance in the absence of interactions with other factors such as pest and pathogen abundance. However, other nonclimatic factors such as changing management practices could be acting simultaneously, potentially contributing to the strong increase of BAI at the southern site since 1960.

Regarding the long-term persistence of relict southernmost Scots pine populations, our results illustrate the variability in plant responses to different climatic drivers along altitudinal gradients (Linares & Tíscar, 2011; Candel-Pérez *et al.*, 2012; Herrero *et al.*, 2013; Galván *et al.*, 2015; Arzac *et al.*, 2016). While the temperature response differed with altitude, a positive growth response to summer rainfall was observed along the whole altitudinal gradient of southernmost Scots pine populations, suggesting the reactivation of cambial activity in response to summer storms. However, while populations at the southernmost range edge appear buffered against rising drought stress to some degree, their recovery could be limited when severe drought impacts occur (Sánchez-Salguero *et al.*, 2015; Cavin & Jump, 2017).

The differential latitudinal and altitudinal growth pattern discussed above relies on different factors controlling growth across the distribution range. Regarding climatic variables, *P. sylvestris* growth is subject to temperature as the most important limiting factor at northern and central latitude (Antonova & Stasova, 1993; Heikkinen *et al.*, 2002; Tuovinen, 2005; Kullman, 2007; Helama *et al.*, 2011; Moir *et al.*, 2011). Increased performance in the central and northern latitudinal sites, where climatic conditions are less stressful (Matías & Jump, 2015), was accompanied by positive growth trends and higher growth rates at the upper elevations of the drought-limited southernmost edge. However, rising temperature during previous autumn, spring and summer imposes negative effects at the low southern edge. Despite the general positive effect of winter temperature, seasonal variables affect this species differentially through the altitudinal gradient, with more negative effects of high temperature as elevation diminishes (Linares & Tíscar, 2011; Candel-Pérez *et al.*, 2012). This finding is in concordance with previous studies indicating that southern lowland populations are more sensitive to increased temperature (Herrero *et al.*, 2013; Sánchez-Salguero *et al.*, 2015) and with impacts on demographic processes already detected (Matías & Jump, 2015).

The effect of precipitation on BAI also differs across the latitudinal and altitudinal gradients. Although precipitation has been traditionally considered to have little effect on tree growth at high latitudes, we detect high importance of winter and spring precipitation at the northern edge (26.4% of the variance explained by precipitation). Higher winter and spring precipitation in boreal forests means higher snow cover, which provides thermoinsulation of roots (Helama *et al.*, 2011), and can prevent the premature yellowing of pine needles (Jalkanen, 1993), translating into a higher radial growth (Tuovinen, 2005). However, precipitation gains in importance at the southern limit of the species (see also Swidrak *et al.*, 2011). Winter precipitation negatively affects tree growth along the studied altitudinal gradient (and during spring at southern treeline). This negative correlation of growth with precipitation might be also explained by the association between precipitation and cloudiness, which reduces the photosynthetic activity and carbon reserves for growth (Gimeno *et al.*, 2012). Higher precipitation during summer enhances tree growth consistently across altitudes (Candel-Pérez *et al.*, 2012; Herrero *et al.*, 2013; Sánchez-Salguero *et al.*, 2015). On the contrary, extended droughts usually lead to reduced growth and, in the most severe cases, to hydraulic failure and/or carbon starvation and the consequent tree death (Martínez-Vilalta & Piñol, 2002; Galiano *et al.*, 2011; Allen *et al.*, 2015).

Forecasted growth for the 21st century

Across the latitudinal gradient, treeline populations are expected to increase BAI up to the end of the present century, although not at the same rate. Current growth is highest at the southern edge, and it will continue rising up to year 2050, when BAI becomes more stable. This stabilization might represent the maximum growth potential of the species, with similar values to those currently found in areas where temperature and water availability are not limiting tree growth (Michelot *et al.*, 2012; Viguera *et al.*, 2013; Zang & Rothe, 2013), and maintaining it until year 2100. Central-latitude populations are expected to present the highest response to the predicted climate alterations, reaching similar values to those of the southern populations by 2100. Consequently, Scots pine populations currently located at treeline at southern and central latitudes will have a similar BAI by the end of the present century, being close to the maximum potential growth of the species (Michelot *et al.*, 2012; Viguera *et al.*, 2013; Zang & Rothe, 2013).

These findings have two main implications: on one hand, current treelines are expected to support healthy populations with higher growth rates and even become denser if there are no recruitment limitations (Camarero & Gutiérrez, 2004). On the other hand, treeline populations have the potential to expand their limits upslope in those areas where topography and soil conditions allow it due to the amelioration of climatic limitations (assuming favourable conditions for establishment; Körner, 2012; Rabasa *et al.*, 2013). Finally, populations located at the northern distribution limit are expected to increase their growth during the 21st century, although at a lower rate than at the other latitudes (Hickler *et al.*, 2012). This implies that northern populations have the potential to continue increasing their growth after 2100, which does not seem to be the case at central and southern latitude.

Across the altitudinal distribution at the southern edge, treeline and mid-elevation populations follow a similar growth trend, with BAI increase during the first part of the century and a stabilized period during the second half (Fig. 3). This finding indicates that the scenario simulated by our model predicts the persistence of these southernmost populations, at least at medium and high elevations. However, a completely different pattern appeared for lowland populations. Our model predicted a short phase of growth increase during the next 10–20 years, but a consistent declining trend is predicted up to the end of the century, which is a strongly negative indication for population persistence (Pedersen, 1998; Jump *et al.*, 2006; Galiano *et al.*, 2011). According to our results, the growth increase predicted for medium and high altitude and the declining growth trends at low elevations, linked with the current mortality trends already detected in the field (Matías & Jump, 2015), might lead to a range migration upslope where physical conditions allow it, or to range contraction from low altitude areas of the southern range edge of the species during the 21st century.

Although geographical variations in climatic sensitivity were evident in our study (see also Martínez-Vilalta *et al.*, 2009), the timing of the climatic response may also shift over time as a response to changing climatic conditions (Lebourgeois *et al.*, 2012; Galván *et al.*, 2015). This possibility could be a shortcoming of our modelling approach, as we assume steady climate sensitivity over the 21st century when forecasting tree growth responses. Although this issue has not been accounted for in this paper, it might be expected that global warming during the past and current centuries may be increasing temperature sensitivity as well as the effect of water limitation (Andreu *et al.*, 2007; Camarero *et al.*, 2015). Furthermore, increased frequency and severity of drought events in future climates may be critical (Giorgi & Lionello, 2008), and that the combined effect drought increase and heat waves (hotter drought, Allen *et al.*, 2015) might induce physiological tipping points, likely resulting in unexpected and long-lasting reductions in growth and subsequent tree mortality (Matías *et al.*, 2012; Cavin *et al.*, 2013). Consequently, our results regarding growth stability at the upper elevations of southern *P. sylvestris* forests over the 21st-century climate change might not be assumed to continue indefinitely.

By simulating future tree growth based on current climate-growth relationships and predicted climate changes, we identified contrasting growth responses along the altitudinal gradient at the southernmost *P. sylvestris* range edge, with stable growth at the mid- to upper-elevation belts but high susceptibility to decline at low elevation. Across a latitudinal gradient, core and northern *P. sylvestris* populations show a sustained temperature-related increase in growth, although water availability also affects overall growth patterns at the northern range edge. While we simulated a conservative climatic scenario, our models forecast a clear increase in radial growth at treeline populations throughout the distribution of the species up to the end of the present century, which would likely lead to upland and northward expansions through the species' distribution. However, these predictions should be interpreted with caution, as other factors such as limiting soil conditions, extreme climatic events or biotic interactions can strongly influence demographic responses. Our results also imply that rear edge populations are able to persist at medium or high elevations but, after an initial growth increase, a rapid decline is expected for those populations located at low elevations. This lowland decline might be even more important than described here when extreme climatic events are considered or if tipping points are reached. The results we present stress the importance of including geographical variability in growth response to improve resolution in predictive models. Our methodology also highlights the value of the use of past responses to climate based on reliable growth data for prediction of future population dynamics under climate change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1 European distribution of *Pinus sylvestris* (source Euforgen; http://www.euforgen.org) with the sampled locations across the latitudinal distribution within the red circles (northern: Kevo, Finland; central: Cairngorms, UK; southern: Sierra de Baza, Spain).
Fig. S2 Number of trees sampled for the period 1900–2011 across the latitudinal (top panel) and altitudinal (down panel) gradients.
Fig. S3 Mean yearly temperature variations during the 1960–2011 period at the three latitudinal study areas: southern (Sierra de Baza, Spain; red dots), central (Cairngorms, UK; green dots) and northern (Kevo, Finland; blue dots). Dashed lines indicate temporal trends.
Fig. S4 Mean basal area increment of Scots pine populations across the latitudinal (top panel) and altitudinal (bottom panel) gradients measured in this study. Data of the two populations per site are pooled.
Fig. S5 Residual adjustment of the different models selected across the latitudinal gradient.
Table S1 Main characteristics: location, latitude, longitude, elevation in m a.s.l., and horizontal (H. dist.) and vertical (V. dist.) distances to sampling sites in m, of the meteorological stations used as data source to build the growth-climate models.