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1 **Title: Contrasting growth forecasts across the geographical range of Scots pine due to**

2 **altitudinal and latitudinal differences in climatic sensitivity.**

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5 Running head: Forecasting Scots pine growth under climate change

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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 rear edge of the distribution (treeline, central 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 stabilises. The highest responsiveness appeared at central latitudes, and moderate growth increase is projected at the northern limit. Contrastingly, the model forecasted growth decline 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

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variability into predictive models for an accurate prediction of species dynamics as climate changes.

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 and 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).

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).

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74 However, precipitation may constrain growth throughout an altitudinal gradient, as is

75 sometimes the case in Mediterranean mountains (Arzac et al., 2016; Camarero et al., 2015;

76 Sánchez-Salguero et al., 2015). Nonetheless, climate effects on growth are not only

77 subjected to regional climate, but also dependent on local conditions or ontogenetic

78 changes such as changes in tree age and size (Voelker, 2011). For example, older trees are

79 usually more susceptible to drought stress than younger adults are, usually related to

80 hydraulic limitations affecting photosynthesis, water-use efficiency and carbon allocation

81 within the tree (Magnani et al., 2000; Martínez-Vilalta & Piñol, 2002; Ryan et al., 2006;

82 Knapp & Soulé 2011). Thus, it is important to explicitly account for factors other than

83 climate such as ontogeny or resource accumulation when predicting the likely

84 consequences of future climate on tree growth. However, species distribution models

85 aimed at predicting future species dynamics usually consider the response of a species to

86 climate as constant through its distribution range (Araújo & Luoto, 2007). Although this

87 may be true for small-ranged species, the high variability of genotypes and climatic

88 conditions make this assumption unrealistic for widely distributed species (Jyske et al.,

89 2014; Matías & Jump, 2014; Matías et al., 2016). Consequently, detailed information about

90 local responses to past changes in climate and its variation through tree ontogeny is

91 urgently needed to predict future species responses under global climate change

92 (Benavides et al., 2013; Mina et al. 2016).

93

94 Scots pine (*Pinus sylvestris* L.) is one the most abundant tree species of the Holarctic, with

95 a distribution ranging from the Arctic to the Mediterranean (Matías & Jump, 2012). The

96 wide distribution of this species implies a broad range of climatic conditions where it is

97 able to survive, from the severe cold winters of northern Fennoscandia to the

98 Mediterranean climate of southern Spain; and from the wet, oceanic climate of the west

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99   coast of Scotland to the dry continental climate of central Europe and Asia (Carlisle and

100   Brown, 1968). Thus, it is logical to expect that different climatic factors are influencing

101   growth across the distribution range of the species (Kullman, 2007; Andreu et al., 2007;

102   Candel-Pérez et al., 2012; Sánchez-Salguero et al., 2015), making this species a valuable

103   study system to evaluate local responses to environmental alterations.

104

105   We sought to model future growth trends across the latitudinal and altitudinal distribution

106   of Scots pine under future climates. We quantified radial growth of Scots pine populations

107   across a latitudinal gradient covering the northernmost and southernmost regions of the

108   species' western distribution and across an altitudinal gradient from the treeline to the

109   lower limit at the southernmost range edge of the species. We analysed past growth

110   patterns at range limits across altitudinal and latitudinal gradients and identified the

111   climatic and ontogenetic variables controlling tree growth at range edges. These

112   fundamental data were then used to construct a predictive model to understand likely

113   consequences of forecasted climate on tree growth at the species' range edges.

114

115   **Materials and Methods**

116   *Field sites*

117   Scots pine populations were selected at locations along the altitudinal and latitudinal

118   distribution of the species. The altitudinal gradient was located at the southernmost limit of

119   this species in the Sierra de Baza, SE Spain (Table 1). Two different populations were

120   selected (mean size 3.9 ± 0.3 ha) in each of the three altitudinal bands: lowermost limit,

121   medium altitudinal distribution and upper (treeline), covering the whole altitudinal range.

122   For the comparison across the latitudinal distribution range, we selected treeline

123   populations across Western Europe (Fig. S1). We used the same populations at the upper

124 limit from the altitudinal range as the southernmost populations and two additional

125 populations at central latitude (Cairngorms, UK), and two close to the northern limit of the

126 distribution (Kevo, Finland), making a total of 10 study populations (see Matías and Jump

127 2015 for more details). The altitudinal gradient was not replicated in latitude since

128 altitudinal distribution diminishes with increasing latitude, presenting a very narrow

129 altitudinal range at the northern limit of the focal species. In order to maintain

130 comparability across the study areas, we selected the different populations maintaining

131 orientation, slope and soil type as constant as possible. To minimise human management

132 impacts as far as is practicable, we selected all population within protected areas: Sierra de

133 Baza Natural Park, Cairngorms National Park, and Kevo Strict Nature Reserve.

134

135 *Sampling and width measurements*

136 Between May and July 2012, 30 trees per population were randomly selected for

137 dendrochronological study. Sampling was performed following standard

138 dendrochronological methods (Fritts, 1976). For each sampled tree, two cores were taken

139 using a 4.3 mm increment borer and diameter was recorded at breast height (DBH, 1.3 m

140 above ground level). Samples were then stored and air-dried in paper straws. The wood

141 core samples were mounted, polished with successively finer grit sand-paper until rings

142 were clearly visible, scanned at 1600 dpi and then measured with an accuracy of 0.001 mm

143 using CooRecorder v7.4 (Larsson 2003a). We examined samples to detect characteristic

144 rings, and cores were cross-dated per population using CDendro v7.4 and COFECHA

145 (Holmes 1983; Larsson 2003b) and a mean ring width value was calculated per tree and

146 year using the two cores. In order to control for the geometric trend of decreasing ring

147 width with increasing tree size, the ring width data were converted into increment of basal

148 area (BAI) using the following formula:

149

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

151

152   where r is the tree radius and t is the year of the ring formation. The resulting chronology

153   included at least 40 trees per site for all the 20th Century (Fig. S2).

154

155   *Climate data*

156   Monthly climatic data series since 1960 were obtained from the nearest meteorological

157   stations for the three latitudinal areas: Kevo Subarctic Research Station (University of

158   Turku), Braemar meteorological station (UK Met Office) and Narvaez meteorological

159   station (Junta de Andalucía) (Table S1). In order to reduce the number of variables used for

160   modelling (see below) and to include general climatic trends, monthly data of mean

161   temperatures were seasonally averaged: temperature of the autumn previous to the

162   formation of the current ring (T_{aup}, September$_{(t-1)}$–November$_{(t-1)}$; winter (T_{wi}, December$_{(t-1)}$

163    $_{1)}$–February$_{(t)}$); spring (T_{sp}, March$_{(t)}$–May$_{(t)}$); summer (T_{su}, June$_{(t)}$–August$_{(t)}$); and autumn

164   (T_{au}, September$_{(t)}$–November$_{(t)}$). To assign the same weight to all variables in the models,

165   variables were normalized by subtracting the average temperature from each value for the

166   period 1961–1990 and dividing by the standard deviation of the same period. Monthly

167   rainfall was also aggregated into seasonal rainfall in the same way as for temperature

168   values (P_{aup}, P_{wi}, P_{sp}, P_{su} and P_{au}) and standardised by means of the Standardised

169   Precipitation Index (SPI) following McKee et al. (1993). SPI shows mean zero and

170   variance of one and represents a Z-score, i.e. the number of standard deviations above or

171   below the mean of a certain event. The SPI allows the determination of the rarity of a

172   drought or an anomalously wet event at a particular time scale and site (McKee et al.

173   1993).

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174

175   Data for the period 1901-2100 were obtained from CRU database (Climate Research Unit,

176   University of East Anglia) for the three latitudinal sites. Forecasted data for the period

177   2012-2100 are projected according with the ECHAM5 General Circulation Model (Max-

178   Planck Institute für Meteorologie) and A1B scenario from IPCC (2013). This scenario is

179   based on a moderate increase of global population, economy and technology with a

180   balanced use of resources and land-use, being among the most conservative predictions.

181   Seasonal standardised temperature and precipitation indices were calculated for projected

182   data in the same way as for past climate.

183

184   The three sites selected for this study across the latitudinal distribution of Scots pine have a

185   strongly contrasted climate. Precipitation has been relatively stable at central and northern

186   latitude sampling sites since 1900, but it has a greater inter-annual variability at the

187   southern edge of the species (variance ± 0.10 at northern, ± 0.11 at central and ± 0.25 mm

188   at southern latitude, respectively; Fig. 1). Temperature had a stronger variability across

189   sites than precipitation. We detected a colder period during the first half of the 20th Century

190   at the three sites, but warmer years have been recorded across the species' range since

191   1990. The three areas presented a positive trend of rising temperature during the past

192   century, but was more steep during the last 50 years with mean yearly increases of 0.05 °C

193   year^{-1} for northern latitude for the 1960-2011 period (0.009 °C year^{-1} for the 1910-1960

194   period), 0.02 °C year^{-1} for central latitude (0.008 °C year^{-1} for the 1910-1960 period) and

195   0.03 °C year^{-1} for the southern edge (0.01 °C year^{-1} for the 1910-1960 period; Fig. S3).

196

197   Climate predicted by the ECHAM5 A1B scenario forecast a generalised rise in mean

198   annual temperature for the studied areas (northern 4.2 °C, central 2.4 °C and southern 4.6

8

199 °C), a total annual precipitation increase at northern and central latitude (48.6 % and 39.2

200 %, respectively) and a reduction at the southern edge (13.6 %) when comparing the

201 periods 1961-1990 with 2071-2100.

202

203 *Data analysis*

204 For modelling the BAI variation across latitudinal and altitudinal gradients, all trees from

205 the same altitude or latitude were pooled together after checking that there were no outliers

206 showing marked discrepancies in growth patterns (N = 60 per altitude or latitude).

207 Following the procedure by González-Muñoz et al. (2014), for each site (altitudinal or

208 latitudinal band) we first fitted the tree age at the year of ring formation using the most

209 accurate function (linear, polynomial or sigmoidal) and kept the residuals. As radial growth

210 strongly depends on tree age, this method allowed us to obtain an estimate of BAI without

211 ontogenetic effects. After that, linear mixed-effects models were used to identify the

212 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

213 residuals of the previous function, using climatic variables for the period 1960-2011 (when

214 instrumental climatic data are available for all sites) as fixed factors and tree as a random

215 factor. Fitted models followed the equation:

216 $$Y_i = Xa_i + Zb + e_i$$

217 where Y_i represents BAI residuals from the age model per year i; a and b are the vectors of

218 fixed (seasonal climatic data) and random effects (tree identity) regression coefficients,

219 respectively; X and Z are regression matrices of fixed and random effects, respectively; and

220 e_i is the within-group error vector (Camarero et al. 2016). Model selection was performed

221 using backward stepwise regression to minimise the Akaike Information Criterion

222 corrected for sample size (AIC_c). The final model was selected for each site as the one with

223 the lowest number of variables among those with the lowest AIC_c (Burnham & Anderson

9

224 2002). The use of standardised seasonal climatic averages instead of monthly data allowed

225 the creation of more parsimonious models, whilst maintaining a reliable representation of

226 climatic trends. Finally, first order autocorrelations were included using a linear regression

227 between the BAI of the previous year (*BAIp*) and the residuals of the climate-growth

228 model. The selected models were run to forecast BAI of each site for the period 1902-

229 2100, using as climatic source CRU data for the period 1902-2011 plus the forecast under

230 the A1B scenario predicted by ECHAM5 for the period 2012-2100. We simulated annual

231 BAI of a group of 1000 individuals per site (either in latitude or in altitude) with initial

232 ages between 5 and 100 years. Accordingly, the individual trees would be a maximum 298

233 years old at the end of the simulated period. All analyses were performed using the

234 packages "nlme" and "mgcv" in R (R Core Team, 2015). Data are shown as mean $\pm$ SE

235 throughout the text.

236

237 **Results**

238 *Past growth*

239 Across the latitudinal gradient we found a contrasting pattern of growth in Scots pine, with

240 BAI at treeline populations decreasing from south to north (Table 1; Fig. S4). All

241 populations showed a positive growth trend during the last 50 years (1960-2011; Fig. S4a),

242 although the slope was highest at the southern edge and lowest at the northern limit

243 (northern: $R^2 = 0.57$, slope = 0.05, $P < 0.0001$; central: $R^2 = 0.81$, slope = 0.11, $P <$

244 0.0001; south: $R^2 = 0.66$, slope = 0.16, $P < 0.0001$). Across the altitudinal gradient at the

245 southern limit of the distribution, medium-altitude populations presented a higher BAI than

246 those at the high or low limits (treeline: 7.3 ± 0.3^a cm^2 year^{-1}; medium: 9.9 ± 0.3^b cm^2 year^{-}

247 ^{1}; low: 7.5 ± 0.4^a cm^2 year^{-1} for the 1900-1990 period; different letters denote significant

248 differences after a post-hoc test; Fig. S4). However, growth of lower populations showed a

10

249   more marked growth decrease in response to especially dry years since the 1990s (such as

250   1998 and 2005) together with a lower mean BAI than at mid or high altitude (treeline: 15.0

251    $\pm$ 0.3^a cm^2 year^{-1}; medium: 15.7 $\pm$ 0.4^a cm^2 year^{-1}; low: 12.5 $\pm$ 0.4^b cm^2 year^{-1} for the 1991-

252   2011 period). Apart from these altitudinal differences, a relatively stable growth trend was

253   evident during the first half of the 20th Century, followed by a steep growth increase since

254   the 1950s (Fig. S4). A positive trend appeared during the last 50 years, but the slope of this

255   trend decreased from high to low altitude (treeline: R^2 = 0.66, slope = 0.16, P < 0.0001;

256   medium: R^2 = 0.34, slope = 0.09, P < 0.0001; low: R^2 = 0.12, slope = 0.05, P = 0.01).

257   However, the majority of this growth increase occurred from 1950 to 1990, followed by an

258   almost steady trend since then (Fig. S4).

259

260   *Factors controlling growth*

261   Growth was controlled by different factors across the distribution of Scots pine. The timing

262   and strength of climatic variables affecting growth shifted with latitude and altitude, with

263   earlier and stronger signals in lower sites, and the intensity of the effect of summer

264   variables related to water availability decreasing with latitude (Tables 2, 3). According to

265   the selected models, temperature is the main factor driving growth at central and northern

266   populations (Table 2). Selected models including climate, age and previous BAI explained

267   between 84 % and 88 % of growth variability across sites (Fig. 2), with climatic variables

268   as the most important factors (Table 3; Fig. S5).

269

270   Across the latitudinal gradient, summer temperature was the main factor positively

271   affecting radial growth in Scots pine at the northern edge, although increased temperature

272   during spring and the previous autumn, and higher precipitation during winter and spring

273   also had a positive effect on growth. At central latitude, all temperature variables except

11

274   that of summer of the year of ring formation positively affected tree growth. In addition,

275   autumn precipitation also had a positive effect on radial growth. By contrast, precipitation

276   exerted a stronger effect on growth at treeline populations from the southern edge of the

277   species. Precipitation during summer was positively related with growth, whereas it had a

278   negative effect during winter and spring. Additionally, higher winter temperature increased

279   radial growth, and growth was reduced in case that higher temperature occurred during

280   autumn.

281

282   Across the altitudinal gradient, temperature of spring and of previous autumn negatively

283   affected tree growth at medium and low elevations. However, the effect of summer

284   temperature differed across the altitudinal gradient, with a positive effect at medium

285   altitude and negative effect at low sites (Table 3). Precipitation had a similar effect across

286   elevations, with a positive effect during summer and negative effect during winter.

287   Although significant, tree age had little effect on tree growth across the species' latitudinal

288   and altitudinal distributions, explaining between 0.2 % and 1.6 % of the variance (Table 3).

289   However, growth of the previous year explained between 9 % and 16 % of the variability

290   of radial growth, with a positive relationship in all cases.

291

292   *Forecasted growth*

293   In response to the changes in climate forecasted by the ECHAM5 A1B scenario, our

294   models predict a growth increase in treeline populations of Scots pine across the latitudinal

295   gradient up to year 2100 (Fig. 3). At the start of the simulations, southern-edge populations

296   present the highest BAI, and BAI is expected to continue rising up to 2060, when growth it

297   becomes more stable ($R^2 = 0.79$, slope $= 0.11$ cm^2 year^{-1}, $P < 0.0001$ for the period 2012-

298   2100). Populations at central latitude present the higher responsiveness ($R^2 = 0.95$, slope $=$

299   $0.23 \text{ cm}^2 \text{ year}^{-1}$, $P < 0.0001$), with a steep BAI increase from 2040 onwards, and reaching

300   similar values to southern populations by the end of the 21$^{\text{st}}$ Century. Finally, trees at the

301   northernmost distribution of the species are also expected to increase growth ($R^2 = 0.97$,

302   slope $= 0.16 \text{ cm}^2 \text{ year}^{-1}$, $P < 0.0001$), but at a lower rate that at central distribution. Across

303   the altitudinal gradient, trees at mid altitude follow a similar growth trend up to year 2100

304   as at treeline ($R^2 = 0.60$, slope $= 0.08 \text{ cm}^2 \text{ year}^{-1}$, $P < 0.0001$). However, trees at the lowest

305   limit follow a completely different pattern, with BAI decreasing after year 2030 ($R^2 = 0.54$,

306   slope $= -0.10 \text{ cm}^2 \text{ year}^{-1}$, $P < 0.0001$ for the 2012-2100 period).

Table 1: Main characteristics of the studied populations across latitudinal (northern, 69º47′ N; 27º02′ E; central, 57º08′ N; 3º40′ W; southern, 37º22′ N; 2º51′W) and altitudinal gradients (treeline, medium, low): climate (TWM, temperature of the warmest month in ºC; TCM, temperature of the coldest month in ºC; 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 year^{-1}) and growth trends during the last century separated in two periods (1910-1960 and 1961-2011). Values are mean ±SD.

Latitude	Altitude	Climate			Elevation	Density	Period	Age	DBH	BAI 1910-1960	Trend 1910-1960	BAI 1961-2011	Trend 1961-2011
		TWM	TCM	PDM									
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

313

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. 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}, T_{au} are standardised temperatures of previous autumn and winter, spring, summer and autumn of current year, respectively. Similar names for standardised precipitation values (P_{aup}, P_{wi}, P_{sp}, P_{su}, P_{au}).

| Latitude	Altitude	Growth model	K	AIC_c	ΔAIC_c	Wi
Northern	Treeline	**$T_{aup}+T_{sp}+T_{su}+P_{wi}+P_{sp}$**	**7**	**13280.3**	**0.0**	**55.5**
		$T_{aup}+T_{sp}+T_{su}+P_{wi}+P_{sp}+P_{au}$	8	13281.6	1.3	29.2
		$T_{aup}+T_{sp}+T_{su}+P_{sp}$	6	13283.1	2.8	13.5
		$T_{aup}+T_{wi}+T_{sp}+T_{su}+P_{wi}+P_{sp}+P_{au}$	9	13287.5	7.2	1.5
		$T_{aup}+T_{wi}+T_{sp}+T_{su}+P_{aup}+P_{wi}+P_{sp}+P_{au}$	10	13291.1	10.8	0.2
		$T_{aup}+T_{wi}+T_{sp}+T_{su}+T_{au}+P_{aup}+P_{wi}+P_{sp}+P_{au}$	11	13296.4	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	13303.0	22.7	0.0
		Null model	2	13456.5	176.2	0.0
Central	Treeline	**$T_{aup}+T_{wi}+T_{sp}+T_{au}+P_{au}$**	**7**	**15232.0**	**0.0**	**47.2**
		$T_{aup}+T_{wi}+T_{sp}+T_{au}+P_{sp}+P_{au}$	8	15233.1	1.2	26.4
		$T_{aup}+T_{sp}+T_{au}+P_{au}$	6	15233.6	1.6	20.9
		$T_{aup}+T_{wi}+T_{sp}+T_{au}+P_{wi}+P_{sp}+P_{au}$	9	15238.9	6.9	1.5
		$T_{aup}+T_{wi}+T_{sp}+T_{su}+T_{au}+P_{wi}+P_{sp}+P_{au}$	10	15245.1	13.1	0.1
		$T_{aup}+T_{wi}+T_{sp}+T_{su}+T_{au}+P_{aup}+P_{wi}+P_{sp}+P_{au}$	11	15251.9	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	15258.6	26.6	0.0
		Null model	2	15611.2	379.3	0.0
Southern	Treeline	**$T_{wi}+T_{au}+P_{wi}+P_{sp}+P_{su}$**	**7**	**17599.9**	**0.0**	**91.7**
		$T_{wi}+T_{au}+P_{aup}+P_{wi}+P_{sp}+P_{su}$	8	17605.3	5.4	6.3
		$T_{wi}+P_{wi}+P_{sp}+P_{su}$	6	17608.3	8.4	1.4
		$T_{wi}+T_{su}+T_{au}+P_{aup}+P_{wi}+P_{sp}+P_{su}$	9	17610.1	10.1	0.6
		$T_{wi}+T_{su}+T_{au}+P_{aup}+P_{wi}+P_{sp}+P_{su}+P_{au}$	10	17617.0	17.0	0.0
		$T_{aup}+T_{wi}+T_{su}+T_{au}+P_{aup}+P_{wi}+P_{sp}+P_{su}+P_{au}$	11	17623.2	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	17628.9	28.9	0.0
		Null model	2	17740.5	140.6	0.0
Southern	Medium	**$T_{aup}+T_{wi}+T_{sp}+T_{su}+T_{au}+P_{wi}+P_{su}$**	**9**	**17278.9**	**0.0**	**44.8**
		$T_{aup}+T_{wi}+T_{sp}+T_{au}+P_{wi}+P_{su}$	8	17279.2	0.3	37.9
		$T_{aup}+T_{wi}+T_{sp}+P_{wi}+P_{su}$	7	17282.0	3.1	9.4
		$T_{aup}+T_{wi}+T_{sp}+T_{su}+T_{au}+P_{wi}+P_{sp}+P_{su}$	10	17282.4	3.6	7.5
		$T_{aup}+T_{wi}+T_{sp}+T_{su}+T_{au}+P_{aup}+P_{wi}+P_{sp}+P_{su}$	11	17289.1	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	17296.5	17.6	0.0
		Null model	2	17370.7	91.8	0.0
Southern	Low	**$T_{aup}+T_{wi}+T_{sp}+T_{su}+P_{wi}+P_{su}$**	**8**	**17284.3**	**0.0**	**71.7**
		$T_{aup}+T_{wi}+T_{sp}+T_{su}+P_{aup}+P_{wi}+P_{su}$	9	17287.6	3.3	14.0
		$T_{aup}+T_{wi}+T_{sp}+T_{su}+P_{aup}+P_{wi}+P_{sp}+P_{su}$	10	17287.8	3.5	12.5
		$T_{aup}+T_{wi}+T_{sp}+P_{wi}+P_{su}$	7	17293.1	8.8	0.9
		$T_{aup}+T_{wi}+T_{sp}+T_{su}+P_{aup}+P_{wi}+P_{sp}+P_{su}+P_{au}$	11	17293.1	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	17299.6	15.3	0.0
		Null model	2	17649.3	365.0	0.0

325 **Table 3**: Regression coefficients of the final full model explaining the basal area

326 increment. Value, standard error (SE) and explained variance (VE, %) are indicated for

327 each variable (see Table 2 for variable names).

328

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**

329

16

330
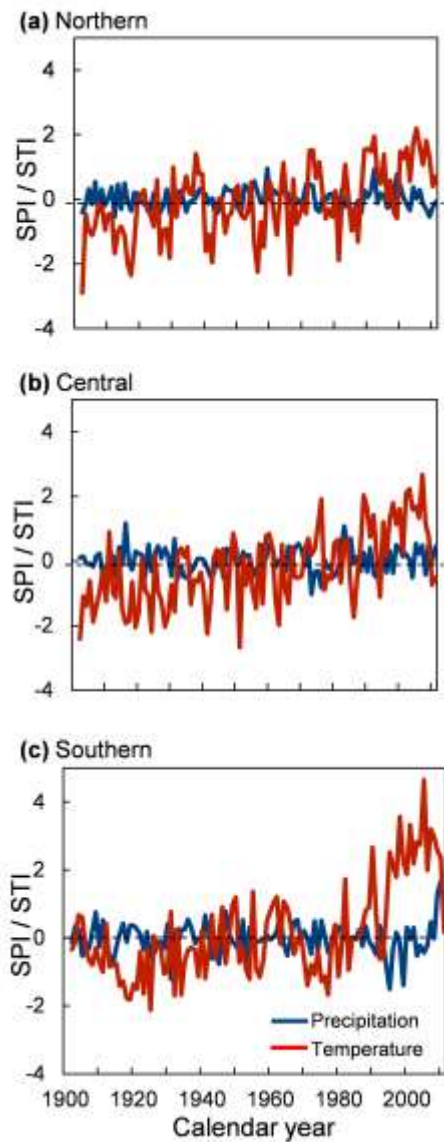
Figure 1: Yearly variations in temperature and precipitation across the latitudinal gradient

(northern: Kevo, Finland; central: Cairngorms, UK; southern: Sierra de Baza, Spain) for

the 1902-2011 period. Standardised precipitation index (SPI, blue lines) and standardised

temperature index (STI, red lines) 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 1960-2011 obtained from Kevo Subarctic Research Station,

Braemar meteorological station and Narvaez meteorological station for northern, central

and southern sites, respectively. Data from 1902-1959 obtained from CRU (Climate

Research Unit, University of East Anglia).

17
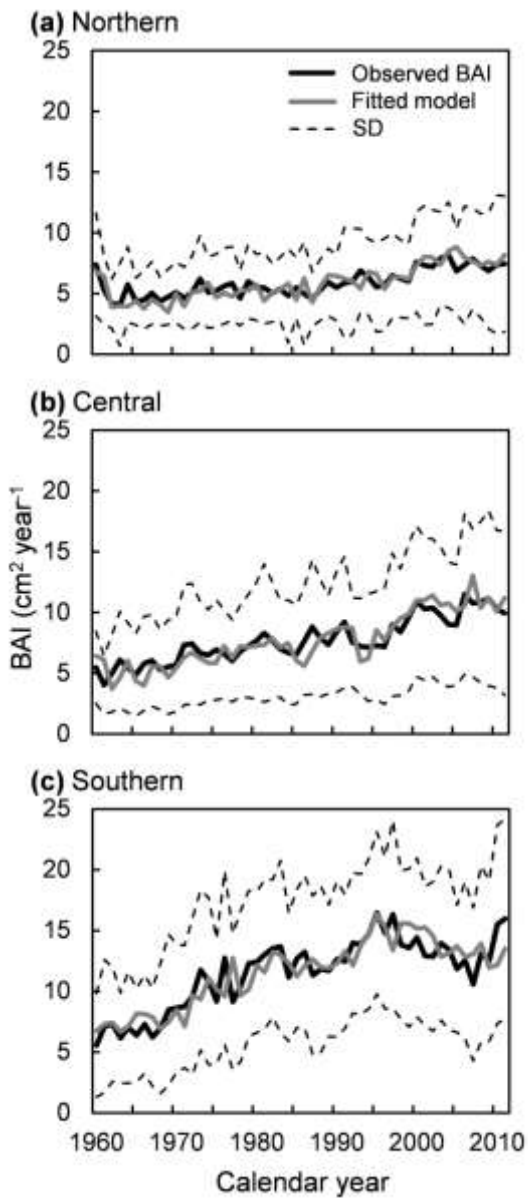
Figure 2: Mean basal area increment (BAI, black line) ± SD (dashed lines) of Scots pine
sites at treeline across its latitudinal distribution gradient during the 1960-2011 period
(period with instrumental climate data availability). Grey line represents the predicted
growth by the full model based on age, climate and previous BAI.

18
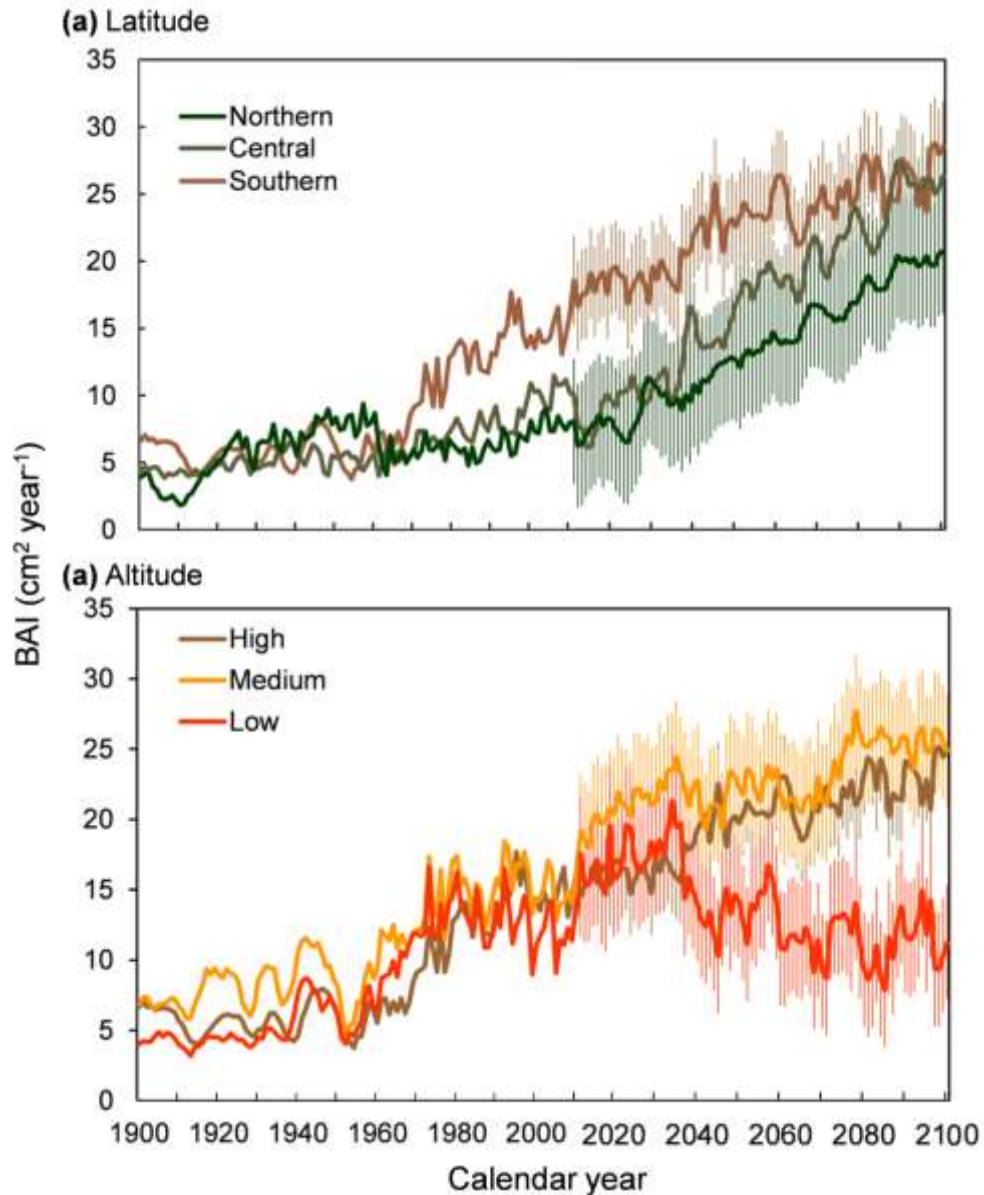
345

346 **Figure 3**: Mean basal area increment (BAI) per site for the different Scots pine sites across

347 the latitudinal (top panel) and altitudinal (bottom panel) gradients. Values for the 1900-

348 2011 series are the site means of observed individual BAI ($N = 60$), whereas for the 2012-

349 2100 period are the predictions for the full model using climatic data predicted by the

350 General Circulation Models, scenario ECHAM A2 (IPCC 2013). Vertical lines represent

351 ±SD for the model predictions based on the simulation of 1000 trees.

352

353 **Discussion**

19

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, 2016).

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

across the 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 generalised growth increase in

response to increasing temperature is consistent across the latitudinal gradient since

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

379 pathogen abundance. However, other non-climatic factors such as changing management

380 practices could be acting simultaneously, potentially contributing to the strong increase of

381 BAI at the southern site since 1960.

382

383 Regarding the long-term persistence of relict southernmost Scots pine populations, our

384 results illustrate the variability in plant responses to different climatic drivers along

385 altitudinal gradients (Linares & Tíscar, 2011; Candel-Pérez et al., 2012; Herrero et al.,

386 2013; Galván et al., 2015; Arzac et al., 2016). While the temperature response differed

387 with altitude, a positive growth response to summer rainfall was observed along the whole

388 altitudinal gradient of southernmost Scots pine populations, suggesting the reactivation of

389 cambial activity in response to summer storms. However, while populations at the

390 southernmost range edge appear buffered against rising drought stress to some degree,

391 their recovery could be limited when severe drought impacts occur (Sánchez-Salguero et

392 al. 2015; Cavin & Jump, 2016).

393

394 The differential latitudinal and altitudinal growth pattern discussed above relies on

395 different factors controlling growth across the distribution range. Regarding climatic

396 variables, *P. sylvestris* growth is subject to temperature as the most important limiting

397 factor at northern and central latitude (Antonova & Stasova, 1993; Heikkinen et al. 2002;

398 Tuovinen, 2005; Kullman, 2007; Helama et al., 2011; Moir et al., 2011). Increased

399 performance in the central and northern latitudinal sites, where climatic conditions are less

400 stressful (Matías & Jump, 2015), was accompanied by positive growth trends and higher

401 growth rates at the upper elevations of the drought-limited southernmost edge. However,

402 rising temperature during previous autumn, spring and summer imposes negative effects at

403 the low southern edge. Despite the general positive effect of winter temperature, seasonal

21

404   variables affect this species differentially through the altitudinal gradient, with more

405   negative effects of high temperature as elevation diminishes (Linares & Tíscar, 2011;

406   Candel-Pérez et al., 2012). This finding is in concordance with previous studies indicating

407   that southern lowland populations are more sensitive to increased temperature (Herrero et

408   al., 2013; Sánchez-Salguero et al., 2015) and with impacts on demographic processes

409   already detected (Matías & Jump, 2015).

410

411   The effect of precipitation on BAI also differs across the latitudinal and altitudinal

412   gradients. Although precipitation has been traditionally considered to have little effect on

413   tree growth at high latitudes, we detect high importance of winter and spring precipitation

414   at the northern edge (26.4 % of the variance explained by precipitation). Higher winter and

415   spring precipitation in boreal forests means higher snow cover, which provides

416   thermoinsulation of roots (Helama et al., 2011), and can prevent the premature yellowing

417   of pine needles (Jalkanen 1993), translating into a higher radial growth (Tuovinen, 2005).

418   However, precipitation gains in importance at the southern limit of the species (see also

419   Swidrak et al., 2011). Winter precipitation negatively affects tree growth along the studied

420   altitudinal gradient (and during spring at southern treeline). This negative correlation of

421   growth with precipitation might be also explained by the association between precipitation

422   and cloudiness, which reduces the photosynthetic activity and carbon reserves for growth

423   (Gimeno et al., 2012). Higher precipitation during summer enhances tree growth

424   consistently across altitudes (Candel-Pérez et al., 2012; Herrero et al., 2013; Sánchez-

425   Salguero et al., 2015). On the contrary, extended droughts usually lead to reduced growth

426   and, in the most severe cases, to hydraulic failure and/or carbon starvation and the

427   consequent tree death (Martínez-Vilalta and Piñol, 2002; Galiano et al., 2011; Allen et al.,

428   2015).

429

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).

443

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

453 increasing their growth after 2100, which does not seem to be the case at central and

454 southern latitude.

455

456 Across the altitudinal distribution at the southern edge, treeline and mid-elevation

457 populations follow a similar growth trend, with BAI increase during the first part of the

458 century and a stabilised period during the second half (Fig. 3). This finding indicates that

459 the scenario simulated by our model predicts the persistence of these southernmost

460 populations, at least at central and high elevations. However, a completely different pattern

461 appeared for lowland populations. Our model predicted a short phase of growth increase

462 during the next 10-20 years, but a consistent declining trend is predicted up to the end of

463 the century, which is a strongly negative indication for population persistence (Pedersen,

464 1998; Jump et al., 2006; Galiano et al., 2011). According to our results, the growth

465 increase predicted for central and high altitude and the declining growth trends at low

466 elevations, linked with the current mortality trends already detected in the field (Matías &

467 Jump, 2015), might lead to a range migration upslope where physical conditions allow it,

468 or to range contraction from low altitude areas of the southern range edge of the species

469 during the 21st Century.

470

471 Although geographical variations in climatic sensitivity were evident in our study (see also

472 Martínez Vilalta et al., 2009), the timing of the climatic response may also shift over time

473 as a response to changing climatic conditions (Lebourgeois et al., 2012; Galván et al.,

474 2015). This possibility could be a shortcoming of our modelling approach, as we assume

475 steady climate sensitivity over the 21st Century when forecasting tree growth responses.

476 Although this issue has not been accounted for in this paper, it might be expected that

477 global warming during the past and current centuries may be increasing temperature

478   sensitivity as well as the effect of water limitation (Andreu et al., 2007; Camarero et al.,

479   2015). Furthermore, increased frequency and severity of drought events in future climates

480   may be critical (Giorgi & Lionello, 2008), and that the combined effect drought increase

481   and heat waves (hotter drought, Allen et al., 2015) might induce physiological tipping

482   points, likely resulting in unexpected and long-lasting reductions in growth and subsequent

483   tree mortality (Cavin et al. 2013; Matías et al., 2012). Consequently, our results regarding

484   growth stability at the upper elevations of southern *P. sylvestris* forests over the 21st-

485   Century climate change might not be assumed to continue indefinitely.

486

487   *Conclusions*

488   By simulating future tree growth based on current climate-growth relationships and

489   predicted climate changes, we identified contrasting growth responses along the altitudinal

490   gradient at the southernmost *P. sylvestris* range edge, with stable growth at the mid- to

491   upper-elevation belts but high susceptibility to decline at low elevation. Across a

492   latitudinal gradient, core and northern *P. sylvestris* populations show a sustained

493   temperature-related increase in growth, although water availability also affects overall

494   growth patterns at the northern range edge. While we simulated a conservative climatic

495   scenario, our models forecast a clear increase in radial growth at treeline populations

496   throughout the distribution of the species up to the end of the present century, which would

497   likely lead to upland and northward expansions through the species' distribution.

498   However, these predictions should be interpreted with caution, since other factors such as

499   limiting soil conditions, extreme climatic events or biotic interactions can strongly

500   influence demographic responses. Our results also imply that rear edge populations are

501   able to persist at medium or high elevations but, after an initial growth increase, a rapid

502   decline is expected for those populations located at low elevations. This lowland decline

25

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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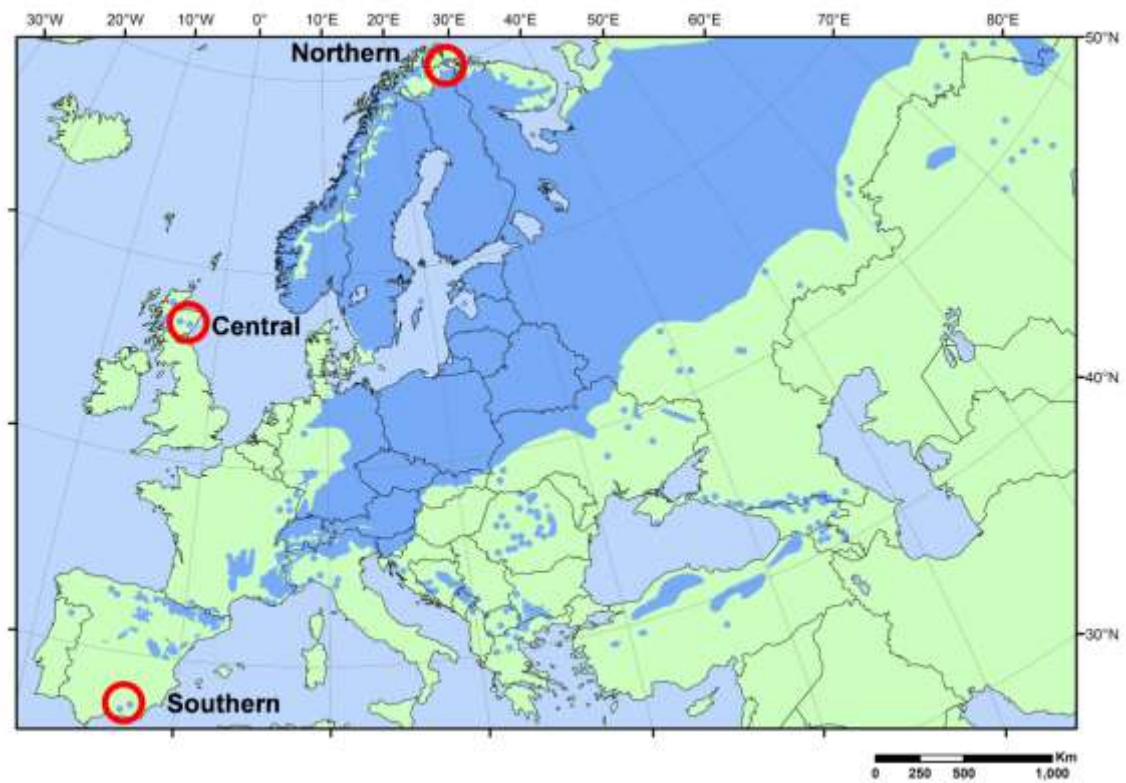
Figure S1: European distribution of *Pinus sylvestris* (source Euforgen; http://www.euforgen.org) with the sampled locations across the latitudinal distribution within the red circles (northern: Kevo, Finland; central: Cairngorms, UK; southern: Sierra de Baza, Spain).
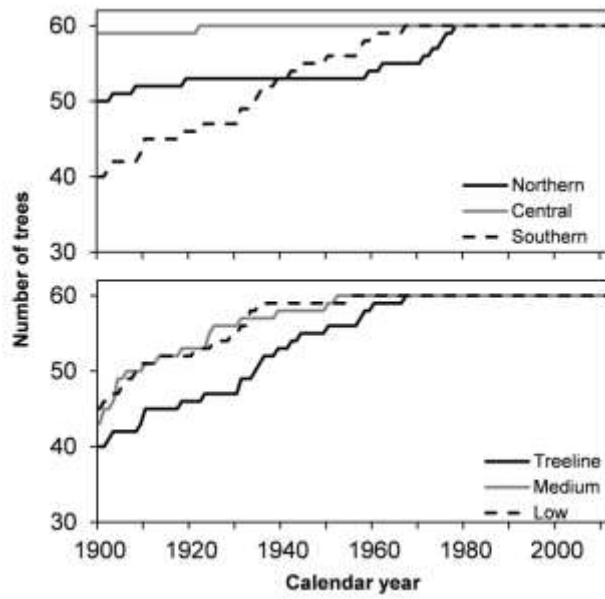
Figure S2: Number of trees sampled for the period 1900-2011 across the latitudinal (top panel) and altitudinal (down panel) gradients.
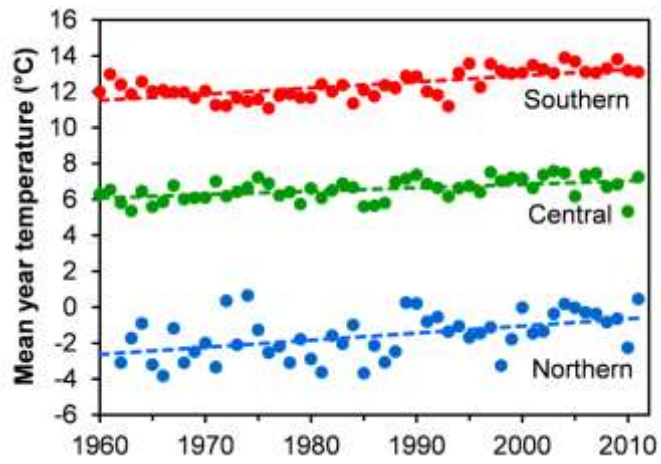
Figure S3: Mean yearly temperature variations during the 1960-2011 period at the three latitudinal study areas: southern (Sierra de Baza, Spain; red dots), central (Cairngorms, UK; green dots) and northern (Kevo, Finland; blue dots). Dashed lines indicate temporal trends.
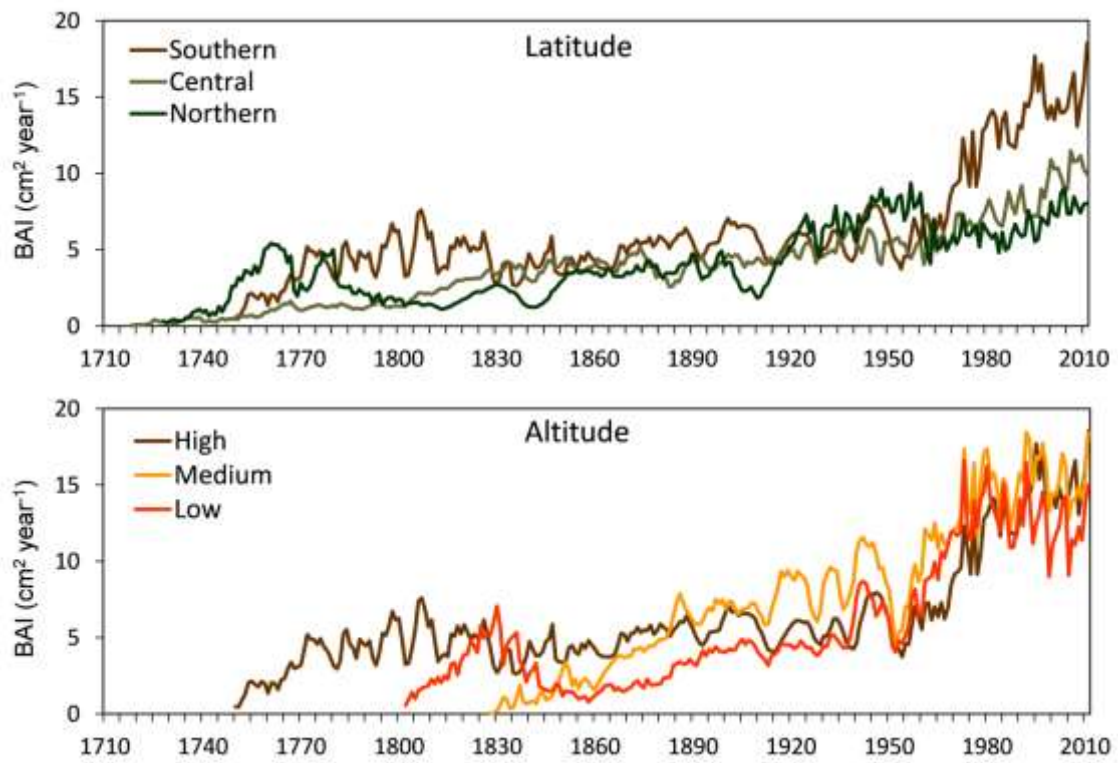
Figure S4: Mean basal area increment of Scots pine populations across the latitudinal (top panel) and altitudinal (bottom panel) gradients measured in this study. Data of the two populations per site are pooled.
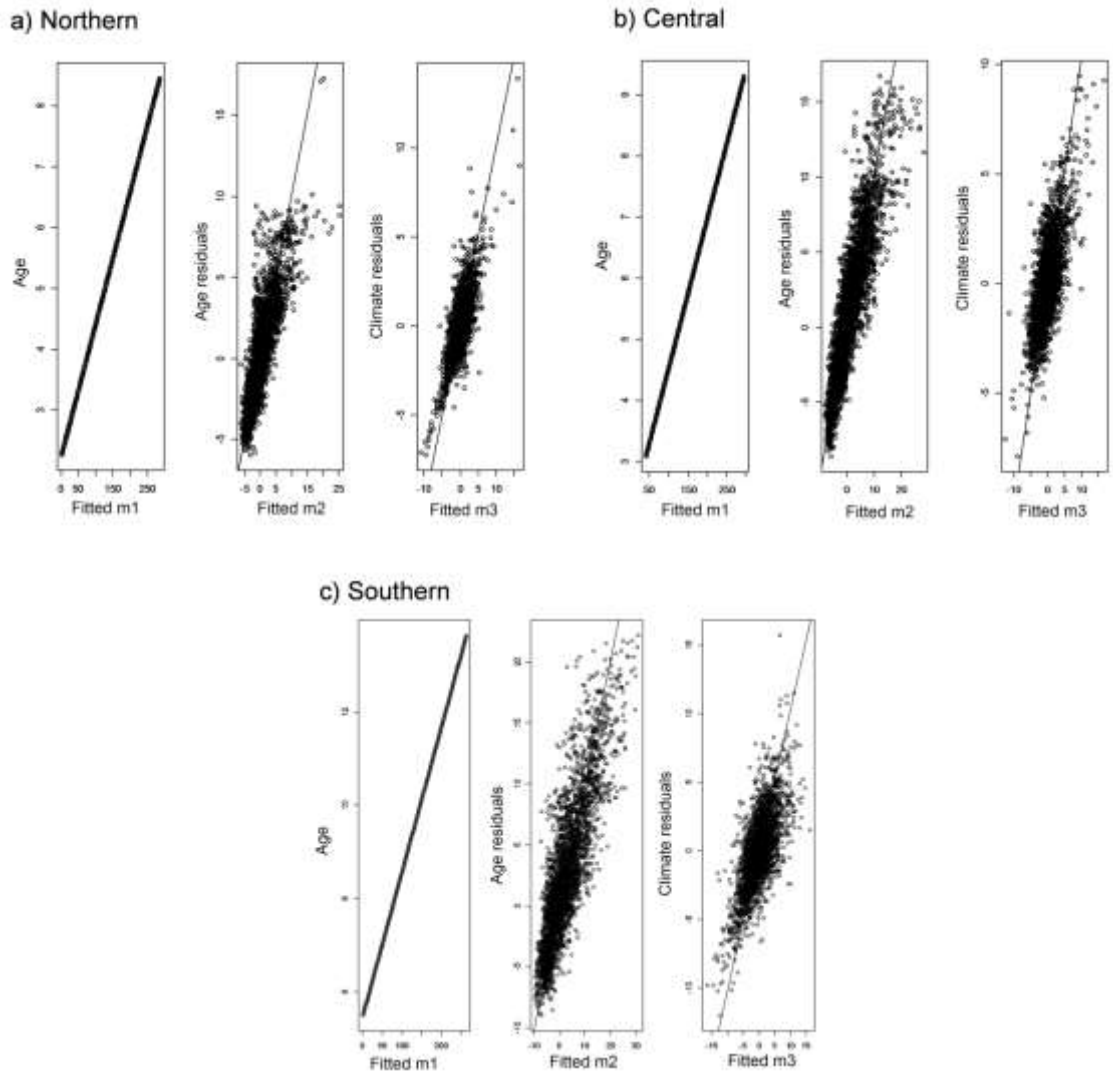
Figure S5: Residual adjustment of the different models selected across the latitudinal gradient

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.

Station	Location	Latitude	Longitude	Elevation	H. dist	V. dist
Kevo	Northern (Finland)	69º45'N	27º01'E	80	4950	156
Braemar	Central (Scotland)	57º00'N	03º23'W	339	21970	109
Narvaez	Southern (Spain)	37º25'N	02º51'W	1354	4520	511