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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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25 **Abstract**

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

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

51

52 **Introduction**

53 Distribution limits of plant species are determined by the ecological conditions that allow
54 them to establish permanent populations (Babst et al., 2013). The long-term persistence of
55 many species within their present distribution limits is, therefore, challenged by global
56 warming (Parmesan, 2006; Allen et al., 2015). Indeed, there is increasing evidence of
57 recent changes in climate affecting the ecological performance of plant species worldwide,
58 from phenology, growth or reproductive investment to recruitment rates (Chmielewski &
59 Rotzer, 2001; Peñuelas et al., 2002; Castro et al., 2004; Jump et al., 2006; Walck et al.,
60 2011; Matías & Jump, 2015). Furthermore, these changes are not likely to homogeneously
61 affect species across their geographical ranges, with populations located at the edges of
62 their distributions being especially sensitive to climate alterations (Andreu et al., 2007;
63 Linares & Tíscar, 2011; Candel-Pérez et al., 2012). The evidence of plant responses to
64 climatic drivers and the mechanisms underlying these responses has risen rapidly during
65 the last decades (Camarero and Gutiérrez, 2004; Jump et al., 2006; Kullman, 2007;
66 Benavides et al., 2013; Matías & Jump, 2015). However, there is an urgent need to move
67 beyond reporting changes underway to increase our predictive capacity, enabling us to
68 better estimate the ecological and biogeographical consequences of climate change for
69 species in the future (Steinkamp & Hickler, 2015).

70

71 Climatic factors constraining plant growth in temperate and boreal environments shift
72 along altitudinal and latitudinal gradients, typically moving from water shortage at lower
73 altitudes to low temperature limitation at higher altitudes or latitudes (Babst et al., 2013).

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

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 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).

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

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:

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

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

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 (*BAI_p*) 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: $7.3 \pm 0.3^a \text{ cm}^2 \text{ year}^{-1}$; medium: $9.9 \pm 0.3^b \text{ cm}^2 \text{ year}^{-1}$;
247 low: $7.5 \pm 0.4^a \text{ cm}^2 \text{ year}^{-1}$ 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

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 $\pm 0.3^a$ $\text{cm}^2 \text{ year}^{-1}$; medium: 15.7 ± 0.4^a $\text{cm}^2 \text{ year}^{-1}$; low: 12.5 ± 0.4^b $\text{cm}^2 \text{ year}^{-1}$ 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

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 = $0.11 \text{ cm}^2 \text{ year}^{-1}$, $P < 0.0001$ for the period 2012-
298 2100). Populations at central latitude present the higher responsiveness ($R^2 = 0.95$, slope =

299 0.23 cm² 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 21st 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 cm² year⁻¹, $P < 0.0001$), but at a lower rate than 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 cm² 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 cm² year⁻¹, $P < 0.0001$ for the 2012-2100 period).

307 **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'
308 N; 2°51'W) and altitudinal gradients (treeline, medium, low): climate (TWM, temperature of the warmest month in °C; TCM, temperature of the
309 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
310 (individuals ha⁻¹), registered period, tree age (estimated at sampling moment from the number of rings measured, in years), diameter at breast
311 height (DBH, in cm), and basal area increment (BAI, in cm² year⁻¹) and growth trends during the last century separated in two periods (1910-
312 1960 and 1961-2011). Values are mean ±SD.

Latitude	Altitude	Climate			Elevation	Density	Period	Age	DBH	BAI		Trend	
		TWM	TCM	PDM						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

313

314 **Table 2:** Linear mixed models explaining the effect of climate on basal area increment
315 (BAI) after accounting for ontogenetic effects for the different sites across the latitudinal
316 and altitudinal gradients. Selected models are highlighted in bold. The null model
317 considered the effect of BAI as a constant. The best models were selected on the basis of
318 the Akaike Information Criteria corrected by sample size (AIC_c). K represents the number
319 of variables included in the model plus constant and error terms, ΔAIC_c is the difference in
320 AIC respect the best model, and Wi is the relative probability to be the best model for the
321 observed data. T_{aup} , T_{wi} , T_{sp} , T_{su} , T_{au} are standardised temperatures of previous autumn and winter,
322 spring, summer and autumn of current year, respectively. Similar names for standardised
323 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		

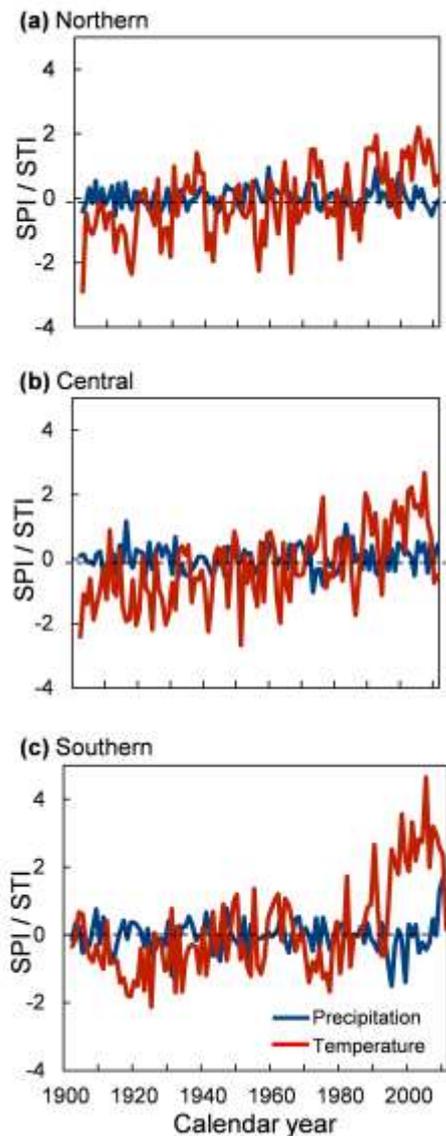
324

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
		<i>BAlp</i>	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
		<i>BAlp</i>	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
		<i>BAlp</i>	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
		<i>BAlp</i>	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
		<i>BAlp</i>	0.523	0.013	9.3
		Age	268.110	5.851	0.3
		Total VE (%)			84.3

329



330

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

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

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

334 temperature index (STI, red lines) are normalized by subtracting the average temperature

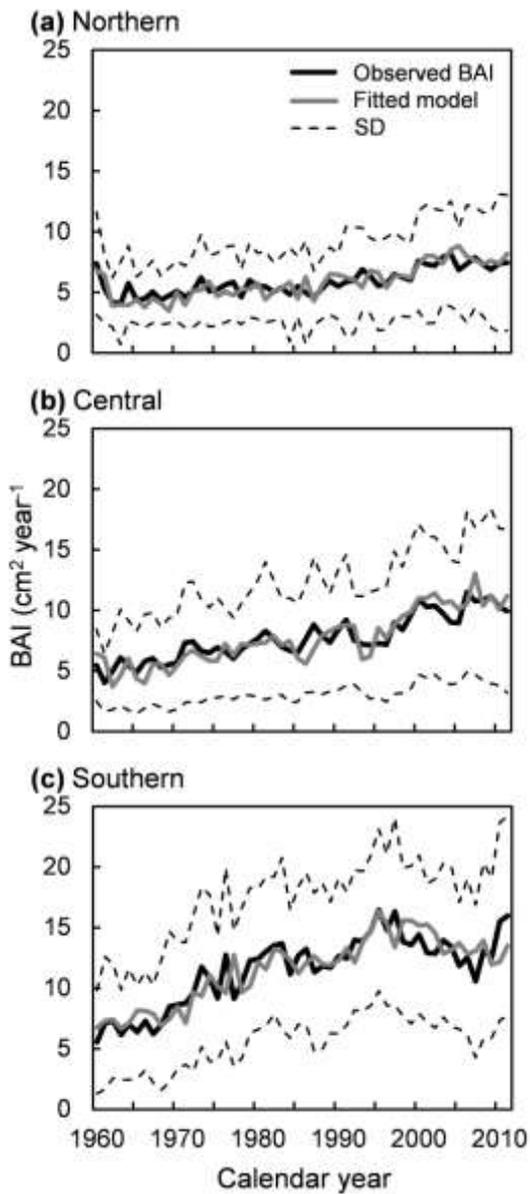
335 from each value for the period 1961–1990 and dividing by the standard deviation of the

336 same period. Data from 1960-2011 obtained from Kevo Subarctic Research Station,

337 Braemar meteorological station and Narvaez meteorological station for northern, central

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

339 Research Unit, University of East Anglia).



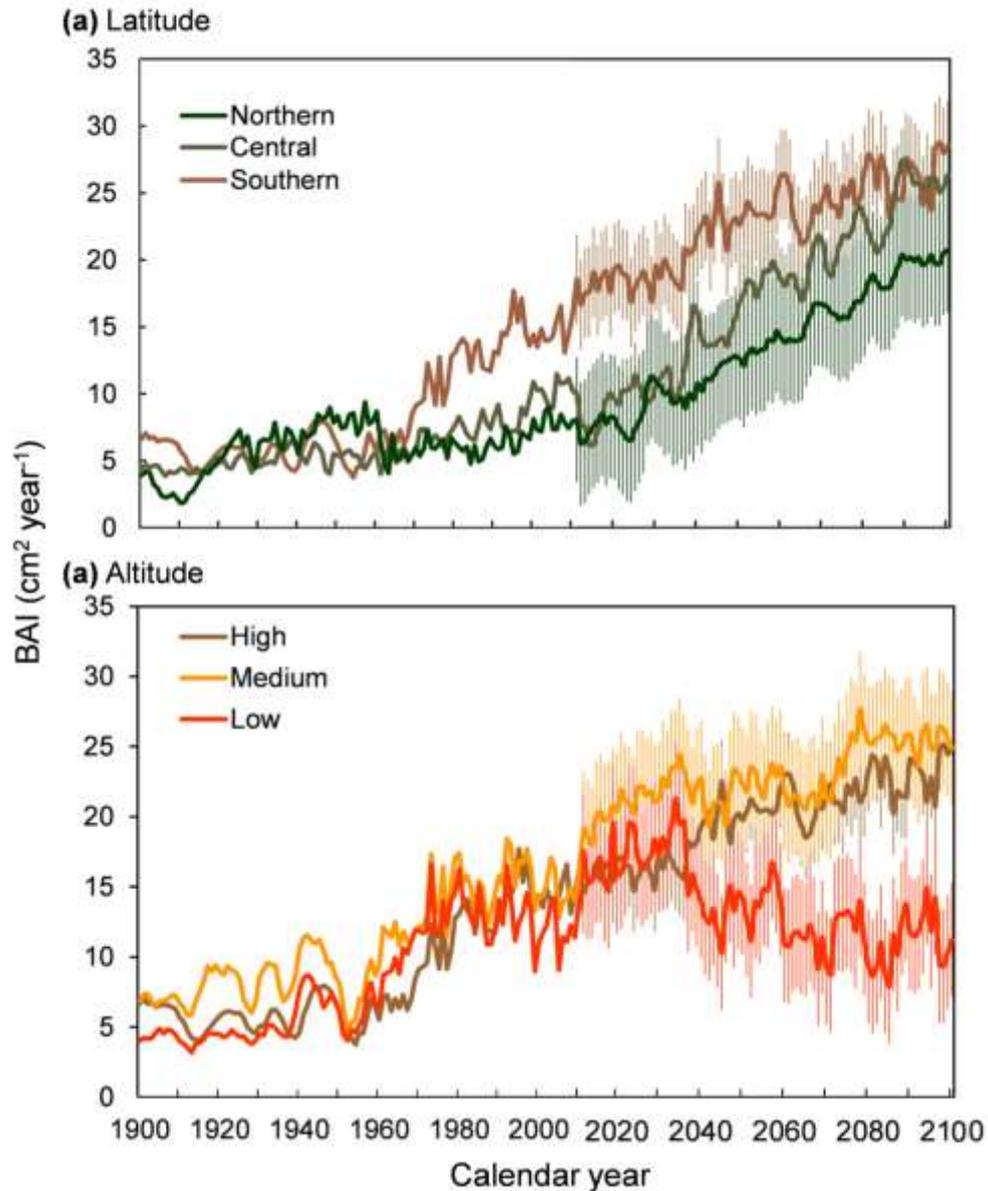
340

341 **Figure 2:** Mean basal area increment (BAI, black line) \pm SD (dashed lines) of Scots pine

342 sites at treeline across its latitudinal distribution gradient during the 1960-2011 period

343 (period with instrumental climate data availability). Grey line represents the predicted

344 growth by the full model based on age, climate and previous BAI.



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 \pm SD for the model predictions based on the simulation of 1000 trees.

352

353 **Discussion**

354 *Latitudinal and altitudinal variation in growth*

355 Ecological theory predicts distribution shifts in woody species as the climate warms.
356 Range expansion to higher altitudes and latitudes, as well as increasing population density,
357 is expected following enhanced growth and reproduction at upper elevation and poleward
358 range limits (Harsch et al., 2009). Decreasing growth, as well as declining recruitment, is
359 expected at the rear range edge (Walther et al., 2002; Linares & Tíscar, 2011; Candel-
360 Pérez et al., 2012). Case studies demonstrate that such processes are underway for a wide
361 variety of species (Walther et al., 2002; Harsch et al., 2009), although widespread growth
362 decline and distributional shifts in some range edges are not necessarily as straightforward
363 as theoretical predictions (Cavin & Jump, 2016).

364

365 Results presented here show positive growth trends in treeline populations of Scots pine
366 across the complete latitudinal distribution during the last 50 years (Table 1). Although this
367 trend was consistent, there were important differences in responsiveness (different rates)
368 among sites. Growth increase was highest at the southernmost limit of the species and
369 lowest at the northern edge, which overall agrees with the trend of increasing temperature
370 detected in these areas (Fig. S3; Galván et al., 2015). This generalised growth increase in
371 response to increasing temperature is consistent across the latitudinal gradient since
372 treeline populations usually are not usually water-limited during the growing period.

373 Although long-term changes in temperature alone are not able to explain the geographical
374 growth trends, they can be also explained by the absolute values of temperature, decreasing
375 as latitude increases. This positive growth trend is consistent with the pattern of increased
376 reproductive investment and recruitment already recorded from the same populations
377 (Hofgaard et al. 2013; Matías & Jump, 2015). Together this evidence points to improved
378 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

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

430 *Forecasted growth for the 21st Century*

431 Across the latitudinal gradient, treeline populations are expected to increase BAI up to the
432 end of the present century, although not at the same rate. Current growth is highest at the
433 southern edge, and it will continue rising up to year 2050, when BAI becomes more stable.
434 This stabilization might represent the maximum growth potential of the species, with
435 similar values to those currently found in areas where temperature and water availability
436 are not limiting tree growth (Michelot et al., 2012; Viguera et al. 2013; Zang & Rothe,
437 2013), and maintaining it until year 2100. Central-latitude populations are expected to
438 present the highest response to the predicted climate alterations, reaching similar values to
439 those of the southern populations by 2100. Consequently, Scots pine populations currently
440 located at treeline at southern and central latitudes will have a similar BAI by the end of
441 the present century, being close to the maximum potential growth of the species (Michelot
442 et al., 2012; Viguera et al. 2013; Zang & Rothe, 2013).

443

444 These findings have two main implications: on one hand, current treelines are expected to
445 support healthy populations with higher growth rates and even become denser if there are
446 no recruitment limitations (Camarero & Gutiérrez, 2004). On the other hand, treeline
447 populations have the potential to expand their limits upslope in those areas where
448 topography and soil conditions allow it due to the amelioration of climatic limitations
449 (assuming favourable conditions for establishment; Körner, 2012; Rabasa et al., 2013).
450 Finally, populations located at the northern distribution limit are expected to increase their
451 growth during the 21st Century, although at a lower rate than at the other latitudes (Hickler
452 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

503 might be even more important than described here when extreme climatic events are
504 considered or if tipping points are reached. The results we present stress the importance of
505 including geographical variability in growth response to improve resolution in predictive
506 models. Our methodology also highlights the value of the use of past responses to climate
507 based on reliable growth data for prediction of future population dynamics under climate
508 change.

509

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517

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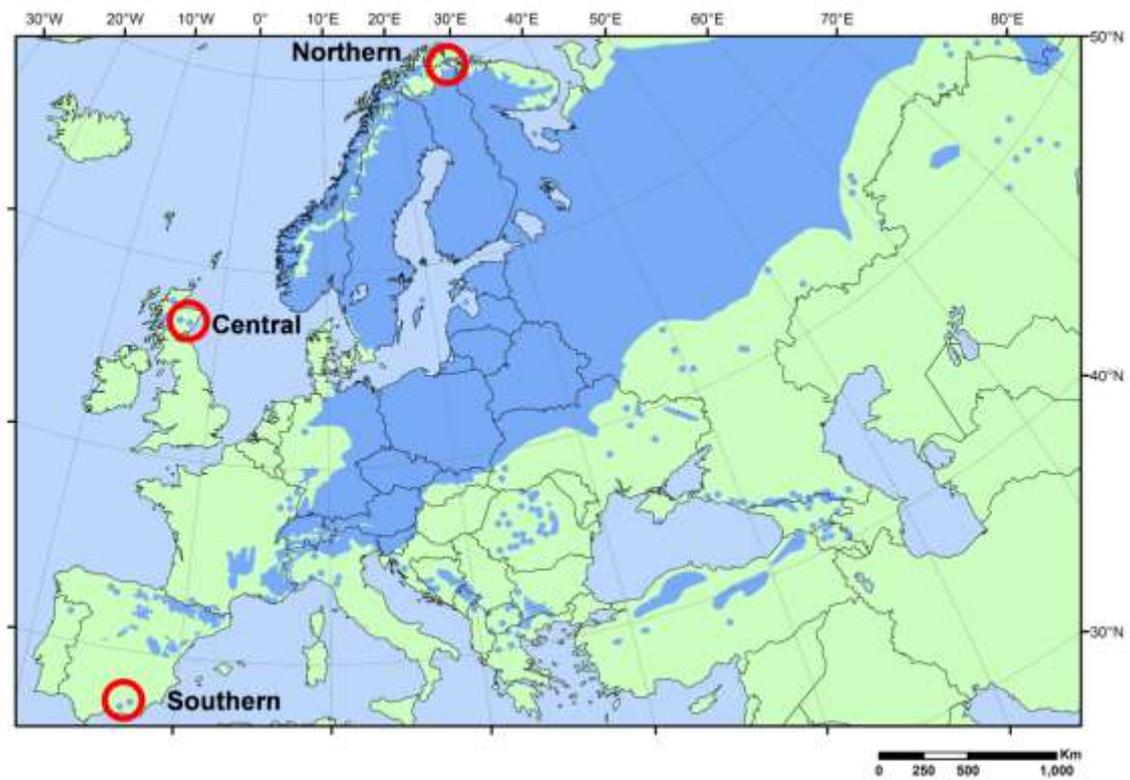


Figure S1: European distribution of *Pinus sylvestris* (source Euforgen; <http://www.euforgen.org>) with the sampled locations across the latitudinal distribution within the red circles (northern: Kevo, Finland; central: Cairngorms, UK; southern: Sierra de Baza, Spain).

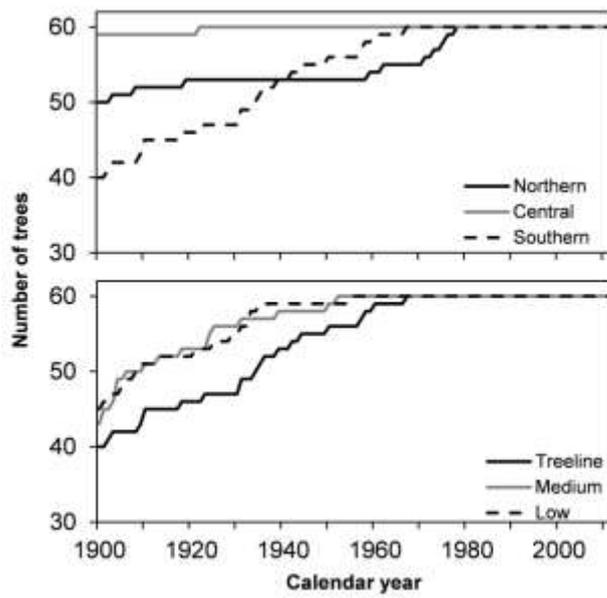


Figure S2: Number of trees sampled for the period 1900-2011 across the latitudinal (top panel) and altitudinal (down panel) gradients.

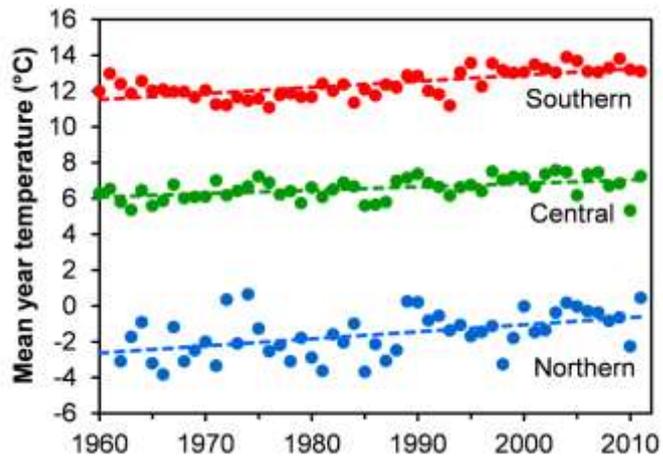


Figure S3: Mean yearly temperature variations during the 1960-2011 period at the three latitudinal study areas: southern (Sierra de Baza, Spain; red dots), central (Cairngorms, UK; green dots) and northern (Kevo, Finland; blue dots). Dashed lines indicate temporal trends.

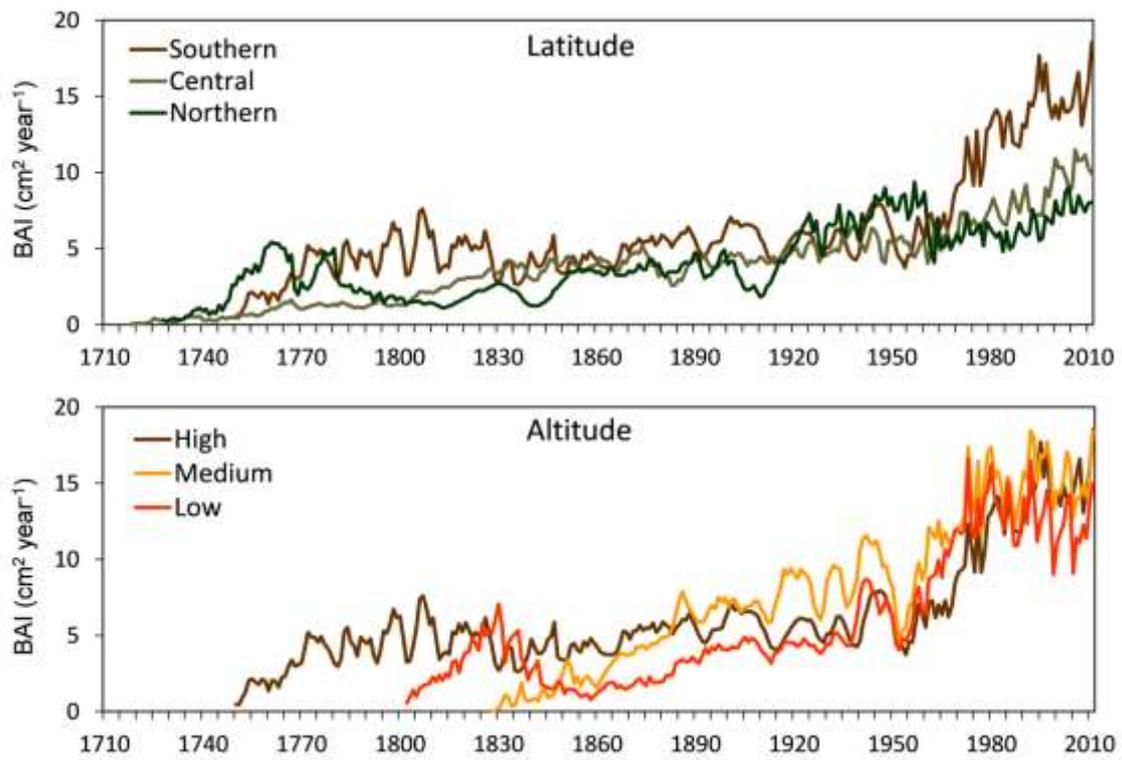


Figure S4: Mean basal area increment of Scots pine populations across the latitudinal (top panel) and altitudinal (bottom panel) gradients measured in this study. Data of the two populations per site are pooled.

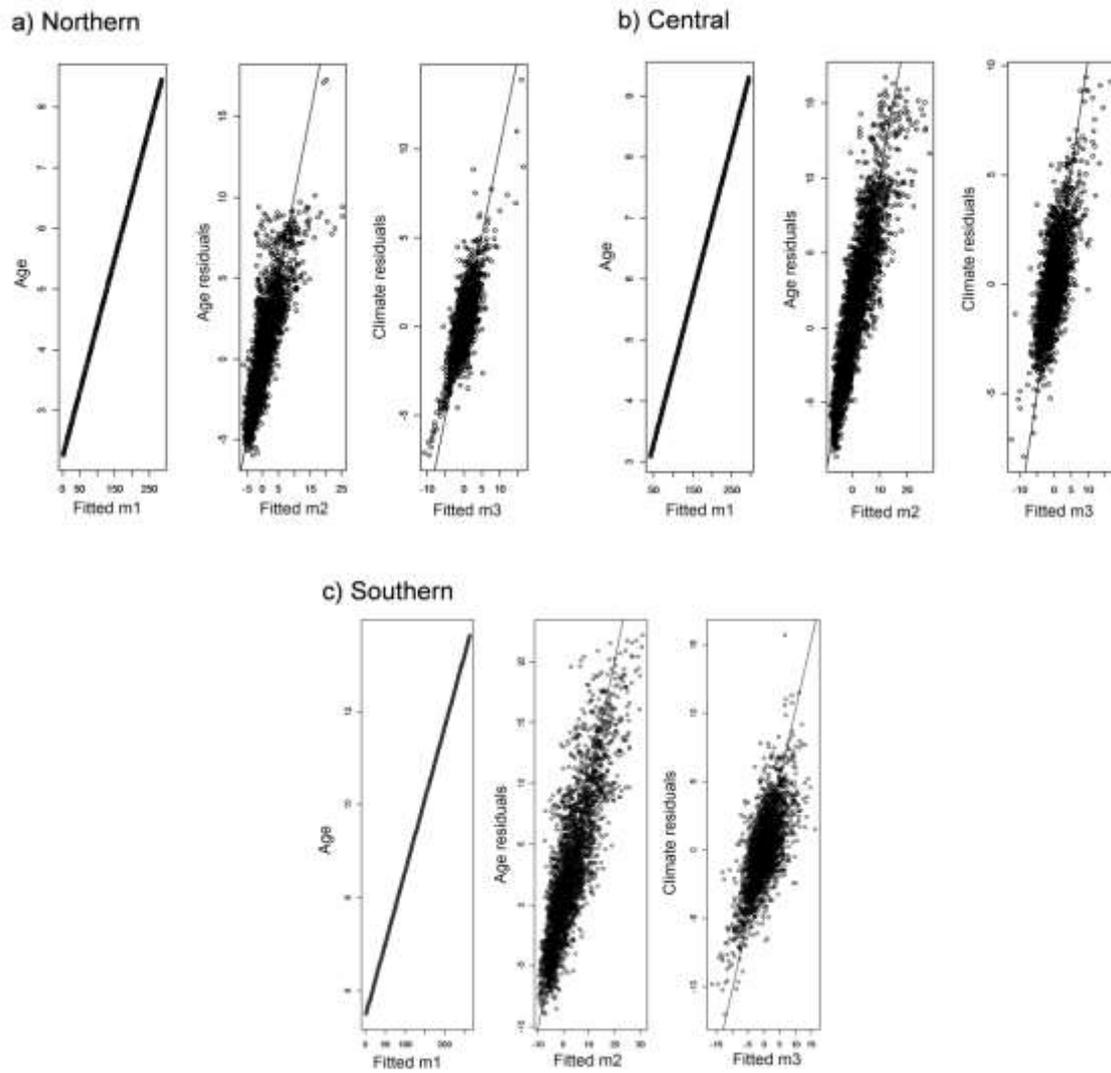


Figure S5: Residual adjustment of the different models selected across the latitudinal gradient

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)	69°45'N	27°01'E	80	4950	156
Braemar	Central (Scotland)	57°00'N	03°23'W	339	21970	109
Narvaez	Southern (Spain)	37°25'N	02°51'W	1354	4520	511