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 tree growth under climate change

6

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20

23 **Abstract**

24 Ongoing changes in global climate are altering ecological conditions for many species. The

25 consequences of such changes are typically most evident at the edge of a species'

26 geographical distribution, where differences in growth or population dynamics may result

27 in range expansions or contractions. Understanding population responses to different

28 climatic drivers along wide latitudinal and altitudinal gradients is necessary in order to gain

29 a better understanding of plant responses to ongoing increases in global temperature and

30 drought severity. We selected Scots pine (*Pinus sylvestris* L.) as a model species to explore

31 growth responses to climatic variability (seasonal temperature and precipitation) over the

32 last century through dendrochronological methods. We developed linear models based on

33 age, climate and previous growth to forecast growth trends up to year 2100 using climatic

34 predictions. Populations were located at the treeline across a latitudinal gradient covering

35 the northern, central and southernmost populations and across an altitudinal gradient at the

36 southern edge of the distribution (treeline, medium and lower elevations). Radial growth

37 was maximal at medium altitude and treeline of the southernmost populations.

38 Temperature was the main factor controlling growth variability along the gradients,

39 although the timing and strength of climatic variables affecting growth shifted with latitude

40 and altitude. Predictive models forecast a general increase in Scots pine growth at treeline

41 across the latitudinal distribution, with southern populations increasing growth up to year

42 2050, when it stabilises. The highest responsiveness appeared at central latitude, and

43 moderate growth increase is projected at the northern limit. Contrastingly, the model

44 forecasted growth decline at lowland-southern populations, suggesting an upslope range

45 displacement over the coming decades. Our results give insight into the geographical

46 responses of tree species to climate change and demonstrate the importance of

47   incorporating biogeographical variability into predictive models for an accurate prediction

48   of species dynamics as climate changes.

49

50   **Introduction**

51   Distribution limits of plant species are determined by the ecological conditions that allow

52   them to establish permanent populations (Babst et al., 2013). The long-term persistence of

53   many species within their present distribution limits is, therefore, challenged by global

54   warming (Parmesan, 2006; Allen et al., 2015). Indeed, there is increasing evidence of

55   recent changes in climate affecting the ecological performance of plant species worldwide,

56   from phenology, growth or reproductive investment to recruitment rates (Chmielewski &

57   Rotzer, 2001; Peñuelas et al., 2002; Castro et al., 2004; Jump et al., 2006; Walck et al.,

58   2011; Matías & Jump, 2015). Furthermore, these changes are not likely to homogeneously

59   affect species across their geographical ranges, with populations located at the edges of

60   their distributions being especially sensitive to climate alterations (Andreu et al., 2007;

61   Linares & Tíscar, 2011; Candel-Pérez et al., 2012). The evidence of plant responses to

62   climatic drivers and the mechanisms underlying these responses has risen rapidly during

63   the last decades (Camarero and Gutiérrez, 2004; Jump et al., 2006; Kullman, 2007;

64   Benavides et al., 2013; Matías & Jump, 2015). However, there is an urgent need to move

65   beyond reporting changes underway to increase our predictive capacity, enabling us to

66   better estimate the ecological and biogeographical consequences of climate change for

67   species in the future (Steinkamp & Hickler, 2015).

68

69   Climatic factors constraining plant growth in temperate and boreal environments shift

70   along altitudinal and latitudinal gradients, typically moving from water shortage at lower

71   altitudes to low temperature limitation at higher altitudes or latitudes (Babst et al., 2013).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

87   2014; Matías & Jump, 2014; Matías et al., 2016). Consequently, detailed information about

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

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

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

91

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

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

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

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

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

4

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

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

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

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

101   study system to evaluate local responses to environmental alterations.

102

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

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

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

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

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

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

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

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

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

112

113   **Materials and Methods**

114   *Field sites*

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

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

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

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

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

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

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

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

123   populations at western-central latitude (Cairngorms, UK), and two close to the northern

124   limit of the distribution (Kevo, Finland), making a total of 10 study populations (see

125   Matías and Jump 2015 for more details). The altitudinal gradient was not replicated in

126   latitude since altitudinal distribution diminishes with increasing latitude, presenting a very

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

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

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

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

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

132

133   *Sampling and width measurements*

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

135   dendrochronological study. Sampling was performed following standard

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

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

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

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

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

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

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

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

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

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

146   area (BAI) using the following formula:

147

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

149

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

151   included 60 trees for the period 1960-2011 and at least 40 trees per site for all the 20th

152   Century (Fig. S2).

153

154   *Climate data*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

172   1993).

173

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

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

176   2012-2100 are projected according with the ECHAM5 General Circulation Model (Max-

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

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

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

180   Seasonal standardised temperature and precipitation indices were calculated for CRU data

181   in the same way as for data from meteorological stations.

182

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

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

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

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

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

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

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

190   1990. The three areas presented a positive trend of rising temperature during the past

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

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

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

194   0.03 °C year^{-1} for the southern edge (0.01 °C year^{-1} for the 1910-1960 period; Fig. S3).

195

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

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

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

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

200   periods 1961-1990 with 2071-2100.

201

202   *Data analysis*

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

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

205   showing marked discrepancies in growth patterns (maximum N = 60 per altitude or

206   latitude). In consequence, all the data shown throughout the text is expressed at site level

207   (n=3 for altitude or latitude). Following the procedure by González-Muñoz et al. (2014),

208   for each site (altitudinal or latitudinal band) we first fitted the tree age at the year of ring

209   formation using the most accurate function (linear, polynomial or sigmoidal) and kept the

210   residuals. As radial growth strongly depends on tree age, this method allowed us to obtain

211   an estimate of BAI without ontogenetic effects. After that, linear mixed-effects models

212   were used to identify the effects of 10 climatic variables (T_{aup}, T_{wi}, T_{sp}, T_{su}, T_{au}, P_{aup}, P_{wi},

213   P_{sp}, P_{su} and P_{au}) on the residuals of the previous function, using climatic variables from

214   meteorological stations for the period 1960-2011 (when instrumental climatic data are

215   available for all sites) as fixed factors and tree as a random factor. Fitted models followed

216   the equation:

$$Y_i = Xa_i + Zb + e_i$$

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

9

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 (*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, also obtained from

231 CRU. We simulated annual BAI of a group of 1000 individuals per site (either in latitude

232 or in altitude) with initial ages between 5 and 100 years. Accordingly, the individual trees

233 would be a maximum 298 years old at the end of the simulated period. All analyses were

234 performed using the packages "nlme" and "mgcv" in R (R Core Team, 2015). Data are

235 shown as mean ± SE 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

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 ± 0.4^a cm^2 year^{-1}; low: 12.5 ± 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 no

258   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 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 cm^2 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 cm^2 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 cm^2 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 cm^2 year^{-1}, $P < 0.0001$ for the 2012-2100 period).

307

308   **Discussion**

309   *Latitudinal and altitudinal variation in growth*

310   Ecological theory predicts distribution shifts in woody species as the climate warms.

311   Range expansion to higher altitudes and latitudes, as well as increasing population density,

312   is expected following enhanced growth and reproduction at upper elevation and poleward

313   range limits (Harsch et al., 2009). Decreasing growth, as well as declining recruitment, is

314   expected at the rear range edge (Walther et al., 2002; Linares & Tíscar, 2011; Candel-

315   Pérez et al., 2012). Case studies demonstrate that such processes are underway for a wide

316   variety of species (Walther et al., 2002; Harsch et al., 2009), although widespread growth

317   decline and distributional shifts in some range edges are not necessarily as straightforward

318   as theoretical predictions (Cavin & Jump, 2016).

319

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

321   across the complete latitudinal distribution during the last 50 years (Table 1). Although this

322   trend was consistent, there were important differences in responsiveness (different rates)

323   among sites. Growth increase was highest at the southernmost limit of the species and

324   lowest at the northern edge, which overall agrees with the trend of increasing temperature

325   detected in these areas (Fig. S3; Galván et al., 2015). This generalised growth increase in

326   response to increasing temperature is consistent across the latitudinal gradient since

327   treeline populations usually are not usually water-limited during the growing period.

328   Although long-term changes in temperature alone are not able to explain the geographical

329   growth trends, they can be also explained by the absolute values of temperature, decreasing

330   as latitude increases. This positive growth trend is consistent with the pattern of increased

331   reproductive investment and recruitment already recorded from the same populations

332   (Hofgaard et al. 2013; Matías & Jump, 2015). Together this evidence points to improved

333   population performance in the absence of interactions with other factors such as pest and

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

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

336   BAI at the southern site since 1960.

337

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

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

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

341   2013; Galván et al., 2015; Arzac et al., 2016). While the temperature response differed

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

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

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

14

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

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

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

348

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

364   already detected (Matías & Jump, 2015).

365

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

383   2015).

384

385   *Forecasted growth for the 21st Century*

386   Across the latitudinal gradient, treeline populations are expected to increase BAI up to the

387   end of the present century, although not at the same rate. Current growth is highest at the

388   southern edge, and it will continue rising up to year 2050, when BAI becomes more stable.

389   This stabilization might represent the maximum growth potential of the species, with

390   similar values to those currently found in areas where temperature and water availability

391   are not limiting tree growth (Michelot et al., 2012; Viguera et al. 2013; Zang & Rothe,

392   2013), and maintaining it until year 2100. Central-latitude populations are expected to

393   present the highest response to the predicted climate alterations, reaching similar values to

394   those of the southern populations by 2100. Consequently, Scots pine populations currently

395   located at treeline at southern and central latitudes will have a similar BAI by the end of

396   the present century, being close to the maximum potential growth of the species (Michelot

397   et al., 2012; Viguera et al. 2013; Zang & Rothe, 2013).

398

399   These findings have two main implications: on one hand, current treelines are expected to

400   support healthy populations with higher growth rates and even become denser if there are

401   no recruitment limitations (Camarero & Gutiérrez, 2004). On the other hand, treeline

402   populations have the potential to expand their limits upslope in those areas where

403   topography and soil conditions allow it due to the amelioration of climatic limitations

404   (assuming favourable conditions for establishment; Körner, 2012; Rabasa et al., 2013).

405   Finally, populations located at the northern distribution limit are expected to increase their

406   growth during the 21st Century, although at a lower rate than at the other latitudes (Hickler

407   et al., 2012). This implies that northern populations have the potential to continue

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

409   southern latitude.

410

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

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

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

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

415   populations, at least at medium and high elevations. However, a completely different

416   pattern appeared for lowland populations. Our model predicted a short phase of growth

417   increase during the next 10-20 years, but a consistent declining trend is predicted up to the

418   end of the century, which is a strongly negative indication for population persistence

419   (Pedersen, 1998; Jump et al., 2006; Galiano et al., 2011). According to our results, the

17

420   growth increase predicted for medium and high altitude and the declining growth trends at

421   low elevations, linked with the current mortality trends already detected in the field

422   (Matías & Jump, 2015), might lead to a range migration upslope where physical conditions

423   allow it, or to range contraction from low altitude areas of the southern range edge of the

424   species during the 21st Century.

425

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

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

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

429   2015). This possibility could be a shortcoming of our modelling approach, as we assume

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

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

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

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

434   2015). Furthermore, increased frequency and severity of drought events in future climates

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

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

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

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

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

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

441

442   *Conclusions*

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

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

18

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

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

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

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

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

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

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

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

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

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

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

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

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

458 might be even more important than described here when extreme climatic events are

459 considered or if tipping points are reached. The results we present stress the importance of

460 including geographical variability in growth response to improve resolution in predictive

461 models. Our methodology also highlights the value of the use of past responses to climate

462 based on reliable growth data for prediction of future population dynamics under climate

463 change.

464

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472

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655 **Table 1**: Main characteristics of the studied populations across latitudinal (northern, 69º47′ N; 27º02′ E; central, 57º08′ N; 3º40′ W; southern, 37º22′

656 N; 2º51′W) and altitudinal gradients (treeline, medium, low): climate (TWM, temperature of the warmest month in ℃; TCM, temperature of the

657 coldest month in ℃; PDM, precipitation of the driest month in mm; mean values for the 1960-211 period), elevation (m a.s.l.), tree density

658 (individuals ha^{-1}), registered period, tree age (estimated at sampling moment from the number of rings measured, in years), diameter at breast

659 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-

660 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

661

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

Table 3: Regression coefficients of the final full model explaining the basal area increment. Value, standard error (SE) and explained variance (VE, %) are indicated for each variable (see Table 2 for variable names).

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**

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).

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.

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

across the latitudinal (top panel) and altitudinal (bottom panel) gradients. Values for the

1900-2011 series are the site means of observed individual BAI ($N = 60$), whereas for

the 2012-2100 period are the predictions for the full model using climatic data predicted

by the General Circulation Models, scenario ECHAM A2 (IPCC 2013). Vertical lines

represent ±SD for the model predictions based on the simulation of 1000 trees.
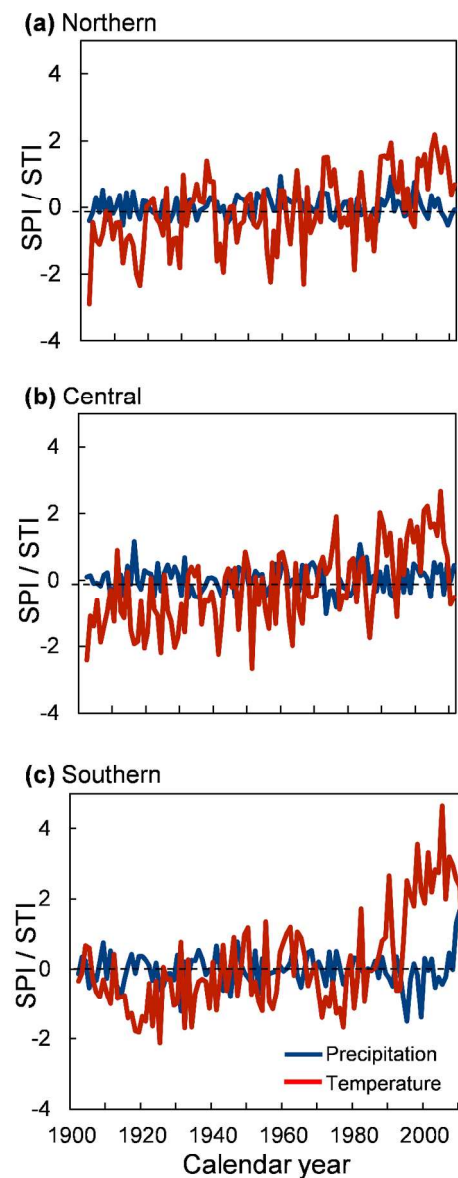
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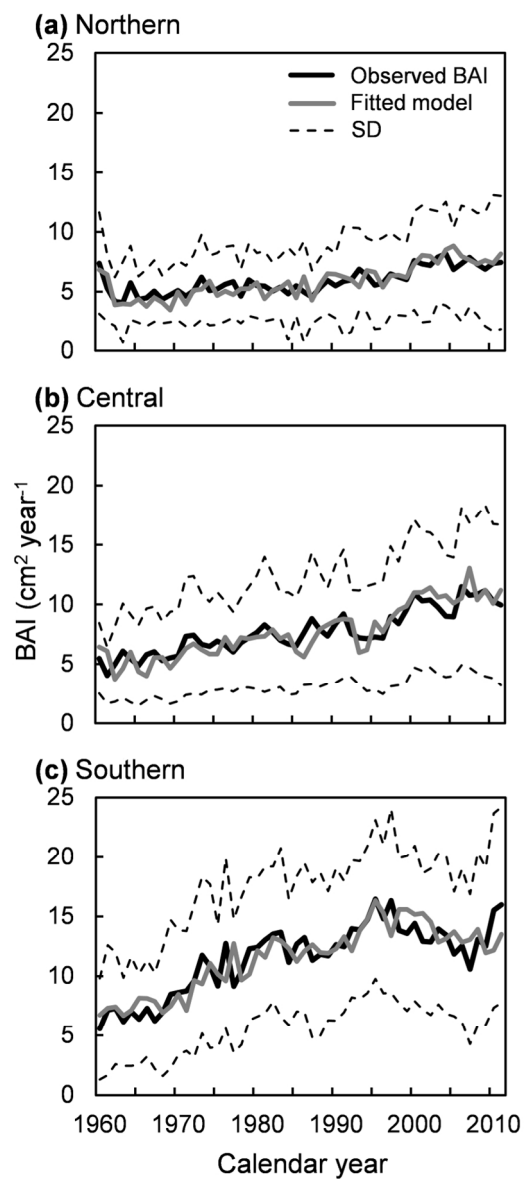Fig. 1
80x188mm (300 x 300 DPI)

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.
Fig. 2
80x172mm (300 x 300 DPI)
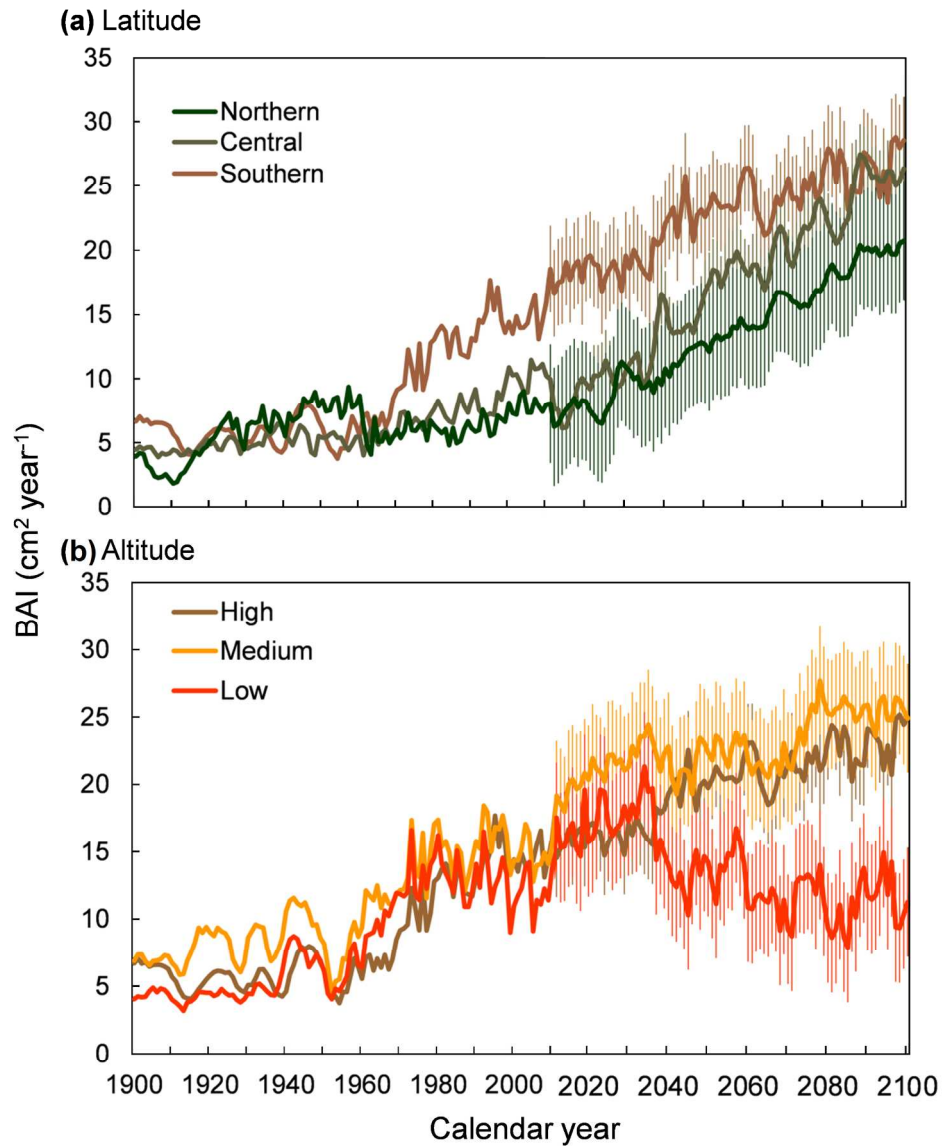
Mean basal area increment (BAI) per site for the different Scots pine sites across the latitudinal (top panel) and altitudinal (bottom panel) gradients. Values for the 1900-2011 series are the site means of observed individual BAI (N = 60), whereas for the 2012-2100 period are the predictions for the full model using climatic data predicted by the General Circulation Models, scenario ECHAM A2 (IPCC 2013). Vertical lines represent ±SD for the model predictions based on the simulation of 1000 trees.

Fig. 3
209x259mm (300 x 300 DPI)