1   Increased growth and reduced summer drought limitation at the southern limit of

2   *Fagus sylvatica* L., despite regionally warmer and drier conditions.

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Abstract

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15   Tree populations at the equatorward edge of their distribution are predicted to respond to increased
16   temperature and drought with declining performance. Empirical studies of *Fagus sylvatica* L., one of the
17   most studied tree species in Europe, have broadly supported these predictions. Using a network of tree
18   ring chronologies from northern Greece, we showed that growth in populations of this species at their
19   southeast distribution limit was limited by summer temperature and precipitation, particularly at low
20   elevations. Furthermore, decadal periods of lower precipitation and higher temperature in the twentieth
21   century were associated with multi-year growth depressions. However, since 1990, growth trends were
22   positive across the network, despite continued dry and hot summer conditions. Growth trends were not
23   correlated with either elevation or tree age. Additionally, correlations between growth and temperature
24   and precipitation were weaker in recent decades. These results are consistent with another recent report
25   from the Balkan Peninsula, and indicate that forests in this region may be more resistant to regional
26   climate change than previously considered.

Keywords

28   Beech; Greece; Balkan; range edge; tree growth; growth trend

Introduction

Populations at the equator-ward or low-elevation edge of their species distribution are expected to respond to increased temperatures and drought with a reduction in performance (Woodward, 1987). In tree species, this response is expected to be evident in declining growth, increased mortality and reduced recruitment (Jump *et al.*, 2010). Changes in demographic and subsequent distribution shifts have already been observed at the trailing edge of many tree species distributions in response to recent climate change (e.g. Beckage *et al.*, 2008). *Fagus sylvatica* L. (European beech) is a widely distributed species in Europe, with great economic and biodiversity value (Gessler *et al.*, 2007), and has often been used as a model species for investigating the current and future impact of climate change on forest ecosystems (e.g. Kramer *et al.*, 2010). It is widely considered to have high sensitivity to growing season drought, based on evidence from experimental and physiological studies (Robson *et al.*, 2012) , forest inventory data (Seynave *et al.*, 2008), dendrochronological studies (Piovesan *et al.*, 2005) and statistical and process-based models of distribution (Kramer *et al.*, 2010). Furthermore, drought stress is widely considered to limit the distribution of *F. sylvatica* at its southern distribution limit, and subsequently the increase in temperature and summer drought in southern Europe over the last half century (Giorgi, 2002) are expected to have led to reduced performance in many of these southern populations (Fyllas and Troumbis, 2009). In contrast, in northern Europe, beech is expected to have increased in competitiveness and expanded into areas currently occupied by boreo-nemoral species as a consequence of increasing survival and seed maturation success, and higher growth rates (Koca *et al.*, 2006). These trends are expected to continue over the next century as climate continues to warm. It is important to test these predictions as they are key to predicting future range shifts, and if species responses to climate change differ from expectations this will have far-reaching consequences for forest carbon cycling, biodiversity and forest-based economic activities.

Until recently, empirical studies have broadly supported predictions, with evidence of increased growth and competiveness reported in northern Europe (Bascietto *et al.*, 2004; Bolte *et al.*, 2010) and growth declines and increased mortality reported at the southern distribution edge (Jump *et al.*, 2006; Piovesan

et al., 2008). Recently however, the picture has become more complex, with climate warming in northern Europe linked with evidence of negative impacts of climate change on forest growth, including declines in growth (Aertsen *et al.*, 2014; Latte *et al.*, 2015). Additionally, a recent study has reported increased tree growth in southern European beech forests, during the ongoing period of regional warming (Tegel *et al.*, 2014). There is therefore a pressing need to improve understanding of the relationships between tree growth and climate in this species, particularly at the southern distribution margin where beech forests are understudied in comparison to central and northern Europe. Furthermore, we require additional understanding of the response of growth in this region to recent changes in climate, which have been characterised by increasing temperatures and summer drought stress (Giorgi, 2002). Tree rings provide a valuable way to investigate such growth responses, allowing reliable assessment of annual aboveground net primary production (Bascietto *et al.*, 2004). However, tree-rings contain multiple biological and environmental signals necessitating careful analysis and interpretation (e.g. Bowman *et al.*, 2013).

This study uses a new network of 21 ring chronologies from across northern Greece to investigate evidence of the impacts of recent climate change on tree growth at the southeast distribution limit of this species. We specifically address the following research questions:

1. What is the relationship between tree growth (ring width) and climate at the southeast distribution limit of beech?
2. How have interannual and decadal variations in growth in beech responded to recent changes in climate?
3. What do growth-climate relationships and growth trends within the network tell us about ongoing and likely future response of this species to climate change?

Material and methods

Study Area

The study was conducted in northern Greece, in forests which represent the most south-easterly populations of beech in Europe. Beech forms the treeline on many mountains (~1900 m a.s.l), and at lower elevations beech is typically replaced by mixed deciduous oak-dominated woodland (~800 m a.s.l.) (Tsiripidis *et al.*, 2007). Research focused on an intensively sampled elevation transect on Mt. Vermio (40.64°N, 21.95 °E), with eleven sampled sites extending from the high elevation treeline at ~1950 m a.s.l. to the lowest elevation site at 880 m a.sl. (Table 1 and Figure 1). Additionally, 10 further sites were sampled across northern Greece to test the regional consistency of results (Table 1 and Figure 1). This additional network of sites included a stand on Mt. Oxia (38.78°N, 21.97°E), the most extreme southeast population of beech in Europe, and the most southerly occurrence in the Balkan peninsula (Tsiripidis *et al.*, 2007).

Climate in this region is typically Mediterranean, with warm dry summers and cold wet winters, although there is geographical and elevational variation (Figure S 1 and S 2). Changes in climate over the last century are consistent with other regions in the Mediterranean, with warming during the first half of the 20th century, followed by a trend of cooling temperature from 1950-1970. Since the 1970s temperatures have risen. Annual precipitation has no significant long-term trend, but summer precipitation was lower during the 1940s and 1950s, and during the decade centred on 2000.

Tree ring sampling

At each site increment cores were extracted from 20-31 canopy dominant trees with two (occasionally three) cores taken per tree from opposite directions and parallel to any slope. Sample preparation followed standard dendrochronological methods, involving the mounting of cores, and then surface sanding until individual ring boundaries were clearly visible. Cores were scanned at either 1600 or 2400 dpi (the latter when rings were particularly narrow), and ring widths for each core was measured using the software CooRecorder v7.3 (Larsson, 2003). Initial cross-dating was conducted in CDendro v7.3 (Larsson, 2010), and then checked for each individual site using the standard dendrochronolgical

104 software COFECHA (Grissino-Mayer, 2001). Some cores could not be successfully measured or cross-
105 dated and these were excluded from subsequent analysis. Commonly used chronology statistics were
106 used to confirm the suitability of our chronologies for dendrochronological analysis (Grissino-Mayer,
107 2001) (Table 2), and PCA analysis was used to quantify the common signal between sites in the network.

108

109 **Tree ring processing**
110 Raw ring width chronologies typically contain low-frequency signals (i.e. decadal and longer), associated
111 with changes in tree age and size, canopy position and long-term changes in the abiotic environment. We
112 used two techniques in order to account for these effects. In the first, we removed low-frequency variance
113 from each individual tree chronology by detrending the ring width time-series using the R package `dplR`
114 (Bunn et al. 2012), individually fitting the raw ring width series from each core with a 32-year cubic spline
115 with a 50% frequency cut off. Dimensionless ring width indices were created for each core by dividing
116 the observed ring width by the spline, with individual indices then averaged to produce a mean ring width
117 index (RWI) for each sampled site, with a prewhitening procedure applied to account for autocorrelation
118 in the RWI time-series. The RWI captures high frequency (i.e. interannual) variation in tree growth. In
119 the second technique we converted raw ring width measurements into basal area increment (BAI) using
120 the formula:

121 $$BAI_t = \pi(r_t^2 - r_{t-1}^2)$$

122 where r is the radius of the tree in year t. BAI chronologies account for the geometric effect (increasing
123 cambium area as tree size increases), but retain low frequency variation due to changes in growing
124 conditions (e.g. climate, canopy position). A mean site BAI chronology is expected to show a long-term
125 positive trend during the juvenile phase, partly due to stand dynamics and changes in tree size. The early
126 parts of a mean BAI chronology represent supressed growth only, with increasing BAI in the mean site
127 chronology as sampled trees increase in size and gain access to the canopy (Bowman *et al.*, 2013). In
128 order to account for this potential bias, individual tree BAI chronologies were truncated to include only
129 mature-phase growth. The cut-off was determined as either the end of the most recent canopy release

5

event, or the transition to mature growth (following the method of Jump et al, (2006), applied to individual trees) (see Figure S 3 for more details). Individual chronologies were averaged for each site to create mature BAI (mBAI) chronologies, and then scaled and centred for plotting and analysis. BAI chronologies created without the removal of juvenile phase growth are included in the supplementary information.

Climate data

Climate data were extracted from the gridded half-degree dataset CRU TS 3.10.01 (Harris *et al.*, 2013). We used monthly-mean daily 24-hour maximum temperature (mean maximum, *MAX*) and monthly precipitation (*PREC*). The location of each grid cell in relation to the sample sites is show in Figure 1. We note that this climate dataset represents regional climates, and so will not fully capture the growing condition experienced at the individual or population scale. Short datasets from high elevation meteorological stations have recently been established by the National Observatory of Athens, and were used for comparison with the gridded dataset (Figure S 1). In addition to temperature and precipitation data, we also quantified drought using the Standardized Precipitation-Evapotranspiration Index (SPEI, Vicente-Serrano *et al.*, 2010) using a 3-month window such that the drought index for July incorporated data for May, June and July (with all months equally weighted). In addition to the gridded climate data, regional climate reconstructions were used to provide information on regional climate trends prior to the observational record (Griggs *et al.*, 2007; Klesse *et al.*, 2015; Levanic *et al.*, 2015).

Ancillary data

The diameter at breast height (DBH) and tree height were measured individually for all sampled trees using a tape measure and a Haglof Vertex III hypsometer. For each sampled tree, age was calculated by estimating the number of missing inner rings for each core (i.e. when the core missed the centre of the tree) and adding this to the number of measured rings. The number of missing rings for each core was estimated by dividing the distance from the innermost measured ring to the pith by the mean ring width of the ten innermost measured rings.

Statistical analysis

To quantify the relationship between annual growth and climate, we calculated bootstrapped correlation coefficients and response functions between the prewhitened RWI chronologies and monthly climate data (*PREC* and *MAX*), using the `bootRes` package in R (Zang and Biondi, 2013). Correlations were calculated for the period 1958-2010, which fully incorporates all site chronologies in the network (Table 2), and limits analysis to the period of more comprehensive climate station data in Greece (although note that the gridded dataset CRU TS 3.2.10 was used for the analysis). Moving Correlation Analysis (MCA) was used to assess the temporal stability of growth-climate relationships. 20 year intervals were used for MCA, with a ten year time-step (i.e. a total of four windows). To assess changes in tree growth, and compare changes in growth between sites, mBAI chronologies were standardised by subtracting the chronology mean and dividing by the standard deviation, and linear trends for the period 1991-2010 calculated using linear regression.

Results

Growth-climate relationships

The growth-climate analysis of the 21 chronologies revealed relationships between *RWI* and both temperature and precipitation for the period 1958-2010 (Figure 2 and S 4). The results of the correlation and response function analyses were broadly consistent, and subsequent analysis therefore focused on the response function analysis only, as it accounts for autocorrelation between monthly climate variables. For temperature (*MAX*) the strongest signals negative relationships between *RWI* and temperature in the summer of growth, and at some sites, with previous summer temperature (Figure 2). However, for the year of growth the relationships were significant in the response function analysis in only four chronologies (all July). In the correlation analysis, 13 chronologies had at least one significant correlation between *RWI* and temperature for either June, July or August in the year of growth (Figure S4). Relationships between *RWI* and summer temperature were stronger at low elevations, both along the Vermio transect and in the rest of the network (Figure 2). At some high elevation sites growth was favoured by warm temperatures in May (significant at two sites), but relationships between growth and temperature were negative for the remaining months of the growing season at all sites.

Strong positive relationships between RWI and precipitation were found at sites across the network, with precipitation in the growing season and previous summer the key factors (Figure 2). The strength of these relationships also showed strong variation with elevation throughout the early- to mid-summer (May-July), with strong and frequently significant positive relationships at low elevation sites. At higher elevations, relationships were weaker, but only rarely negative (Figure 2). However, RWI was negatively related to precipitation in April, especially at low elevation sites along the Vermio transect. RWI was generally positively related to precipitation in the late summer prior to the growing season (July-September), with signification response functions at six high or medium elevation sites.

Growth-climate relationships through time

Testing the stability of growth-climate relationships was challenging due to the relatively short length of reliable climate records in this region, with CRU TS 3.10.01 based on increasingly sparse station data

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194 prior to 1958. However, moving correlation analysis (MCA) showed that the strength of growth-climate

195 relationships varied through time during the period 1961-2010 (Figure 3). Overall, correlations between

196 RWI and summer temperature (MAX_{JJA}) were negative across all 21 sites, but generally became weaker

197 in recent decades (i.e. the 1981-2000 and 1991-2010 windows), particularly at low elevations along the

198 Vermio transect (although relationships were rarely significant). For example, along the Vermio transect,

199 5 of the 11 sites had significant negative correlations between *RWI* and MAX_{JJA} for the window 1971-1990,

200 but for the most recent window 1991-2010 only one of these correlations was still significant, and the

201 correlation coefficient had declined for 10 of the sites.

202 For precipitation, the most recent window was also associated with an apparent a decline in the strength

203 of correlations (Figure 3). This decline in correlation was stronger for sites on the Vermio transect, where

204 the correlation coefficients shifted to <0.2 (i.e. close to zero) for the 1991-2010 window for all but one

205 site. Correlations were >0.2 for at least eight sites for all the previous three windows. Similar shifts in

206 correlations were found in the rest of the network, especially at low and medium elevations.

207 **Long-term growth trends**

208 Throughout most of the twentieth century, decadal trends in mBAI broadly mirrored decadal trends in

209 summer drought stress with lower growth during periods with drier and warmer summers (Figure 4).

210 This was particularly evident along the Vermio transect. For example, the periods 1920-1930 and 1945-

211 1955 were associated with lower mBAI at most sites. However, recent mBAI trends were positive across

212 the network, including at high and low elevations, and at the most southerly sites (Figure 4). Importantly,

213 trends for the period 1991-2010 were not significantly correlated with the age of the sampled trees

214 (mean sampled tree age). Additionally, in all but two cases, trends for the period 1991-2010 were more

215 positive than the period 1971-1990, indicating that positive trends were not due to age effects (Table S

216 1). Furthermore, the decade centred on the year 2000, which had consistently low summer precipitation

217 was generally not associated with a strong growth suppressions, in contrast to previous periods with

218 similar climate conditions. Indeed, at most sites mBAI showed strongly positive trends through this

219 period (significant at seven of the eleven sites on Mt Vermio, and at two of the ten sites in the rest of the

9

220   network). Only three sites showed evidence of negative mBAI trends in the period 1991-2010; these were

221   two treeline site (VERM19 and VERMTL) and the lowest elevation site in the network (OSSA06), although

222   at both these sites the trends were close to zero and not statistically significant. Consequently, there was

223   no overall significant relationship between mBAI trend and elevation across the network, and with the

224   exception of OSSA06 all low elevation sites had positive trends in mBAI.

225

Discussion

Response of growth to recent changes in climate

The response function analysis revealed summer temperature and precipitation control on interannual variations in growth, with strong and frequently significant relationships between RWI and summer temperature and precipitation across the network (Figure 2). The relationships were particularly strong at low elevations. The association between mBAI and climate also indicated drought limitation on growth with mBAI decreases associated with dry (and hot) periods in the 1920s, during the 1940s and 1950s, and to a more limited extent during the 1980s (Figure 4). These results were consistent along the Vermio transect (11 sites) and, to a more limited extent, across the rest of northern Greece (10 sites). Previous studies have reported strong coherence between beech growth trends in southern Europe and decadal changes in climate (Piovesan *et al.*, 2008; Castagneri *et al.*, 2014; Tegel *et al.*, 2014). Together with the results of the response function analysis, these results have important implications for the future of this species in southern Europe. If climate continues to warm without an increase in precipitation (Giorgi and Lionello, 2008), this will be expected to lead to a general reduction in the growth of beech at all elevations in Greece (although the response at the population level will be determined by a combination of regional climate changes and local factors, such as soil depth or nutrients). We see evidence to support this is our network, with declines in mBAI during the late 1970s and 1980s in many sites. However, since 1990 the association between growth trends and climate has weakened. For example, mBAI increased at most sites from around ~1990, despite many parts of the study region experiencing decadal-scale drought through the late 1990s and early 2000s (Figure 4). Additionally, MCA revealed weaker correlations between *RWI* and summer temperature and precipitation in recent decades (and specifically for the period associated with these positive mBAI trends, 1991-2010). The positive mBAI trends, and the apparent decoupling of both decadal growth trends and *RWI* from regional summer climate, are consistent with some recent studies of beech elsewhere in southern Europe (Tegel *et al.*, 2014), but contradict other tree ring studies and also model simulations of growth declines in low elevation beech forests (Jump *et al.*, 2006; Piovesan *et al.*, 2008; Fyllas and Troumbis, 2009). Furthermore, while Tegel *et al.* (2014) also reported strong

253 recent increases in beech growth in the Balkan region, these forests were located in regions of higher

254 summer precipitation, while the sites in this network are located in the drier southeast of the Balkan

255 peninsula, close to the xeric limit of the species distribution. Additionally, while Cavin and Jump (2016)

256 found little evidence of growth declines in southern beech forests in the Iberian peninsula, these sites

257 were also associated with weak growth-climate correlations. This can be interpreted as indicating that

258 these sampled trees represent "climate-relics", occupying specific locations where microclimates

259 dominate (Cavin and Jump, 2016). In contrast, the sites in the Greek network reported in this study show

260 stronger relationships between *RWI* and regional summer temperature and precipitation, indicating

261 coupling of forest growth to regional weather conditions. Consequently, these forests are expected to also

262 respond to decadal changes in regional climate, including the recent increases in summer temperature.

263 The lack of evidence for a decline in recent growth in Greek beech populations over recent decades,

264 despite increasing drought stress could result from biases in tree-ring chronologies (Bowman *et al.*,

265 2013), but these are unlikely to fully explain the positive trends we detect, particularly as we account for

266 a major source of bias by considering only mature-phase growth (mBAI). Alternatively, the recent

267 increases in BAI across the whole elevation gradient could be the result of environmental changes such

268 as increasing atmospheric CO_2, reduction in air pollutants including ozone, or changes in management.

269 Carbon assimilation in Greek beech forests is strongly limited by stomatal conductance during dry

270 conditions (Raftoyannis and Radoglou, 2002), and an increase in water use efficiency (WUE) as a

271 consequence of higher atmospheric CO_2 will be expected to lead to increased growth in a carbon-limited

272 ecosystem (assuming negligible effects of any changes in humidity). However, numerous studies have

273 failed to detect growth increases, despite increased WUE, including in other southern European beech

274 forests (e.g. Penuelas *et al.*, 2008).

275 **Relationships between growth and climate**

276 The analysis of relationships between growth and regional climate revealed that summer temperature

277 and precipitation were the key climate signals in beech tree ring chronologies from across Greece (Figure

278 4). Summer drought has been identified as the key driver of beech tree-ring chronologies across the

279 species distribution of beech, including at the southern distribution edge (Dittmar *et al.*, 2003; Piovesan

280 *et al.*, 2005; Hacket Pain *et al.*, 2016). In the only other published investigations of beech chronologies

281 from the Balkan peninsula, Tegel *et al.* (2014) and Castagneri *et al.* (2014) also found that growth of beech

282 was sensitive to summer climate, but that temperature was a stronger control than precipitation.

283 However both of these studies noted the poor quality of climate data in the western Balkans, which likely

284 influenced the strength of statistical relationships. Additionally, annual and summer precipitation is

285 much higher in mountains of the western Balkans than in the region studied here (Figure S 2). While

286 growth was limited by summer temperature and precipitation across the network in this study, the

287 strength of the relationships were stronger at the lowest elevation sites (Figure 2). This variation in

288 response function coefficients with elevation was particularly strong for summer precipitation,

289 consistent with numerous previous studies of beech (e.g. Hartl-Meier *et al.*, 2014), and indicates that

290 growth at low elevation sites is more strongly controlled by water availability. The low elevation sites in

291 this study represent trees growing close to the distribution limit, which according to previous studies

292 and the classic dendrochronological literature are expected to show stronger relationships between

293 growth and summer drought (Fritts, 1966).

294 However, while relationships between growth and summer climate were strongest at low elevations, the

295 ~~strength of the~~ negative relationships with temperature at high elevations, including at the treeline, was

296 surprising (although note that these were only ever significant in tehn correlation analysis, Fig S 4). Low

297 temperatures are commonly thought to limit tree growth in high elevation or latitude forests, and tree-

298 ring studies have tended to find a positive effect of higher temperatures on growth at high elevations

299 (Wettstein *et al.*, 2011), including in beech forests (Dittmar *et al.*, 2003; Latte *et al.*, 2015). However,

300 Piovesan *et al.*, (2005) found strong summer drought signals in high elevation beech forests in Italy, and

301 recent studies from conifer treelines in the Balkans have found similar results (Panayotov *et al.*, 2010;

302 Klesse *et al.*, 2015). This has been linked to thin soils and steep slopes at high elevations, which also

303 applies in this study (Supplementary Table 1).

304   Strong and significant relationships between growth and the temperature and precipitation of the

305   previous summer were also common across the network (Figure 4 and S4), but were strongest at highest

306   elevations and in the sites with the oldest trees. Unfortunately, as the site elevation and mean site tree

307   age are correlated in our network, it is difficult to distinguish these two influences, although future

308   analysis at the individual tree level may allow separation of age and elevation effects. In conifers, the

309   importance of previous summer weather in treeline chronologies has been linked to the short growing

310   season, which reduces the availability of carbohydrates at the start of the following growing season

311   (Panayotov *et al.*, 2010). Similarly, in beech, 20-30% of annual growth is thought to rely on carbon

312   assimilated in the previous year (Cufar *et al.*, 2008). An alternative explanation for the correlations

313   between growth and previous summer climate is related to masting phenomenon (Hacket-Pain *et al.*,

314   2015). Years of heavy seed production are cued by conditions in the previous summer, and are

315   themselves associated with strong growth reductions (Drobyshev *et al.*, 2010). The increase in the

316   strength of correlations with previous summer temperature with increased elevation (and age) might

317   result from greater growth reductions in mast years, due to stronger growth-reproduction trade-offs at

318   sites with longer growing seasons or with older trees (Thomas, 2011).These hypotheses are difficult to

319   test in this study due to the lack of data on seed production in the Balkan region, but two mast years

320   reported in beech forests in northern Greece by Gerasimidis *et al.* (2006) correspond to years of low

321   growth across the network (1998 and 2001).

Conclusions

We found inter-annual growth of *F. sylvatica*, as estimated using tree-ring chronologies, in southeastern Europe to be correlated with summer precipitation and temperature. Trees at all elevations were sensitive to summer drought, including sites at the treeline. Until the end of the 1990s, decadal trends in mBAI closely matched regional summer climate, with growth decreases during periods of drier and warmer summers. However, in recent decades relationships between inter-annual and decadal climate variability and growth have weakened. Recent mBAI trends are positive across the network, including at low elevation sites, despite an ongoing warming trend in the region. These results were consistent along both an intensively sampled elevation transect (Mt. Vermio) and in a network of sites across northern Greece. We suggest that these results indicate that beech forests in this region may be more resistant to regional climate changes than previously considered.

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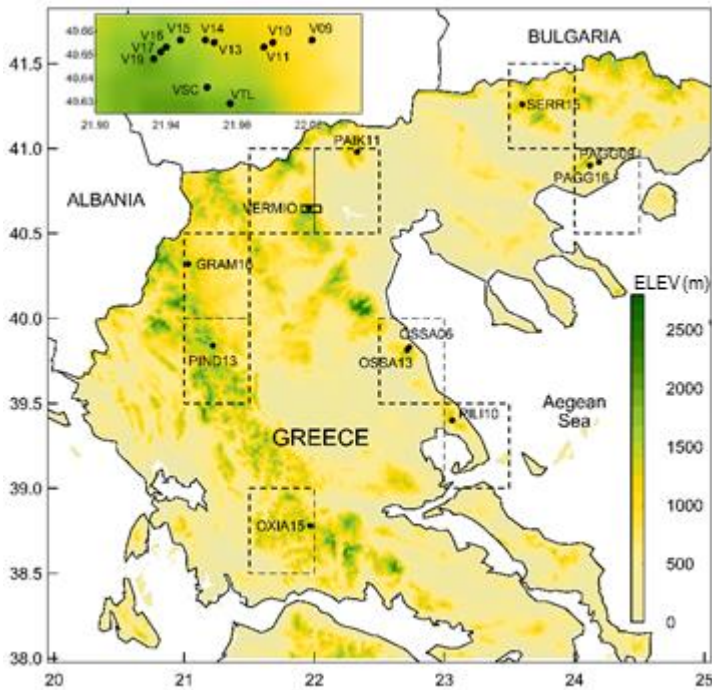
Figure 1. The location of the sites included in the *F. sylvatica* tree ring network in Greece. The rectangle
labelled VERMIO shows the location of the transect on Mt. Vermio, enlarged in the inset map. The dashed
boxes represent the grid cells for the gridded climate data (CRU TS 3.10.01). Note that the two lowest
elevation sites in the Vermio transect (VERM10 and VERM08) fall slightly outside grid cell, but the
decision was taken to use the same climate data as the rest of the transect for consistency.

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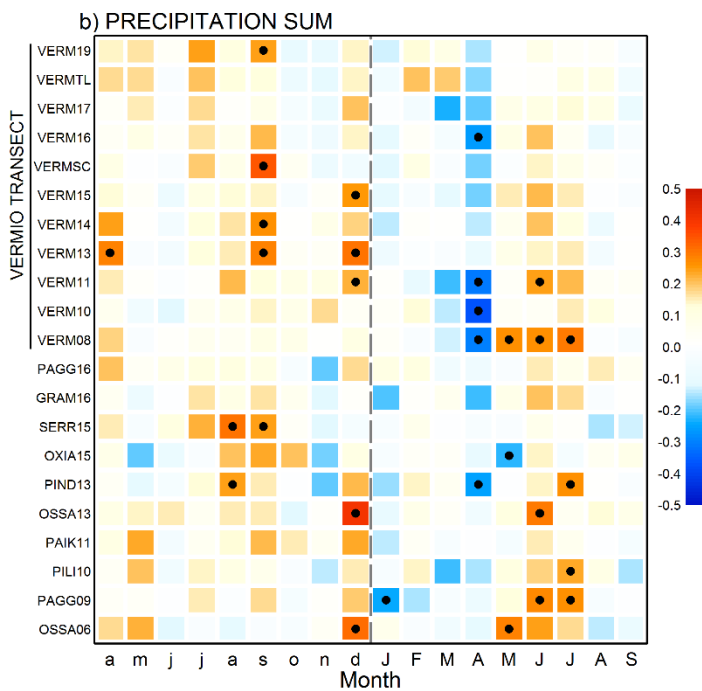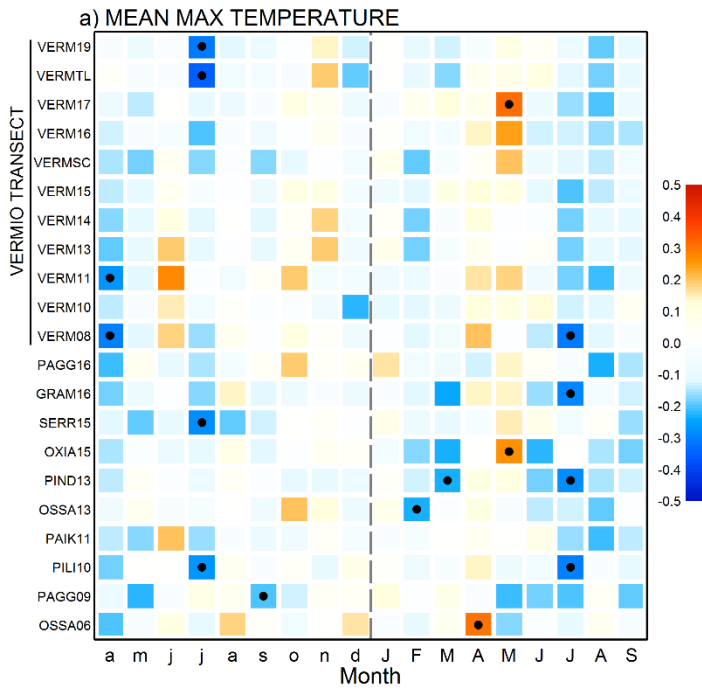
Figure 2. Response function coefficients of ring width index (*RWI*) and monthly climate variables for each site. a) Monthly mean maximum temperature (*MAX*). b) Monthly total precipitation (*PRE*). Response functions were calculated for the period 1958-2010 (common to all sites) and significance was calculated using bootstrapping (95% confidence level), and indicated by black circles. Sites are ordered by elevation.

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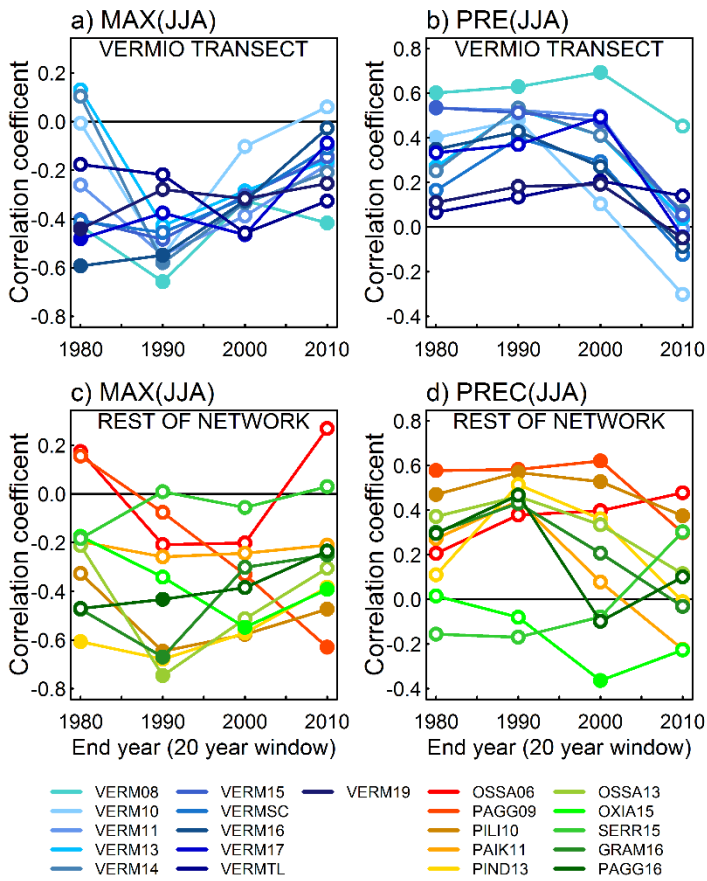
Figure 3. Moving Correlation Analysis, calculated using 20 year windows with 10 year time-steps, and plotted according to the end year of each window. Filled points indicate significance at the 95% confidence level, estimated using bootstrapping. a) MAX_{JJA} for the Vermio transect. b) PRE_{MJJ} for the Vermio transect. c) MAX_{JJA} for the rest of the network. d) PRE_{MJJ} for the rest of the network.
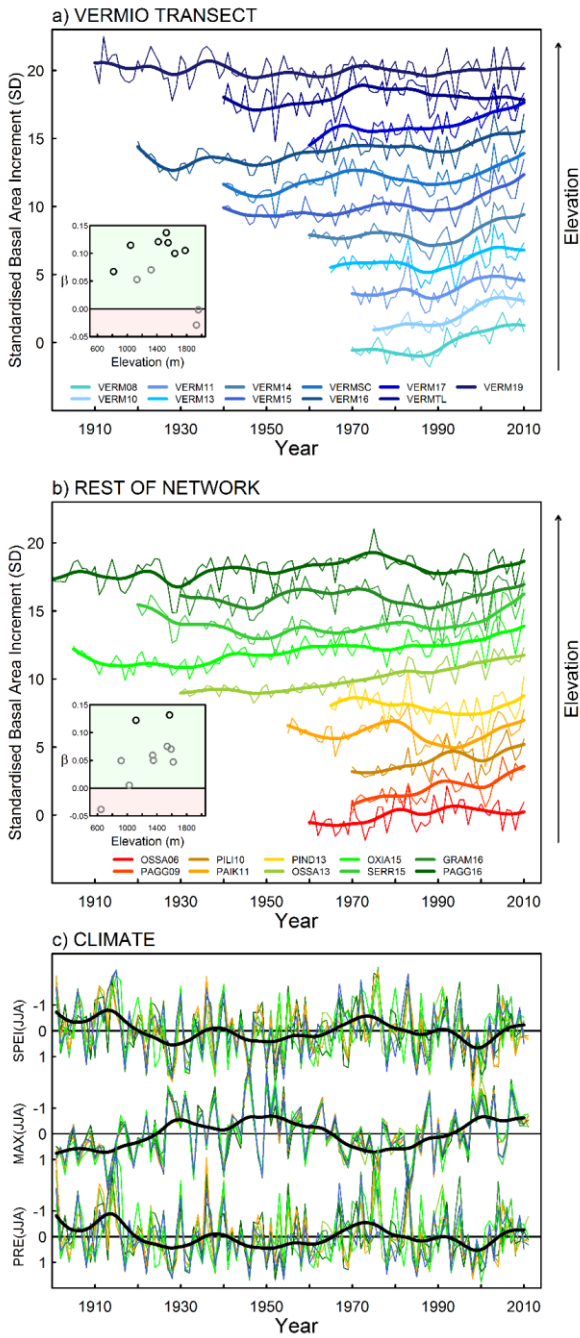
Figure 4. Mature phase standardised Basal Area Increment (mBAI) chronologies for each site. a) mBAI chronologies for sites on the Vermio transect, ordered vertically by elevation (with an cumulative offset of 2 SD units). Splines of mBAI chronologies are used to highlight growth trends (frequency response = 50%, wavelength = 16 years). Sites are ordered by elevation. The inset plot shows the slope of the linear trend in mBAI over the period 1991-2010, plotted against the elevation of the site. Significant slopes (p<0.05) are plotted in black. b) as for a), but for the rest of the network. c) CRU TS 3.10.01 climate data for the period 1901-2010, with splines plotted to highlight trends. Climate data was scaled and centred.

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