Original Article

Geographically structured and temporally unstable growth responses of *Juniperus thurifera* to recent climate variability in the Iberian Peninsula

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Abstract

Geographically structured tree-ring networks are needed to fully understand the spatio-temporal variability in climatic sensitiveness of trees and to study their future responses to global warming. We aim to identify the spatially-constrained structure of radial-growth patterns of the Spanish juniper (*Juniperus thurifera* L.) and to assess whether their climate-growth responses were unstable during the late twentieth century. Tree-ring width chronologies were built for 13 *J. thurifera* stands in Spain using dendrochronological methods and related to monthly climatic data. Sites were grouped according to their growth patterns using hierarchical cluster analysis. The relationships among geographical, climatic and stand features and their influence on radial growth were evaluated using redundancy analysis. The climate-growth relationships and their temporal stability were assessed using Pearson's and moving bootstrapped correlations, respectively. Stands formed three geographical groups according to their high-frequency growth variation: North West and Centre, North East, and South East. We found that *J. thurifera* radial-growth patterns depended on geographical and climatic factors, but not on the stand structure, and responded to a northwest-southeast gradient of decreasing rainfall and influence of Atlantic Westerlies and Mediterranean cyclonic activity. The positive response to June precipitation was unstable during the late 20th century and started earlier in populations from western mesic sites than in eastern xeric sites. This pattern may be related to either decreasing water availability in western than in eastern sites, or the resilience of *J. thurifera* growth from xeric sites in response to the increasing summer aridity.

Keywords: climate warming; dendrochronology; juniper; Mediterranean Basin; network; tree-ring.

Introduction

The current distribution areas of tree species in Europe are a consequence of historical processes such as glaciations or land-use changes and the capacity of each species to respond to environmental constraints such as climate (Svenning and Skov 2004). The role of these factors on determining the present range of several species has been evaluated (Davis and Shaw 2001) although detail studies about how past and current climatic constraints influence tree growth across the distribution area of selected European tree species are still needed. Such spatiotemporal assessment is required to forecast potential responses of tree growth to current climate warming throughout the species' distribution range. First, populations at the geographical margin of the range may show negative growth responses and decline processes (e.g. Macias et al. 2006). Second, nonlinear growth responses to the unprecedented rates of temperature rise and to the increase of climatic variability (e.g. more frequent and severe droughts) may also be expected and their effects may be more evident in harsh environments, such as marginal areas with pronounced water deficit (Andreu et al. 2007; Sarris et al. 2007). Finally, critical reviews of simulation models have emphasized that tree growth in central locations does not only respond to climate but also to other environmental factors (Loehle and LeBlanc 1996).

Nevertheless, few insights of growth patterns throughout most of the distribution area of tree species exist so as to compare the growth response to climate in central and marginal populations (Jump et al. 2006; Gaston 2009 and refs. therein). Such studies would provide a preliminary spatiotemporal analogy of growth responses to a changing climate because they would include central and marginal populations, potentially yielding divergent responses to contrasting climatic conditions. The current geographically diverse climates throughout the ranges of tree species might include climatic conditions similar to some of those predicted under the future warming.

Dendrochronology is an appropriate tool to describe tree-growth patterns and their dependence on climate at multiple spatial and temporal scales ranging from stands to whole distribution range and from years to centuries (e.g. Tardif et al. 2003). Common or divergent growth patterns among neighbouring or distant tree populations can reflect ecologically and climatically homogeneous territories (Cook et al. 2001; Piovesan et al. 2005; Di Filippo et al. 2007) and can be used to detect geographical gradients for tree growth and forest productivity (Mäkinen et al. 2002; Carrer et al. 2007). Furthermore, networks of tree-ring chronologies have been increasingly used to detect geographical patterns in climate-growth relationships and even to describe the temporal stability of such relationships (Tardif et al. 2003; Carrer et al. 2007; Di Filippo et al. 2007). Nonetheless, the geographical and temporal variations of tree-ring growth across most of the distribution range of a tree species have been rarely assessed. Such spatiotemporal description would benefit from including climatically constraining sites (e.g. both water- and temperature-limited sites) which can provide a valuable analogue to the forecasted climate change conditions.

In the continental areas of the western Mediterranean Basin such as the Iberian Peninsula, summer drought and low winter temperatures are the main constraints of tree growth (Mitrakos 1980). Consequently, the growing season is split in two separated periods, spring and autumn, corresponding to the periods with enough water availability and mild temperatures (Camarero et al. 2010). In this area, several studies have reported a pronounced warming trend in the last decades, and a general decrease in precipitation in the Mediterranean margin of the Iberian Peninsula has been predicted (van Oldenborgh et al. 2008). There is a great uncertainty on how such warming will affect tree growth in continental Mediterranean areas, where we can expect that rising temperatures may enhance growth in spring or autumn but increase water deficit in summer (Christensen et al. 2007). The observed growth declines and time-dependent climate-growth relationships in several Mediterranean

100 tree species have been attributed to increasingly drought-stress conditions induced by climate
101 warming (Jump et al. 2006; Macias et al. 2006; Andreu et al. 2007; Carrer et al. 2007; Sarris
102 et al. 2007; Linares et al. 2009). However, most of these studies were focused in reduced
103 mountainous areas where the interaction between climatic and topographic factors causes
104 complex spatiotemporal patterns of tree growth (Tardif et al. 2003; Leonelli et al. 2009).
105 Hence, we need a detailed assessment of the impacts of climatic constraints on tree growth
106 across most of the species distribution range but taking also into account the effects of
107 topography on growth responses to climate.

108 The Iberian forests of Spanish juniper (*Juniperus thurifera* L.) provide the opportunity to
109 solve the mentioned shortcomings since over 80 % of the world range of this tree, endemic to
110 the western Mediterranean Basin, is located in Spain (Gauquelin et al. 1999). *Juniperus*
111 *thurifera* is a long-lived evergreen species growing under continental and cold climatic
112 conditions, dominating valuable ecosystems and forming unique landscapes (Fig. A1). Most
113 extant populations are located at 300-3300 m elevation in Spain and Morocco, whereas relict
114 populations exist in the French Alps and Pyrenees, Corsica and Algeria (Gauquelin et al.
115 1999). These inland forests are affected by diverse climatic influences such as warmer and
116 drier conditions in low-elevation sites towards the Mediterranean coast, and colder and more
117 humid conditions towards the north-western Atlantic coast (Esteban-Parra et al. 1998;
118 Rodríguez-Puebla et al. 1998). The comparative study of the sensitivity of this species to
119 climatic patterns across geographical gradients in the Iberian Peninsula can provide a deeper
120 understanding of the potential effects of climate change on inland Mediterranean ecosystems.

121 Thus, we can expect a geographic variation in the climatic response across the Iberian *J.*
122 *thurifera* range, as a consequence to the west-east gradient of decreasing water availability in
123 the Iberian Peninsula. We may also hypothesize that such growth response would be unstable
124 through time being more marked during recent decades in response to warmer conditions and

lower water availability. To test whether the tree-growth sensitivity to climate is spatially structured and temporally stable over the last decades, we established a network of *J. thurifera* tree-ring chronologies in the Iberian Peninsula. Our specifics aims were: (1) to characterize the spatiotemporal heterogeneity of radial-growth patterns across the Iberian distribution range of *J. thurifera*, (2) to identify the main geographical, topographical and climatic factors that determine this heterogeneity, and (3) to ascertain the temporal consistency of the limiting climatic factors that influence the growth of *J. thurifera* across its Iberian range.

Material and methods

Study sites

We sampled 13 *J. thurifera* stands located across its Iberian distribution range (38.5–43.5º N latitude and 0–6º W longitude), with elevations ranging from 350 to 1400 m (Table 1). *J. thurifera* was the dominant tree species in the stands and frequently coexisted with *Pinus* and *Quercus* species of diverse biogeographical origin (Table A1). Most *J. thurifera* forests in Spain are found typically in northern mountains (Fig. A1a; sites LA, LU), plateaus or canyons in calcareous ranges in the central Spanish Meseta (Fig. A1b; sites AR, BU, CA, CH, CI, OL, VE), and in semiarid or xeric eastern sites (Fig. A1c; sites RE, SA, VI). All study sites are subjected to a continental Mediterranean climate characterized by (1) summer drought, which increases from the North West to the South East in Spain (Fig. 1a), and (2) low winter temperatures with frequent frosts and snowfall throughout the continental Iberian distribution range of the species.

148 **Climatic data**

149 The climatic database used in this study corresponds to the TS 3.0 dataset produced by the
150 Climate Research Unit (CRU 2008). This dataset is based on instrumental records from a
151 network of meteorological stations over the global land surface which have been subjected to
152 homogeneity tests and relative adjustments, and finally gridded onto a 0.5º network (Mitchell
153 and Jones 2005). We downloaded monthly mean temperature (T) and total precipitation (P)
154 data for the studied period using the Climate Explorer of the Royal Netherlands
155 Meteorological Institute (http://climexp.knmi.nl).

156 Mean annual temperature ranged from 9.2 to 14.9 ºC among study sites. January was the
157 coldest month (mean minimum temperatures ranging from –3.4 to 2.2 ºC) and July the
158 warmest (mean maximum temperatures ranging from 23.7 to 33.0 ºC). Mean annual
159 precipitation was highly variable among study sites, ranging from 435 to 824 mm. May was
160 the wettest month (45.0 – 79.2 mm) and July the driest one (7.1 – 37.7 mm), and water deficit
161 occurred from June to September in most of the sites.

162

163 **Field sampling and dendrochronological methods**

164 We randomly selected 20 dominant mature trees without external signs of bole dieback in
165 each stand. Diameter at breast height (DBH) and total height were measured in the main stem
166 of each sampled tree. Two cores per tree were taken from opposite sides of the stem at 1.3 m
167 above ground using an increment borer. At the Cabrejas site, the samples were stem disks
168 from 23 mature trees taken at 1.3 m above ground (Rozas et al. 2009).

169 Wood samples were processed using standard dendrochronological procedures (Stokes and
170 Smiley 1996). Cores and disks were dried, mechanically surfaced and then manually polished
171 with a series of successively finer grades of sandpaper until the xylem cellular structure was
172 clearly visible. After visual cross-dating, tree-ring widths were measured to the nearest 0.001

mm using a sliding-stage micrometer (Velmex Inc., Bloomfield, NY, US) interfaced with a computer. The individual tree-ring series were statistically compared with a site master chronology using the COFECHA program and checked for dating accuracy (Holmes 1983; Grissino-Mayer 2001). All series with potential errors were corrected when possible, including those containing missing or false rings, or discarded.

A site chronology was calculated from those ring-width series correctly synchronised within each site. Tree-ring width series were standardised with the ARSTAN program by using a two-step procedure (Cook and Holmes 1996). The series were first fit to a negative exponential function, and then to a cubic smoothing spline with a 50% frequency response of 64 years, which was flexible enough to reduce the non-climatic variance by preserving high-frequency climatic information (Cook and Peters 1981). The obtained indices were averaged on a year-by-year basis using a biweight robust mean, and the mean series subjected to autoregressive modelling to obtain residual site chronologies of prewhitened growth indices (see Fig. 2). Several descriptive statistics were calculated for the common interval 1951-2002 (Cook and Kairiukstis 1990; Fritts 1976) from the raw tree-ring widths (MW, SD and AC), and the residual site chronologies (ms_x, r_{bt}, EPS, E1 and SNR). MW and SD are mean tree-ring width and their standard deviation, AC is the first-order autocorrelation, a measure of the year-to-year growth similarity. Mean sensitivity (ms_x) is a measure of the year-to-year variability in width of consecutive tree rings, mean between-trees correlation (r_{bt}) is a measure of the similarity in growth among trees, expressed population signal (EPS) is a measure of the statistical quality of the mean site chronology as compared with a perfect infinitely replicated chronology, percentage of variance explained by the first principal component (E1) is an estimate of the common variability in growth among all trees at each site, and signal-to-noise ratio (SNR) is a measure of the strength of the common high-frequency signal in the ring-

width indices of trees from the same site. The period with at least five trees in all site chronologies was regarded as the statistically reliable common period.

Characterization of growth heterogeneity

A hierarchical cluster analysis (HCA) was performed using the euclidean distances matrix between residual chronologies and based on the Minimum Evolution algorithm of Desper and Gascuel (2002) which fits the dendrogram to the data and determines the branch lengths (distances) by using unweighted least square methods. Therefore, least squares dendrograms were obtained for different topologies and then the topology of shortest total lengths among the sites was selected. The obtained clusters of residual chronologies were considered as homogeneous groups with similar high-frequency growth variation and validated by the bootstrap technique. We calculated the proportion of bootstrapped clusterings that support the groupings displayed in HCA analysis and stated them for each dendrogram node. HCA was performed with the *ape* package (Paradis et al. 2004) in the R environment (R Development Core Team 2010).

Geographical determinants of tree-growth variability

Distance-dependent relationships among site chronologies were assessed comparing their common growth variability, computed as the Pearson's correlations between all the site chronologies for the common period 1951-2002, as a function of the distance for all site pairs (teleconnection), calculated from the sites latitudes and longitudes (Carrer et al. 2010). To summarize the relationships among site chronologies a principal component analysis (PCA) was performed on a correlation matrix calculated among the chronologies considering the common period. The first two components of the PCA (PC1, PC2) were selected because they had eigenvalues greater than one (Garfin 1998). Lastly, linear or quadratic regressions

between stand characteristics (latitude, longitude, elevation) and statistics (MW, SD, AC, ms_x, r_{bt}, EPS, SNR, PC1 and PC2 of the network) were performed to recognise the geographical dependency of growth patterns.

Growth-variation partitioning among geographical, climatic and stand variables

The relative importance of geographical, climatic and stand features in determining the high-frequency variation of radial growth was evaluated via constrained ordinations (ter Braak 1986). Since the expected gradient was short, we performed a Redundancy Analysis (RDA) on the correlation matrix calculated among residual chronologies matrix. RDA searches those linear combinations of environmental factors (geographical, climatic and stand features) that are correlated to linear combinations of responses variables, in this case site residual chronologies (Legendre and Legendre 1998). We used three distinct environmental constraining matrices corresponding to three variance components to carry out RDAs: (a) a geographical matrix including elevation, longitude, latitude and the interaction term "longitude × latitude"; (b) a climatic matrix including seasonal precipitations, Continentality Index (Gorczynski 1922), Mediterraneity Index (Rivas-Martínez and Rivas-Sáenz 2009), Aridity Index (De Martonne 1925) and annual average temperature; and (c) a stand-features matrix comprising mean tree age, DBH and height.

The total variation explained (TVE) by each environmental matrix was calculated as the sum of all canonical axes obtained using each of these matrices as a constraining data matrix (Borcard et al. 1992). The significance of the relationship was assessed using a Monte Carlo permutation test based on 999 randomizations. The sum of all canonical eigenvalues corresponded to the *F*-ratio statistic (ter Braak 1988), and it was considered significant when $P < 0.05$. A forward stepwise procedure was carried out to select a reduced RDA model including only significant environmental variables for each environmental matrix. The

247 improvement of the reduced model with each new selected variable was determined by a
248 Monte Carlo permutation test with 999 randomizations. Variance partitioning was performed
249 to evaluate the relative importance of each component by adjusting the variability of the other
250 components considered as covariables (Borcard et al. 1992). In this procedure, called partial
251 RDA (pRDA), we calculated the fraction of growth variance explained independently by each
252 environmental component. These analyses were done using Canoco v4.51 program for
253 Windows (ter Braak and Šmilauer 1997; CANOCO Biometris, Wageningen, The
254 Netherlands).
255
256 **Spatiotemporal variation of climate-growth relationships**
257 The climate-growth relationships were analysed at the regional level based on the
258 composite chronologies corresponding to the geographical groups previously identified with
259 HCA. The composite chronologies were computed averaging the site series of the same
260 cluster (Carrer et al. 2007). To obtain climatic data for each regional group of chronologies,
261 we used the MET routine in the Dendrochronology Program Library package (Holmes 1994).
262 The mean temperature and precipitation data for each regional group were calculated as the
263 average of the gridded temperature and precipitation data from all sites included in that group.
264 A temporal window of 13 months was selected to identify limiting climatic factors from
265 September of the previous year (*t*–1) to September of the year of tree-ring formation (*t*).
266 Pearson's correlations and bootstrapped response functions between growth indices and the
267 climatic variables were calculated for the period 1951-2002 with the PRECON v5.17 program
268 (Fritts et al. 1991). Bootstrapped moving correlations between these climatic variables and the
269 composite regional chronologies were calculated considering 25-year intervals for the period
270 1930-2006 using the Dendroclim2002 program (Biondi and Waikul 2004).

Results

Geographical structure of tree growth variation

Tree size showed high variability among sites, with mean DBH ranging between 13.9 and 60.9 cm and mean height between 5.0 and 8.3 m (Table 1). Mean tree age varied from 50 to 154 years. Tree-ring width ranged from 0.56 to 1.27 mm (Table 2), and differed significantly among sites (Kruskal-Wallis test: $\chi^2_{12} = 301.2$; $P < 0.001$) (Fig. 3a).

The first (PC1) and second (PC2) principal components of the entire *J. thurifera* network explained 43.57% and 10.65% of the growth variance, respectively, indicating a common signal at broad scales among all chronologies. No clear relationships between chronology statistics and geographical descriptors were evident, with the exceptions of PC2 loadings of residual chronologies that showed an inverse relationship with longitude (Fig. 3b), and mean sensitivities which increased with decreasing site elevation (Fig. 3c). The correlation between trees within each site ranged from 0.37 to 0.54, whereas the variance explained by the first eigenvector ranged from 34.5 to 58.8 % (Table 2). EPS varied from 0.84 to 0.94 confirming that the amount of local year-to-year growth variation shared by co-occurring trees was consistently high. Finally, the correlation among site chronologies decreased linearly as distance increased showing significant site-to-site correlations up to approximately 300 km (Fig. 3d).

Three groups with a consistent geographic pattern were established based on the HCA (Fig. 1b). Most of the bootstrapped cluster values within the groups highly supported the reliability of the clustering. The group of stands located in North West and Central Spain (40–43º N, 2.5–6.0º W; hereafter NW-C group) included six sites (LU, LA, AR, SI, CA and BU)

296 and 150 tree-ring series, and the first two principal components of this group explained 72 %
297 of the total growth variance. A second group comprised four sites (CI, CH, RE and SA) in
298 North East Spain (41–42º N, 0.0–2.5º W; hereafter NE group) and 94 tree-ring series, and its
299 first two principal components explained 77 % of the growth variability. Finally, the last
300 group included three sites (OL, VE and VI) from South East Spain (38.5–40.5º N, 0.5–3.0º
301 W; hereafter SE group) and 71 tree-ring series, and its first two principal components
302 explained 91 % of the common growth variance.
303
304 **Geographical and climatic constraints of tree growth**
305 The geographical and climatic components explained significant fractions of the total high-
306 frequency variation of tree growth, whereas the stand-structure component did not
307 significantly influence growth patterns (Table 3). The reduced RDA model of the
308 geographical component included elevation and latitude as significant factors, and accounted
309 for 30.5 % of the growth variance. The reduced model of climate included the Mediterraneity
310 Index and annual mean temperature, and accounted for 31.7 % of the variance. TVE
311 explained by geographical and climatic data sets together was 49.4 % (F_{ratio} = 1.95, P =
312 0.001), with an important fraction of shared variation (12.9 %). In fact, their separate effects
313 on tree growth were only marginally significant (pRDA of climatic variables with
314 geographical factors as covariates: F_{ratio} = 1.50, P = 0.063; pRDA of geographical factors with
315 climatic variables as covariates: F_{ratio} = 1.34, P = 0.077), suggesting a strong spatial structure
316 of the climatic component.
317
318 **Spatial structure of climatic factors limiting growth**
319 In the period 1951-2002, growth indices of the composite NW-C chronology were
320 positively correlated with April temperature and May-June precipitation, whereas February-

March precipitation and June temperature were negatively related to growth (Fig. 4a). Composite chronologies of the NE group were also positively correlated with April temperature and May-June precipitation. Conversely, tree growth in NE sites was positively correlated with December precipitation of the previous year (Fig. 4b). The SE group chronology was positively correlated with precipitation in previous September and December, February temperature and May-June and August precipitation (Fig. 4c). Bootstrapped response functions showed that the main climatic factors limiting growth were April temperature and June temperature and precipitation in the NW-C group, December precipitation in the NE, and previous September and current May and August precipitation in SE (Fig. 4).

Temporal instability of the growth-climate relationships

The responses of composite group chronologies to the main limiting climatic factors were unstable during the late 20th century, reflecting a regional differentiation in the timing and duration of this non-stationary response. Radial growth in eastern groups was positively correlated with precipitation in previous December in 1947-1970 for the NE group, and since 1985 for both NE and SE groups (Fig. 5a). By contrast, growth in both northern groups (NW-C and NE) showed positive relationship with April temperature since 1967, while this climatic variable was not limiting for growth in SE (Fig. 5b). All three groups showed positive relationships of growth with precipitation in May, but in particular periods for each group: 1965-1974 in NW-C, 1949-1969 in NE, and since 1994 in SE (Fig. 5c). June temperature was negatively correlated with growth in the NW-C group since 1964, and for the periods 1979-1983 for NE and 1982-1989 for SE groups. The positive response to June precipitation increased during the late decades in all groups, being significant since 1964 in NW-C, 1975 in NE and 1981 in SE (Fig. 5e).

Discussion

On a broad scale, the high correlation among site chronologies indicated a shared climatic signal in the growth patterns of Spanish *J. thurifera* populations. The geographical and climatic components explained significant fractions of the total high-frequency variation of tree growth, whereas the stand-structure component did not significantly influence growth patterns at the regional scale of study (Table 3). The degree of correlation was highly related to between-site distance, suggesting that the climatic response was spatially structured. Such spatial structure allowed us to differentiate three distinct geographical groups according to their common growth patterns in the Iberian Peninsula (NW-C, NE and SE), comprising most of the world distribution range of *J. thurifera*.

Elevation exerted an independent influence in structuring the between-site correlation and affected negatively the mean sensitivity of chronologies, i.e. the high-frequency variability in radial growth. The sensitivity of *J. thurifera* growth increased in the low-elevation sites (RE, SA) located in the semi-arid Middle Ebro Basin where summer droughts are more intense and frequent than in higher-elevation sites. In these semi-arid sites annual precipitation greatly fluctuates between consecutive years and likely controls tree-ring development which shows higher interannual variability. Probably, the negative relationship between elevation and mean sensitivity may be considered a characteristic of inland areas with pronounced water deficit where precipitation increases at higher elevations due to topographical effects, as occurs in other conifer forests under continental Mediterranean climates (e.g., Linares et al. 2009). Contrastingly, in wetter subalpine mountain forests, elevation and mean sensitivity are usually positively related because tree growth is mainly dependent on temperature, which is more

limiting for growth at higher elevation (e.g. Tardif et al. 2003; Piovesan et al. 2005; Di Filippo et al. 2007). Nevertheless, our findings need further verification since few stands appeared in mid-elevation sites (600-900 m) due to the topographical distribution of *J. thurifera* in the Iberian Peninsula.

In Mediterranean inland areas, summer drought and winter cold are the major constraints of radial growth, whereas spring is usually the most favourable season for xylem growth (Cherubini et al. 2003; Camarero et al. 2010). The secondary growth of *J. thurifera* was mostly associated to spring and early summer conditions being enhanced by warmer conditions in April and higher precipitation in May and June, in accordance with previous studies on the species (Bertaudière et al. 1999; Camarero 2006; Rozas et al. 2009). Our results are consistent with recent xylogenesis analyses in *J. thurifera*, which found that spring cambial onset, started in April or May in a warm xeric and a cold mesic site, respectively, whereas the maximum rate of wood formation was observed respectively in May or June (Camarero et al. 2010). Contrastingly, a warmer June or July, which was related to a lower growth, probably induces greater evapotranspiration, showing that water availability in late spring and early summer was crucial for growth in this species. These findings agree with the observed low growth rates in north western sites (LA and LU) and in both eastern groups, suggesting that their growing season was respectively constrained by cold spring and summer drought. These patterns indicate a strong longitudinal gradient of climate-growth relationships at broad scales, probably associated to atmospheric patterns, which is consistent with: (1) the mean size of observed regional groups of site chronologies (ca. 300 km), (2) the strong connection between geographical longitude and the second principal component of all chronologies, and (3) the geographically structured growth-climate relationships observed in the composite regional chronologies.

We found similarities in growth responses to climate in all composite regional chronologies, with *J. thurifera* growth being enhanced by late-winter (February) to early-spring (April) temperatures and late-Spring (May) to early-summer (June) precipitation. However, distinctive patterns were also detected which may be associated to particular climatic conditions in each region affecting carbon gain during winter. In north western and central sites growth was mainly enhanced by warm and dry conditions in late-winter and early-spring and wet summer conditions. This winter effect could be explained as the indirect influence of anticyclonic events on diurnal temperatures and the increase of solar radiation received, with the consequent rise in carbon assimilation (DeSoto 2010) and likely more intense spring growth in these cold sites (Chapin et al. 1990 and refs. therein; Larcher 2000). In high-latitude forests, this result has been interpreted as a delay in the start of the growing season due to both cold winter temperatures and high snowfall, which result in a greater depth of soil freezing and a delay of snow melt in the spring (Mäkinen et al. 2002; Euskirchen et al. 2006).

In contrast, early winter precipitation (previous December) enhanced growth in NE and SE groups which may be caused by a greater replenishment of the soil water budget in these semi-arid areas, before tree-ring formation starts in spring when water deficit can be noticeable (Camarero et al. 2010). Furthermore, evergreen Mediterranean conifers are able to maintain the photosynthetic activity during the winter, although at lower rates than during the growing season (Larcher 2000). The surplus of carbohydrates assimilated before tree-ring formation may be stored and subsequently allocated to earlywood formation in spring after cambial reactivation (Kagawa et al. 2006). Therefore, the influence of winter precipitation on subsequent *J. thurifera* growth in all groups may be also a response to mild winter conditions leading to an increase in the assimilation of carbohydrates (Skomarkova et al. 2006; DeSoto 2010), and an earlier cambial resumption. Moreover, the positive response of *J. thurifera*

radial growth to precipitation in the previous fall and the current spring was more important in semi-arid eastern sites (NE and SE groups) than in mesic sites westwards. Latter difference agrees with observed phenological differences between mesic and xeric sites, since spring cambial reactivation occurred *ca.* one month earlier and lasted longer under warmer (e.g. sites from the NE and SE groups) than under colder conditions (e.g. sites from the NW-C group) (Camarero et al. 2010).

This geographically structured climatic response of *J. thurifera* was also verified by the spatial field correlations with climatic data (see Appendix B in supplementary material). North western sites (NW-C group) were under the influence of Atlantic atmospheric patterns controlling spring precipitation and temperature at broad spatial scales. However, the positive effect of previous winter and spring precipitation on growth of eastern sites (NE and SE groups) suggested a more localised influence of cyclonic activity from the Mediterranean Sea in the eastern sites. These results confirm that the effects of atmospheric circulation patterns on *J. thurifera* growth in the Iberian Peninsula are an indirect expression of large-scale influences on local weather types and ultimate climatic factors such as precipitation, temperature and radiation as has been observed in *Pinus halepensis* (Pasho et al. 2011).

The shared positive response of growth to June precipitation detected over the whole Iberian distribution area of *J. thurifera* was not stationary and markedly increased during the late 20^{th} century (Fig. 5). This increasing sensitivity to late-spring and early-summer precipitation coincided with a noticeable rise in the response of growth to April temperatures which we interpret as a consequence of the significant rise in spring temperatures and the decrease in precipitation observed since the 1970s over the Spanish Mediterranean region (Romero et al. 1998; Trenberth et al. 2007). Such increasing aridity and the occurrence of severe droughts have been revealed as one of the main factors constraining the recent growth of pine species in the Iberian Peninsula (Andreu et al. 2007). Nevertheless, we additionally

found that this trend of growth response was spatially structured. The timing in the climate response to the main controlling factor, i.e. June precipitation, changed among the regional groups, showing the NW-C populations an earlier and stronger responsiveness than the NE and SE ones. This pattern suggests that the positive effect of water availability in June was perceived earlier by populations in mesic sites from the NW-C group under more humid conditions than in the more xeric sites from NE and SE groups. Such pattern was not mediated by changes in the response to the previous-winter precipitation which remained high or increased slightly in xeric sites.

Two possible, but not mutually excluding, explanations can be proposed. First, drought stress might have begun to increase in NW-C sites earlier than in NE and SE sites, as the greater relative rise of summer temperatures in the NW-C sites as compared with eastern sites suggests (see Appendix C in supplementary material ; Christensen et al. 2007; Trenberth et al. 2007). Second, *J. thurifera* populations established in more xeric sites might be more resilient and less sensitive to the decrease water availability in late spring associated with rising temperatures than those living in more humid sites, which is consistent with previous findings in *Pinus virginiana* (Orwig and Abrams 1997). Moreover, populations subjected to extreme climatic events or close to physiological limits, such as frequent severe droughts and thermal stress, might be better adapted to a warming climate than those in less hazardous and stressful environments, likely due to a directional selection for resistance (Kuparinen et al. 2010; Hoffmann and Sgrò 2011).

Conclusions

The responses of *J. thurifera* to climatic variability throughout most of its distribution range shows a strong spatial structure along its Iberian range, with a northwest-southeast shift

in limiting factors and response timings as a consequence of the noticeable gradient of increasing aridity. This spatial pattern may also determine future responses to global warming as non-stationary responses to water availability in late spring-early summer during the 20th century indicate that the sensitivity to climatic change may increase, especially in mesic populations at the northwest and central Iberian range of *J. thurifera*. This study foregrounds the need of comprising a major part of the geographical range of a species, including a diversity of physiographic and climatic conditions, to fully understand tree growth responses to limiting climatic factors.

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664 **Table 1.** Geographical and structural features of the thirteen study sites. Site name, code,
665 geographical latitude and longitude, elevation, mean (range) values for tree age, diameter at
666 breast height (DBH) and height are displayed. Sites' locations are displayed in Figure 1a.
667

Group	Site	Code	Latitude (N)	Longitude (W)	Elevation (m a.s.l.)	Age (years)*	DBH (cm)	Height (m)
NW-C	Arlanza	AR	42º 02' 49"	3º 26' 42"	932	72 (57-87)	24.8 (18.5-30.1)	8.0 (6.1-12.2)
	Sigueruelo	SI	41º 10' 04"	3º 38' 15"	1114	206 (102-413)	60.9 (33.4-85.3)	8.3 (6.0-12.0)
	Cabrejas del Pinar	CA	41º 47' 37"	2º 50' 42"	1130	132 (87-209)	20.2 (12.8-35.1)	6.5 (4.2-10.8)
	Peña Lampa	LA	42º 50' 31"	4º 51' 36"	1187	97 (77-125)	20.1 (12.4-31.7)	6.0 (4.1-9.2)
	Mirantes de Luna	LU	42º 52' 39"	5º 51' 05"	1284	103 (60-136)	13.9 (9.1-22)	5.0 (3.3-8.2)
	Buenache de la Sierra	BU	40º 07' 46"	1º 58' 26"	1319	85 (46-115)	29.5 (21.3-37.6)	8.2 (5.7-10.8)
NE	Retuerta de Pina	RE	41º 28' 00"	0º 16' 31"	358	50 (32-63)	22.4 (5.6-35.5)	7.1 (4.5-10.0)
	Santa Engracia	SA	41º 46' 35"	0º 32' 29"	530	73 (40-136)	19.6 (12.9-24.8)	5.6 (4.5-6.2)
	Ciria	CI	41º 37' 43"	1º 56' 17"	1157	91 (66-114)	32.3 (21.6-41.8)	7.9 (4.7-10.8)
	Chaorna	CH	41º 07' 45"	2º 11' 21'	1210	93 (48-137)	37.4 (20.0-72.0)	6.9 (4.0-8.9)
SE	Viveros	VI	38º 47' 55"	2º 31' 34"	1030	83 (56-115)	25.9 (19.1-31.8)	5.9 (4.9-7.8)
	Veguillas de la Sierra	VE	40º 09' 26"	1º 25' 51"	1375	154 (61-199)	38.8 (25.0-56.5)	5.7 (4.0-8.0)
	Olmedilla	OL	40º 19' 12"	0º 44' 01"	1400	75 (58-98)	28.5 (19.0-42.5)	7.4 (6.1-9.9)

668 *Age was estimated as the maximum number of rings counted at 1.3 m.

669 **Table 2.** Summary of the dendrochronological statistics calculated for the ring-width
670 chronologies of each site for the common period 1951-2002. Sites' codes are as in Table 1.
671

				Raw tree-ring data		Residual chronology				
Group	Site	Period	No. trees/radii	MW ± SD (mm)	AC	ms_x	r_{bt}	EPS	E1 (%)	SNR
NW-C	AR	1925-2007	14 / 26	1.21 ± 0.59	0.67	0.16	0.41	0.86	45.40	9.40
	SI	1894-2006	11 / 21	1.09 ± 0.43	0.67	0.32	0.39	0.88	43.94	7.03
	CA	1850-2004	23 / 31	1.13 ± 0.41	0.72	0.21	0.37	0.93	42.44	13.48
	LA	1902-2006	14 / 21	0.70 ± 0.32	0.69	0.22	0.45	0.86	46.89	6.35
	LU	1876-2002	18 / 29	0.56 ± 0.20	0.80	0.30	0.47	0.93	48.43	13.46
	BU	1920-2006	15 / 22	1.24 ± 0.48	0.67	0.19	0.39	0.91	43.94	9.72
NE	RE	1945-2005	12 / 20	0.93 ± 0.52	0.54	0.31	0.54	0.94	58.80	14.36
	SA	1924-2006	13 / 28	0.96 ± 0.58	0.42	0.45	0.37	0.85	44.50	5.73
	CI	1911-2006	14 / 24	1.17 ± 0.54	0.63	0.31	0.38	0.90	43.12	8.61
	CH	1920-2006	13 / 22	1.13 ± 0.40	0.59	0.16	0.38	0.84	43.60	7.14
SE	VI	1922-2006	13 / 19	1.27 ± 0.57	0.57	0.33	0.38	0.85	43.47	5.10
	VE	1840-2006	19 / 31	0.62 ± 0.25	0.72	0.17	0.41	0.89	34.50	8.41
	OL	1909-2005	12 / 21	0.86 ± 0.38	0.65	0.24	0.42	0.90	46.51	8.71

672

673 MW, mean ring-width; SD, ring-width standard deviation; AC, first-order autocorrelation;
674 ms_x, mean sensitivity; r_{bt}, mean between-trees correlation; EPS, expressed population signal;
675 E1, variance explained by the first principal component; SNR, signal-to-noise ratio.

676 **Table 3.** Variables included in the RDA models of tree growth for the period 1951-2002 after
677 a stepwise forward procedure. The *F*-ratio statistic and the probability level (*P*) are also
678 displayed. The significance level of the model was based on 999 randomizations. Only those
679 environmental variables with significant effects ($P < 0.05$) on tree-ring growth, according to a
680 stepwise selection procedure, are included. Reduced models included all environmental
681 variables with significant effects on tree growth variability.

682

Reduced model	*F*-ratio	*P*	Variables	λ[a]	*F*-ratio	*P*
Geographical variables	2.20	< 0.001	Elevation	0.19	2.50	0.004
			Latitude	0.11	1.72	0.030
Climatic variables	2.32	< 0.001	Mean temperature	0.16	2.25	0.010
			Mediterraneity index	0.15	2.16	0.009

683 [a] λ: eigenvalues for the corresponding extracted axes, equivalent to the proportion of site
684 growth variance explained by each environmental variable.

Figures

Figure 1

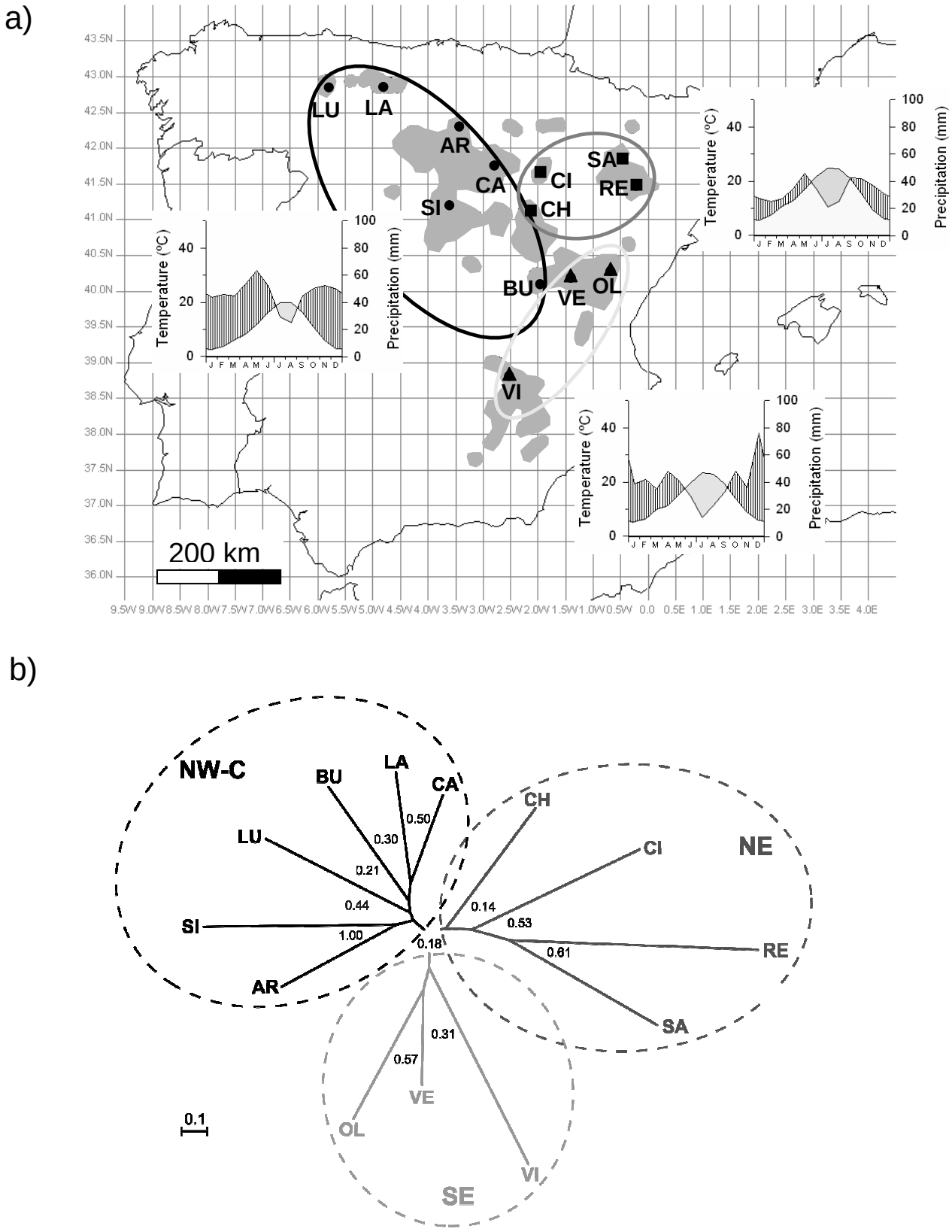
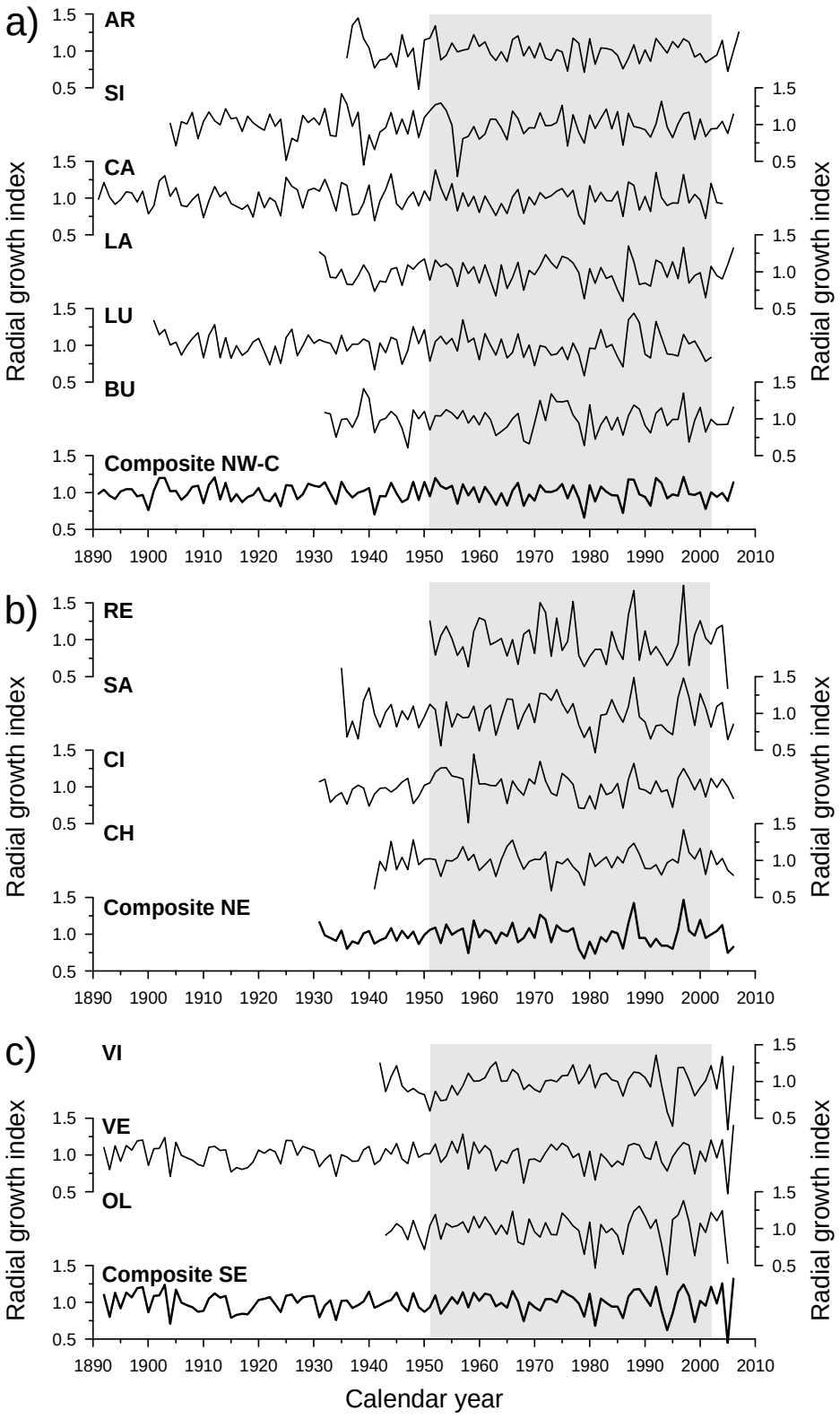
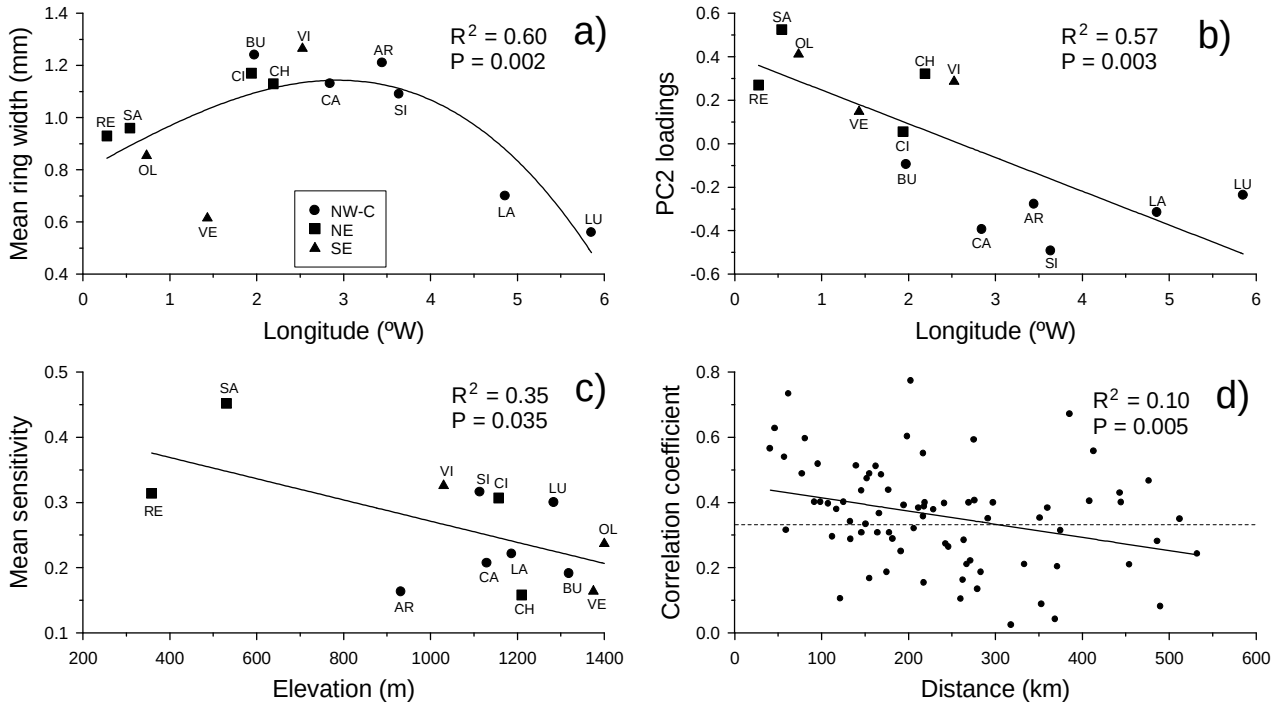


Figure 2


a)
AR
SI
CA
LA
LU
BU
Composite NW-C
b)
RE
SA
CI
CH
Composite NE
c)
VI
VE
OL
Composite SE
Radial growth index
1.5
1.0
0.5
1890
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
2000
2010
Calendar year

705 **Figure 3**

706



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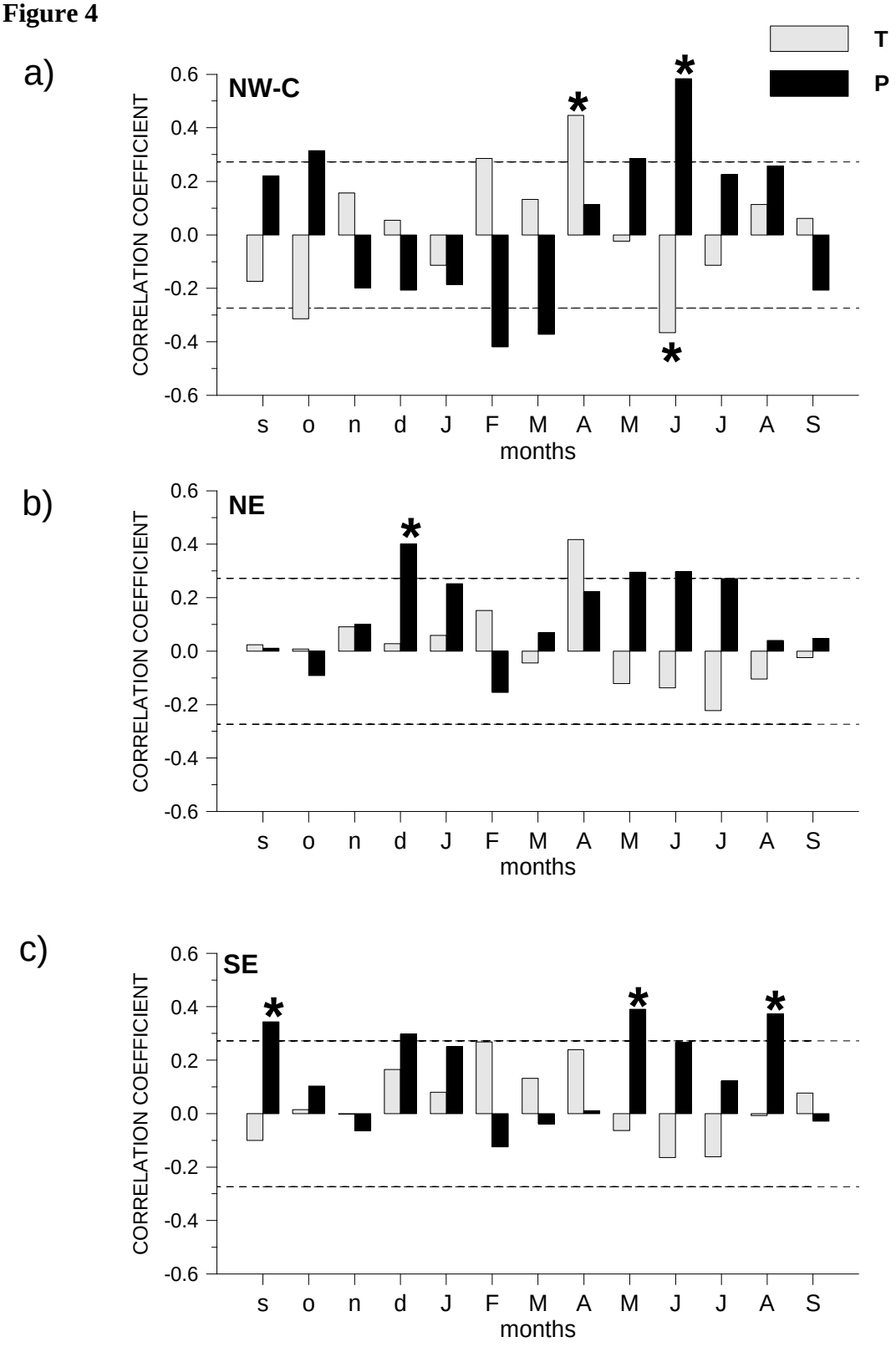
708 **Figure 4**



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713 **Figure 5**

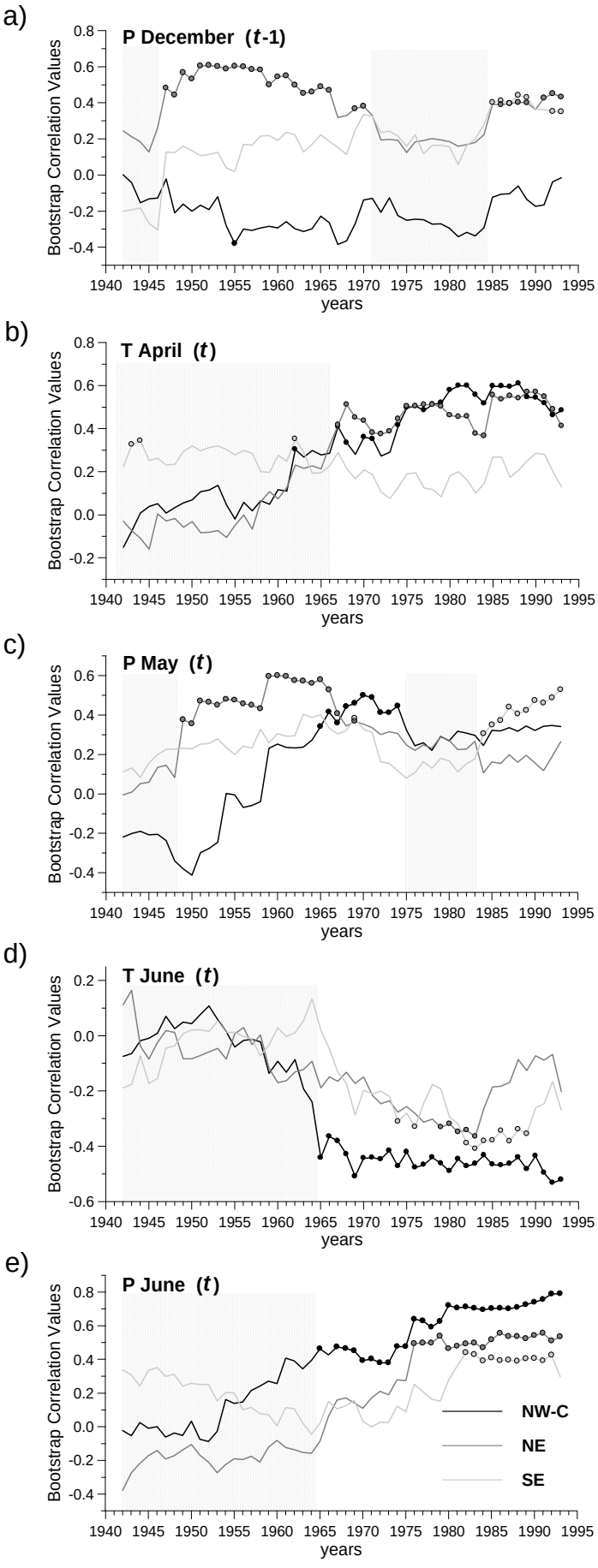
a)
P December (t-1)
b)
T April (t)
c)
P May (t)
d)
T June (t)
e)
P June (t)
Bootstrap Correlation Values
years
NW-C
NE
SE

Figure legends

Figure 1. (a) Sampled *Juniperus thurifera* stands within the species distribution area in Spain (grey areas) and corresponding regional groups detected using hierarchical cluster analysis for the period 1951-2002: North West and Centre (NW-C), North East (NE) and South East (SE). Climate diagrams of representative climatic stations for each group are displayed (NW-C, Soria, 41º 46' N, 2º 28' W, 1063 m a.s.l.; NE, Pallaruelo de Monegros, 41º 42' N, 0º 12' W, 356 m; SE; Nerpio, 38º 09' N, 02º 18' W, 1082 m). (b) Regional groups recognised using hierarchical cluster analysis for the period 1951-2002. NW-C in black, NE sites in dark grey, and SE in light grey. The values on nodes are the proportion of bootstrapped clusters that support the groupings showed in HCA analysis. Sites' codes are indicated in Table 1.

Figure 2. Residual ring-width chronologies of the thirteen *J. thurifera* study sites belonging to NW-C (a), NE (b) and SE (c) groups. The site chronologies and the composite regional chronologies of each group are shown. The common period 1951-2002 is shaded.

Figure 3. Relationships of (a) mean tree-ring width and (b) second principal component (PC2) loadings for the site chronologies vs. geographical longitude, (c) mean sensitivity of the site chronologies vs. elevation, and (d) correlation coefficient between site chronologies vs. inter-site distance (teleconnection pattern). Solid lines represent quadratic (a) or linear (b, c, d) regressions with their corresponding R^2 and P values. Different symbols correspond to different regional groups (NW-C, North West and Centre; NE, North East; SE, South East). The dotted line in Figure 3d indicates the significance level ($P < 0.05$) for correlation coefficients.

Figure 4. Correlation coefficients calculated between radial growth and climate for the period 1951-2002 among the ring-width indices of the regional composite chronologies (a, NW-C; b, NE; c, SE) and gridded monthly climatic data (T, mean temperature, and P, total precipitation), over a 13-month window. Months before (year *t*-1) and during tree-ring formation (year *t*) are abbreviated by lower- and upper-case letters, respectively. Black lines indicate the 95% significance level for the Pearson correlation coefficients, and asterisks indicate significant ($P < 0.05$) response function coefficients.

Figure 5. Temporal shifts of correlations between *J. thurifera* regional composite chronologies (NW-C, North West-Central; NE, North East; SE, South East) and selected monthly precipitation (P) and mean temperature (T) data of the previous (*t*-1) and current (*t*) years: previous December P (a); current April T (b); current May P (c); current June T (d), current June P (e). Moving bootstrap correlations were calculated for 25-year intervals in the period 1930-2006, and each correlation corresponds to the middle of the interval. Significant correlations are displayed as circles ($P < 0.05$). The grey background highlights the periods with non-significant correlations in at least five consecutive intervals.