Tree rings reflect growth adjustments and enhanced synchrony among sites in Iberian stone pine (*Pinus pinea* L.) under climate change

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Abstract

Context. Understanding the response of Mediterranean forests to climate change is required to assess their vulnerability and to develop measures that may limit the impact of future climate change.

Aims. We analyzed the sensitivity of several populations of *Pinus pinea* (Stone pine) in Southern and Central Spain and Portugal to climate and identified some responses to climate change.

Methods. We constructed tree-ring chronologies and studied the dendroclimatic signal over the last century.

Results. There were similarities in tree ring growth and response to climate among sites. Growth was enhanced after precipitation during the previous autumn and the current spring, and was limited by water shortage. In recent decades, aridity increased in the study region and the sensitivity of tree-ring growth to water availability increased at all study sites. We also observed an enhanced growth synchrony among chronologies as well as an increase in ring-width variability during the last decades.

Conclusion. The radial growth of *Pinus pinea* indicated strong effects of climate change. The climatic signal in tree ring chronologies suggested a plastic growth response to climate of this species, although the enhanced growth synchrony and variability in recent years suggest the presence of conditions that are limiting for growth. This study provides the first assessment of the responses of Iberian populations of *Pinus pinea* to changes in climate.

Key-words: Mediterranean pines, tree-ring sensitivity, climate-growth relationships, regional growth synchrony

Executive summary. We used tree ring analysis to assess the response of *Pinus pinea* to climate change in South Iberia. Climate-growth relationships changed over time, with greater sensitivity in recent years due to increasing aridity. A common dendroclimatic signal among sites was found suggesting that climate change is the main responsible for the observed variation in tree growth.

1 Introduction

Climate change significantly affects the conservation, productivity and management of forest ecosystems worldwide (see *e.g.* Ciesla 1995). Climate models for the Mediterranean region forecast atmospheric warming, reduced rainfall, longer dry spells, and more frequent heat waves and heavy precipitation events (Kovats et al. 2014). These changes will alter plant phenology, decrease growth (especially in the southern provenances and at the edges of species ranges), reduce non-wood forest products, increase forest decline and die-back processes, change species distributions, and increase pests and fires (Lindner et al. 2010; Lindner and Calama 2013; Resco de Dios 2007). Thus, studying the driving factors and the extent of changes in Mediterranean forests will provide important information on their ecological behavior and vulnerability, and guide the implementation of management options that may improve their response to future climate change.

Dendrochronology and dendroecology provide valuable information on the response of forests to environmental factors (Fritts 1976; Schweingruber 1996; Cook and Kairiukstis 1990). Recent dendroecological studies in the Mediterranean basin demonstrated that tree-ring data can be used as climate proxies in this region (*e.g.* Bogino and Bravo 2008; Campelo et al. 2009; Gea-Izquierdo et al. 2009, 2011; Vieira et al. 2010).

Stone pine (*Pinus pinea* L.) is native to southern Europe, occurs around the northern and eastern Mediterranean (Online Resource 1), and is present in more than 500 000 ha in the Iberian Peninsula (Montero González et al. 2004). In southern and central Iberia, stone pine stands are considered multifunctional forests, because they provide wood and edible pine nuts that are highly valued in international markets (see Mutke et al. 2005). These trees also provide soil protection, sand dune stabilization, biodiversity refuge, space for public and recreational activities, and carbon sequestration (Montero González et al. 2004). Previous studies of *P. pinea* indicated a close relationship between radial growth and climatic factors, and highlighted that tree ring formation in this species is sensitive to drought (Campelo et al. 2006; De Luis et al. 2009; Mazza et al. 2011; Novak et al. 2011; Raventós et al. 2001). Thus, tree-ring analysis in this species can be potentially useful in climate change studies in the Mediterranean basin, which is considered particularly vulnerable to climate change (de Sherbinin 2014; Giorgi 2006). Nevertheless, no studies have yet thoroughly assessed climate change response in *P. pinea* populations, particularly those in Southern Iberia.

In this paper we investigated the growth response of *P. pinea* populations to climate change in South and Central Spain and Portugal by examining the climatic signal in tree ring chronologies. Our working hypothesis were the following: (1) variations in climate entail a response in wood growth that will be reflected in temporal changes of the high-frequency response to climate; (2) if climate in a given region becomes more limiting for growth, different population from the same region will intensify their response to climate and will increase the shared variance in growth trends. To test the first hypothesis, we related the annual tree-ring growth to the climate of the study areas and checked if climate-growth relationships varied over recent decades. To test the second hypothesis, we compared the high-frequency growth variability of the studied stands to detect similarities in the growth patterns and check whether these similarities were stable over time.

2 Materials and methods

2.1 Study sites, samples and tree-ring analysis

Samples were collected from six sites in the province of Huelva, in southwestern Spain (Campo común, El Portil, Moguer, Hinojos, Punta Umbría, and Valverde del Camino) and one site in Pegões, in central Portugal (Table 1, Online Resource 1). These woodlands are managed for production of pine nuts and timber, and for the protection of coastal ecosystems. We also used three chronologies from the International Tree Ring Data Base (ITRDB, www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring) in the area of La Mancha (central-eastern Spain; Table 1, Online Resource 1): Dehesa del Peral, Pinar viejo and La Pasadilla (ITRDB codes: spai057, spai056 and spai059, respectively; contributors: Briongos and Del Cerro-Barja). The woodlands in this area are mainly managed for forest ecosystem conservation and timber production.

The climate in all areas is Mediterranean (Online Resource 2), but presents gradients in drought and precipitation regimes. Based on data from the meteorological stations of Huelva, Lisbon, Albacete, and Molina de Aragón (Online Resource 1), total annual precipitation and mean temperature are 520 mm and 18.2°C in Huelva, 730 mm and 16.9°C in Pegões, 362 mm and 13.8°C in Pinar Viejo and La Pasadilla, and 496 mm and 10.2°C in Dehesa del Peral. The annual distribution of rainfalls reaches a peak between November and February in Huelva and Pegões, while in the areas of La Mancha rainfall maximums normally occur in April-May and October. The dry period is larger in Huelva and Pegões (three months, from June to August), normally lasts for two months in Pinar Viejo and La Pasadilla (July-August) and one month in Dehesa del Peral (August) (Online Resource 2).

For the construction of the chronologies (Table 2) we used stem cross sections at breast height from previous harvests in Pegões (Correia et al. 2010). For Huelva, samples were extracted with an increment borer at breast height (two cores per tree), glued onto wooden mounts, and sanded along the transverse sections to make the rings visible. Tree ring widths were measured with a stereomicroscope and a LINTAB^{TM} table (Rinntech®) connected to a TSAP-Win^{TM} tree-ring analysis system (Rinntech®). Ring width curves were plotted for visual inspection and cross-dated with determination of the coefficient of parallel variation (*Gleichlaeufigkeit*, *Glk*), *t*-value and cross-date index (CDI). The *Glk* tests if two chronologies are simultaneously increasing or decreasing in each year-to-year interval and is calculated as the percentage of intervals showing matching growth variations (see Speer 2010, p. 108). The CDI was calculated in the TSAP-Win^{TM} software as a combination of the *t*-value and the *Glk* (Rinn 2011). The cross-dating was verified using COFECHA (Grissino-Mayer 2001). For the stands from La Mancha the ITRDB provided individual cross-dated ring-width series.

Each cross-dated ring-width series was standardized by applying a smoothing spline with a 50% frequency cutoff at 32 years, the autocorrelation was removed, and growth indexes (Gi) were computed as the ratios between the observed ring widths and the values from the fitted spline (Cook et al. 1990). The 32-year wavelength produces a rather flexible spline which is a good filter to smooth the medium-frequency variability in the growth trends due to management and enhance the high-frequency climatic signal (see *e.g.* Gea-Izquierdo et al. 2009, 2011; Helama et al. 2004). By averaging the Gi-series with a biweight robust mean, a residual chronology was obtained for each stand (Cook et al. 1990). The standardization and computation of residual series were performed using the R software package (Venables and Smith 2015) with the dplR library (Bunn 2008). The residual chronologies eventually used in the subsequent dendroecological analyses only included years with at least five cross-dated series (Gea-Izquierdo et al. 2011) and we checked that the included years had an Expressed Population Signal higher than 0.85, which is a measure of the confidence of the chronology in expressing the signal attributable to climate (Briffa and Jones 1990).

To identify the common dendroclimatic signal in the areas of Huelva and La Mancha, we performed principal component analyses (PCA). The use of PCA in dendroclimatic studies enables finding the common signal from a set of chronologies (*e.g.* Fritts 1990; D'Arrigo et al. 1999). For La Mancha, we computed the PCA of the correlation matrix of the residual series of Dehesa del Peral, Pinar Viejo and La Pasadilla. The first principal component (PC) was used in subsequent analyses. The PCA was also performed for successive windows of 30 years to determine the stability of the common dendroclimatic signal.

The selected stands in Huelva are included in even-aged plots originated from plantations, with similar tree ages within each plot, but different ages between plots. Since tree response to climate can be age-dependent (*e.g.* Carrer and Urbinati 2004), we grouped the stands in Huelva into age clusters to increase the resolution of dendroclimatic signals (see Vieira et al. 2008). The age of the trees was firstly estimated by counting rings on each individual cross-dated chronology, from the ring closest to the pith up to the ring beneath the bark. Subsequently, the oldest and youngest trees were determined for each stand. On the basis of the observed tree age structure, the stands were eventually grouped into two age clusters: young (≤70 years old) and old (≥100 years old). The tree ages in the "young" cluster are equal or lower than the shortest rotation age for timber production in *Pinus pinea* in Spain, which is between 60 and 80 years, while tree ages in the "old" cluster are equal or higher than the optimal rotation age for timber and nut production, which ranges from 80 to 120 years (Montero González et al. 2004). The PCA of the correlation matrix of the series of each age cluster was then performed. The PC that contained the common dendroclimatic signal of each age cluster was used in subsequent analyses. As above, the PCA was performed for successive windows of 30 years.

2.2 Climate and dendroecological analyses

For climate change analysis over time, we used the series of self-calibrating Palmer Drought Severity Index (PDSI), which is based on the high-resolution surface climate data set CRU TS 2.1 of the Climate Research Unit of University of East Anglia, UK, and available in the KMNI Climate Explorer (http://climexp.knmi.nl; van der Schrier et al. 2006). Drought is the main growth-limiting factor in Mediterranean forests (see *e.g.* Cherubini et al. 2003), so we considered this index to be a good descriptor of the impact of climate in our study areas.

For the analysis of the high-frequency response of radial growth to climate, we computed bootstrapped correlations and response functions, using climatic covariates as independent variables and tree-ring data as dependent variables. The climatic covariates were the monthly cumulative precipitation and the monthly averages of minimum and maximum temperatures computed from daily observations at the closest meteorological stations of the national weather services (see Online Resource 1), which were available in the KMNI Climate Explorer (Klein Tank et al. 2002). For the area of Huelva, the dependent variables used in correlation and response function analysis were the PCs of each tree age class and the climatic covariates were from the meteorological station of Huelva (37.26ºN, 6.9ºW; 19 m a.s.l.; time-span of precipitation and temperature records: 1920-2011). For Portugal, the analysis included the residual chronology of Pegões and the climatic data from the station of Lisbon (38.72ºN, 9.15ºW; 77 m a.s.l.; time-span of precipitation and temperature data: 1901-2012). For the area of La Mancha, in which the sites were farther apart and had larger climatic gradients, no single meteorological station was suitable; thus correlation and response function analysis was performed separately for the residual chronologies of Dehesa del Peral, Pinar Viejo and La Pasadilla, using the closest available meteorological station for each site (see Online Resource 1). In particular, the station of Albacete (38.95ºN, 1.86ºW; 704 m a.s.l.; time-span of precipitation data: 1940-2010; time-span of temperature data 1919-2010) was used for Pinar Viejo and La Pasadilla, and the station of Molina de Aragón (40.84ºN, 1.89ºW; 1056 m a.s.l.; time-span of precipitation data: 1950-2010; time-span of temperature data: 1960-2010) was used for Dehesa del Peral. The bootstrapped correlations and response functions were computed with the bootRes library (Zang and Biondi 2012) in the R software package. Bootstrapped correlations were also performed for successive windows of 30 years to verify whether climate-growth relationships were stable over time.

We used mean sensitivity (Ms, average of the relative differences in width from one ring to the next [Fritts, 1976]) to determine the intensity of tree response to climate. Ms was calculated as:

$$Ms = \left(\frac{1}{n-1}\right) \times \sum_{t=1}^{t=n-1} \left| \frac{2 \times \left(x_{t+1} - x_t\right)}{x_{t+1} + x_t} \right|$$

where x is the growth index and n is the number of annual rings in the tree-ring sequence. Thus, sensitivity ranges annually from 0 (in which adjacent rings have the same value) to 2 (in which a zero [“missing ring”] occurs next to a non-zero value) (Fritts 1976). As above, the Ms was computed for successive windows of 30 years to check if the intensity of response to climate varied over time.

For examination of the common dendroclimatic signal at a large scale, we compared the growth patterns by checking the cross-dating through the Glk coefficient and computing Pearson correlations between the study sites, using the residual chronology from Pegões and the PCs from Huelva and La Mancha. Again, the correlations were computed for successive 30-year windows to test the stability of the common signal.

3 Results

3.1 Chronologies

In the area of Huelva, the youngest and oldest trees were 47 and 68 years old in El Portil, 53 and 70 in Campo Común, 52 and 69 in Moguer, 127 and 150 years old in Hinojos, 100 and 110 in Punta Umbría, and 120 and 139 in Valverde del Camino. Therefore, the chronologies from El Portil, Campo Común and Moguer were included in the "young" cluster, while the chronologies from Hinojos, Punta Umbría and Valverde del Camino were included in the "old" cluster. One PC, with eigenvalue > 1, explained 70% of the variance of the chronologies included of the "young" cluster, and one PC, with eigenvalue > 1, explained 72% of the variance of the chronologies in the "old" cluster. The variance accounted for by the first PC increased over recent decades for both old and young trees (Online Resource 3). The tree ages in Pegões ranged from 50 to 60 years. In the area of La Mancha, the youngest and oldest trees were 82 and 119 years old in Pinar Viejo, 65 and 113 in Dehesa del Peral, and 50 and 89 in La Pasadilla. One PC, with eigenvalue > 1, explained 67% of the variance of the chronologies from La Mancha and the amount of variance explained by this PC tended to increase over time (Online Resource 3).

3.2 Dendroecological analyses

Analysis of the PDSI series indicated increasing aridity during recent decades in Central Portugal, SW Spain, and CE Spain (Fig. 1). In particular, these regions had prolonged droughts, mainly in the 1970s, early 1980s, and mid-1990s. Furthermore, 30-year running inter-correlations between the PDSI series of the three areas showed an increase over time, with a mean value equal to 0.5 up to 1965 and a mean value of 0.75 in the subsequent decades, which suggests that the increase of aridity, with more frequent and severe droughts, is common at the large scale in our study region.

Radial growth of *P. pinea* trees in Huelva had a significant positive correlation with precipitation from the previous November to the current spring (up to May in old trees, March in young trees) (Fig. 2). Except for the young trees in Huelva (in which growth correlated with maximum temperature in the previous October), the relationship of growth and maximum temperature was not significant. However, there was a positive correlation of growth with minimum temperatures from December to February in old trees and from the previous October to the current January in young trees. In Pegões, radial growth correlated with precipitation from the previous October to February of the current year, had no significant relationship with maximum temperature, and had a positive correlation with minimum temperatures of December and January.

The chronologies in La Mancha indicated correlations of radial growth with precipitation in the previous November, winter, and the current May (Fig. 3). There was a negative correlation between maximum temperature and radial growth in La Pasadilla and Pinar Viejo in the previous October-November and the current May; in Dehesa del Peral the correlation was negative in May and in summer. The relationship between minimum temperature and growth in La Pasadilla and Pinar Viejo was positive in winter and negative in May and July; in Dehesa del Peral, the correlation was positive in the previous November, winter, and current April.

The relationship of climate and radial growth changed over time in all study areas (Figs. 4 and 5). In particular, growth of old trees in Huelva had an increasing correlation with precipitation and minimum temperature of the previous December, and a declining correlation with spring rainfall. Growth of young trees in Huelva had negative correlations with May maximum temperature in the most recent decades, did not have significant correlations with March rainfalls between the 1960s and the 2000s, and became insensitive to rainfall in June since the 1960s, but was more correlated with temperature in February and precipitation of the previous October and the current September. The trees in Pegões had increasing dependence on rainfall of the previous November (there was also decreasing correlation with rainfalls in April, although not statistically significant). In Huelva, Pegões and La Pasadilla we found significantly negative correlations with temperature in June from the 1970s to the mid-1990s (Fig. 4, 5), suggesting that radial growth was sensitive to high temperature during these years, characterized by extreme and prolonged droughts (Fig. 1). In La Mancha, analysis of all chronologies indicated increasing correlation with winter and current November precipitation, but decreasing correlation with rainfalls in March (and in June for Pinar Viejo), whereas the correlation with temperatures (Fig. 5) increased during winter and became negative in the current November.

The mean sensitivity of all tree-ring series increased over the last decades (Online Resource 4), indicating an increasing intensity of the response to climate. Up to the 1960s, Ms in Huelva ranged from 0.1 to 0.3, but increased in the subsequent decades and reached values between 0.3 and 0.5. In Pegões, Ms increased up to 0.3 from the 1970s and in La Mancha increased from 0.2-0.3 before the 1960s to 0.3-0.4 in subsequent decades.

The residual chronologies from Pegões and the PCs extracted from the chronologies in Huelva and La Mancha had good cross-dating and were significantly correlated (Table 3). Moreover, the correlations among these series increased over time, with a notable increase from the mid-1960s (Fig. 6). The mean correlations of the old trees in Huelva with Pegões, La Mancha and the young trees in Huelva were 0.60, 0.34 and 0.68, respectively, before the 1965; whereas after this year were 0.63, 0.58 and 0.81. The mean correlation of the young trees in Huelva with Pegões and La Mancha increased from 0.30 and 0.26 to 0.38 and 0.51 (the running correlation analysis between Pegões and La Mancha was not meaningful due to the short overlap).

4 Discussion

The *P. pinea* trees from the three study areas showed similarities in the high-frequency growth patterns and response to climate during the study period. These similarities indicate the presence of a common signal in the tree-ring chronologies, suggesting that climatic factors control tree growth variability at a large scale irrespective of population distribution and local environmental conditions (Andreu et al. 2007; Čufar et al. 2014).

The correlations of radial growth with previous autumn and winter rainfall reflect the importance of soil recharge for improving water availability and subsequent growth in the spring. These results agree with previous studies of *P. pinea* in Portugal (Campelo et al. 2006) and Spain (Raventós et al. 2001) and with studies of other Mediterranean species (*e.g.* Campelo et al. 2009; Corcuera et al. 2004; David et al. 2007). Moreover, for evergreen trees, the positive response to rainfall and mild temperature in winter suggests the dependency of ring formation on the photosynthesis and carbohydrates produced during this period (Baldocchi et al. 2010). Mild temperatures during the winter can also alter phenological patterns, inducing an early dormancy interruption and consequently the formation of wider rings (Begum et al. 2010; Oribe and Kubo 1997).

The dendroclimatic signal that we recorded also reflected the influence of local climatic factors. The stands in La Mancha had higher responses to precipitation in May; this can be partly explained by the rainfall maximum occurring in May in this area (Online Resource 2), which provides an important water supply for ring formation. We found no relationship between summer climate and radial growth in the drier sites, Huelva and Pegões (Fig. 2). This can be expected for trees growing under these conditions (Campelo et al. 2009; Gea-Izquierdo et al. 2011), in which scarce and irregular summer rainfall is insufficient to alleviate water stress due to the high temperature, and there may even be a contraction of the radial growth. In contrast, trees in La Mancha were sensitive to summer temperatures although did not correlate to precipitation in this season. This suggests that in La Mancha, even though summer rainfall is scarce, the growing season is extended throughout summer, so that the radial growth can be affected by high temperatures during this season (Gea-Izquierdo et al. 2009).

Age-mediated response to climate has been observed in different species and climates and the interpretation of forest dynamics can be improved if the age effect is accounted for (Carrer and Urbinati 2004). In Huelva, the growth of young trees correlated with temperature and was more sensitive to rainfall in the previous autumn than old trees (Fig. 2). This may indicate that, under the same climatic conditions, young trees respond more rapidly to climate than older trees, and xylogenesis in young trees is higher in the earlier phases of the growing season (Rossi et al. 2008). Vieira et al. (2008) reported similar observations for *P. pinaster* in the Mediterranean climate of central Portugal.

Previous studies reported that spring precipitation increased radial growth in Mediterranean pines (*e.g.* Vieira et al. 2010; Campelo et al. 2006; De Luis et al. 2009, 2013; Piraino et al. 2013; Novak et al. 2013) and other Mediterranean trees (*e.g.* Campelo et al. 2009; Gea-Izquierdo et al. 2011). Although we found similar results for the old trees in Huelva, showing a positive correlation with rainfall up to May (Fig 2), the young trees in Huelva and in Pegões (see Fig. 2 and 4) were less sensitive to spring precipitation. The time span covered by the tree-ring sequences of the young trees (El Portil, Campo Común and Moguer in Huelva and Pegões, see Table 2) largely overlapped with the downward slope of the PDSI curves (Fig. 1). This means that the young trees grew under more xeric conditions, which possibly limited the cambial activity in the warmer months and consequently led to a weak chronology signal related to spring rainfall. This also suggests that the different dendroclimatic signals observed in trees of different ages depends not only on endogenous growth factors (*i.e.* physiological changes related to aging, see *e.g.* Rossi et al. 2008, Szeicz and Macdonald 1994) but also on the climatic conditions in which the trees were established and developed.

The observed changes in the relationships between climate and growth reflect the non-stationary nature of the growth responses of trees to climate (Carrer and Urbinati 2006). Other Iberian Mediterranean tree stands exhibited changes in high-frequency responses to climate suggesting a reaction to warming and increased water stress (Gea-Izquierdo et al. 2009; Martín-Benito et al. 2010). Wood anatomy and physiological studies indicate that tree species present some degree of plasticity to changing environmental conditions, *i.e.* the ability of a genotype to adjust the phenotype as a result of the physiological responses to environmental variability (see Fonti et al. 2010). For example, alterations in plant phenology, including seasonal xylem growth patterns, have been observed with atmospheric warming (Peñuelas et al. 2002; Rossi et al. 2011; Deslauriers et al. 2008). We may speculate that the plastic variations in climate-growth relationships observed in our study can be the result of a phenological adjustment of the cambial activity in relation to the distribution of water availability over the year (de Luis et al. 2011; Camarero et al. 2010). This could explain that, under more xeric conditions observed in recent decades, *P. pinea* ring growth became less sensitive to climatic conditions in the spring, when higher temperatures increased the water stress, and enhanced its dependence on water availability in the previous autumn-winter and current autumn, when climate is milder. We made similar observations in our dendroecological studies for *Quercus ilex* in Huelva (data not published). Although in the young trees we observed that the chronology signal related to spring climate was weak (in Huelva) or absent (in Pegões), improved relationships with autumn/winter climate were found. Therefore, an alteration of climate-growth relationships was observed in all sites with a reduction of the growth sensitivity to climate in the warmer months and an enhanced dependence of growth on the milder months (also see Fig. 7 in Gea-Izquierdo et al. 2009; and Fig. 7 in Martín-Benito et al. 2010). This suggests that climate variability in the region induce similar responses in the cambial activity of trees from different populations.

The similarity in the high-frequency growth variability among sites can be interpreted as a common response to the regional climate (Andreu et al. 2007; Macias et al. 2006; Tardif et al. 2003). Trees with Ms values greater than 0.4 are considered extremely sensitive to climate, while trees with Ms values lower than 0.2 are less climate-sensitive (Speer 2010, p. 107). In our sites, the Ms values increased in recent years (Online Resource 4), indicating that trees were exposed to harsh environmental conditions that controlled growth to a wider extent. In agreement with our findings, previous research in Iberian forests also reported high year-to-year variability of growth at dry sites (Campelo et al. 2006; Nabais et al. 2014) and increases in Ms over time (Andreu et al. 2007; Martín-Benito et al. 2010; Tardif et al. 2003; Gea-Izquierdo et al. 2009). Furthermore, the good cross-dating and correlation among sites in our study region support the presence of a significant dendroclimatic signal at the large scale. In particular, the increased similarity in growth patterns (Online Resource 3 and Fig. 6) indicates increasing growth synchrony. This suggests that, despite the differences in the dendroclimatic signal related to local environmental conditions and tree age structure, the climate of the region becomes increasingly important as a factor driving the variability of ecosystem growth. The increase of aridity over the second half of the 20th century matching the increase of Ms and growth synchrony (Fig. 1, Online Resource 4 and Fig. 6), together with the clear dependence of growth on water availability (Figs. 2-5), suggests that the observed changes in the growth patterns were linked to the higher frequency, severity and duration of droughts (Andreu et al. 2007).

5 Conclusions

In this study we have found a robust dendroclimatic signal in newly established *P. pinea* tree-ring chronologies in Southwestern Spain and Central Portugal and archived chronologies from Central-Eastern Spain. We provide a valuable assessment of the sensitivity of Iberian sites of *P. pinea* to changing growing conditions. The growth of studied trees was sensitive to high temperatures and water shortage, as the most limiting factors in Mediterranean forests. Our findings suggest that cambial activity adjusted to the increased water stress. In recent decades, the inter-annual variability of growth increased, indicating an intensified response to climate, and there was enhancement of growth synchrony among forests, reflecting that climatic conditions became more limiting for growth. We also observed that climate change induced similar responses in the cambial activity over wide areas, including forests with different site characteristics and ages. Further research is needed to assess the degree to which climate change impacts can be mediated by the stand age structure and local site conditions. These issues can improve the knowledge regarding species vulnerability to climate change and should be taken into account for forest growth modeling and adaptive management.

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Captions of figures

Figure 1. Annual mean Palmer Drought Severity Index in south-west Spain, Central Portugal, and central-eastern Spain (the upper *x* axis shows the years of the PDSI series). The dotted lines indicate 30-year moving averages, centered in the mid-year of the window (the lower *x* axis shows the 30-year windows of the moving averages).

Figure 2. Bootstrapped correlations (bars) and response functions (lines with dots) for monthly values of climatic covariates (precipitation, maximum temperature, minimum temperature) with the first principal component of old trees and young trees from Huelva and residual series from Pegões. Grey bars and black dots indicate statistically significant relationships ($p < 0.05$).

Figure 3. Bootstrapped correlations (bars) and response functions (lines with dots) between monthly values of climatic covariates (precipitation, maximum temperature, minimum temperature) and residual chronologies from La Mancha. Grey bars and black dots indicate statistically significant relationships ($p < 0.05$).

Figure 4. Thirty-year running-window bootstrapped correlations between monthly values of precipitation and temperature (months of previous year are in capital letters) with the first PC of old trees and young trees from Huelva and residual series from Pegões. Horizontal solid and dotted lines indicate thresholds for statistically critical values ($\alpha = 0.01$ and $\alpha = 0.05$, respectively).

Figure 5. Thirty-year running-window bootstrapped correlations between monthly values of precipitation and temperature (months of previous year are in capital letters) and chronologies from La Mancha. Horizontal solid and dotted lines indicate thresholds for statistically critical values ($\alpha = 0.01$ and $\alpha = 0.05$, respectively). There were no significant results after the correlation analysis between Dehesa del Peral and temperatures due to the short time-span of the temperature records in the meteorological station of Molina de Aragón.

Figure 6. Pearson's correlations for 30-year moving windows, calculated as pair-wise comparisons between the residual chronologies from Pegões and the PCs from Huelva and La Mancha. The *x* axis shows the 30-yr intervals

Geographic area	**Site name**	**Lat (º N)**	**Long (º W)**	**Elevation (ma.s.l.)**	**mean diameter ± st.dev. (cm)**	**main height ± st.dev. (m)**	**stand density (trees/ha)**
Huelva (south-west Spain)	Campo Común	37.39	7.19	100	67±7	22±1	209
	El Portil	37.21	7.04	20	22±8	5±1	264
	Moguer	37.21	6.84	30	55±9	17±3	158
	Hinojos	37.29	6.39	70	72±8	20±1	197
	Punta Umbría	37.20	7.00	20	28±7	7±1	237
	Valverde del Camino	37.53	6.78	260	62±6	19±3	300
Central Portugal	Pegões	38.63	8.62	60	19±4	15±3	135
La Mancha (central-eastern Spain)	Dehesa del Peral (*)	40.67	2.77	1057	34±6	9±1	450
	Pinar Viejo (*)	39.55	2.77	750	26±5	8±1	350
	La Pasadilla (*)	39.28	1.35	705	27±7	9±1	250

Table 1. Geographic coordinates, elevations and stand structural attributes of the study sites. (*) The chronologies in the area of La Mancha are from the International Tree Ring Data Base (ITRDB, see text for details).

	El Portil	Campo Común	Moguer	Hinojos	Punta Umbría	Valverde del Camino	Pegões	Pinar Viejo	Dehesa del Peral	La Pasadilla
Time-span (years)	1952-2011 (60)	1945-2012 (68)	1946-2012 (67)	1866-2012 (147)	1902-2011 (110)	1881-2011 (131)	1958-2007 (50)	1906-1999 (94)	1899-2001 (103)	1919-2001 (83)
No. of trees (no. of cores)	20 (40)	17 (34)	17 (34)	19 (38)	17 (34)	20 (40)	24 (*)	13 (**)	21 (**)	26 (**)
Mean width (mm)	2.4	3.7	2.7	2.1	1.4	1.8	3.2	1.4	2.0	2.5
Median width (mm)	2	3	2.2	1.7	1.2	1.4	2.3	1.0	1.7	2.1
Standard deviation (mm)	1.5	2.3	1.9	1.5	0.8	1.3	2.5	1.2	1.1	1.6
Mean sensitivity	0.28	0.20	0.32	0.37	0.28	0.23	0.26	0.36	0.24	0.30
First-order autocorrelation										
• raw series	0.68	0.73	0.54	0.68	0.67	0.79	0.77	0.77	0.77	0.72
• after standardization	0.007	0.013	0.024	0.034	0.066	0.052	0.027	0.036	0.020	0.040
Mean correlation:										
• series *vs.* master chronology	0.64	0.52	0.68	0.70	0.70	0.69	0.69	0.65	0.63	0.65
• among series	0.37	0.36	0.55	0.48	0.40	0.49	0.77	0.54	0.45	0.41

Table 2. Statistics of tree ring chronologies from Huelva (El Portil, Campo Común, Moguer, Hinojos, Punta Umbría and Valverde del Camino), Pegões and La Mancha (Pinar Viejo, Dehesa del Peral and La Pasadilla). Time-spans include at least 5 cross-dated series with Expressed Population Signal>0.85 (see text for details). (*) 24 stem cross sections were used for Pegões. (**) Individual tree chronologies of the area of La Mancha (Pinar Viejo, Dehesa del Peral and La Pasadilla) were from the International Tree Ring Data Base (ITRDB, see text for details).

	Huelva (young)	La Mancha	Pegões
Huelva (old)	*Glk*:76% *r*: 0.76 (p<0.01)	*Glk*: 67% *r*: 0.54 (p<0.01)	*Glk*: 75% *r*: 0.64 (p<0.01)
Huelva (young)		*Glk*: 62% *r*: 0.36 (p<0.05)	*Glk*: 67% *r*: 0.41 (p<0.01)
La Mancha			*Glk*: 75% *r*: 0.55 (p<0.01)

Table 3. *Glk* and Pearson correlation coefficients (*r*) calculated from pair-wise comparisons between the residual chronologies from Pegões and the PCs from Huelva and La Mancha. Significance of Pearson correlation coefficients is indicated in brackets.

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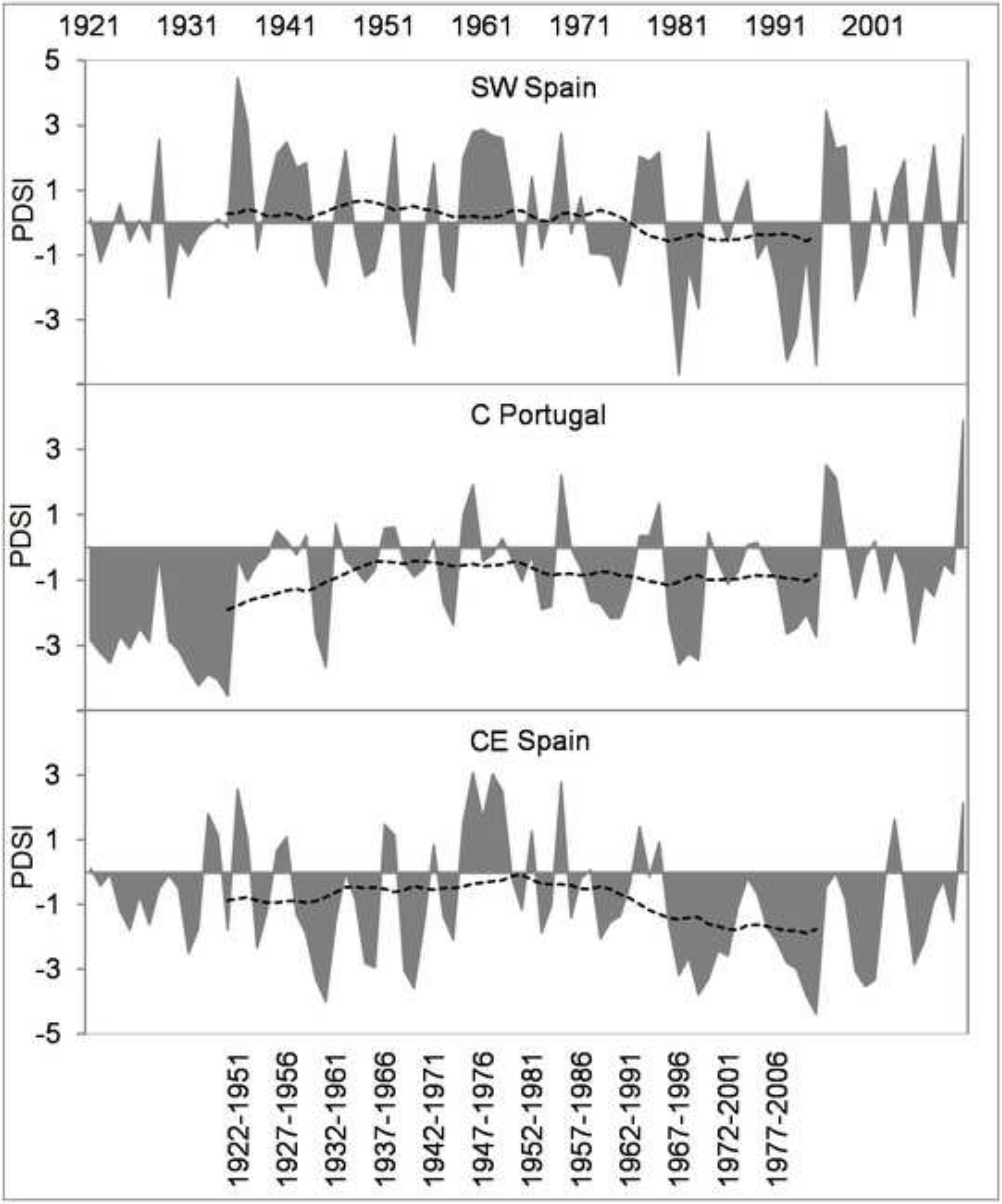

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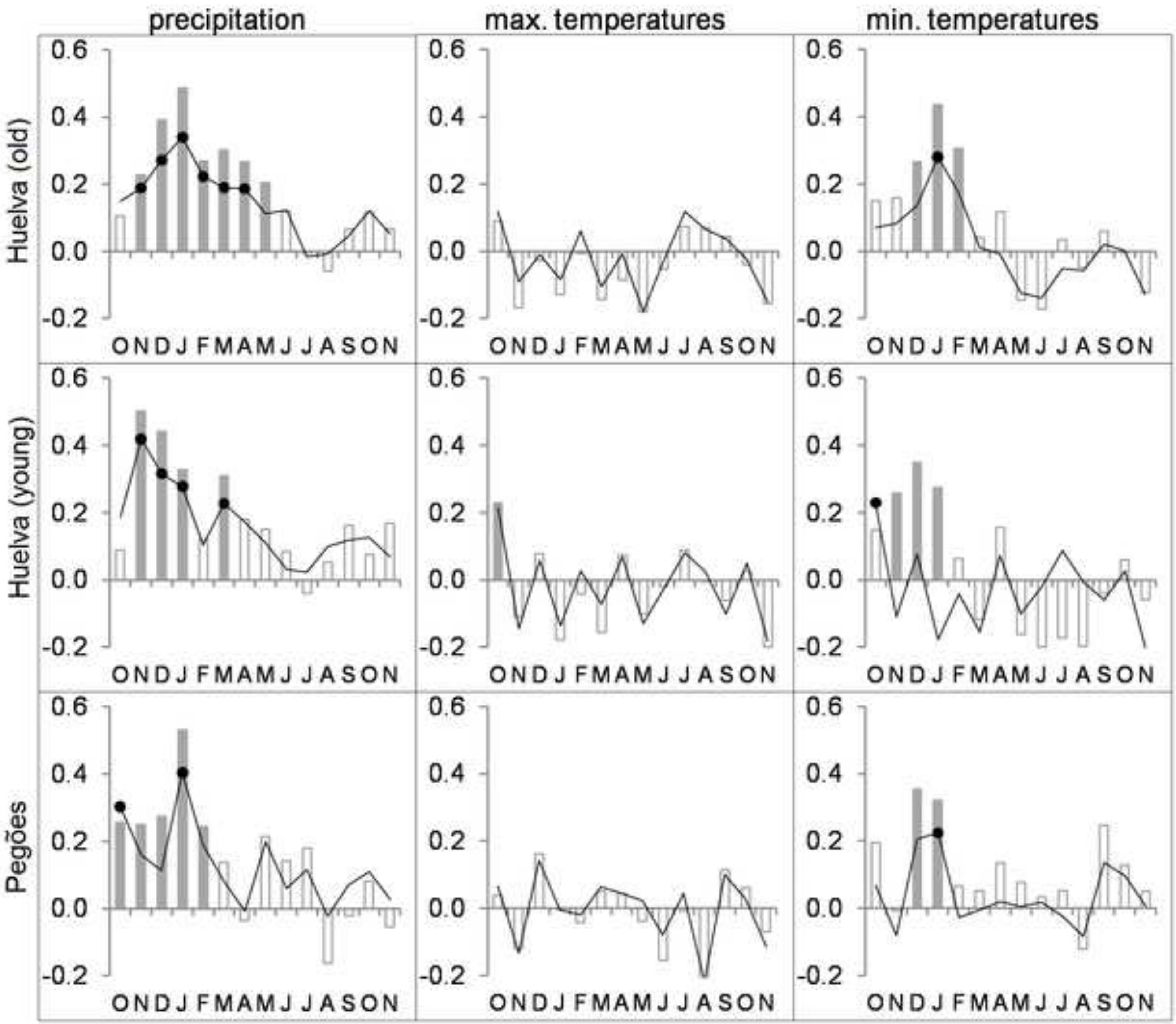

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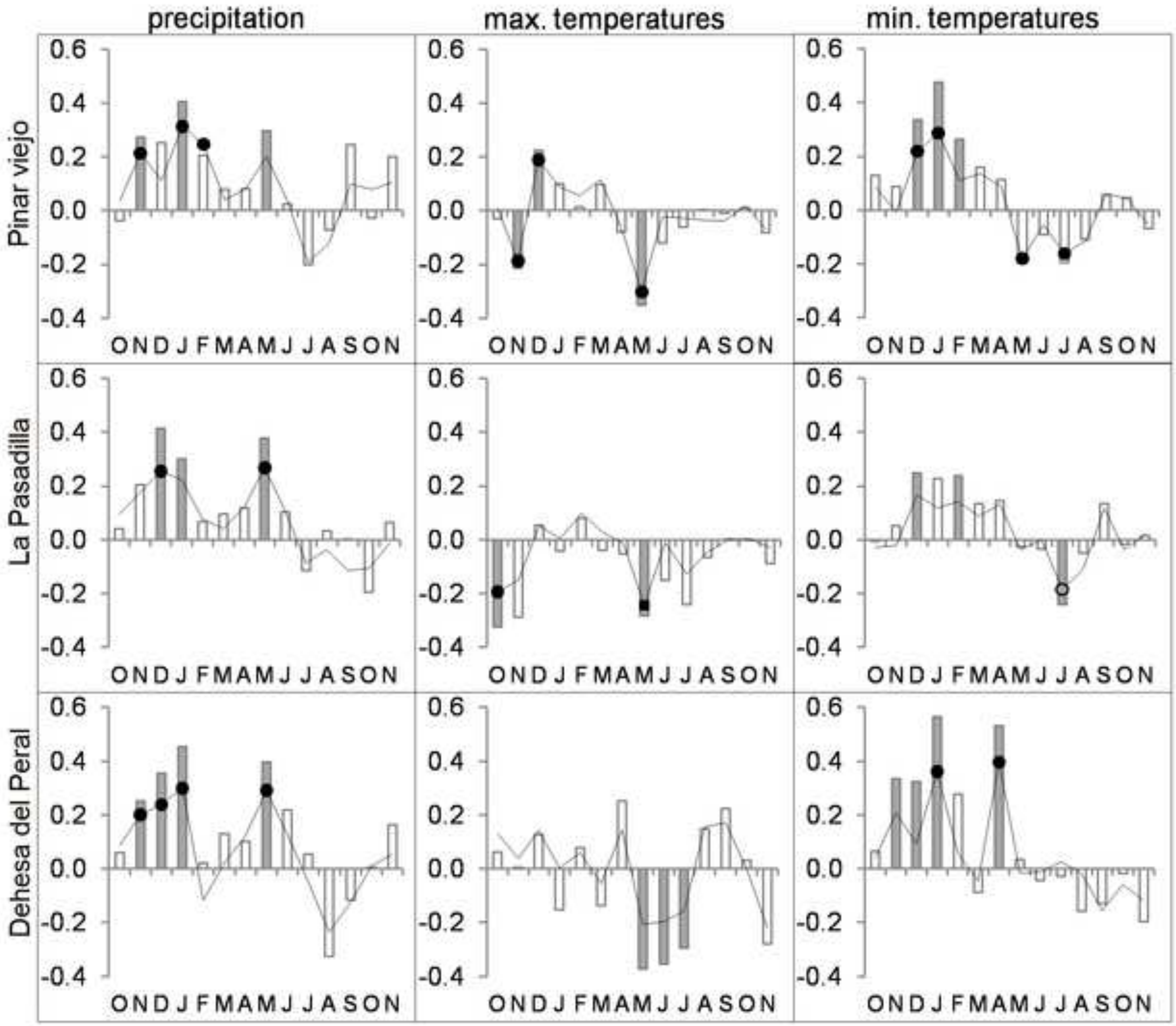

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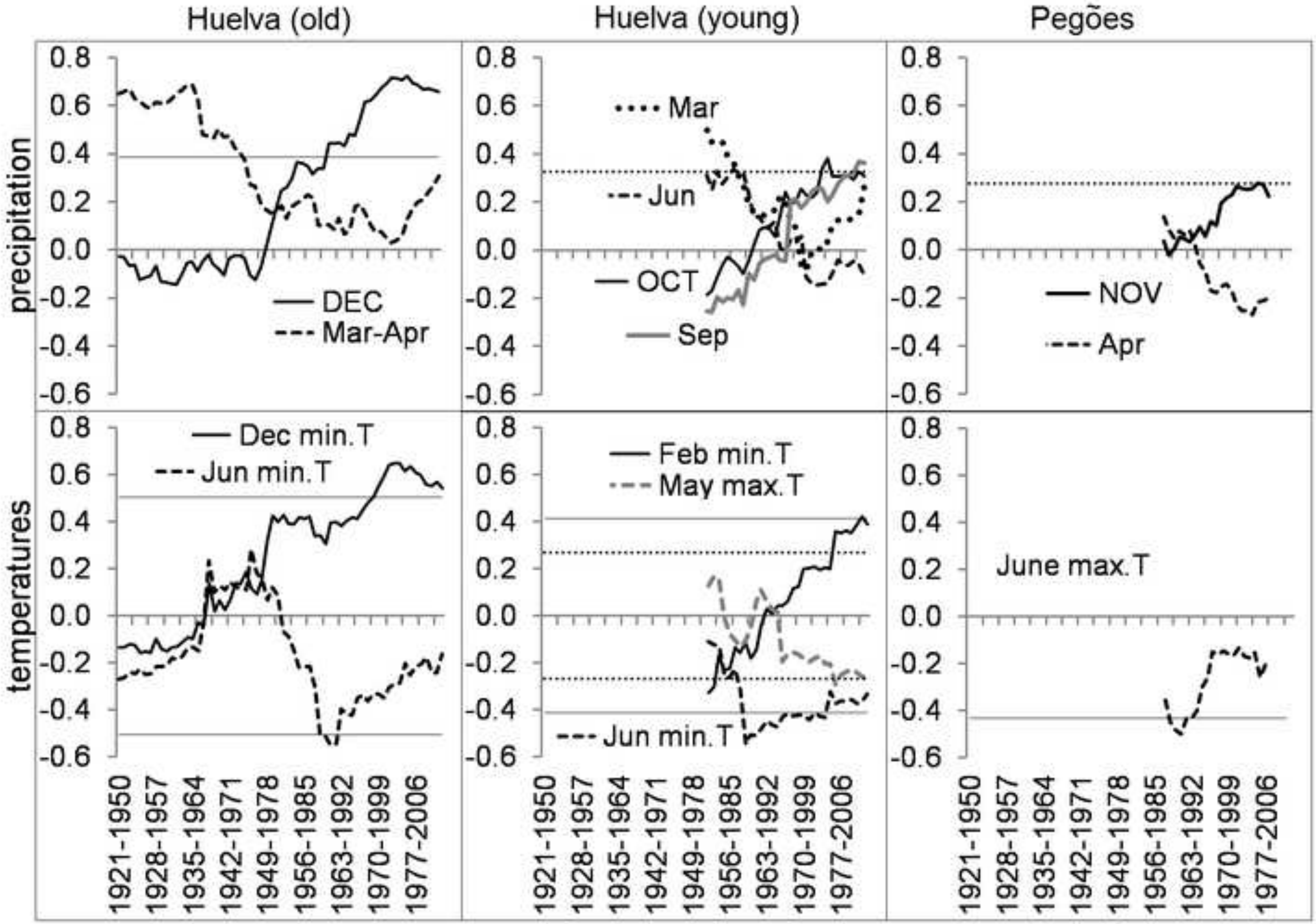

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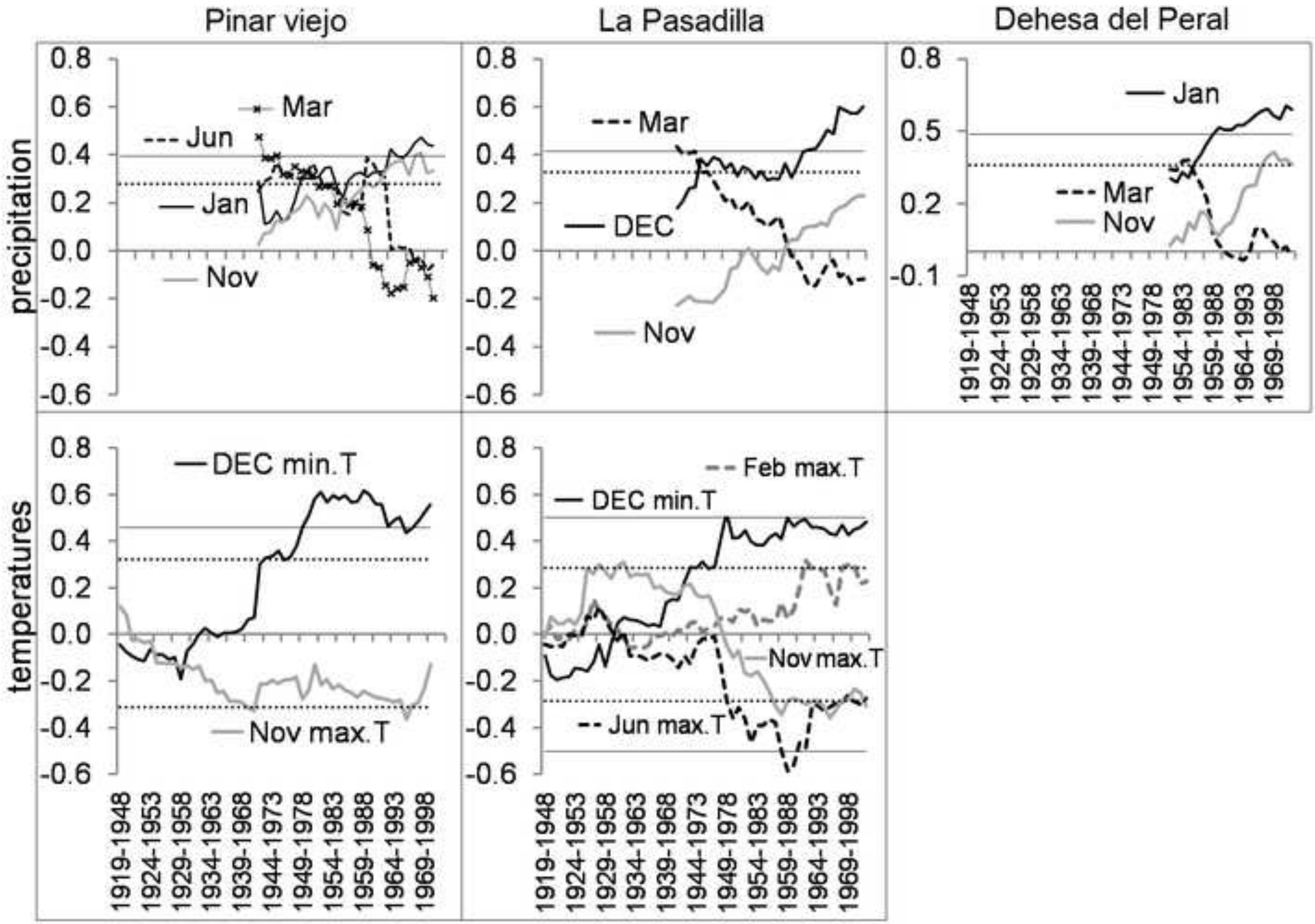

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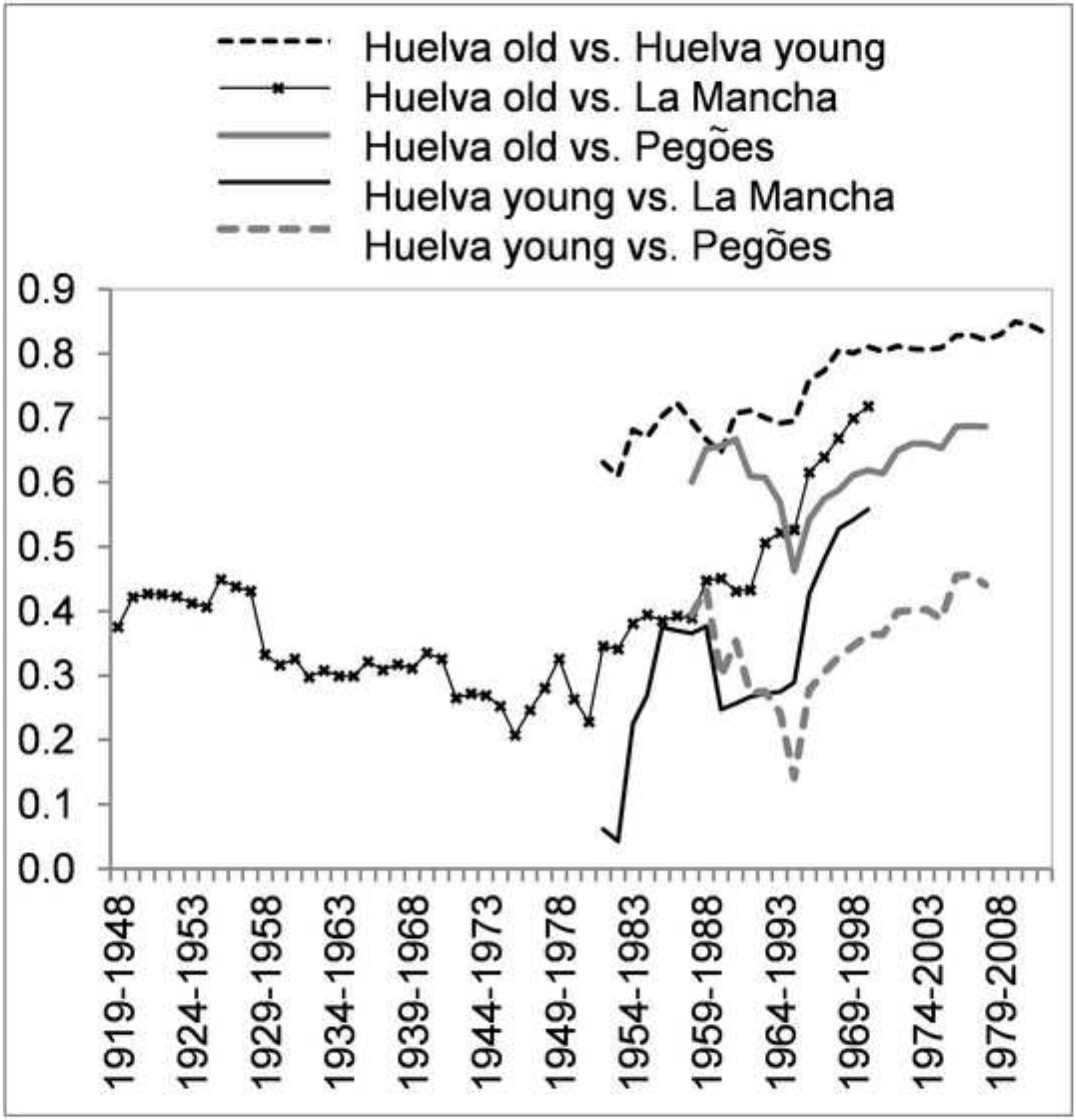
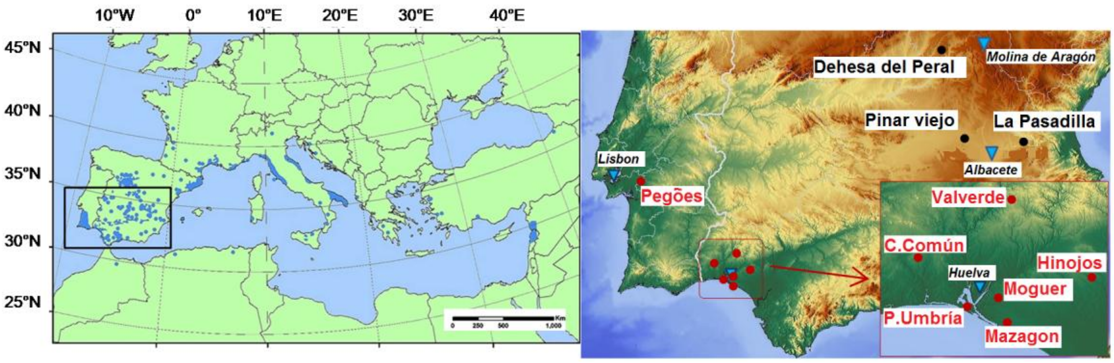
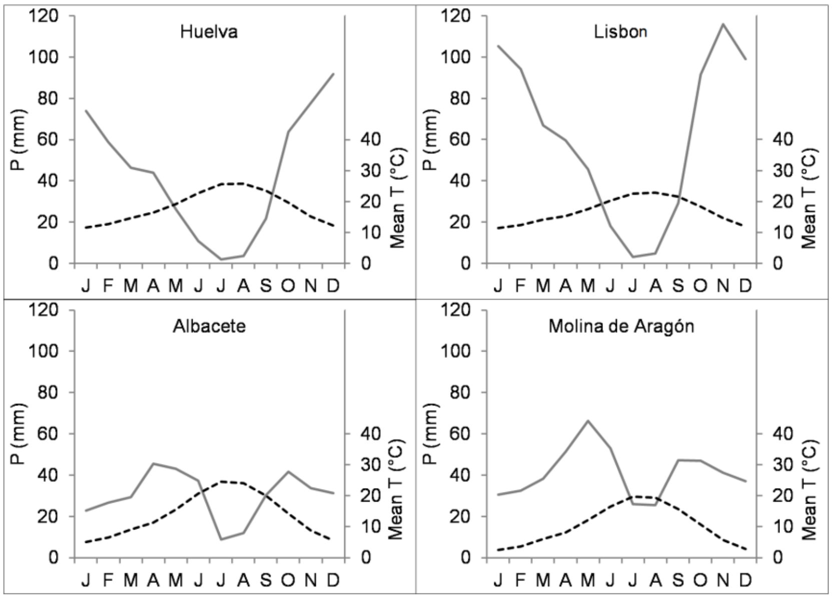


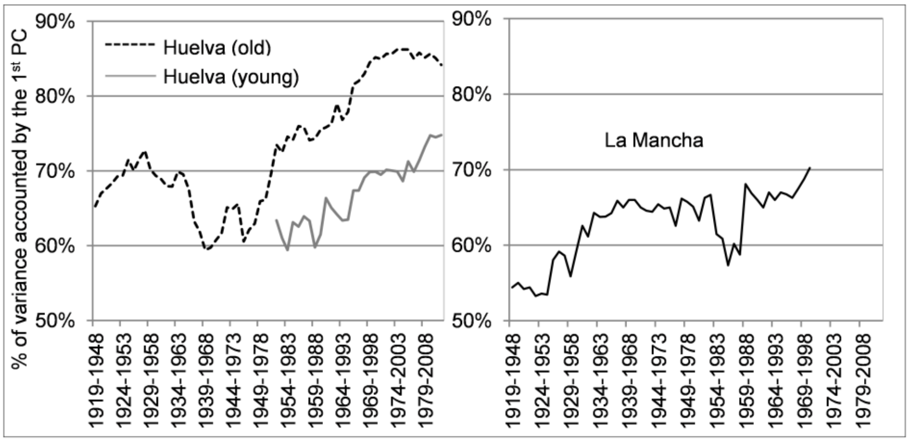
Online resource 1. Distribution of *Pinus pinea* (left, from EUFORGEN 2009 [www.euforgen.org]), and location of study sites (right). Blue triangles indicate meteorological stations, red dots indicate newly established chronologies, and black dots indicate chronologies from the International Tree Ring Data Base (see Table 1 and text for details).



Online resource 2. Climatic diagrams of the meteorological stations of Huelva (SW Spain), Lisbon (C Portugal), Albacete, and Molina de Aragón (CE Spain) (grey solid lines: precipitation; black dotted lines: mean temperature).



Online resource 3. Percentage of variance accounted by the first PC with 30-year running window PCA of the chronologies of young and old trees from Huelva (left) and chronologies from La Mancha (right). The *x* axis shows the 30-yr intervals.



Online resource 4

Online resource 4. 30-year running mean sensitivity (Ms) of the chronologies of young trees from Huelva (top left), old trees from Huelva (top right), trees from Pegões (bottom left), and trees La Mancha (bottom right). The *x* axis shows the 30-yr intervals.