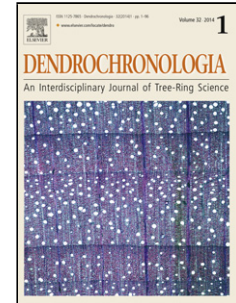


## Accepted Manuscript

Title: Spatiotemporal variability of stone pine (*Pinus pinea* L.) growth response to climate across the Iberian Peninsula

Author: Fabio Natalini Reyes Alejano Javier Vázquez-Piqué  
Marta Pardos Rafael Calama Ulf Büntgen



PII: S1125-7865(16)30077-7  
DOI: <http://dx.doi.org/doi:10.1016/j.dendro.2016.07.001>  
Reference: DENDRO 25394

To appear in:

Received date: 3-3-2016  
Revised date: 12-7-2016  
Accepted date: 16-7-2016

Please cite this article as: Natalini, Fabio, Alejano, Reyes, Vázquez-Piqué, Javier, Pardos, Marta, Calama, Rafael, Büntgen, Ulf, Spatiotemporal variability of stone pine (*Pinus pinea* L.) growth response to climate across the Iberian Peninsula. *Dendrochronologia* <http://dx.doi.org/10.1016/j.dendro.2016.07.001>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

**Spatiotemporal variability of stone pine (*Pinus pinea* L.) growth response to climate across the Iberian Peninsula**

Fabio Natalini <sup>1,2\*</sup>, Reyes Alejano <sup>1,2</sup>, Javier Vázquez-Piqué <sup>1,2</sup>,

Marta Pardos <sup>3</sup>, Rafael Calama <sup>3</sup>, Ulf Büntgen <sup>4,5,6</sup>

<sup>1</sup>Departamento de Ciencias Agroforestales, Escuela Técnica Superior de Ingeniería, Universidad de Huelva, Campus de La Rábida, 21819 Palos de la Frontera, Huelva, Spain

<sup>2</sup>Análisis y Planificación del Medio Natural, Campus of Excellence CeiCambio

<sup>3</sup>CIFOR-INIA, Ctra. de la Coruña km 7.5, Madrid 28040, Spain

<sup>4</sup>Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

<sup>5</sup>Oeschger Centre for Climate Change Research, Bern, Switzerland

<sup>6</sup>Global Change Research Centre AS CR, Brno, Czech Republic.

\*corresponding author: fabio.natalini@dcaf.uhu.es, fabionatalini@gmail.com

**Abstract**

Climate warming and increasing aridity have impacted diverse ecosystems in the Mediterranean region since at least the 1970s. *Pinus pinea* L. has significant environmental and socio-economic importance for the Iberian Peninsula, so a detailed understanding of its response to climate change is necessary to predict its status under future climatic conditions. However, variability of climate and uncertainties in dendroclimatological approach complicate the understanding of forest growth dynamics. We use an ensemble approach to analyze growth-climate responses of *P. pinea* trees from five sites along a latitudinal gradient in Spain over time. The growth responses to April-June precipitation totals were stronger in the north than in the south. Since the 1950s, the sensitivity of growth to April-June precipitation increased in the north and decreased in the south. Meteorological drought usually started in May in the southern sites, but in June-July in the northern sites. The water deficit in the southern sites is thus greater and more limiting for tree growth, and this likely accounts for the lower growth sensitivity during these months. Our results indicate that *P. pinea* has a high degree of plasticity, suggesting the species will withstand changing climatic conditions. However, growth response to drought regimes varies among *P. pinea* populations, suggesting that different populations have different capacities for acclimation to warmer and drier climate, and this may influence future vegetation composition.

**Keywords:** climate change; dendroecology; growth plasticity; Mediterranean; tree rings; drought

## 1. Introduction

Climate forecasts for the Mediterranean region indicate there will be an increase of temperature, decrease of rainfall, longer dry spells, more frequent heat waves, and more heavy precipitation events, all of which will exacerbate the existing problems of soil loss and desertification (Kovats et al., 2014). Significant changes in climate and related social dynamics, such as land use and food production, migration, and social conflicts, make the Mediterranean region a major climate change “hotspot” (Giorgi, 2006; Scheffran and Battaglini, 2011). The Iberian Peninsula, located in the western sector of the Mediterranean basin, has diverse climatic conditions: the northern zones have a Eurosiberian climate, and large parts of the peninsula have a Mediterranean-type climate, with warm summers and cold winters in the center and hot summers and mild winters in the south. The Iberian Peninsula has become drier in recent decades, and research indicates this change will continue (Pérez and Boscolo, 2010). There is evidence that climate change has already impacted forest ecosystems in this region. These impacts include shifts in species distributions and phenology (Peñuelas et al. 2002), decreases of growth, at least in the southern provenances and at lower edges of species altitudinal ranges (Jump et al. 2006; Martín-Benito et al. 2010), reductions of non-wood forest products (Büntgen et al. 2015a), stand decline processes and increased mortality (Carnicer et al. 2011; Natalini et al., 2016), and increased disturbances such as pests and fires (Hódar et al., 2003; Pausas, 2004). Distribution shifts of tree species are also expected for the future (Benito-Garzón et al. 2008).

*Pinus pinea* L. is an important tree species of Iberian Mediterranean forests. This species occurs throughout southern Europe and the eastern and southern Mediterranean coasts, and is native to the Iberian Peninsula (Martínez and Montero, 2004). *P. pinea* forests in Spain have considerable socio-economic value and, because of the easy access to areas where it grows (for the most part flat terrains at low elevations), it is exposed to human disturbances. Most *P. pinea* forests in Spain originated from plantations during the 20<sup>th</sup> century. These forests occupy more than 500,000 ha and are managed as multifunctional forests that provide timber, biomass, non-wood forest products (especially pine “nuts”), soil protection, sand dune stabilization, biodiversity refuge, space for public and recreational activities, and carbon sequestration (Montero González et al. 2004). It is necessary to understand the effects of climate change on the ecology of *P. pinea* forests to assess the adaptive capacity of this species and to develop management programs that ensure the conservation of this environmentally and socio-economically important species.

*P. pinea* tree ring data can provide accurate information about the relationships between growth and climate (Campelo et al., 2006). Natalini et al. (2015) studied *P. pinea* tree ring growth in relation to climate

change in southern Iberian Peninsula. In particular, they focused on temporal shifts of growth-climate relationships and increasing high-frequency variability and synchrony of growth in different populations as common responses to drier and warmer climate. However, trees also have diverse responses to climate depending on site-specific conditions (e.g. De Luis et al., 2013; Mazza et al., 2014). In fact, *P. pinea* grows under very different environmental conditions (Montero González et al. 2004), and variable growth responses to climate may be therefore expected across its geographical distribution range. The range of climatic conditions to which a species is adapted potentially determines its capacity to acclimate to future climatic conditions, and this should be considered when investigating the effects of climate change on forest dynamics (Tardif et al., 2003). For a proper assessment of growth-climate relationships, tree-ring detrending procedures also must be carefully considered. In particular, detrending curves with different degree of flexibility enhance the climatic signal and remove the non-climatic variance at different frequencies, and their suitability depends on the frequency domain of the tree-ring series (Helama et al., 2004). Moreover, uncertainties in growth-climate relationships can derive from the climate data, especially the choice of climate parameters and the lack of homogeneity of meteorological records (Frank et al., 2007; Büntgen et al., 2015b). Therefore, the spatiotemporal variability of species' response to climate, and the influence of different dendroclimatological approaches, make the assessment of climate-related forest growth dynamics more complex.

The purpose of this study is to provide a better understanding of climate-related *P. pinea* forest growth dynamics in Spain. We hypothesize that the species-specific growth response to climate varies over space and time in association with climatic spatial variability and temporal changes. To test our hypothesis, we examined growth-climate relationships and their variability over time in climatologically distinct sites along a latitudinal gradient in Spain. We tested the suitability of different tree-ring detrending methods and we used a comprehensive set of climatic parameters and climate data sources to check for uncertainties in climate data that could influence the assessment of growth-climate relationships. Finally, we discuss the observed variability of growth response to climate and its potential implications in Iberian *P. pinea* forest dynamics.

## **2. Materials and methods**

### ***2.1 Sampling sites***

The sampling sites are along a latitudinal gradient in Spain and present different environmental conditions (Figure 1, Table 1). Two sites (“Carrascal” – hereinafter CAR -- and “Viana de Cega” – VIA) are in the province of Valladolid on the “Meseta Norte” (northern Spain), one site (“Hoyo de Pinares” -- HOY) is in

the province of Ávila (Central Spain), on the “Sistema Central” mountain range, and two sites (“Hinojos” – HNJ -- and “Valverde” -- VAL) are in the province of Huelva, Southwestern Spain. The Meseta Norte is a vast plateau of Tertiary and Quaternary deposits with altitudes of ~600 to ~900 m a.s.l., where *P. pinea* grows within nemoro-Mediterranean vegetation, i.e. transitional areas where evergreen sclerophyll and deciduous broad-leaf forests occur (Allué et al., 1990). The Sistema Central is composed of Paleozoic and Mesozoic granitic rocks with patches of Cenozoic sediments, runs in an ENE-WSW direction (between the Meseta Norte to the north and the Meseta Sur to the south). Here, several peaks are higher than 2000 m a.s.l., and *P. pinea* grows at 600-1000 m a.s.l. within Mediterranean and nemoro-Mediterranean vegetation. VAL is on the southernmost limit of the “Sierra Morena” mountain range, HNJ is on the coastal zone of the Baetic depression (alluvial plain of the Guadalquivir river), and both have Tertiary and Quaternary deposits and low elevations (under 300 m). In this area, vegetation is Mediterranean including the most xeric *P. pinea* forests of Spain. In Carrascal and Viana de Cega, they are on flat terrains and are managed as protection forests (with an important function of fixing continental fossil dunes) and for production of timber and pine nuts. In Hinojos and Valverde del Camino, *P. pinea* forests are on flat terrains, they are primarily managed for timber production and nowadays biomass, and secondarily for pine nuts. Silvicultural measures for productive functions typically involve thinning and pruning for improving wood production and crown development. In Hoyo de Pinares, *P. pinea* trees grow on a south-facing slope within less disturbed protection forests, where productive functions are not important. The sampled stands in VIA, HOY, VAL and HNJ are pure, even-aged, single-canopied *P. pinea* stands, and the stand in CAR is a single-cohort stratified mixture, with a dominant storey of *P. pinea* trees and a lower storey of *Quercus ilex* L. subsp. *ballota* [Desf.] Samp. and *Juniperus thurifera* L. Climatic conditions are similar between the two northern sites (VIA and CAR) and between the two southern sites (VAL and HNJ), but differ along the latitudinal gradient. Annual precipitation and mean temperature are 404 mm and 12°C in CAR, 357 mm and 12°C in VIA, 548 mm and 11°C in HOY, 525 mm and 17°C in VAL, 527 mm and 18°C in HNJ (climate values calculated over the period 1950-2013 using the E-OBS gridded climate dataset).

## 2.2 Tree-ring chronologies

All samples (2 cores per tree) were extracted with an increment borer at breast height from the largest dominant or co-dominant trees. The cores were 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™ table connected to a TSAP-Win™ tree ring analysis system (Rinntech®). Ring width curves were plotted for visual inspection and cross-dated by determination of the coefficient of parallel variation (*Gleichlauefigkeit*, Glk;

see Speer, 2010, p. 108),  $t$ -value, and cross-date index (CDI) using TSAP-Win™ software. The cross-dating was verified using COFECHA (Grissino-Mayer, 2001).

The stands in the study sites are subjected to forestry treatments that affect growth trends and may mask the climatic signals stored in the ring width measurements. To remove the non-climatic growth variance from the ring-width measurements, we applied 2 detrending techniques: a negative exponential curve (NEXP), and a cubic smoothing spline with 50% frequency-response cutoffs at 30 years (SP30). The NEXP removes the age-related trends and retain other low-frequency variability, allowing the detection of low-frequency climatic signals, while the SP30 removes the low-frequency variance and enhances the high-frequency climatic signal (Helama et al., 2004; Cook et al., 1990a). To obtain dimensionless tree ring series and to remove the heteroscedasticity, tree ring indexes were annually calculated for each individual series as ratios between the raw ring width measurement and the corresponding statistical fit (Cook et al., 1990a). The final mean chronology of each site was computed as a bi-weight robust mean of the indexed series, which removes the effects of outliers (Cook et al., 1990b). To assess the strength of the site chronologies we used the expressed population signal (EPS), which is a measure of the confidence of a mean chronology in expressing the population-level signal (Briffa and Jones, 1990). To verify the stability of the chronology signal strength over time, we computed the EPS for each site using 30-year windows lagged by 15 years along the mean ring-width chronology.

### **2.3 Climate data**

A composite database of meteorological parameters from different climate data sources was created to check for uncertainties in climate data and to develop a robust assessment of climate variability. Specifically, we used 6 climate parameters (precipitation, self-calibrating Palmer Drought Severity Index [scPDSI], diurnal temperature range [DTR], and maximum, minimum, and mean temperature), from 6 climate data sources (3 meteorological stations and 3 gridded datasets) (Table S2). The scPDSI is suitable to assess growth sensitivity and has been widely used in dendroclimatological studies (e.g. Cook et al., 2015). The scPDSI improves upon the Palmer Drought Severity Index (PDSI) by maintaining a consistent behavior of the index over diverse climatological regions, thus making spatial comparisons of the drought index values on large scales more meaningful (van der Schrier et al., 2006). The DTR is a metric used in climate change studies and is linked to cloud cover (Karl et al., 1993). Since cloud cover controls solar radiation, that influences terrestrial temperatures and soil moisture, the DTR can be an appropriate hydroclimatic metric to study tree growth (Gimeno et al., 2012; Büntgen et al., 2013).

The meteorological station records were obtained from the European Climate Assessment Dataset project (ECAD, Klok and Klein Tank, 2008; <http://eca.knmi.nl>). We used homogenized meteorological records from three stations: “Valladolid-Villanubla”, which was the closest station to CAR and VIA, “Ávila”, the closest station to HOY, and “Huelva”, the closest station to HNJ and VAL. The ECAD does not provide any other station to characterize separately the climate conditions of the two northernmost sites (VIA and CAR) nor of the two southernmost sites (HNJ and VAL) (see “Meteorological station data” in Supplementary Material).

The sources of the gridded data were: (i) the E-OBS v11.0 dataset by the EU-FP6 project ENSEMBLES (Haylock et al., 2008; hereinafter “E-OBS”); (ii) the CRU scPDSI 3.21 (van der Schrier et al., 2006) and (iii) the CRU TS3.23 (Harris and Jones, 2014) by the Climatic Research Unit, University of East Anglia, UK (hereinafter “CRU”) (see Table S2). The E-OBS provides climate data with higher geographical resolution, but the CRU covers a longer period (see Table S2); therefore, we used the CRU to study the long-term climatic changes, and we included the E-OBS to have more detailed information about site-specific climate. For each gridded dataset, we selected the closest grid point to each study site through the KNMI Climate Explorer (<http://climexp.knmi.nl>). There was a distinct grid point for each study site.

We computed monthly sums of precipitation and monthly averages of scPDSI, DTR and maximum, minimum, and mean temperatures. Hence there was a total of 62 sets of monthly resolved climate data (Table S1).

The monthly climate values were very similar between CAR and VIA and between HNJ and VAL (compared using the gridded datasets), but varied with latitude. Therefore, we distinguished three climatic regions: the north (including CAR and VIA), the centre (HOY) and the south (VIA and HNJ). A climate diagram was produced for each climatic region by averaging per year the monthly values of precipitation and temperature within the common period of the climate datasets. To study the temporal variability of climate in each region, climate diagrams were also produced for two successive time windows by dividing the common period of the datasets into two sub-periods of equal length. In the climate diagrams, all months with  $P$  less than  $2T$  (where  $P$  is mm of total precipitation and  $T$  is mean temperature in Celsius degrees) were classified as “dry”.

Moreover, we calculated the departures of the climate data from the average of the last 30 years of the climate datasets. The values so obtained for the months April, May, June, July, August, and September (AMJJAS) were averaged per year. AMJJAS were used following previous tree ring studies (*e.g.* Büntgen et al., 2007; Nicault et al., 2008; Galván et al., 2014) and taken as a general time window comprising months in which high temperatures and water deficit significantly influence Mediterranean tree growth (*e.g.* de Luis et al., 2013, Seim et al., 2014). Subsequently, the AMJJAS time series were plotted for each region to study the temporal



trends. Moreover, correlations between the AMJJAS series of different climate data sources were computed to examine the discrepancies among the different climate data sources.

#### **2.4 Analysis of growth-climate relationship**

The relationships of growth with climate were analyzed with bootstrapped correlation and response functions, which remove the multicollinearity between climatic variables (Zang and Biondi, 2015), using the standardized tree ring chronologies and the climate datasets. We applied an ensemble approach (Büntgen et al., 2012) to assess how *P. pinea* growth response varies with climate in space and time, and to evaluate how the assessment of growth-climate relationships can be influenced by the choice of tree-ring detrending methods, climate data sources and climate parameters. This approach was accomplished in three successive steps:

- 1) Growth-climate correlations were computed for each site using all monthly resolved climate datasets and standardized tree ring chronologies. Unsuitable tree ring detrending methods, and climate data sources that generated uncertainties in the growth-climate relationships, were excluded from the analyses. Moreover, we identified the climate parameters which best explained tree growth.
- 2) We examined the spatial variability of growth-climate correlations and response functions in association with the spatial variability of climate.
- 3) Correlations and response functions were computed over two successive time periods – by dividing the common period between tree-ring and climate data into two sub-periods of equal length – to examine the temporal shifts of the growth response to climate and their connection with climate change.

A total of 240 correlation analyses were performed (Table S3).

### **3. Results**

#### **3.1 Tree-ring chronologies**

The number of cross-dated ring width measurement series per site ranged from 38 (19 trees, in HOY and 5) to 52 (26 trees, in VIA). The oldest trees were in HOY and the youngest in CAR, and the ranges of the chronologies were: 43-94 years in CAR, 102-144 years in VIA, 75-228 years in HOY, 91-139 years in VAL, and 69-150 years in HNJ (Table 2). These differences in chronology length within each stand were due to the uneven distances between the pith and the innermost cross-dated ring, rather than the age structure of the stands (which are even-aged). The EPS value for each site and consistently was above the minimum threshold of 0.85 back to ~1880 in CA, VIA, HNJ and VAL, and above 0.85 back to 1842 in HOY (Figure 3).

### ***3.2 Influence of detrending methods on growth-climate relationships and uncertainties from climate data***

There were discrepancies between the NEXP chronologies and the SP30 chronologies, especially in VIA and HNJ, while CAR and HOY the agreement between the detrending methods was greater (Figure 2B). The discrepancies were due to non-climatic growth releases (in the 2000s in VIA and in the 1960s in HNJ) that were not removed by the NEXP curve. The highest between-site correlations were found with the SP30 detrending method between CAR and VIA and between VAL and HNJ (Table 3). Therefore, the SP30 enhanced the climatic signal and confirmed the existence of three distinct dendroclimatic signals, one in the north (common to CAR and VIA), one in the center (HOY), and one in the south (common to VAL and HNJ).

The effects of different detrending methods were also visible in the growth-climate correlation patterns. In particular, the growth-climate correlations obtained with the NEXP chronologies differed from those obtained with the SP30 chronologies in VIA, VAL and HNJ (Figures S2, S4 and S5). On the other hand, the similarities between VIA and CAR and between VAL and HNJ were higher when we applied the SP30 (compare Figures S1 with S2, and S4 with S5), supporting the notion of similar growth response within each region.

Uncertainties in the assessment of growth-climate relationships occurred when we used different climate data sources. In particular, growth-climate correlation patterns differed within HOY, VAL and HNJ when we used temperature data from meteorological stations (Figures S3, S4, d, S5). Notably, the AMJJAS series computed using meteorological station records had disagreements with the other climate data sources (Table S4). In particular, the correlations were low ( $\sim 0.50$ ) for the mean temperature series in the south and even lower ( $\leq 0.3$ ) for the minimum temperature series in the south and center (Table S4).

Consequently, because the NEXP detrending method was less appropriate to remove the non-climatic variance from the tree ring chronologies and the uncertainties mainly derived from the use of meteorological station data, we only considered the results obtained with the gridded climate data and the SP30 chronologies.

### ***3.3 Climate variability***

The climate diagrams of the three climatic regions show different patterns (Figure 4). In the south, the winters were mild and most precipitation was during winter; in the northern and central sites, the winters were cold and the maximum of precipitation was during spring and autumn. In the north, there was a more delayed onset of meteorological droughts than in the south. Moreover, meteorological droughts in the south lasted longer and were more intense due to higher temperatures and less precipitation.

The intensity and duration of meteorological droughts increased over time (Figure 4). Specifically, from the “early” (1950-1980) to the “late” (1981-2011) period, the number of dry months (*i.e.*  $P < 2T$ ) increased from 3 (Jul-Sep) to 4 (Jun-Sep) in the north and from 2 (Jul-Aug) to 3 (Jul-Sep) in the central region. In the south, the number of dry months was 5 (May-Sep) during both periods, but drought intensity increased due to higher temperatures from May to August and less precipitation during June (Figure 4).

The AMJJAS scPDSI series showed different patterns of droughts before 1980 in the three regions, but the droughts in the early 1980s and mid 1990s were similar (Figure 5). The long-term trends of temperature were similar in all regions, with a warm period from the 1940s to 1960s and an increase of temperature during the last 40 years, although only the north and center had increases in DTR (Figure 5).

### **3.4 Growth response to climate variability**

We can distinguish the patterns of growth-climate relationships by latitude. In particular, the growth-climate correlations in the northern sites had similar bimodal patterns (CAR and VIA in Figure 6). In particular, there were positive correlations with precipitation from the previous October/November to January and from April to June; the correlations with temperature were positive from December to February and negative from May to June/July. There were similar correlation patterns in HOY (Figure 6). A distinct growth-climate response pattern occurred in the south (VAL and HNJ in Figure 6). In particular, there were positive correlations with precipitation from November to January, but these correlations were not significant during spring and absent during summer. There were positive correlations with temperature in the south during winter, but only for mean and minimum temperatures, and these were absent during spring/summer.

The growth-climate relationships were unstable over time and had distinct temporal changes along the latitudinal gradient. In the northern sites, the bimodal patterns in the growth-climate correlations were more marked during the “late” (1981-2011) than the “early” (1950-1980) period. Specifically, in the “late” period the correlation with precipitation in spring was greater and the correlation with temperatures in May/June was more negative (Figures 7, 8). There were similar changes in the center (although there was a loss of positive correlation with precipitation during June, Figure 9). In the southern sites the correlation with precipitation in spring was low during both periods, and the growth response to precipitation in June was significant during the “early” period but absent during the “late” period (Figures 10, 11) Moreover, there was a marked increase of positive correlations with precipitation and mean/minimum temperatures in autumn/winter (Figures 10, 11).

The correlations with the scPDSI and DTR reflected the overall patterns observed with precipitation and temperature data (Figures S6, S7), The response function analysis led to a lower number of statistically

significant coefficients, but confirmed the overall patterns and temporal changes of growth-climate relationships found with the bootstrapped correlation analysis (Figures 6-11, Figures S6, S7).

#### 4. Discussion

##### *4.1 Influence of detrending methods on growth-climate relationships, uncertainties from climate data and choice of climate parameters*

The dendroclimatic signal was not properly assessed using the NEXP method in VIA, VAL and HNJ. The NEXP is a parametric method which retains low-frequency growth variance (other than the age-related one) which can be a proxy of long-term climatic changes (Esper et al., 2002). In this sense, it can be referred to as a “conservative” detrending method (Cook et al., 1990a; Biondi and Qeadan, 2008). Nevertheless, conservative methods are suitable for wood specimens from sites with minimal ecological and anthropogenic disturbances, which are preferred for climatic reconstructions (Schweingruber et al., 1990). In contrast, the goodness-of-fit is reduced in managed forests and shade-tolerant interior-forest trees, where stand dynamics produce stochastic perturbations in growth trends (Piovesan et al., 2005; Gea-Izquierdo et al., 2011). In such cases, non-climatic noise is better removed by data-adaptive detrending curves (Cook et al., 1990a). Growth releases due to thinning can be found in tree-ring samples from Iberian *P. pinea* productive forests, and in fact were evident in VIA and HNJ. In these two cases, growth pulses could be wrongly interpreted as climate-induced if conservative methods were used, thus the tree-ring series are better filtered by flexible curves that extract the middle/high-frequency climatic signal. Notably, the NEXP and SP30 chronologies were comparable in CAR and HOY, where the silviculture-induced noise is absent, although the NEXP estimated lower ring indexes in HOY during the 1920s and 1930s, that probably reflect droughts occurred in these decades (Figure 2) and may suggest the extraction of low-frequency climatic signals. However, we applied the SP30 method in all sites to obtain the same type of climatic information for a coherent spatial comparison of growth responses.

A possible explanation of the uncertainties arisen from the meteorological records can be the uneven quality of instrumental measurements over time, which actually causes biases in tree-ring based climate reconstructions (Dessen and Bücher, 1995; Frank et al., 2007; Dorado Liñán et al., 2012; Büntgen et al., 2015b). The uncertainties are also partly explained by the location of the stations. Indeed, differences in temperatures and humidity can be expected from the different elevation between the stations and the study sites, in particular between “Ávila” and HOY and between “Huelva” and VAL (a difference of around 240 m in both cases). However, there were no closer stations with long-term records, and our analysis indicated that the available

meteorological station data are somewhat inappropriate for calibrating tree-ring proxy data in these sites. The grid boxes constituted the most suitable source of information about site-specific climate available for our study.

The relationships between tree ring chronologies and scPDSI reflect the suitability of this metric for dendroclimatological studies in the southern Europe (Cook et al., 2015). However, the combined use of precipitation and temperature data provided clearer seasonal patterns of statistically significant correlation values, permitting a better dendroecological comparison between sites. The DTR provided meaningful results, reinforcing its potential use to calibrate tree-ring proxy data. Negative growth response to DTR may refer to cloud-free sky, associated with high DTR, which generally boosts temperatures and reduces soil moisture, at least during the warm seasons, but the possible negative effects of atmospheric brightening on forest productivity needs further studies (Büntgen et al., 2013).

#### ***4.2 Spatiotemporal variability of climate***

The three studied regions all have a Mediterranean macroclimate that is characterized by hot and dry summers. However, there were also climatic differences among the sites. The annual distribution of precipitation varied among regions, and the duration and intensity of meteorological droughts was greater at lower latitudes. The lower amount of rainfall during spring and summer in the southern sites is related to the dominant atmospheric circulation patterns in southern Spain (Romero et al., 1999). Furthermore, winter temperatures in the northern and central regions were lower, attributable to the “sub-continental” type of the Mediterranean climate which characterizes the supra-Mediterranean belt in central-northern Spain (Rivas-Martinez, 2007; Olano et al., 2012). In the central region, the annual precipitation is higher and the meteorological droughts are shorter than in the northern sites, due to humid winds from the Atlantic Ocean through the Tagus river valley, which lead to more frequent precipitation events (see Benito et al., 2003, and Figure 69 in AEMET-IM, 2011). The greater precipitation amount of this area is also associated with the higher elevation (Rodríguez-Puebla et al., 1998).

The dry periods during the 1980s and 1990s (scPDSI series in Figure 5) and the increase of temperature since the 1980s (Figure 5) occurred in all three regions. This confirms the existence of a large-scale climate change process characterized by increasing temperature and aridity, in line with previous findings in the Iberian Peninsula (Pérez and Boscolo, 2010). However, there were different dynamics in the drying process in the three study regions (Figure 4). In the northern and central regions, meteorological droughts increased in intensity and duration because of higher temperature and lower rainfall from June to September. In the south, meteorological droughts did not change in duration but increased in intensity due to higher temperature from May to August and

decreased precipitation during June. Our observations indicate that our three study regions, although affected by a common macroclimate and by similar climate change processes, have different climate dynamics at the local level (Vicente-Serrano et al., 2004).

#### **4.3 Spatiotemporal variability of growth-climate relationships**

The differences in the duration and intensity of meteorological droughts among the study regions can explain the differences in tree growth sensitivity during the late spring and early summer. During this period, the moisture conditions were more limiting in the south, so the precipitation-related signal strength was lower in this region than in the other sites. This may indicate lower rates of wood formation under water deficit during spring/summer (Vieira et al., 2014). Moreover, the stronger growth response to spring precipitation in CAR, VIA and HOY may also be due to the spring maximum rainfall in these areas. In the northern and central sites, growth sensitivity to May/June temperature was also greater than in the southern sites. In fact, during late spring and early summer, an increase of temperature without an increase of precipitation can negatively affect cambial activity, and this underlies the sensitivity of ring formation to high temperature in this period of the year (de Luis et al., 2011; Martín-Benito et al., 2013).

Differences in additional factors other than climate, especially soils, probably influence growth rates and forest productivity in our study sites (Bravo-Oviedo and Montero, 2005). However, when stand dynamics were removed with appropriate tree ring detrending methods, the chronology signals were noticeably similar between sites of a same climatic region (north and south), despite the geological and edaphic differences. Therefore, non-climatic site-specific ecological characteristic barely influenced the assessment of dendroclimatic signals and did not affect our dendroecological comparison between regions.

The capacity of *P. pinea* trees to establish site-specific relationships with the local climate may be explained by the plasticity of this species. The genetic variability of *P. pinea* is low (Fallour et al., 1997; Vendramin et al., 2008; Pinzauti et al., 2012). However, this is a widespread species that grows under diverse environmental conditions, indicating that genetic variability does not entirely explain its adaptability (Vendramin et al., 2008; Soto et al., 2010). In fact, the successful adaptation of *P. pinea* seems to depend largely on the variability of phenotypic traits, which is high in this species (Mutke et al., 2010, 2013; Sánchez-Gómez et al., 2011; Sáez-Laguna et al., 2014). Thus, phenotypic plasticity may explain the observed variability of the growth response to climate in different regions, that could suggest the capacity of *P. pinea* to adapt the annual distribution of cambial activity depending on site-specific climatic conditions. Tree-ring analysis and xylogenesis indicate plastic cambial activity in *Pinus halepensis* (de Luis et al., 2011, 2013), an ecologically

similar species that also has little genetic variability (Soto et al., 2010). However, experimental data on xylogenesis of *P. pinea* to verify plastic cambial activity are still very scarce (Luz et al., 2014)

The growth-climate correlations in our sites varied over the study period. This reflects the non-stationary nature of growth responses to climate (Carrer and Urbinati 2006) which can be interpreted as physiological plasticity that enables an individual to acclimate to changing conditions (Meyers and Bull, 2002). In fact, individual trees can alter their physiology in response to environmental changes (Walther et al., 2002; Rossi et al., 2011). In our study sites, climatic changes over time drove the shift of the growth-climate response patterns, as also reported in other tree-ring studies (Martín-Benito et al., 2010; Latte et al., 2015). This suggests an adjustment of growth physiology during the life of trees in response to a warmer and drier climate, as discussed in a previous study (Natalini et al., 2015). However, the response shifts observed in the present study also seem to be mediated by site-specific climate dynamics. In fact, the increased growth response to spring precipitation (and the increased sensitivity to temperature in May) in the northern and central sites appear linked to the higher spring rainfall during the “late” period in these regions. There were different changes in the south, where spring precipitation did not increase and growth response to climate was always low in this season. Hence, in this region, the climate change-related risk of water deficit during spring is higher and induces a distinct response in growth physiology. In the south there was also a significant decrease of the positive correlation with precipitation in June, which may be linked to the marked increase in drought intensity in this month in this region. These findings indicate that temporal changes and spatial variability in climate simultaneously influence tree growth and the acclimation response.

The plasticity of plant species may play an important role in future vegetation dynamics following climate change (Nicoltra et al., 2010). Based on our results, we suggest that *P. pinea* in northern sites have some capacity to resist a future increase of drought by adjusting cambial activity and thus becoming more similar to trees in southern sites (which are currently adapted to drier conditions). On the other hand, the southern populations may already be approaching or exceeding their ecological limit, and their persistence under future conditions may be threatened. This could be in agreement with predicted vegetation dynamics. In fact, global warming induces spatial shifts in the ecological ranges of plant species (Walther et al., 2002), and in Spain this will likely lead to a northward shift of the distribution of tree species (Benito-Garzón et al. 2008; Pardos et al., 2015). Alternatively, the southern *P. pinea* populations could acclimate by activating the cambium during winter if winter temperatures continue increasing (Prieto et al., 2004). In fact, maintaining cambial activity during winter is an adaptive trait that some Mediterranean trees show in certain precipitation and temperature conditions (Cherubini et al., 2003). For instance, previous research in Portuguese stands of *Pinus pinaster*, a species

ecologically close to *P. pinea*, indicates some cambial activity during winter, although evidences are restricted to coastal (oceanic) zones during mild winters (Vieira et al., 2014). The tree-ring growth response of *P. pinea* during winter, also previously reported in Spain and Italy (de Luis et al., 2009; Mazza et al., 2014; Natalini et al., 2015), may reflect that this species can be physiologically active during winter (Pardos et al., 2010). In fact, cells in differentiation during winter have been observed in *P. pinea* in coastal areas of central Portugal, although this needs further investigation (Luz et al., 2014). There is no basis for making further speculations about future changes in cambial activity for trees in our southern sites because there is no species-specific experimental evidence in drier locations which could be used for such predictions. However, our results suggests that the species' plastic response to warmer and drier climate can vary among populations, and some measure of such variable plasticity should be considered in long-terms forecasts of vegetation dynamics (Alla and Camarero, 2012).

## 5. Conclusions

The study regions had similar Mediterranean macro-climates and were all affected by the long-term increases of temperature and aridity. However, climatic patterns and climate change dynamics were not uniform among sites. The *P. pinea* growth response to climate changed over time in response to climate change, but this varied in space according to site-specific climatic conditions. The variable growth-climate relationships suggested that *P. pinea* can adapt to a range of climatic conditions, and will be able to acclimate to temporal variations in climate. Few studies have investigated the plasticity of plants from a dendrochronological perspective (de Luis et al., 2013). In this context, the present study provides a tree ring-based assessment of the plastic growth response of *P. pinea* to climate variability in Spain. Our results do not support or contradict the persistence of *P. pinea* near its xeric distribution limit under future warmer and drier climate, but they indicate that the species' plasticity can be crucial for prediction of vegetation dynamics under climate change scenarios.

The dendroecological approach to climate-related forest growth dynamics requires a careful evaluation of the most suitable tree-ring detrending methods and climate data. There are no universally valid detrending methods, because chronologies from different stands, especially from managed stands, show different non-climatic perturbations, which determine the appropriate method and the type of climate signal that can be extracted. Uncertainties in growth-climate correlations can be related to climate data, thus the type, quality, sources and geographical validity of climate data should also be screened. To study the variability of climate and tree growth response in managed stands of our study areas, the most appropriate approach involved flexible splines and gridded climate data. We suggest that an ensemble approach, involving the evaluation of



dendroclimatological procedures, and comparing species' responses across diverse site-specific climatic conditions and time periods, can enhance our understanding of forest growth dynamics.

### **Acknowledgements**

This study was supported by the Spanish Ministry of Economy and Competitiveness, the European Union (FEDER funds), and the Spanish National Agriculture Research Institute (project ref:RTA2013-00011-C02-02). FN was supported by the International Campus of Excellence for Environment, Biodiversity and Global Change (CeiCambio) with a scholarship for a scientific stay at the Swiss Federal Research Institute-WSL (Birmensdorf, Switzerland) in 2015. Paolo Cherubini (WSL, Birmensdorf, Switzerland) provided useful suggestions to improve the discussion.

## References

- AEMET-IM, 2011. Iberian Climate Atlas. Agencia Estatal de Meteorología-Instituto de Meteorología de Portugal, <http://www.aemet.es/documentos/es/conocerlas/publicaciones/Atlas-climatologico/Atlas.pdf>
- Alla, A.Q., Camarero, J.J., 2012. Contrasting responses of radial growth and wood anatomy to climate in a Mediterranean ring-porous oak: implications for its future persistence or why the variance matters more than the mean. *Eur J For Res* 131 (5), 1537-1550.
- Allué, J.L., 1990. Atlas fitoclimático de España. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain.
- Benito, G., Sopena, A., Sánchez-Moya, Y., Machado, M. J., & Pérez-González, A.. 2003. Palaeoflood record of the Tagus River (central Spain) during the Late Pleistocene and Holocene. *Quaternary Sci Rev* 22 (15), 1737-1756.
- Benito Garzón, M., Sánchez de Dios, R., Sainz Ollero, H., 2008. Effects of climate change on the distribution of Iberian tree species. *Appl Veg Sci* 11 (2), 169-178.
- Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Res* 64 (2), 81-96.
- Bravo-Oviedo, A., & Montero, G., 2005. Site index in relation to edaphic variables in stone pine (*Pinus pinea* L.) stands in south west Spain. *Ann For Sci* 62 (1), 61-72.
- Briffa, K., Jones, P.D., 1990. Basic chronology statistics and assessment. In: Cook, E.R., Kairiukstis, L.A. (Eds.), *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 137-152.
- Büntgen, U., Egli, S., Galván, J. D., Diez, J. M., Aldea, J., Latorre, J., Martínez-Peña, F., 2015a. Drought-induced changes in the phenology, productivity and diversity of Spanish fungi. *Fungal Ecol* 16, 6-18.
- Büntgen, U., Trnka, M., Krusic, P. J., Kyncl, T., Kyncl, J., Luterbacher, J. et al., 2015b. Tree-Ring Amplification of the Early Nineteenth-Century Summer Cooling in Central Europe. *J Climate* 28 (13), 5272-5288.
- Büntgen, U., Martínez-Peña, F., Aldea, J., Rigling, A., Fischer, E. M., Camarero, J. J., Hayes, M.J., Fatton, V., Egli, S., 2013. Declining pine growth in Central Spain coincides with increasing diurnal temperature range since the 1970s. *Global Planet Change* 107, 177-185.
- Büntgen, U., Kaczka, R.J., Trnka, M., Rigling, A., 2012. Ensemble estimates reveal a complex hydroclimatic sensitivity of pine growth at Carpathian cliff sites. *Agr Forest Meteorol* 160, 100-109.

- Büntgen, U., Frank, D. C., Kaczka, R. J., Verstege, A., Zwijacz-Kozica, T., Esper, J., 2007. Growth responses to climate in a multi-species tree-ring network in the Western Carpathian Tatra Mountains, Poland and Slovakia. *Tree Physiol* 27 (5), 689-702.
- Campelo, F., Nabais, C., Freitas, H., Gutiérrez, E., 2006. Climatic significance of tree ring width and intra-annual density fluctuations in *Pinus pinea* from a dry Mediterranean area in Portugal. *Ann For Sci* 64, 229–238.
- Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., Peñuelas, J., 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *P Natl Acad Sci USA* 108(4), 1474-1478.
- Carrer, M., Urbinati, C., 2006. Long-term change in the sensitivity of tree-ring growth to climate forcing in *Larix deciduas*. *New Phytol* 170(4), 861-872.
- Cherubini, P., Gartner, B. L., Tognetti, R., Braker, O. U., Schoch, W., Innes, J. L., 2003. Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. *Biol Rev* 78 (01), 119-148.
- Cook, E.R., Briffa, K.R., Shiyatov, S., Mazepa, V., 1990a. Tree-ring standardization and growth-trend estimation. In: Cook, E.R., Kairiukstis, L.A. (Eds.) *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 104-123
- Cook, E.R., Shiyatov, S., Mazepa, V., 1990b. Estimation of the Mean Chronology. In: Cook, E.R., Kairiukstis, L.A. (Eds.), *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 123-132
- Cook, E. R., Seager, R., Kushnir, Y., Briffa, K. R., Büntgen, U., Frank, D. et al., 2015. Old World megadroughts and pluvials during the Common Era. *Science Advances* 1(10), e1500561, DOI: 10.1126/sciadv.1500561
- de Luis, M., Cufar, K., Di Filippo, A., Novak, K., Papadopoulos, A., Piovesan, G., Rathgeber C.B.K., Raventos, J., Saz, M.A., Smith K.Y., 2013. Plasticity in dendroclimatic response across the distribution range of Aleppo pine (*Pinus halepensis*). *Plos One* 8 (12), e83550, DOI:10.1371/journal.pone.0083550
- de Luis, M., Novak, K., Čufar, K., Raventós, J., 2009. Size mediated climate–growth relationships in *Pinus halepensis* and *Pinus pinea*. *Trees-Struct Funct* 23 (5), 1065-1073.
- de Luis, M., Novak, K., Raventós, J., Gričar, J., Prislán, P., Čufar, K., 2011. Cambial activity, wood formation and sapling survival of *Pinus halepensis* exposed to different irrigation regimes. *Forest Ecol Manag* 262 (8), 1630-1638.

- Dessens, J., Bücher, A., 1997. A critical examination of the precipitation records at the Pic du Midi observatory, Pyrenees, France. In: Diaz, H.F., Beniston, M., Bradley, R.S. (Eds.) *Climatic Change at High Elevation Sites*. Springer, pp. 113-121
- Dorado Liñán, I. D., Büntgen, U., González-Rouco, F., Zorita, E., Montávez, J. P., Gómez-Navarro, J. J., Brunet, M., Heinrich, I., Helle, G., Gutiérrez, E., 2012. Estimating 750 years of temperature variations and uncertainties in the Pyrenees by tree ring reconstructions and climate simulations. *Clim Past* 8 (3), 919-933.
- Esper, J., Cook, E. R., Schweingruber, F. H., 2002. Low-frequency signals in long tree-ring chronologies or reconstructing past temperature variability. *Science* 295 (5563), 2250-2253
- Fallour, D., Fady, B., Lefevre, F., 1997. Study on isozyme variation in *Pinus pinea* L.: evidence for low polymorphism. *Silvae Genetica* 46 (4), 201-206.
- Frank, D., Büntgen, U., Böhm, R., Maugeri, M., Esper, J., 2007. Warmer early instrumental measurements versus colder reconstructed temperatures: shooting at a moving target. *Quaternary Sci Rev* 26 (25), 3298-3310.
- Galván, J. D., Camarero, J. J., Ginzler, C., Büntgen, U., 2014. Spatial diversity of recent trends in Mediterranean tree growth. *Environ Res Lett* 9 (8), 084001
- Gea-Izquierdo, G., Cherubini, P., Cañellas, I., 2011. Tree-rings reflect the impact of climate change on *Quercus ilex* L. along a temperature gradient in Spain over the last 100 years. *Forest Ecol Manag* 262 (9), 1807-1816.
- Gimeno, T. E., Camarero, J. J., Granda, E., Pías, B., Valladares, F., 2012. Enhanced growth of *Juniperus thurifera* under a warmer climate is explained by a positive carbon gain under cold and drought. *Tree Physiol* 32 (3), 326-336
- Giorgi, F., 2006. Climate change hot-spots. *Geophys Res Lett* 33 (8).
- Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Bull* 57, 205–221
- Harris, I., Jones, P.D., 2014. CRU TS3.22: Climatic Research Unit (CRU) Time-Series (TS) Version 3.22 of High Resolution Gridded Data of Month-by-month Variation in Climate (Jan. 1901- Dec. 2013). NCAS British Atmospheric Data Centre, 24 September 2014. DOI:10.5285/18BE23F8-D252-482D-8AF9-5D6A2D40990C
- Haylock, M.R., Hofstra, H., Klein Tank, A.M.G., Klok, E.J., Jones, P.D., New, M., 2008. A European daily high-resolution gridded dataset of surface temperature and precipitation for 1950-2006. *J Geophys Res - Atmos* 113, D20119, DOI:10.1029/2008JD10201

- Helama, S., Lindholm, M., Timonen, M., Eronen, M., 2004. Detection of climate signal in dendrochronological data analysis: a comparison of tree-ring standardization methods. *Theor Appl Climatol* 79 (3-4), 239-254.
- Hódar, J. A., Castro, J., Zamora, R., 2003. Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming. *Biol Conserv* 110 (1), 123-129.
- Jump, A. S., Hunt, J. M., Penuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob Change Biol* 12 (11), 2163-2174.
- Karl, T. R., Knight, R. W., Gallo, K. P., Peterson, T. C., Jones, P. D., Kukla, G. et al., 1993. A new perspective on recent global warming: asymmetric trends of daily maximum and minimum temperature. *B Am Meteorol Soc* 74 (6), 1007-1023.
- Klok, E.J., Klein Tank, A.M.G., 2008. Updated and extended European dataset of daily climate observations. *Int J Climatol* 29, 1182–1191
- Kovats, R.S., Valentini, R., Bouwer, L.M., Georgopoulou, E., Jacob, D., Martin, E., Rounsevell, M., Soussana, J.F., 2014. Europe. In: Barros, V.R., Field, C.B., Dokken, D.J., Mastrandrea, M.D., Mach, K.J., Bilir, T.E., Chatterjee, M.E., Ebi K.L., Estrada, Y.O., Genova, R.C., Girma, G., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.) *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp 1267–1326
- Latte, N., Lebourgeois, F., Claessens, H., 2015. Increased tree-growth synchronization of beech (*Fagus sylvatica* L.) in response to climate change in northwestern Europe. *Dendrochronologia* 33, 69-77.
- Luz, A.L., Pereira, H., Lauw, A. and Leal, S., 2014. Monitoring intra-annual cambial activity based on the periodic collection of twigs—A feasibility study. *Dendrochronologia* 32 (2), 162-170.
- Martin-Benito, D., Beekman, H., Cañellas, I., 2013. Influence of drought on tree rings and tracheid features of *Pinus nigra* and *Pinus sylvestris* in a mesic Mediterranean forest. *European J For Res* 132 (1), 33-45.
- Martín-Benito, D., Del Río, M., Cañellas, I., 2010. Black pine (*Pinus nigra* Arn.) growth divergence along a latitudinal gradient in Western Mediterranean mountains. *Ann For Sci* 67 (4), 401.
- Martínez, F., Montero, G., 2004. The *Pinus pinea* L. woodlands along the coast of South-western Spain: data for a new geobotanical interpretation. *Plant Ecology* 175 (1), 1-18.
- Mazza, G., Cutini, A., Manetti, M. C., 2014. Site-specific growth responses to climate drivers of *Pinus pinea* L. tree rings in Italian coastal stands. *Ann For Sci* 71 (8), 927-936.
- Meyers, L. A., Bull, J. J., 2002. Fighting change with change: adaptive variation in an uncertain world. *Trends Ecol Evol* 17 (12), 551-557.

- Montero González, G., Candela Plaza, J.A., Rodríguez Navarro, A. (Eds.), 2004. El pino piñonero en Andalucía: ecología distribución y silvicultura. Dirección General de Gestión del Medio Natural, Consejería de Medio Ambiente, Junta de Andalucía, Sevilla, [http://www.juntadeandalucia.es/medioambiente/consolidado/publicacionesdigitales/80-409\\_EL\\_PINO\\_PINHONERO\\_EN\\_ANDALUCIA/80-409.htm?lr=lang\\_es](http://www.juntadeandalucia.es/medioambiente/consolidado/publicacionesdigitales/80-409_EL_PINO_PINHONERO_EN_ANDALUCIA/80-409.htm?lr=lang_es)
- Mutke, S., Gordo, J., Khouja, M.L., Fady, B., 2013. Low genetic and high environmental diversity at adaptive traits in *Pinus pinea* from provenance tests in France and Spain. In : Mutke, S., Piqué, M., Calama, R. (Eds.) Mediterranean stone pine for agroforestry. Zaragoza: CIHEAM / FAO / INIA / IRTA / CESEFOR / CTFC, pp. 73-79. (Options Méditerranéennes: Série A. Séminaires Méditerranéens; n. 105). AGROPINE 2011 International Meeting on Mediterranean Stone Pine for Agroforestry, 2011/11/17-19, Valladolid (Spain), <http://om.ciheam.org/om/pdf/a105/00006784.pdf>
- Mutke, S., Gordo, J., Chambel, M. R., Prada, M. A., Álvarez, D., Iglesias, S., Gil, L., 2010. Phenotypic plasticity is stronger than adaptive differentiation among Mediterranean stone pine provenances. *Forest Systems* 19 (3), 354-366.
- Natalini, F., Correia, A. C., Vázquez-Piqué, J., Alejano, R., 2015. Tree rings reflect growth adjustments and enhanced synchrony among sites in Iberian stone pine (*Pinus pinea* L.) under climate change. *Ann For Sci* 72 (8), 1023-1033, DOI: 10.1007/s13595-015-0521-6
- Natalini, F., Alejano, R., Vázquez-Piqué, J., Cañellas, I., & Gea-Izquierdo, G., 2016. The role of climate change in the widespread mortality of holm oak in open woodlands of Southwestern Spain. *Dendrochronologia* 38, 51-60, DOI: 10.1016/j.dendro.2016.03.003.
- Nicault, A., Alleaume, S., Brewer, S., Carrer, M., Nola, P., Guiot, J., 2008. Mediterranean drought fluctuation during the last 500 years based on tree-ring data. *Clim Dynam* 31 (2-3), 227-245.
- Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M.D., Richards, C.L., Valladares, F., and van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. *Trends Plant Sci* 15 (12), 684-692.
- Olano, J. M., Eugenio, M., García-Cervigón, A. I., Folch, M., & Rozas, V., 2012. Quantitative tracheid anatomy reveals a complex environmental control of wood structure in continental Mediterranean climate. *Int J Plant Sci* 173 (2), 137-149
- Pardos, M., Calama, R., Maroschek, M., Rammer, W., Lexer, M. J., 2015. A model-based analysis of climate change vulnerability of *Pinus pinea* stands under multiobjective management in the Northern Plateau of Spain. *Ann For Sci* 72 (8), 1009-1021.

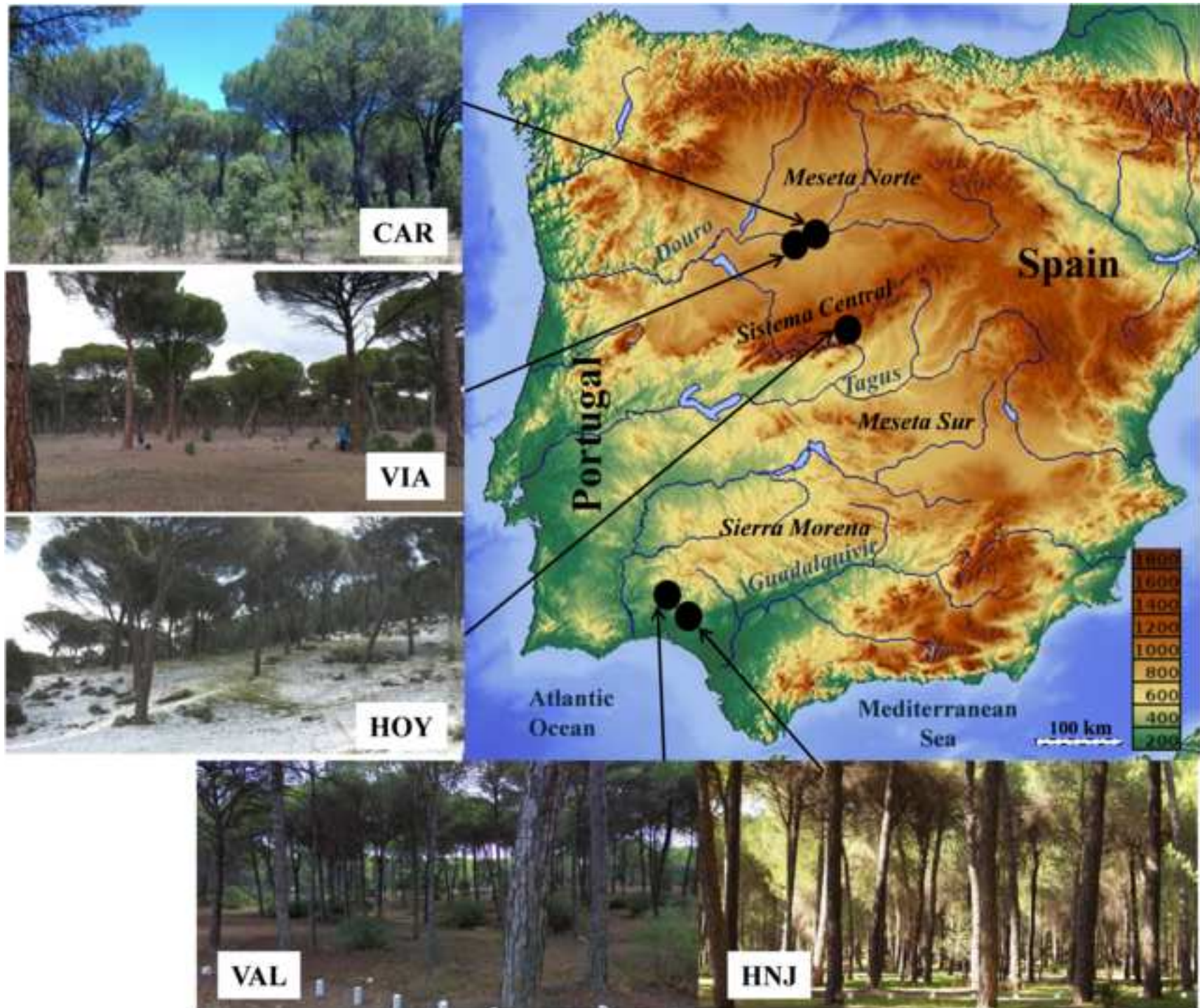
- Pardos, M., Puértolas, J., Madrigal, G., Garriga, E., de Blas, S., Calama, R., 2010. Seasonal changes in the physiological activity of regeneration under a natural light gradient in a *Pinus pinea* regular stand. *Forest Systems*, 19 (3), 367-380.
- Pausas, J. G., 2004. Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Climatic Change* 63 (3), 337-350.
- Peñuelas, J., Filella, I., Comas, P., 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Glob Change Biol* 8 (6), 531-544.
- Pérez, F.F., Boscolo, R. (Eds.), 2010. Climate in Spain: past, present and future. Regional climate change assessment report. CLIVAR: Ministerio de Medio Ambiente y Medio Rural y Marino : Ministerio de Ciencia e Innovacion. 83 pp., <http://digital.csic.es/handle/10261/33470>
- Pinzauti, F., Sebastiani, F., Budde, K. B., Fady, B., González-Martínez, S. C., Vendramin, G. G., 2012. Nuclear microsatellites for *Pinus pinea* (Pinaceae), a genetically depauperate tree, and their transferability to *P. halepensis*. *Am J Bot* e362–e365, DOI: 10.3732/ajb.1200064
- Piovesan, G., Di Filippo, A., Alessandrini, A., Biondi, F., Schirone, B., 2005. Structure, dynamics and dendroecology of an old-growth *Fagus* forest in the Apennines. *J Veg Sci* 16 (1), 13-28.
- Prieto, L., Herrera, R. G., Díaz, J., Hernández, E., del Teso, T., 2004. Minimum extreme temperatures over Peninsular Spain. *Global Planet Change* 44 (1), 59-71.
- Rivas-Martínez, S., 2007. Mapa de series, geoserias y geopermaseries de vegetación de España. *Itinera Geobotanica* 17, 5-436
- Rodríguez-Puebla, C., Encinas, A. H., Nieto, S., & Garmendia, J., 1998. Spatial and temporal patterns of annual precipitation variability over the Iberian Peninsula. *Int J Climatol* 18 (3), 299-316.
- Romero, R., Sumner, G., Ramis, C., Genovés, A., 1999. A classification of the atmospheric circulation patterns producing significant daily rainfall in the Spanish Mediterranean area. *Int J Climatol* 19(7), 765-785.
- Rossi, S., Morin, H., Deslauriers, A., Plourde, P. Y., 2011. Predicting xylem phenology in black spruce under climate warming. *Glob Change Biol* 17 (1), 614-625.
- Sáez-Laguna, E., Guevara, M. Á., Díaz, L. M., Sánchez-Gómez, D., Collada, C., Aranda, I., Cervera, M. T., 2014. Epigenetic variability in the genetically uniform forest tree species *Pinus pinea* L. *Plos One*, DOI: 10.1371/journal.pone.0103145
- Sánchez-Gómez, D., Velasco-Conde, T., Cano-Martín, F. J., Guevara, M. Á., Cervera, M. T., Aranda, I., 2011. Inter-clonal variation in functional traits in response to drought for a genetically homogeneous Mediterranean conifer. *Environ Exp Bot* 70 (2), 104-109.

- Scheffran, J., Battaglini, A., 2011. Climate and conflicts: the security risks of global warming. *Reg Environ Change* 11 (1), 27-39.
- Schweingruber FH, Kairiukstis L, Shiyatov S., 1990. Sample selection. In: Cook, E.R., Kairiukstis, L.A. (Eds.) *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 23-35
- Seim, A., Treydte, K., Trouet, V., Frank, D., Fonti, P., Tegel, W., Panayotov, M., Fernández-Donado, L., Krusic, P. and Büntgen, U., 2014. Climate sensitivity of Mediterranean pine growth reveals distinct east–west dipole. *Int J Climatol* 35 (9), 2503-2513, DOI: 10.1002/joc.4137
- Soto, A., Robledo-Arnuncio J. J., Gpnzález-Martínez S. C., Smouse, P. E., Alia, R., 2010. Climatic niche and neutral genetic diversity of the six Iberian pine species: a retrospective and prospective view. *Mol Ecol* 19 (7), 1396-1409.
- Speer, J., 2010. *Fundamentals of tree-ring research*. The University of Arizona Press, Tucson
- Tardif, J., Camarero, J. J., Ribas, M., Gutiérrez, E., 2003. Spatiotemporal variability in tree growth in the Central Pyrenees: climatic and site influences. *Ecol Monogr* 73 (2), 241-257.
- van der Schrier, G., Briffa, K.R., Jones, P.D., Osborn, T.J., 2006a. Summer moisture variability across Europe. *J Climate* 19, 2818-2834, DOI:10.1175/JCLI3734.1
- Vendramin, G.G., Fady, B., González-Martínez, S.C., Hu, F.S., Scotti, I., Sebastiani, F., Soto, Á. Petit, R.J., 2008. Genetically depauperate but widespread: the case of an emblematic Mediterranean pine. *Evolution* 62 (3), pp.680-688.
- Vicente Serrano, S. M., González-Hidalgo, J. C., Luis, M. D., Raventós, J., 2004. Drought patterns in the Mediterranean area: the Valencia region (eastern Spain). *Clim Res* 26 (1), 5-15.
- Vieira, J., Rossi, S., Campelo, F., Freitas, H., Nabais, C., 2014. Xylogenesis of *Pinus pinaster* under a Mediterranean climate. *Ann For Sci* 71 (1), 71-80.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.M., Hoegh-Guldberg, O. and Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416 (6879), pp.389-395
- Zang, C., Biondi, F., 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. *Ecography* 38 (4), 431-436.



Figure1

[Click here to download high resolution image](#)



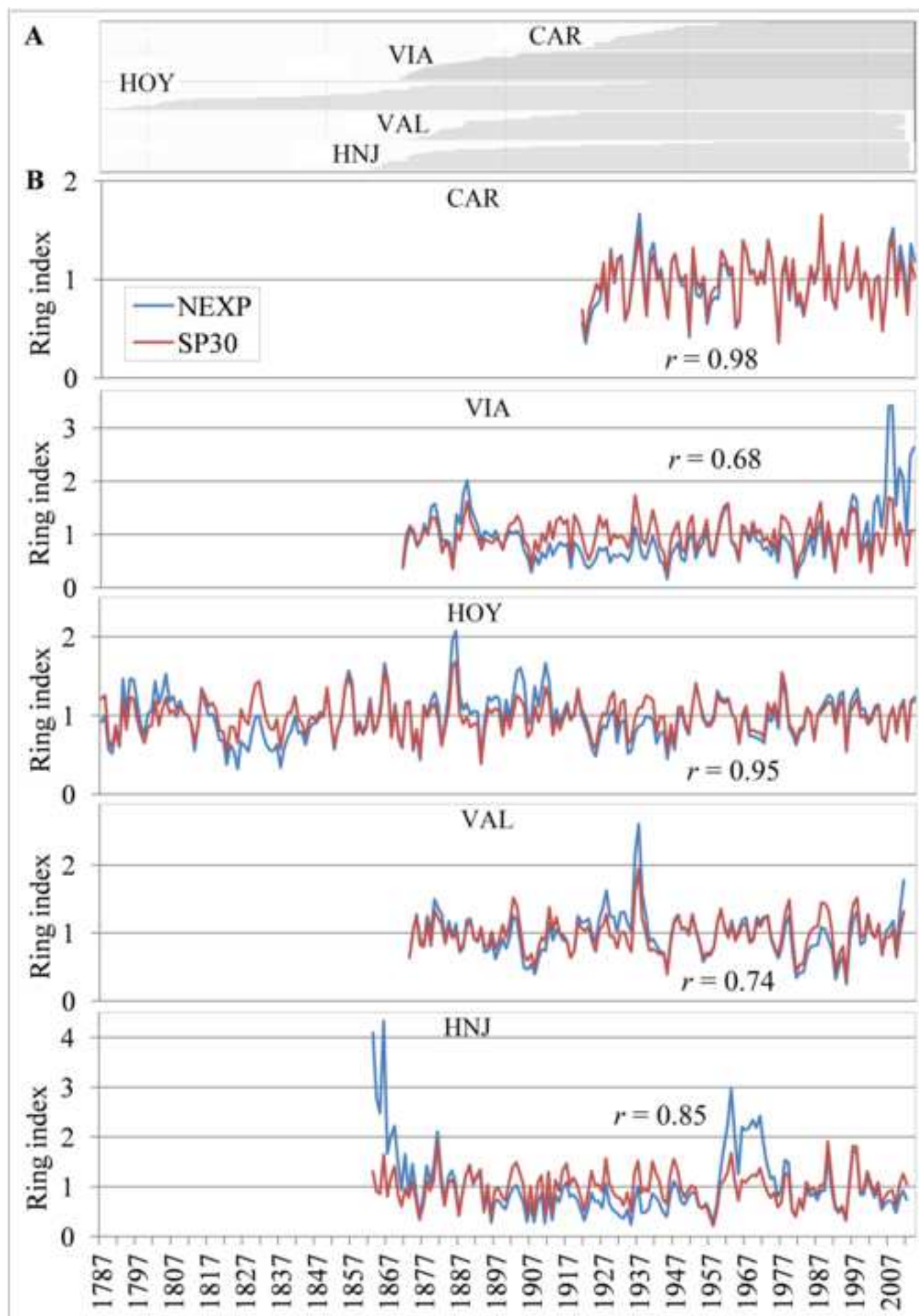
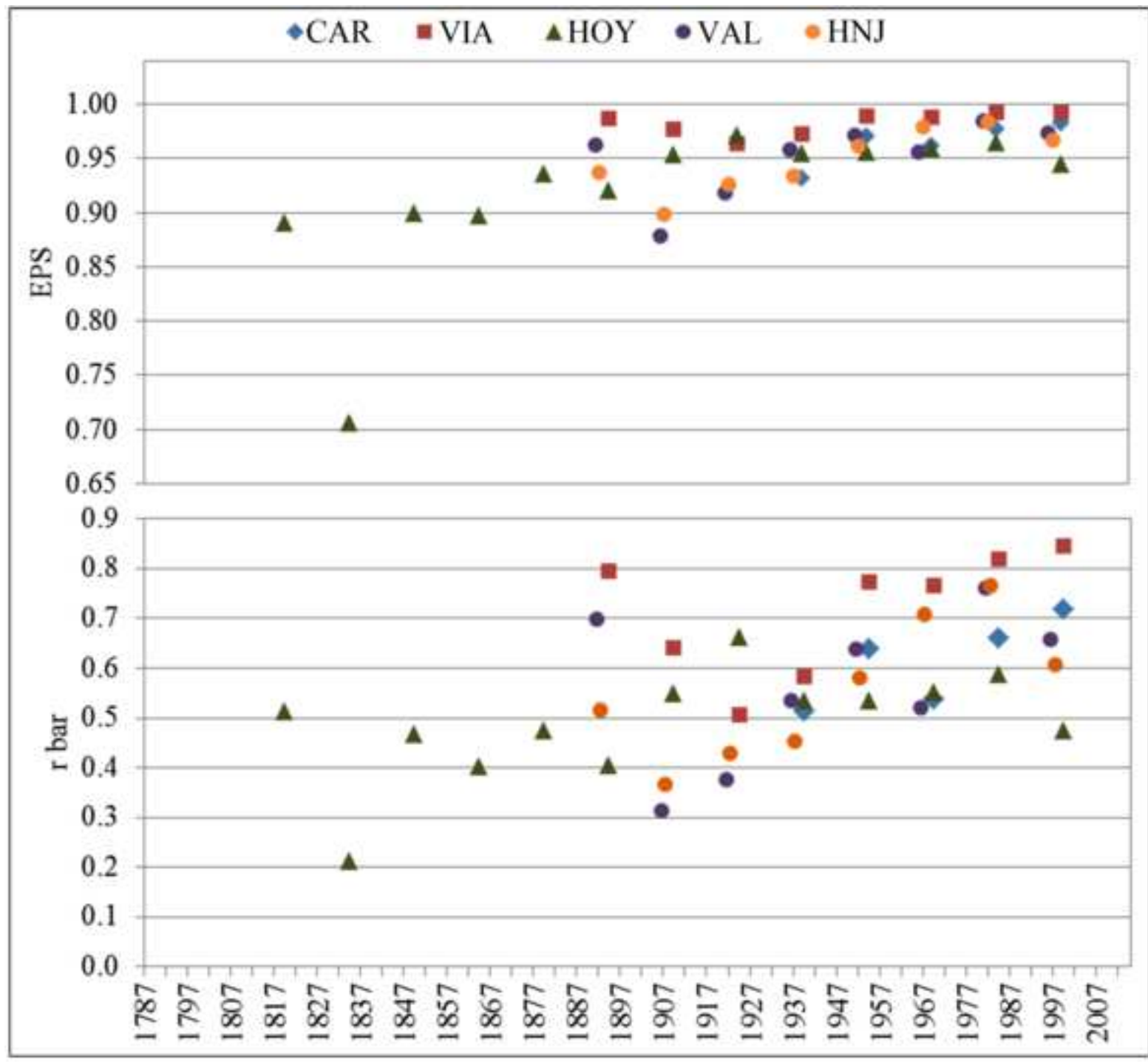
[Click here to download high resolution image](#)



Figure3

[Click here to download high resolution image](#)



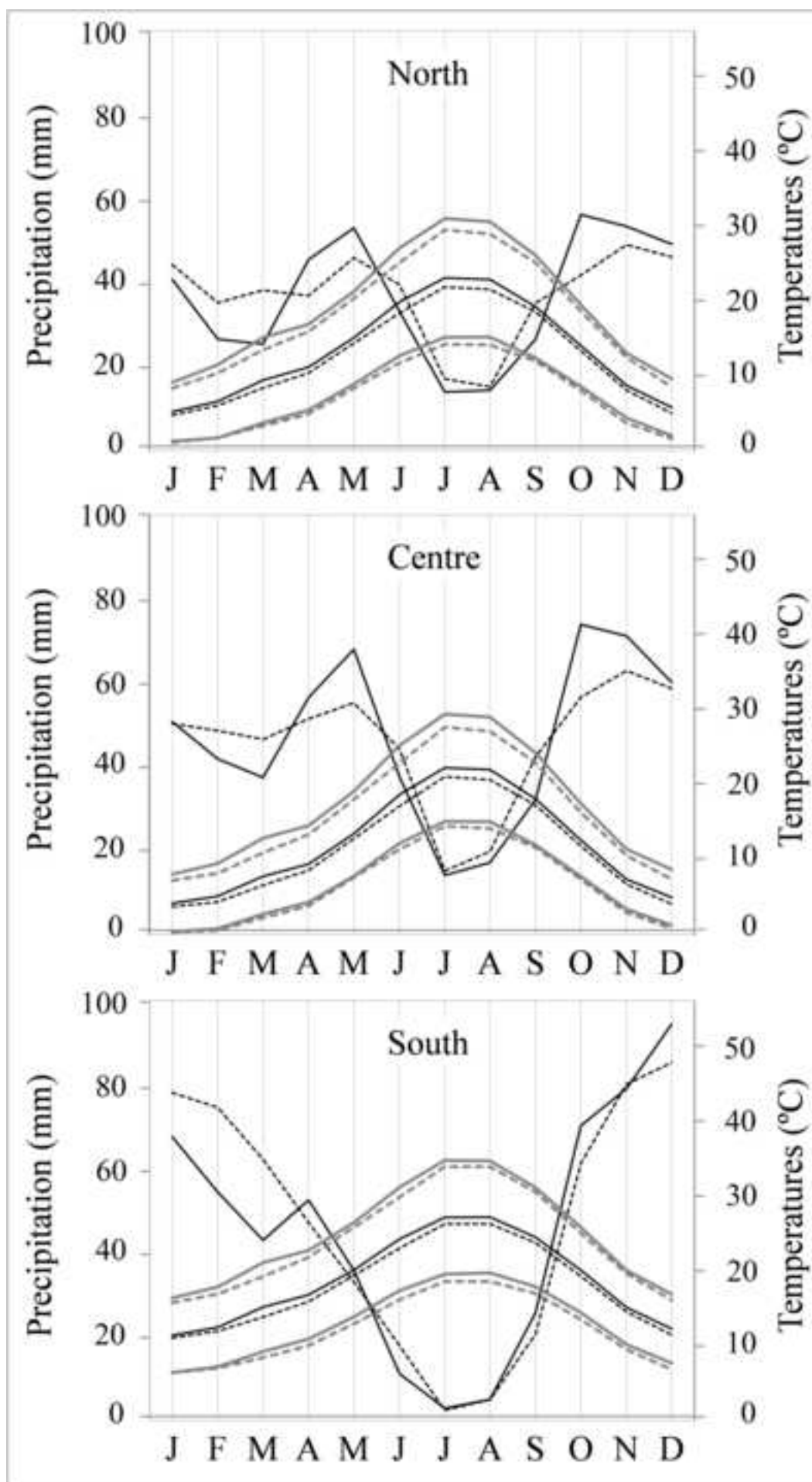


Figure5

[Click here to download high resolution image](#)

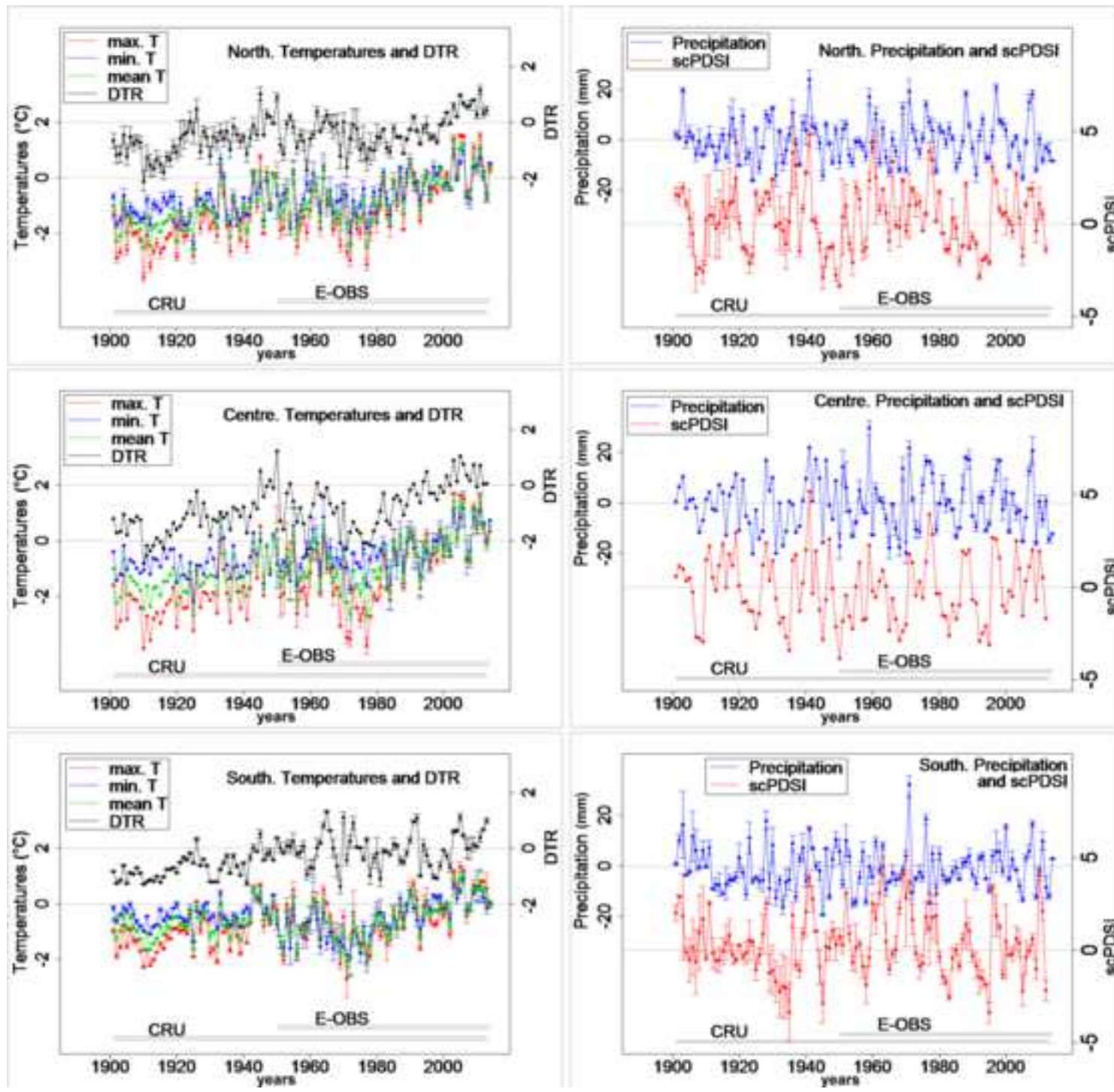


Figure6

[Click here to download high resolution image](#)

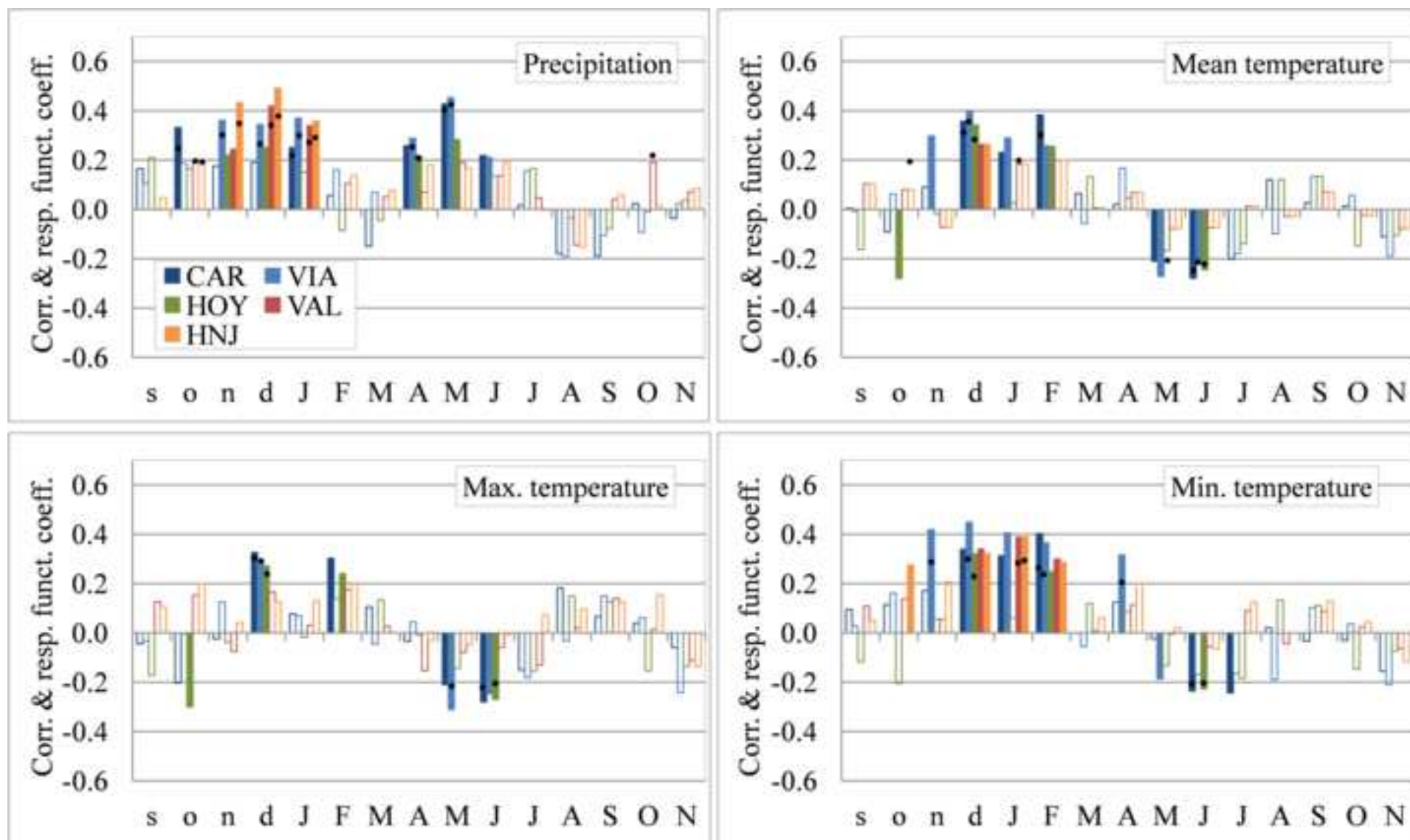




Figure7

[Click here to download high resolution image](#)

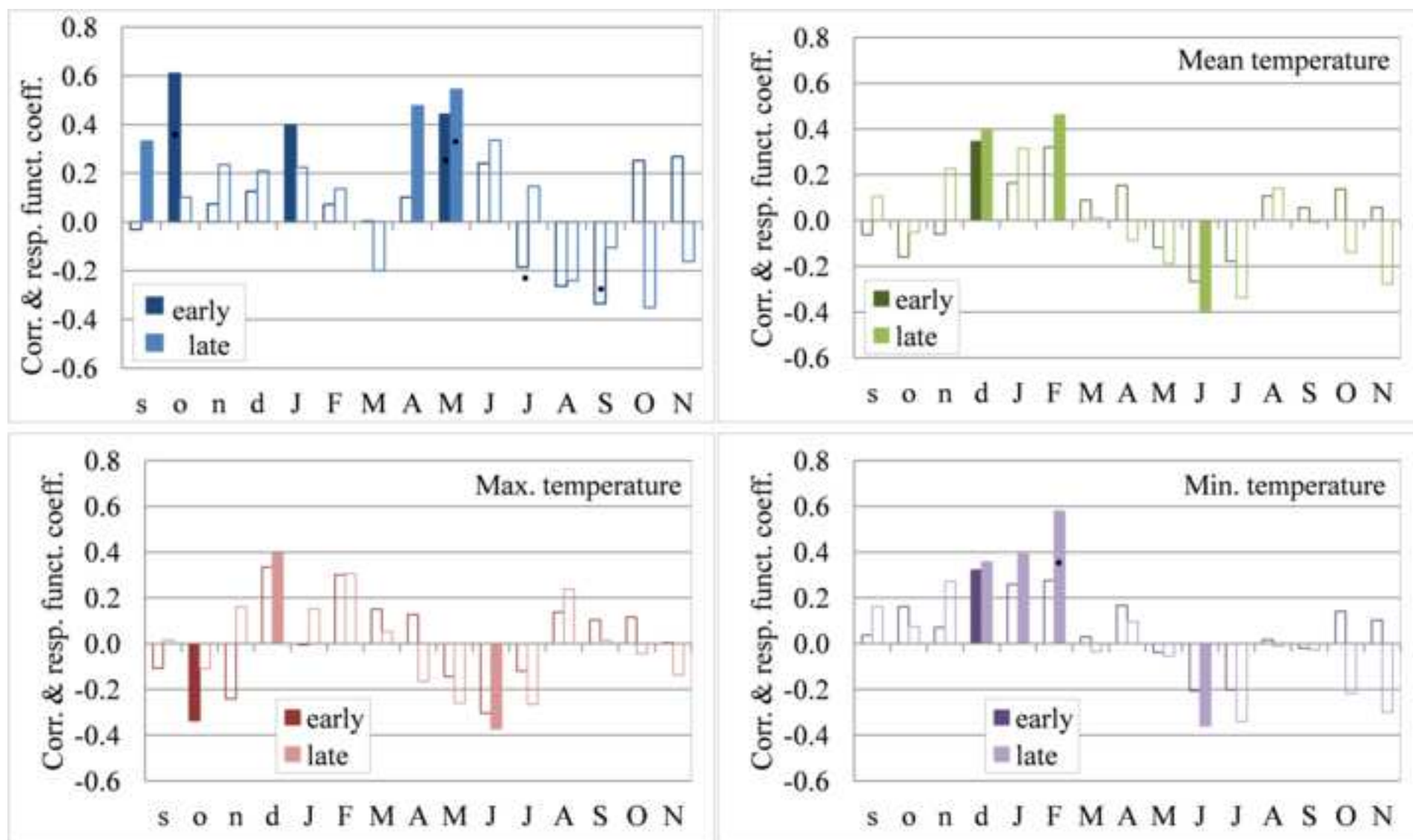


Figure8

[Click here to download high resolution image](#)

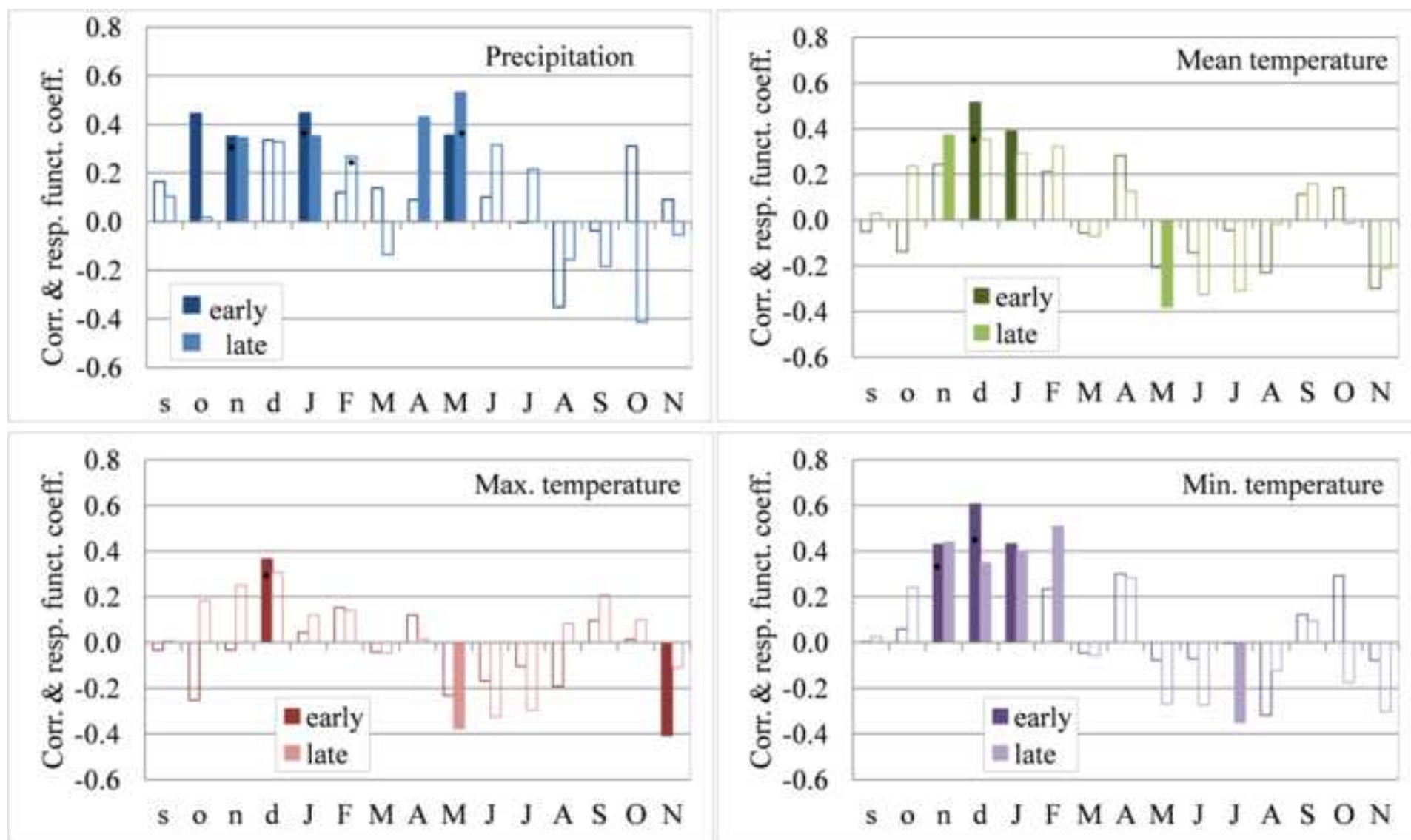
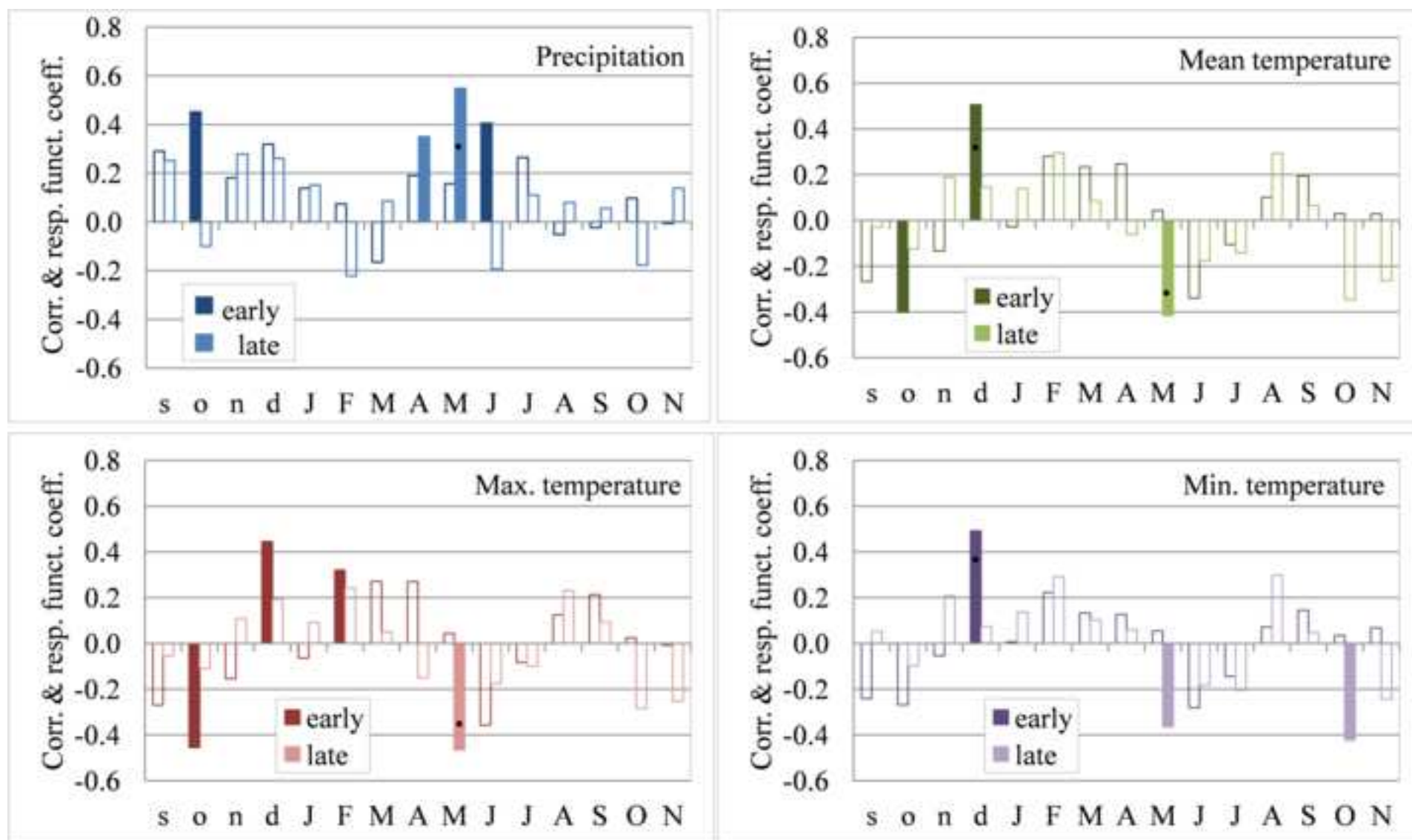




Figure9

[Click here to download high resolution image](#)



□

Figure10

[Click here to download high resolution image](#)

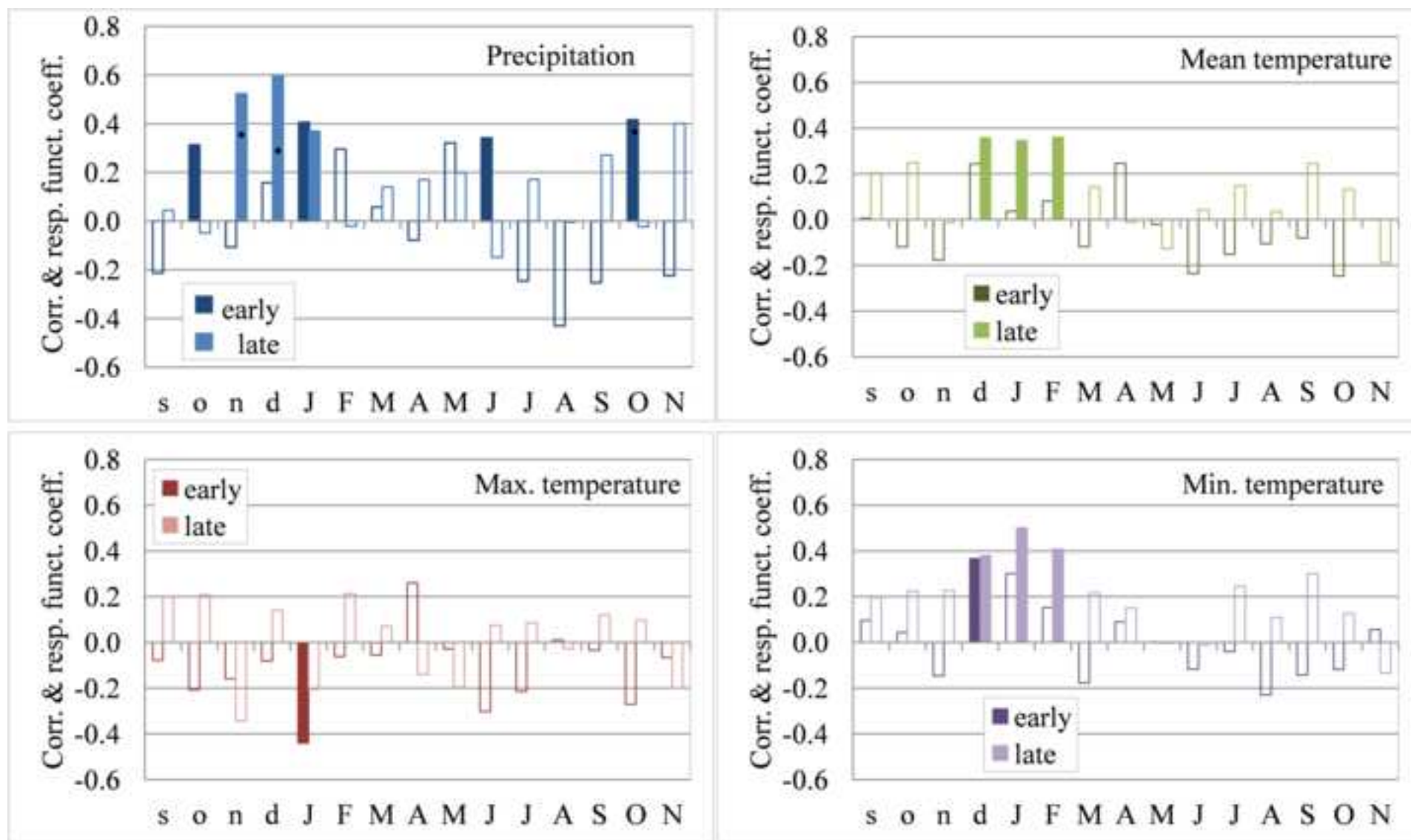
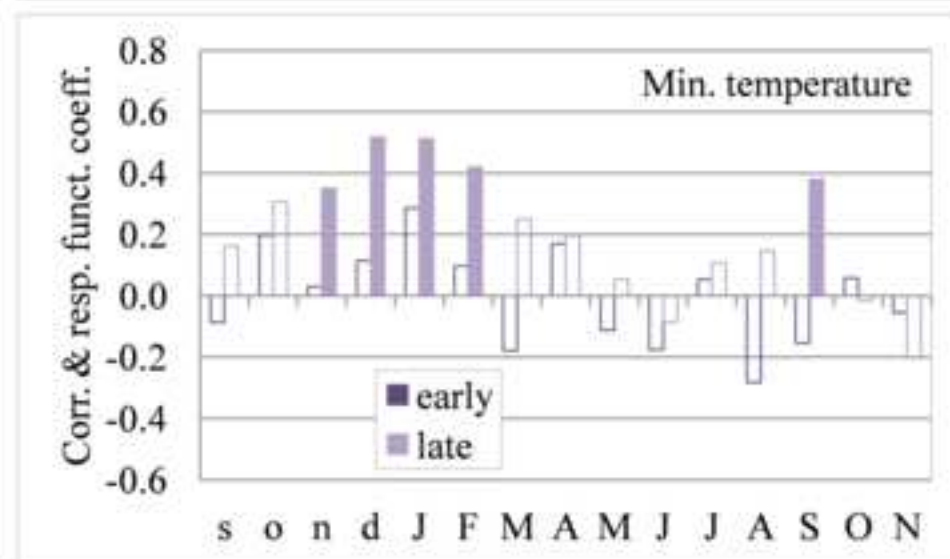
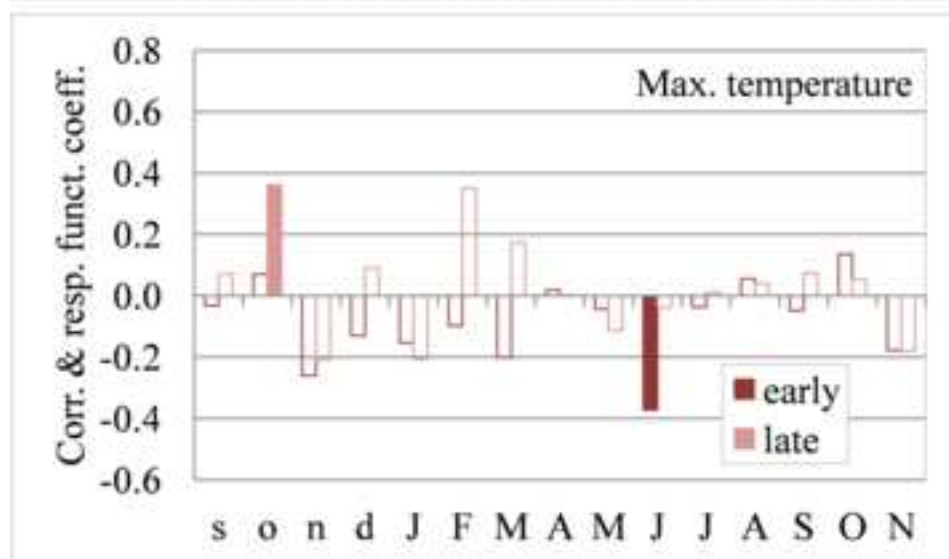
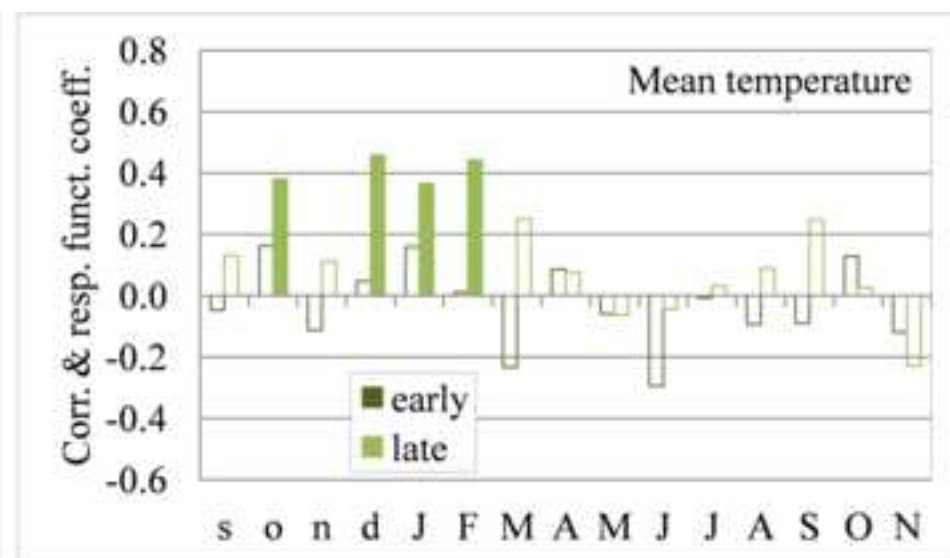
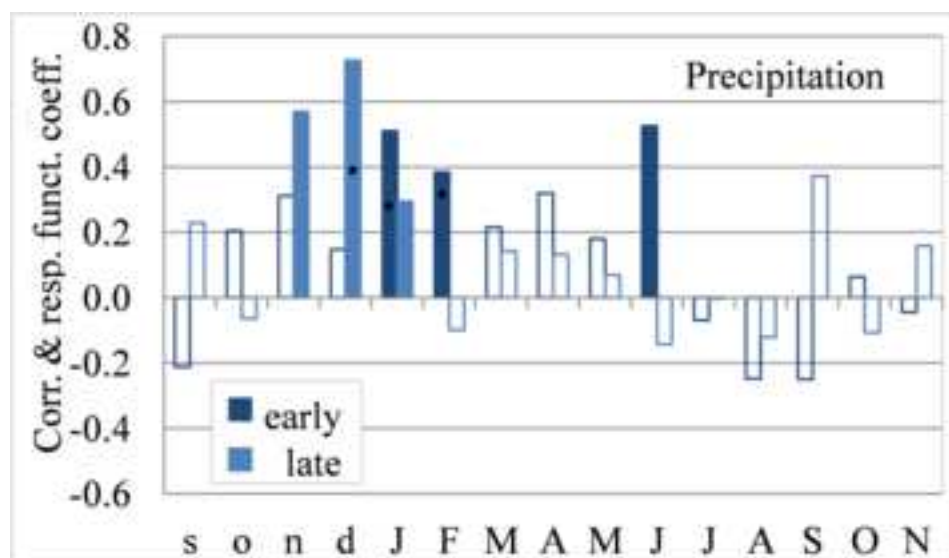


Figure11

[Click here to download high resolution image](#)



**Table 1.** Site locations and characteristics.

	<b>Carrascal</b>	<b>Viana de Cega</b>	<b>Hoyo de Pinares</b>	<b>Valverde del Camino</b>	<b>Hinojos</b>
Latitude [°N]	41.59	41.47	40.51	37.53	37.28
Longitude [°W]	4.33	4.72	4.38	6.78	6.39
Elevation [m a.s.l.]	880	710	890	260	80
Soils (FAO classification)	Cambisols	Arenosols	Leptosols	Luvisols	Cambisols/Regosols
Slope [%]	0	0	50-60	0	0
Species composition	Mixed ( <i>P. pinea</i> - <i>Quercus ilex</i> - <i>Juniperus thurifera</i> )	Pure ( <i>P. pinea</i> )	Pure ( <i>P. pinea</i> )	Pure ( <i>P. pinea</i> )	Pure ( <i>P. pinea</i> )
Mean tree height [m]	10	17	19	18	18
Mean tree diameter [cm]	45	50	75	65	70

**Table 2.** Characteristics of tree ring chronologies at the different sites. Chronology length refers to the longest cross-dated individual tree series in each site. A chronology length with “ $\geq 10$  trees” refers to the interval with a minimum of 10 cross-dated individual tree series. The mean growth rate refers to the average ring width over each chronology. Standard chronology refers to the mean ring index chronology calculated as ratios and detrended with a negative exponential curve (NEXP), or cubic smoothing splines with 50% frequency-response cutoffs at 30 years (SP30).  $EPS > 0.85$  indicates the period covered by the chronologies with an Expressed Population Signal greater than 0.85.

		<b>Carrascal</b>	<b>Viana de Cega</b>	<b>Hoyo de Pinares</b>	<b>Valverde del Camino</b>	<b>Hinojos</b>
No. of trees		22	26	19	20	19
Chronology length (years)		1921-2014 (94)	1871-2014 (144)	1787-2014 (228)	1873-2011 (139)	1863-2012 (150)
Chronology length with $\geq 10$ trees (years)		1931-2014 (84)	1877-2014 (138)	1844-2014 (171)	1888-2011 (124)	1874-2012 (139)
Mean series length (years)		77	130	172	120	127
Mean growth rate (mm)		2.28	1.52	1.74	2.08	2.04
1 <sup>st</sup> order autocorrelation	Raw ring width series	0.616	0.867	0.609	0.844	0.765
	Standard chronologies					
	NEXP	0.203	0.638	0.541	0.600	0.673
	SP30	0.070	0.268	0.311	0.444	0.259
EPS > 0.85		1925-2014	1873-2014	1842-2014	1881-2011	1866-2012

**Table 3.** Correlation coefficients between sites using the mean standard chronologies after detrending with a negative exponential curve (NEXP), or cubic smoothing splines with 50% frequency-response cutoffs at 30 years (SP30). Correlations were calculated over the common interval with at least 10 trees (1931-2011).

(NEXP)	Carrascal	Viana de Cega	Hoyo de Pinares	Valverde del Camino
Viana de Cega	0.45			
Hoyo de Pinares	0.24	0.35		
Valverde del Camino	0.48	0.29	0.13	
Hinojos	0.21	0.14	0.14	0.26
(SP30)	Carrascal	Viana de Cega	Hoyo de Pinares	Valverde del Camino
Viana de Cega	0.63			
Hoyo de Pinares	0.38	0.41		
Valverde del Camino	0.47	0.52	0.40	
Hinojos	0.38	0.47	0.23	0.66