VARYING CLIMATE SENSITIVITY AT THE DRY DISTRIBUTION EDGE OF *PINUS SYLVESTRIS* AND *P. NIGRA*

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EPS: Expressed population signal
MS: Mean sensitivity
SD: Standard deviation
r1: first-order autocorrelation
SNR: signal-to-noise ratio
VARpc1: variance explained by the first principal component
s_x: annual sensitivity
ms_x: mean annual sensitivity
HSD: honestly significant difference

Abstract

Rear edge populations, those residing at the low-latitude margins of species ranges, represent a critical genetic diversity for species conservation, management, and evolutionary potential. The present study analyses climate-radial growth relations for *Pinus sylvestris* and *P. nigra* at their dry distribution limit in the Mediterranean basin. The study was conducted in native relict forests of the two species in SE Spain, analyzing radial growth variability and climate-growth relations over time and between different ecological conditions. The lack of strong precipitation signals found could be due to high tree density, appropriate microclimatic conditions and/or high local adaptation. However, previous September temperatures exerted a negative impact on radial growth at all sites, presumably as a result of a prolonged summer drought. By contrast, high temperatures during winter and spring boosted radial growth at most locations. Both the negative and positive effects of temperature have gained relevancy in the last decades and can determine future performance of these Mediterranean pinewoods. Besides common patterns, recorded site-specific signals in climate-growth relationships reveal the influence of different ecological conditions. In this respect, tree-growth variability increased at low elevation coupled with increasing aridity, indicating higher vulnerability to rapid climate changes at low elevations. In contrast, the lack of strong precipitation signals and positive effects of temperatures at high elevation, could buffer the impact of drought and favor the persistence of *P. sylvestris* and *P. nigra* rear edge populations.

Keywords: rear edge populations; dendroecology; climate-growth relations; tree growth variability; climate change; *Pinus*.

1. INTRODUCTION

The study of ecological dynamics of species' borders provides insights into the potential ability of species to respond to climate change (Holt and Kleitt, 2005). Populations residing at the low-latitude margin of species distribution ranges, defined as rear edge populations, represent a critical genetic diversity for species conservation, management and future evolutionary potential (Hampe and Petit, 2005; Jump et al., 2009). Therefore, the understanding of rear edge population performance becomes increasingly urgent.

Many tree species reach their southern distribution limit in the Mediterranean basin, where drought constrains their main demographic rates (Castro et al., 2004a; Galiano et al., 2010; Linares and Tíscar, 2010; Peñuelas et al., 2001). Expected upward migrations of plant populations as the climate warms up, could convert mountains into dead-end streets for many rear edge populations, exacerbated by the recurrence of extreme droughts (Beniston et al., 2007; Christensen et al., 2007; Briffa et al., 2009) and associated growth declines and mortality events (Galiano et al., 2010; Jump et al., 2006; Linares et al., 2009). However, stabilizing processes, which compensate or minimize performance reductions at individual and population level (see Lloret et al., 2012), could buffer the impact of rapid climate changes. In this context, site-specific ecological conditions, such as high moisture and low competition, can provide adequate sites for persistence of rear edge populations (Hampe and Pettit, 2005).

Although precipitation variability severely hampers plant performance in southern distribution limits (Dobbertin et al., 2010; Matías et al., 2012; Mendoza et al., 2009), temperature can also play a key role. High temperatures are a common factor in massive tree-mortality events, in part through temperature-driven increase in water deficit (Allen et al., 2010; vanMantgen and Stephenson, 2007). Although in cold climates moderate warming can be beneficial for tree growth (Devi et al., 2008; Scholze et al., 2006), temperature-induced drought stress can also limit tree radial growth at high latitudes (Barber et al., 2000; Wilmking et al., 2004). Thus, both temperature and precipitation could entail plant drought stress, notably affecting plant performance in rear edge populations.

The main objective of the present study is to analyze climate-tree growth relationships of *Pinus sylvestris* L. and *P. nigra* Arnold in rear edge populations in SE Spain. Both species are characterized by wide distribution areas, with their dry limits occurring in the southern Mediterranean basin. As climatic conditions are changing persistently, there is need not only to assess climate-tree growth relationships for a given time period, but also to assess changes over time, allowing us to discuss future shifts in rear edge population performance (Weber et al., 2012). Tree growth variability was also measured for each species and location, in order to test whether these rear edge populations follow the increasing trend recorded at the regional scale in the Iberian Peninsula for *P. sylvestris* and *P. nigra* (Andreu et al., 2007; Martín-Benito et al., 2010; Tardif et al., 2003). These analyses were performed along environmental gradients of altitude and exposure. The combined analyses of climate-tree growth relations varying in space and time will provide insight into tree performance at the dry limits of *P. sylvestris* and *P. nigra*.

In summary, the present study analyses changes in climate-tree growth relationships and tree growth variability over time and between different ecological conditions at *P. sylvestris* and *P. nigra* rear edge populations. We examine differences in growth response over time and along the environmental gradients for *P. sylvestris* growing with northern and southern exposures, and for *P. nigra* growing across an altitudinal gradient. We hypothesise a stronger response both to high summer temperatures and to precipitation for *P. sylvestris* at locations with southern exposures, with usually warmer and drier conditions. Accordingly, the strongest response to rainfall and high summer temperatures for *P. nigra* is expected at the low elevation site. Differences in growth response between *P. sylvestris* and *P. nigra* were also compared at the high elevation with a southern exposure, where the two species coexist. We expect *P. nigra* radial growth to depend less on water availability and to be less harmed by high summer temperatures than *P. sylvestris*, as Mediterranean *P. nigra* often occur at warmer and drier sites than do boreo-alpine *P. sylvestris* (Rouget et al. 2001). In fact, *P. nigra* displayed less vulnerability to drought-related mortality over ontogeny than *P. sylvestris* where the two species coexist (Boulant et al., 2008; Castro et al., 2004a; Herrero et al., 2013; Martínez-Vilalta and Piñol, 2002). In addition, adult trees of *P. sylvestris* seem to be more sensitive than *P. nigra* to summer potential evapotranspiration effects (Eilmann and Rigling 2012; Lévèsque et al. 2013; Sánchez-Salguero et al., 2012a).

2. MATERIALS AND METHODS

2.1 Study site and sampling design

The study was conducted at Sierra de Baza Natural Park (SE Spain, 2º51’48’’W, 37º22’57’’N), at the southernmost distribution limit for both *Pinus sylvestris* and *P.*

nigra (Barbéro et al., 1998; Fig. 1). The climate is Mediterranean, characterized by cold winters and hot summers, with pronounced summer drought (June-August). Figure 2 shows a climatic diagram for the period 1920-2007 using data from CRU T.S 2.1 database (see 2.4 Climatic data subsection), with a mean annual rainfall of 482 ± 12 mm (mean ± SE). The bedrock is predominantly calcareous and the soil type is cambisol for all the sampled sites (CSIC-IARA, 1989).

(Figure 1)

(Figure 2)

The study was performed on *P. sylvestris* subsp. *nevadensis* (Christ) and *P. nigra* relict native forests. *P. sylvestris* populations occur mainly at 1900-2000 m a.s.l., whereas *P. nigra* formations extend from 1500 m to 2000 m. However, at the highest altitude (2000 m) *P. nigra* is associated with warmer southern exposures while at lower altitudes (1500-1700 m) it appear more frequently with northern exposures. At the lowest altitude (1500 m), *P. nigra* commonly intermingle with *Quercus ilex* L subsp. *ballota* (Desf.) Samp. To test the influence of exposure on *P. sylvestris* radial growth, we sampled two different sites at 2000 m a.s.l. only 300 m apart from each other in the same valley, one site with a northern and the other with a southern exposure. While the forest with the northern exposure was formed exclusively by *P. sylvestris*, the forest with southern exposure was composed of both *P. sylvestris* (56 ± 5% of total tree density) and *P. nigra* (44 ± 5%), allowing growth responses of the two species to be compared. In addition, two *P. nigra* sites were sampled at 1700 (almost pure *P. nigra*) and 1500 m (63 ± 5% *P. nigra*, 37 ± 5% *Quercus ilex*) to analyze *P. nigra* growth responses along an altitudinal gradient. Figure 1 shows the location of sampled sites in the study area, and Table 1 describes its characteristics. At each site, 20 trees were cored with an increment borer at breast height (1.30 m). Two cores were taken from each tree in two opposite radial directions. Diameter at breast height and tree height were recorded for each tree.

2.2 Sample processing and chronology building

Cores were mounted and sanded with progressively finer grades of sandpaper to highlight ring-width patterns. All cores were visually cross-dated following the procedures described by Yamaguchi (1991). Afterwards, tree-ring width was measured using a combination of a Lintab digital positioning table and the Time Series Analysis Program (TSAP, Rinntech, Germany). Because of numerous missing rings, cross-dating was not always possible and the corresponding cores were discarded. Cores from young trees were also discarded. The final number of trees used and tree characteristics are shown in Table 1.

Each ring-width series was detrended using a 30-year cubic smoothing spline with a 50% frequency response (Cook and Peters, 1981) using the software ARSTAN (Cook, 1985). Each measured series was standardized dividing observed values by predicted values to obtain dimensionless ring-width indices series. Index series were averaged using a bi-weight robust mean to develop the mean standard chronology. Additionally, temporal autocorrelation was removed by applying autoregressive modelling and the residual chronology developed.

The reliable time span was calculated for each chronology, based on a minimum expressed population signal (EPS) value of 0.85 (Wigley et al., 1984). EPS quantifies the degree to which a particular sample chronology depicts a hypothetically perfect chronology (Briffa and Jones, 1990). Several descriptive statistics were calculated for the period 1935-2007 for all chronologies, as this period was common for all the chronologies (see Table 1). Mean radial growth, mean sensitivity (MS), standard deviation (SD), first-order autocorrelation (r1), signal-to-noise ratio (SNR) and variance explained by the first principal component (VARpc1) were calculated. MS measures the relative differences in the widths of adjacent growth rings, and r1 describes the influence of the previous growth on the growth of the current year (Fritts, 1976). Thus, while MS measures high-frequency variation in radial growth, r1 measures low-frequency variation. The chronology SD is a measure of the total amount of ring-width variation through time. Mean radial growth, MS, SD and r1 were also calculated for individual trees, in order to compare species and sites using a one-way ANOVA. *Post hoc* differences between elevations for *P. nigra* were analyzed using Tukey's honestly significant difference (HSD) test. Finally, SNR measures the common variance in a chronology scaled by a measure of the total variance of the chronology (Cook et al., 1990; Wigley et al., 1984), and VARpc1 the strength of the common growth signal. SNR and VARpc1 were calculated for detrended series.

2.3 Tree-growth variability

For the analysis of tree-growth variability between different species and sites, years with extreme growth values at tree level were identified for the period 1935-2007. Averaged ring-width indices for individual trees greater and lower than 1.75 standard deviations from the mean of the residual chronology were considered wide and narrow indices, respectively. The relative frequencies of wide and narrow indices for each year were calculated as a percentage of trees showing extreme indices from the total number of trees. In addition, annual sensitivity (s_x) was calculated by dividing the absolute value of the differences between each pair of ring-width indices by the mean of the paired index (Fritts, 1976). For the assessment of trends in s_x, the mean annual sensitivity (ms_x) was computed for 37-year periods and shifted by 5-year intervals of 5 years. Trends in annual mean temperature and total precipitation for the same intervals were also considered. Linear regressions between the variables and time intervals were performed in order to identify significant trends through time.

2.4 Climatic data

The climatic data used were monthly mean temperature and total precipitation for the study area taken from the CRU TS 2.1 high-resolution gridded data set (Mitchell and Jones, 2005). The spatial resolution of the data set is 0.5º latitude by 0.5º longitude. As this set spanned only the 1901-2002 period, we performed linear regressions using data from nearby meteorological stations to extend monthly data to 2007 (all the regressions were significant at $P < 0.05$, with R^2 ranging from 0.39 to 0.89). To test climate trends for the period 1920-2007, linear regressions were performed between monthly and annual mean values and time (years). This period was selected to correspond to the same interval used in the moving response function analysis (see 2.6 Growth-climate relationships).

2.5 Microclimatic conditions

The differences in microclimatic conditions between sampled sites were tested by measuring temperature and relative humidity from 2008 March to 2010 January. Ambient temperature and relative humidity were measured by an external sensor connected to a HOBO prov2 data logger (Onset, Pocasset, USA) at each site, recording data at 15-min intervals. We checked for differences in mean, maximum and minimum daily values during two different periods: June-August and November-January. Only the first 14 days of August were considered due to logistical problems. On the one hand, we compared southern and northern exposures; on the other hand, the high, medium and low altitudes were compared across the elevation gradient. Differences between elevations and exposures were tested using a one-way ANOVA. *Post hoc* differences between elevations were analyzed using Tukey's HSD test.

2.6 Growth-climate relationships

To quantify growth-climate relationships between residual chronologies of each species and site and climate series (monthly mean temperature and precipitation sums), correlation and response function analyses were performed using the software Dendroclim2002 (Biondi and Waikul, 2004). Correlation analysis was made using Pearson's product moment correlation. The response function is a principal-component regression which accounts for multicollinearity in multivariable sets of climatic data (Fritts, 1976). Significance of correlation and response function coefficients were tested at 0.05 level using 1000 bootstrapped estimates, drawn at random with replacement from the initial data set (Biondi and Waikul, 2004). The temporal window used for calculating growth-climate relations extend from the previous June to October of the growth year. Growth-climate relationships were analyzed for the common period 1935-2007.

Changes in radial growth response to climate through time were assessed using moving response function analysis with 68-year fixed intervals, increasing both the starting and ending year by one for each iteration. A base length of 68 years was selected as it had to be at least twice the number of predictors (34 monthly mean temperature and precipitation sums), in order to provide a large enough number of degrees of freedom (Biondi and Waikul 2004). The moving response function also required a base length lower than the 80% of the common interval of climate data and ring-width indices, in order to generate a large enough number of intervals (Biondi and Waikul 2004). Thus, the analysis was performed for the period 1920-2007, excluding *P. nigra* chronology at 1700 m in elevation as its reliable time span covered only the period 1935-2007. Finally, linear regressions between response function coefficients and time intervals were performed to identify significant trends.

3. RESULTS

3.1 Chronology statistics

Table 2 summarizes the statistics for the mean chronologies while Figure 3 shows the residual chronologies and associated core numbers. For *P. sylvestris*, the northern exposure site showed significantly higher mean radial growth than did the southern exposure (F=6.09, *P*=0.02). However, MS and SD were significantly higher with a southern exposure than with a northern one for both standard and residual chronologies (*P*<0.05 for all the comparisons). Regarding r1, no significant differences were found between northern and southern exposures (F=0.35, *P*=0.56).

(Figure 3)

For *P. nigra*, marginal significant differences in mean radial growth were found between elevations (F=3.19, *P*=0.053), with the medium elevation site showing significantly higher mean radial growth than the high elevation one (*P*<0.05). However, no significant differences were found between high and low elevations in radial growth. MS and SD displayed a decreasing trend with altitude, with the low elevation site showing significantly the highest values and the high elevation one significantly the lowest values (*P*<0.05 for all the cases and chronologies). Finally, no significant differences in r1 were detected between elevations (F=2.26, *P*=0.12).

At the high elevation with a southern exposure, where *P. sylvestris* and *P. nigra* coexist, no significant differences between species in mean radial growth were detected (F=1.54, P=0.23). *P. sylvestris* showed significantly higher MS than *P. nigra* for both standard and residual chronologies (*P*<0.05 for both cases). However, SD was significantly higher for *P. sylvestris* only for the standard chronology (F=6.55, *P*=0.0017), but not for the residual chronology (F=2.29, *P*=0.14). r1 was only marginally significantly higher for *P. sylvestris* than for *P. nigra* (F=3.50, *P*=0.073).

3.2 Tree-growth variability

The frequency of narrow (< 1.75 SD) and wide (> 1.75 SD) ring-width indices displayed differences between species and locations (Fig. 4). *P. nigra* at medium and low elevations presented the highest frequency of extreme values, both showing increasing trends in the last few decades. *P. sylvestris* with a southern exposure showed higher frequency of extreme narrow ring-width indices for the period 1945-1955 than *P. sylvestris* with a northern exposure (Fig. 4).

(Figure 4)

Regarding ms_x, contrasting trends over the last seven decades were recorded across species and sites. While significant decreasing trends in ms_x were detected for *P. sylvestris* with northern and southern exposures, a significant increasing trend was recorded for *P. nigra* at the low elevation (Fig. 5). In the case of *P. nigra* at the medium elevation, the increasing trend in ms_x was only marginally significant (R^2=479, P=0.0573). Along with these results, a decreasing trend in annual total precipitation with time was detected (Fig. 5).

(Figure 5)

3.3 Climatic data

Annual mean temperature and the monthly temperatures in March and especially in June and July significantly increased (Appendix A). Total precipitation decreased significantly in March and increased slightly in August. Overall, annual precipitation showed a significantly negative trend (Appendix A).

3.4 Microclimatic conditions

Clear differences were recorded in ambient temperatures across the elevation gradient. Differences in mean, minimum and maximum daily temperatures were registered between elevations, with the high elevation registering significantly lower temperatures than at the low elevation for both June-August and November-January periods ($P < 0.05$ for all the cases; Appendix B). Minimum relative humidity showed an increasing trend with elevation, differences between elevations being marginally significant in 2008 ($F = 2.56$, $P = 0.0793$) and significant in 2009 ($F = 4.10$, $P = 0.0196$; Appendix B) for June-August period. Similar differences in minimum relative humidity were found for the November-January period, with the high elevation showing significantly higher values than low elevation ($P < 0.05$ for both years). Finally, maximum daily temperatures were significantly higher on southern exposure than on northern exposure for the November-January period ($P < 0.05$ for both years, Appendix B). The rest of the variables showed no significant differences among elevations or exposures.

3.5 Growth-climate relationships

The negative effect of temperature during the previous September was a strong common signal for both species and all the study sites, significant for both correlation and response function analyses (Fig. 6). Temperature signals prevailed over precipitation and, in fact, only current May precipitation showed both a significant positive correlation and response function coefficients for *P. nigra* at the low elevation. Other significant positive signals in precipitation were recorded only for the correlation analysis: current June at the high elevation for the two species, previous October for *P. nigra* at the high and medium elevations, and current October for *P. sylvestris* with a southern exposure. Finally, current September precipitation showed a significant negative correlation with radial growth for *P. nigra* at the high elevation (Fig. 6).

Temperature showed stronger signals, often significant for both correlation and response function analysis (Fig. 6). Positive strong signals detected by both analyses were concentrated in the winter and spring months: current May for *P. sylvestris* northern exposure, current March for *P. nigra* at the high elevation, current February for *P. nigra* at medium and low elevations, and previous December for *P. nigra* at low elevation. Apart from the aforementioned previous September temperature signal, only previous August temperature for *P. nigra* at the high elevation displayed significant negative correlation and response function coefficients. Other negative relationships between monthly temperatures and growth were significant only for correlation analysis: current July for *P. nigra* at all elevations, previous July for *P. nigra* at the high elevation, and previous August for *P. nigra* at medium elevation. In addition, current May temperature displayed a significant positive response function coefficient for *P. nigra* at the high elevation (Fig. 6).

(Figure 6)

3.6 Growth-climate relationship through time

Figure 7 shows the time course of response function coefficients of variables that were significant for both correlation and response function analyses per species and site (with the exception of *P. nigra* at the medium elevation, excluded due to analysis requirements). On one hand, there was a significant increasing trend for the negative effect of previous September temperature for *P. nigra* at high and low elevations (Fig. 8), and a marginally significant trend for *P. sylvestris* with southern exposure (R^2=0.647, *P*=0.0536). For *P. nigra* at high elevation, the negative effect of previous

August temperature also showed a marginally significant increasing trend (R^2=0.575, *P*=0.0807). On the other hand, the positive effect of winter temperatures (previous December, current February) increased significantly over the last nine decades for *P. nigra* at low elevation (Fig. 7). In addition, the positive effect of current May temperature also increased with time for *P. sylvestris* with the northern exposure (Fig. 7).

(Figure 7)

4. DISCUSSION

4.1 Growth-climate relationship at the dry distribution limit

Our climate-tree growth analysis revealed prevailing temperature signals at the dry distribution edge of *P. sylvestris* and *P. nigra*. The lack of strong precipitation signals, with the exception of *P. nigra* at the low elevation, is unexpected because establishment, growth, and survival of both species are constrained by water availability at this latitude (Castro et al., 2004a, 2004b; Linares and Tíscar, 2010, 2011; Martínez-Vilalta and Piñol, 2002). Thus, we expected stronger positive precipitation signals, and even more so considering the negative trend in the precipitation recorded in the study area. In fact, our results contrast with those of other studies performed in southern populations of Spain and other drought-limited areas of, for example, the European Alps, showing a dominant negative influence of precipitation (Affolter et al., 2010; Eilmann et al., 2009; Martín-Benito et al., 2010; Weber et al., 2007). Such results could be related to different abiotic (microclimatic conditions, distribution of precipitation, soil characteristics) and biotic factors (tree density, local adaptation).

Among abiotic conditions, site-specific microclimatic conditions could explain the observed lack of strong precipitation signals at high elevation. In fact, lower temperatures and higher minimum values of relative humidity were recorded at the high elevation, which may diminish the impact of summer drought on tree performance. In addition, high frequency and persistence of fog at the high elevation (author's personal observation) could provide additional water input, improving tree water status. Fine aspects of precipitation distribution (those not well captured by monthly sums) may also influence the observed climate-growth relationships. However, the overall lack of strong positive effects of precipitation for summer months is surprising because previous studies indicate relevant physiological activity for *P. sylvestris* and *P. nigra* during the summer dry season (Lebourgeois, 2000; Weber et al., 2007; Eilmann et al., 2010). Soil characteristics could also play a role in observed climate-growth relationships, although the cambisols of the study area do not show especially high water-holding capacity (CSIC-IARA, 1989).

Regarding biotic factors, tree competition has been revealed as an outstanding interaction able to shape the dynamics and distribution of forest communities (Linares et al., 2009; Gómez-Aparicio et al., 2011). Our results contrast with those registered in *P. sylvestris* and *P. nigra* reforestations located close to the study area, where strong precipitation signals were recorded (Sánchez-Salguero et al., 2012b). These reforestations were characterized by high tree densities, more than twice the tree density of natural populations sampled in the present study (250-470 ind/ha in natural populations vs. 1000 ind/ha or even higher in reforestations; Sánchez-Salguero et al., 2012b). High tree density increases the competition for water, increasing tree vulnerability to drought stress (Linares et al., 2009; Moreno-Gutiérrez et al., 2011; Rigling et al., 2013; Vilá-Cabrera et al., 2011). Thus, competition could be a relevant factor to keep in mind interpreting growth-climate relationships (Weber et al. 2008). It is also important to consider the degree of local adaptation, which can favor the persistence of rear edge populations (Hampe and Petit, 2005; Hampe and Jump, 2011). High genetic differentiation found at southern populations of *P. nigra* and *P. sylvestris* in Spain (Afzal-Rafii and Dodd, 2007; Prus-Glowacki and Stephan, 1994), might entail high local adaptation to seasonally dry conditions and could influence the observed responses to precipitation. In fact, *P. sylvestris* in the study area showed lower vulnerability to embolism than did northern populations (Martinez-Vilalta et al., 2009, unpublished data). In addition, Mediterranean *P. sylvestris* provenance showed higher seedling emergence and survival than a more northern provenance under experimental dry conditions (Richter et al., 2012).

The weak precipitation signals are of special importance under the current climatic change scenario. Climatic models predict reductions of -4 to -27% in annual total precipitation for Southern Europe at the end of the 21st century, with the largest decreases expected for the summer season (Christensen et al., 2007). However, high temperatures can also exacerbate drought stress for trees (Adams et al., 2009). The observed widespread negative impact of previous September temperature has been previously reported for *P. nigra* and *P. sylvestris* (Andreu et al., 2007; Martín-Benito et al., 2010; Rigling et al., 2002), and may be a result of prolonged summer drought.

Intense drought stress in late summer can impact storage of carbon reserves and thereby negatively affect radial growth the following year (Fritts, 1976; Rolland and Schueller, 1994). By contrast, high winter and spring temperatures boosted radial growth in most locations. On the one hand, current May temperature positively influenced *P. sylvestris* radial growth in northern exposures, probably as a result of earlier onset of growing season (Richter and Eckstein, 1990). On the other hand, high temperatures may allow *P. nigra* to perform photosynthesis during wet winter when temperature is above the critical threshold of about 4ºC (Körner, 1998, and references within). Carbohydrates produced throughout winter might be useful for diverse tree functions during spring and dry summer, encouraging subsequent growth.

Thus, in this context of prevailing temperature signals, the future growth of these rear edge populations will be determined to a large extent by the magnitude of the negative (autumn) and positive temperature (winter, spring) effects. If the magnitude of negative effects is greater than the magnitude of positive effects, a future decline in radial growth will occur. However, if the positive effects prevail upon negative ones, radial growth levels will be sustained or even increased. Climatic models predict a rise in annual mean temperatures of 3-4ºC until the end of 21st century for the European Mediterranean area (Christensen et al., 2007), but the increase will be higher in summer (4-5 ºC) than in winter (2-3 ºC). Therefore, the detrimental impacts of temperature will presumably be greater than the beneficial ones, although this will depend on specific physiological mechanisms of each effect.

4.2 Differences in growth responses between species and sites

In addition to common patterns, site- and species-specific growth responses were recorded at the dry distribution limit of *P. sylvestris* and *P. nigra*. At high altitude, a southern exposure appears to be more stressful than the northern exposure for *P. sylvestris*. Firstly, *P. sylvestris* showed lower mean growth and higher MS with a southern exposure. Previous studies have recorded greater MS with more severe drought stress (Fritts et al., 1965; Rigling et al., 2001, 2003). Secondly, *P. sylvestris* with a southern exposure showed a higher frequency of narrow extreme values for the period 1945-1955, which was characterized by recurrent severe droughts (data not shown). Although no differences were recorded in ambient temperature and relative humidity between the northern and southern exposures during summer, we did not measure other variables such as soil temperature and soil water availability, which can be affected by higher irradiance with a southern exposure (Weber et al., 2007). The differences in microclimatic conditions between southern and northern exposures may be more accentuated in extreme dry years and less in average dry years such as 2008 and 2009, when microclimatic data were recorded. In contrast to measured summer temperatures, maximum winter temperatures (November-January) were lower with the northern exposure, possibly explaining the beneficial effect of a warm May for the onset of tree growth.

The altitudinal gradient displayed striking differences in growth responses for *P. nigra*. The low elevation site appeared to be most vulnerable to water stress, as suggested by high MS and SD values at this location. In addition, the only strong precipitation signal, that of current May precipitation, was recorded at the low elevation site. The highest temperatures and the lowest humidity values were recorded at the low elevation, together with higher tree density than at high elevation, findings that could explain this vulnerability to drought stress. These results agree with other studies performed with southern *P. nigra* populations, which recorded drought-induced growth declines at drier and lower locations (Linares and Tíscar, 2010, 2011).

Tree growth variability data also point to the low elevation site as the most stressful one. At the low elevation, and also at the medium one, higher extreme growth values were detected for *P. nigra* in recent decades, which denote stronger climatic influence for these locations (Tardif et al., 2003). In addition, ms_x showed an increasing trend at the low elevation for the last seven decades, coupled with decreasing annual precipitation. This contrasts with the decreasing trend in ms_x observed for *P. sylvestris*, although it was rather low (approx. 25%) in comparison to the recorded increase for *P. nigra* at the low elevation (approx. 45%). The decrease in growth sensitivity for *P. sylvestris* might be associated with a decrease of precipitation variability over the last seven decades (data not shown) and the more favorable microclimatic conditions plus lower tree density at the high elevation sites, where *P. sylvestris* grow. Thus, registered differences in growth variability across elevations and exposures demonstrate the importance of the local scale, and associated site-specific ecological conditions, when analyzing tree growth variability trends.

Finally, at the high elevation with the southern exposure, where *P. sylvestris* and *P. nigra* coexist, the two species also differed in growth responses. Summer temperatures of the previous and the current year exerted a stronger negative influence on Mediterranean *P. nigra* than on coexisting boreo-alpine *P. sylvestris*. We expected the opposite pattern inferred by their biogeographical origin and the lower vulnerability to drought of *P. nigra* (Boulant et al., 2008; Castro et al., 2004a; Herrero et al., 2013; Lévèsque et al. 2013; Martínez-Vilalta and Piñol, 2002). However, this negative impact of warm temperatures could be counteracted by higher positive influences of winter and spring temperatures for *P. nigra*.

4.3 Growth-climate relationship through time

Climate-growth relationships varied not only across space, also through time. In this context, moving response function analyses are helpful to predict future changes in radial growth under future climate projections. On one hand, the widespread negative effect of previous September temperatures increased over the last decades for *P. nigra* at high and low elevations, probably as a result of increasing temperatures. Surprisingly, no specific trend was reported either for September temperature or precipitation (Appendix A). However, September is a key month when the drought period normally ends and even a slight increase in temperature could extend drought stress. This might be amplified by the overall declining precipitation in the Mediterranean during the past decades, resulting in generally drier conditions (Carnicer et al., 2011). The projected increase in summer temperatures would also aggravate the detrimental impact of previous September temperature, even more under predictions of longer and more frequent drought periods (Christensen et al., 2007). On the other hand, positive impacts of spring temperature (current May) for *P. sylvestris* with northern exposure and winter temperatures (previous December, current February) for *P. nigra* at low elevations also increased in the last few decades, according to the overall increasing trend of temperatures in the study area. Thus, in a warmer future, *P. sylvestris* would benefit from a northern exposure in comparison with a more stressful southern exposure (Martínez-Vilalta et al. 2008). The increasing trend of the positive impacts of temperature for *P. nigra* at the low altitudinal margin is noteworthy, since these populations are the most vulnerable ones to future climate change, where retractions of tree species distribution are predicted and already observed through growth reductions and/or mortality events (Allen and Breshears, 1998; Adams and Kolb, 2004; Peñuelas et al. 2007).

4.4 Implications for management

Our results suggest that tree competition could increase the vulnerability to drought of trees, especially at low elevation, drought-prone sites. Prescribed thinning could diminish the vulnerability to drought stress of low elevation populations (Giuggiola et al., unpublished results) and might boost the positive impacts of winter temperatures, favoring the persistence of these rear-edge forest formations. Although more research is needed to link genetic differentiation and local adaptation, the vulnerability against heat and drought of *P. sylvestris* and *P. nigra* plantations in southeast Spain could be reduced by promoting local varieties (since these plantations often consist of non-native varieties of diverse origins (Montero, 1997)). Finally, the long-term monitoring of local climatic but also microclimatic conditions, such as soil moisture and water inputs through fog, must be intensified as these data are crucial to understand the water cycle of forest communities located at the dry distribution edge under climatic change scenarios.

4.5 Conclusions

An outstanding result of our study is that, even at the dry distribution limit, temperature effects appear to be more important than precipitation variability in mountain populations of *P. sylvestris* and *P. nigra*. The balance between positive and negative effects of seasonal temperatures on radial growth, and factors such site-specific ecological conditions, can determine future performance and persistence of *P. sylvestris* and *P. nigra* rear edge populations. This balance is altitudinally dependent, with lower populations being more prone to suffer drought and heat stress, whereas higher populations remain more buffered. Thus it appears necessary to include site-specific conditions as well as local adaptation data in theoretical models in order to improve the predictions concerning distributional shifts and local extinctions of species. This information can also be used to improve management practices and conservation strategies. Promoting low tree density stands and local varieties of species would aid the persistence of rear edge populations, which harbor considerable and valuable genetic diversity (Hampe and Petit, 2005; Jump et al., 2009).

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Table 1 Characteristics of sampled sites and trees, and reliable time span. Elevation, aspect, geographical location and tree density refer to whole sites. Age at coring height, tree height and DBH are related to sampled trees. Finally, reliable time span for each chronology is shown. Note that *P. sylvestris* and *P. nigra* sites with a southern exposure are the same (mixed forest of both species)

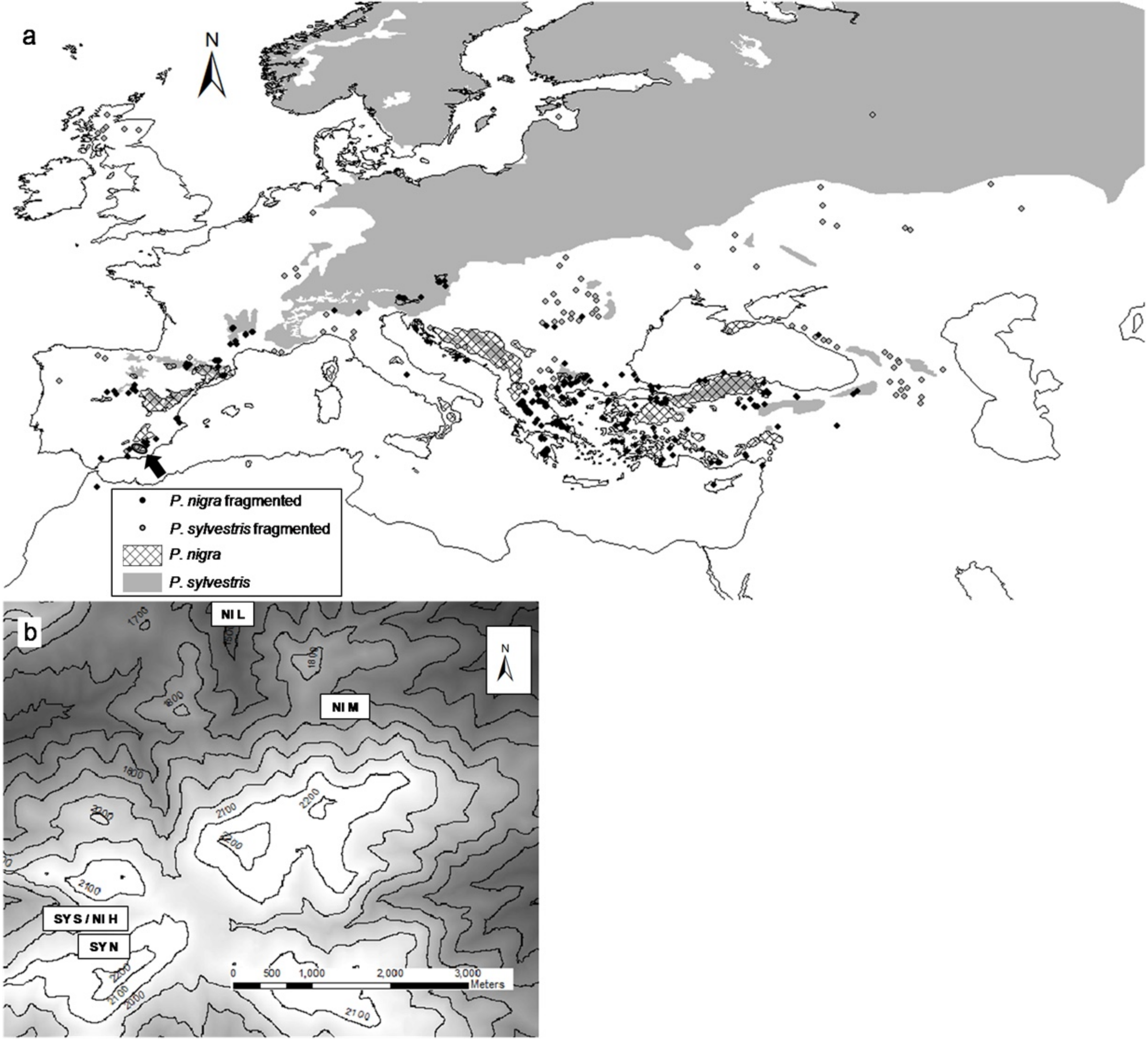
Species	**Elevation (m)**	**Aspect**	**Latitude (N)**	**Longitude (W)**	**Tree density (ind/ha)**[a]	**Nº of trees**	**Age at coring height (yr)**	**Tree height (m)**	**DBH (cm)**	**Reliable time span**[b]
P. sylvestris	2000	N	37º 22’	2º 51’	365 ± 29.08	17	104 ± 5.57	8.88 ± 0.46	45.22 ± 1.99	1908-2007
P. sylvestris	2000	S	37º 22’	2º 51’	252 ± 30.52	13	115.54 ± 6.57	8.68 ± 0.46	47.62 ± 3.61	1879-2007
P. nigra	2000	S	37º 22’	2º 51’	252 ± 30.52	15	139.6 ± 8.92	9.66 ± 0.51	49.70 ± 1.77	1867-2007
P. nigra	1700	NW	37º 24	2º 49’	461 ± 39.80	11	97.72 ± 8.25	9.58 ± 0.40	36.72 ± 1.93	1935-2007
P. nigra	1500	NW	37º 24	2º 50’	471 ± 46.64	12	104.17 ± 6.83	8.88 ± 0.34	34.79 ± 1.23	1916-2007

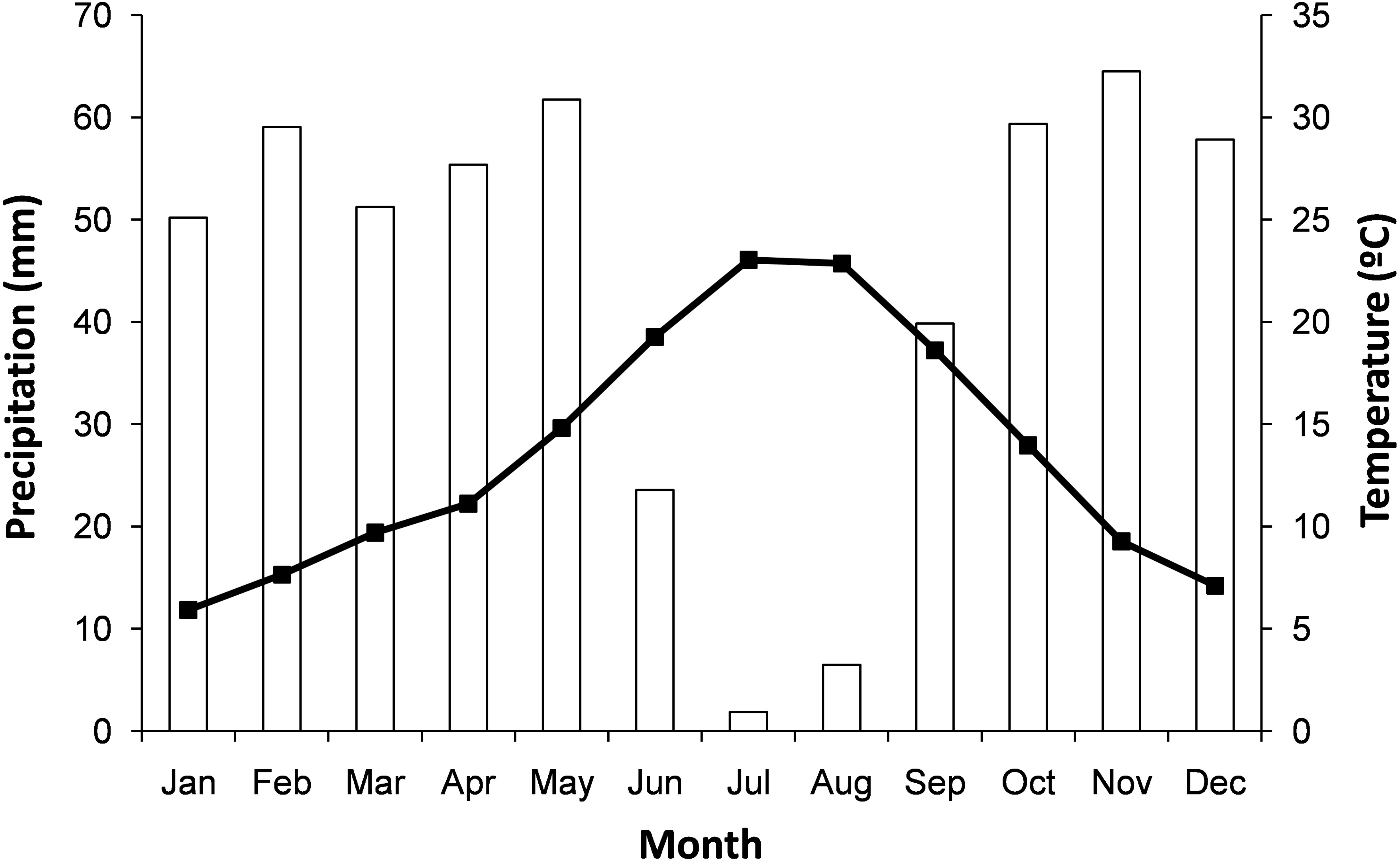
[a] Tree density was measured with 20 transects of 50 m length and 10 m wide

[b] EPS > 0.85

Table 2 Summary statistics for *P. sylvestris* and *P. nigra* chronologies for period 1935-2007: nº of trees, mean radial growth, mean sensitivity (MS), standard deviation (SD), first-order autocorrelation (r1), signal-to-noise ratio (SNR) and variance explained by the first principal component (VARpc1)

					Standard chronology			**Residual chronology**		**Detrended series: common period analysis**	
Species	**Elevation (m)**	**Aspect**	**Nº of trees (radii)**	**Radial growth mean (SD) (mm)**	**MS**	**SD**	**r1**	**MS**	**SD**	**SNR**	**VARpc1 (%)**
P. sylvestris	2000	N	17 (34)	1.74 (0.72)	0.15	0.17	0.51	0.17	0.15	17.87	40.0
P. sylvestris	2000	S	13 (26)	1.30 (0.62)	0.19	0.24	0.66	0.18	0.18	25.78	52.1
P. nigra	2000	S	15 (30)	1.11 (0.42)	0.15	0.20	0.49	0.17	0.17	22.62	46.7
P. nigra	1700	NW	11 (22)	1.53 (0.88)	0.30	0.28	0.42	0.27	0.23	6.31	35.2
P. nigra	1500	NW	12 (24)	1.29 (0.84)	0.37	0.33	0.38	0.35	0.28	12.11	43.3


a
N
P. nigra fragmented
P. sylvestris fragmented
P. nigra
P. sylvestris
b
N
NI L
NI M
SY S / NI H
SY N
1700
1800
2000
2100
2200
0
500
1,000
2,000
3,000
Meters


Precipitation (mm)
70
60
50
40
30
20
10
0
Temperature (ºC)
35
30
25
20
15
10
5
0
Jan
Feb
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Apr
May
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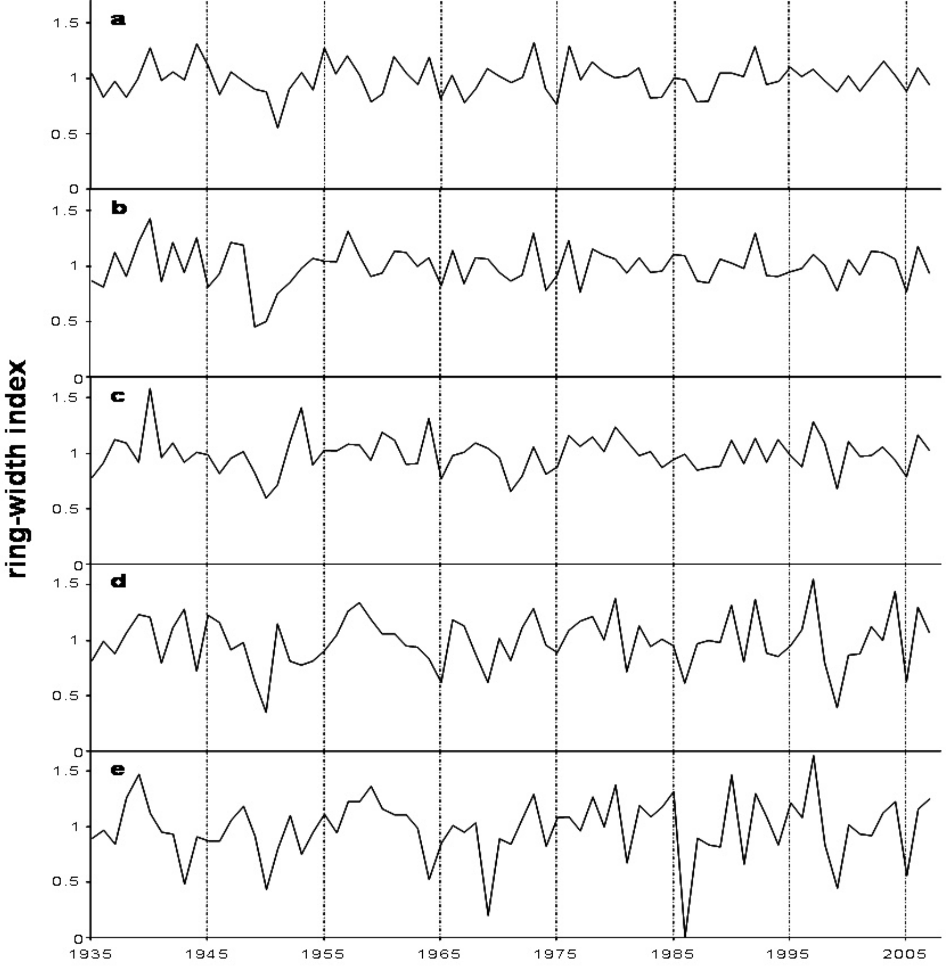
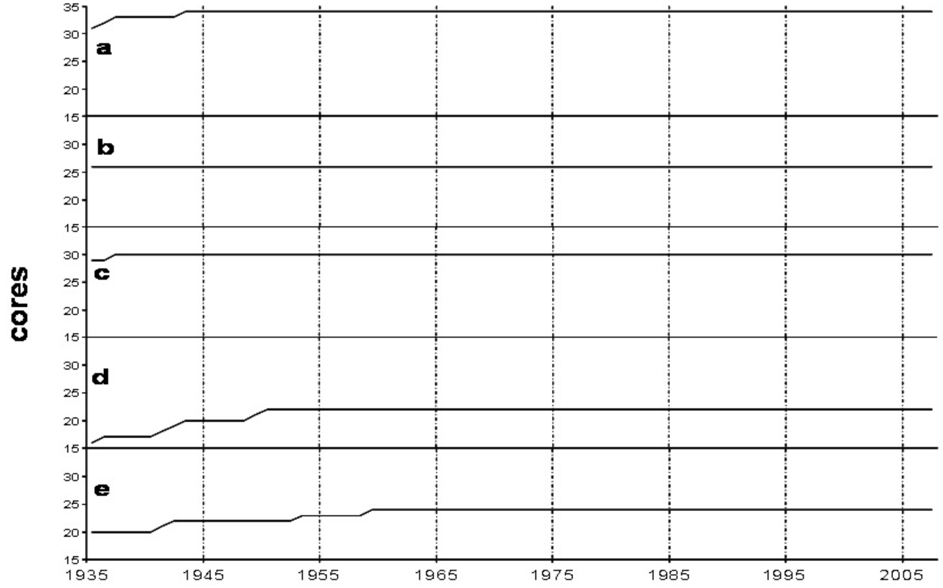
Month


ring-width index
a
b
c
d
e
0
0.5
1
1.5
1935
1945
1955
1965
1975
1985
1995
2005


cores
a
b
c
d
e
15
20
25
30
35
1935
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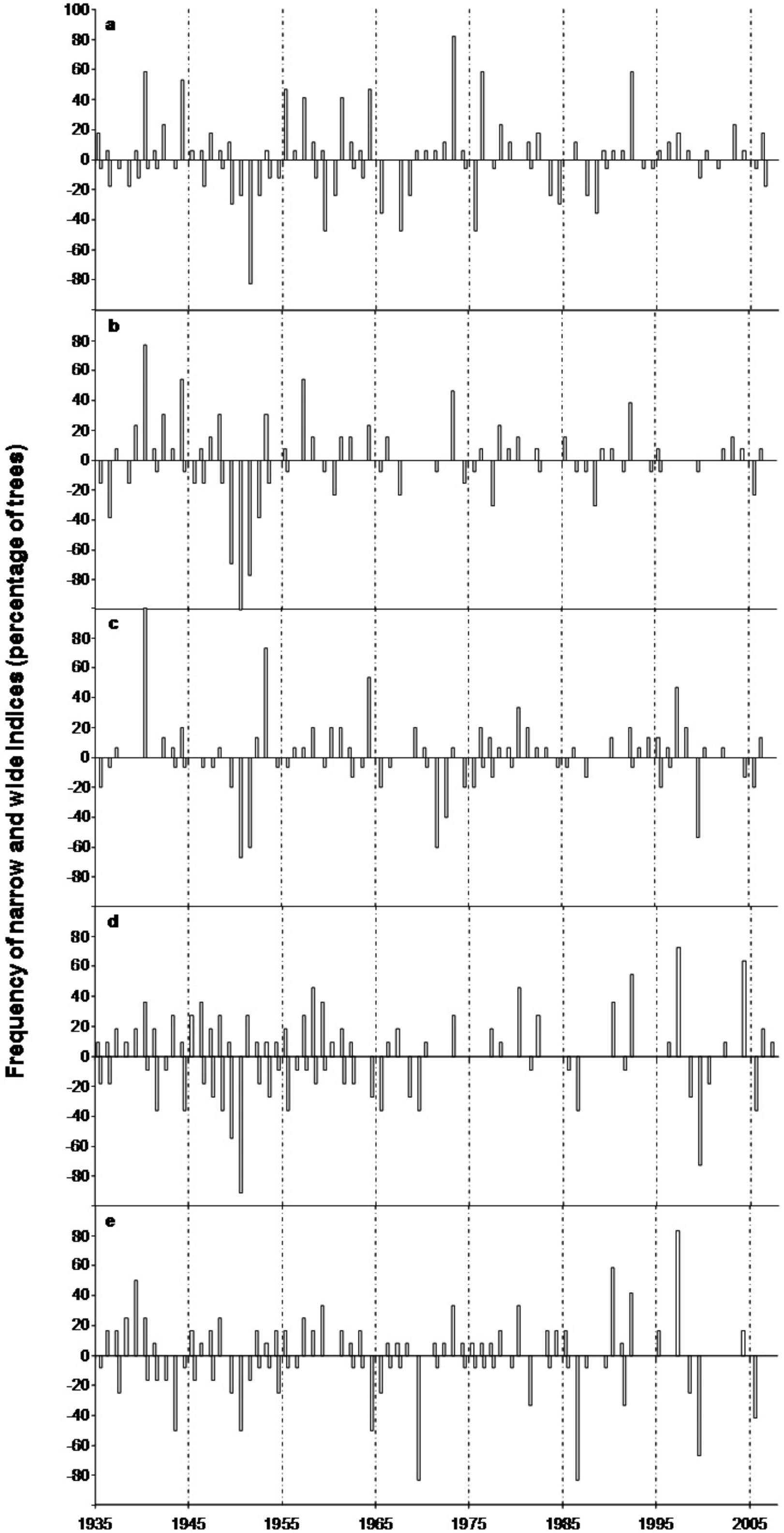
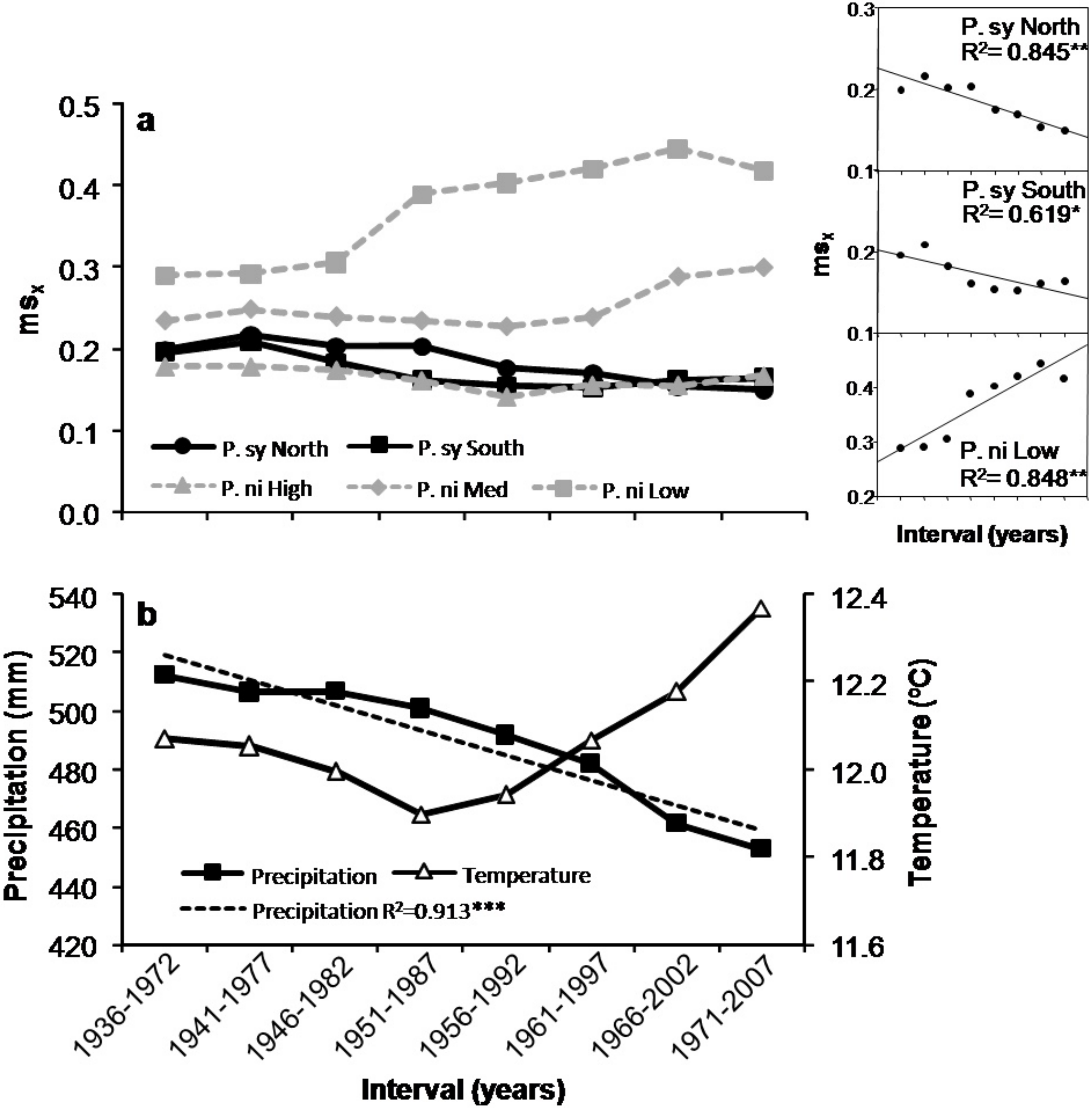
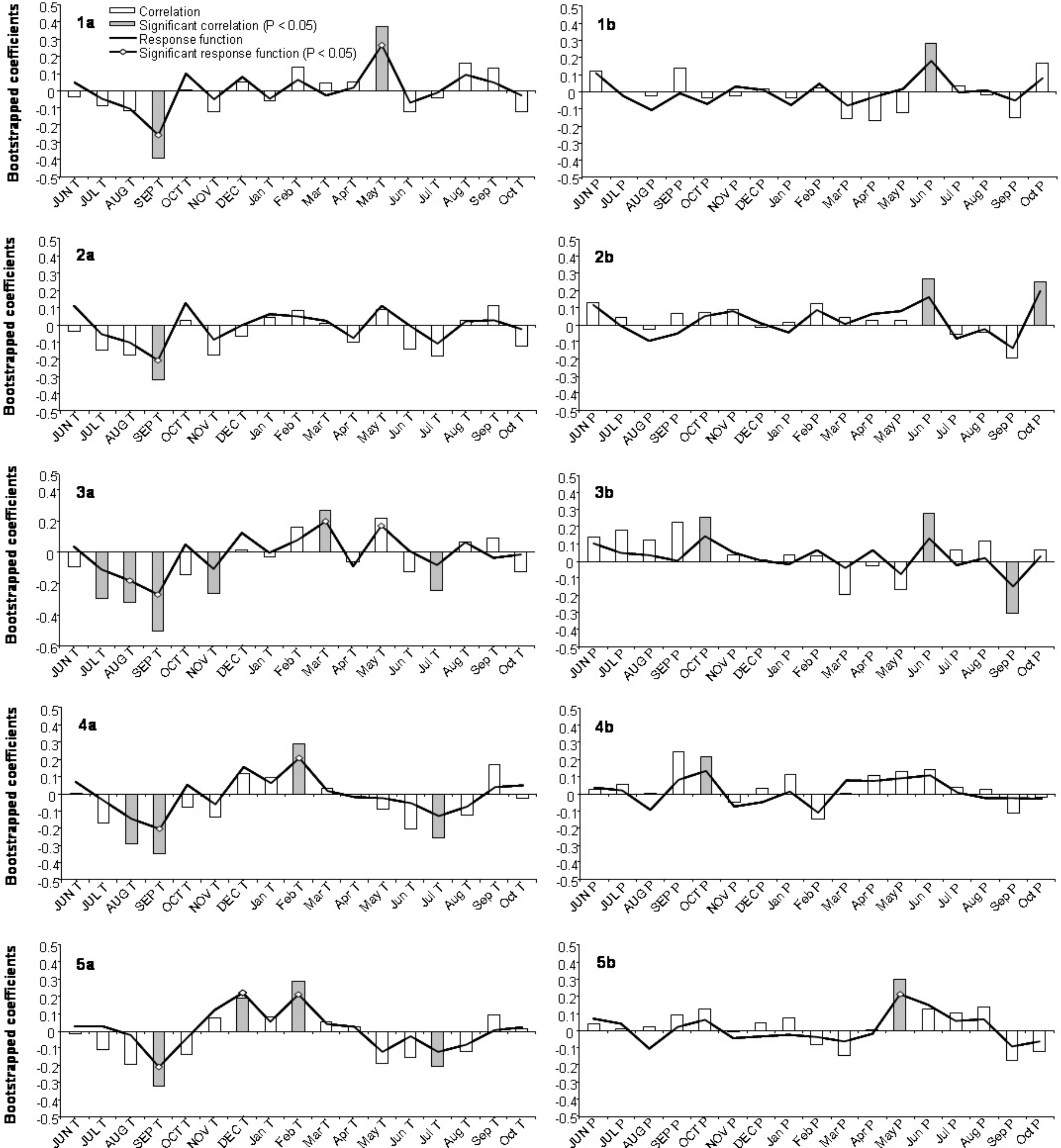
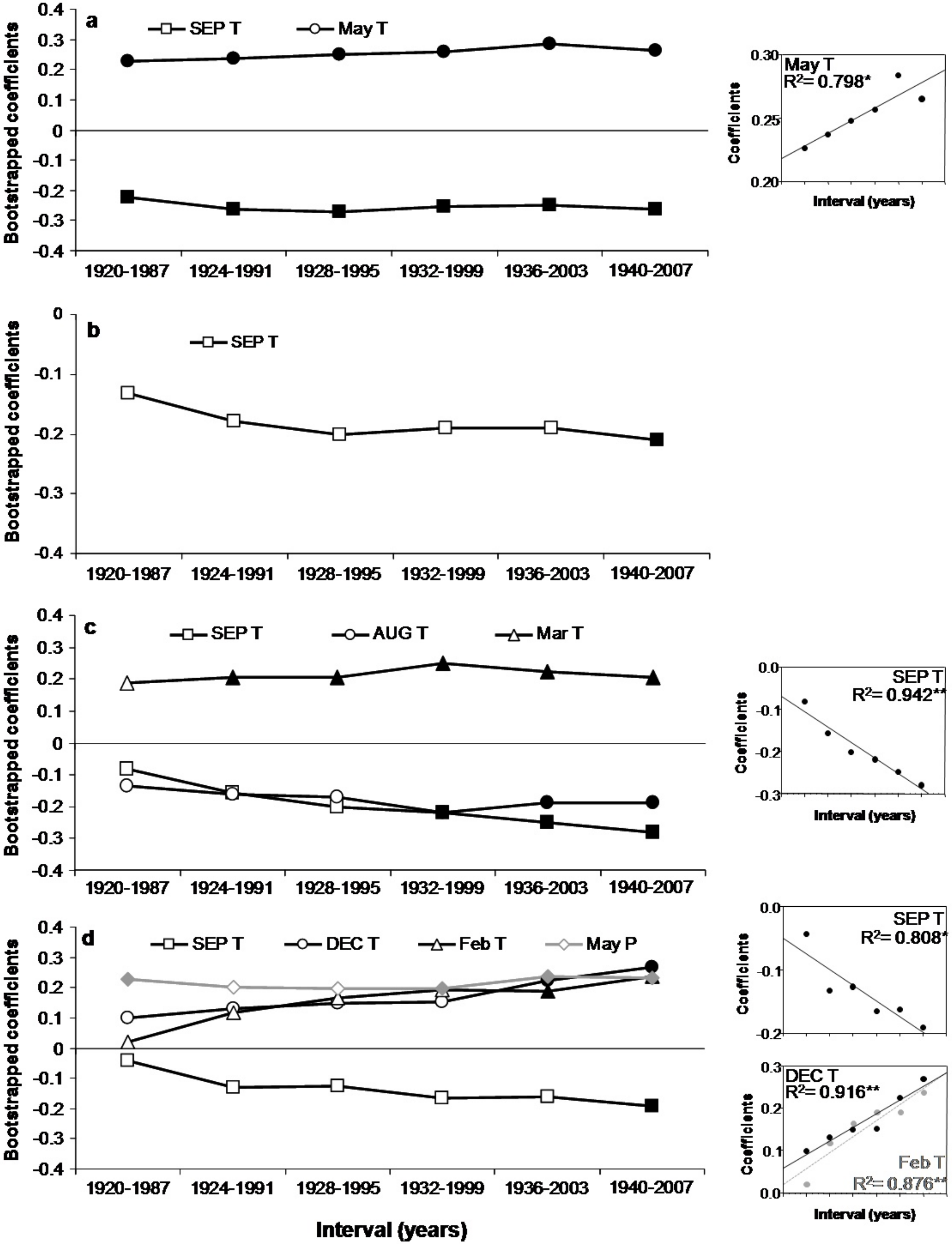

Frequency of narrow and wide indices (percentage of trees)
a
b
c
d
e
100
80
60
40
20
0
-20
-40
-60
-80
1935
1945
1955
1965
1975
1985
1995
2005


a
0.5
0.4
0.3
0.2
0.1
0.0
ms_x
P. sy North
P. sy South
P. ni High
P. ni Med
P. ni Low
P. sy North R²= 0.845**
P. sy South R²= 0.619*
P. ni Low R²= 0.848**
0.3
0.2
0.1
0.4
Interval (years)
b
540
520
500
480
460
440
420
Precipitation (mm)
12.4
12.2
12.0
11.8
11.6
Temperature (°C)
Precipitation
Temperature
Precipitation R²=0.913***
1936-1972
1941-1977
1946-1982
1951-1987
1956-1992
1961-1997
1966-2002
1971-2007
Interval (years)


Correlation
Significant correlation (P < 0.05)
Response function
Significant response function (P < 0.05)
Bootstrapped coefficients
1a
1b
2a
2b
3a
3b
4a
4b
5a
5b
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
JUN T
JUL T
AUG T
SEP T
OCT T
NOV T
DEC T
Jan T
Feb T
Mar T
Apr T
May T
Jun T
Jul T
Aug T
Sep T
Oct T
JUN P
JUL P
AUG P
SEP P
OCT P
NOV P
DEC P
Jan P
Feb P
Mar P
Apr P
May P
Jun P
Jul P
Aug P
Sep P
Oct P


a
SEP T
May T
b
SEP T
c
SEP T
AUG T
Mar T
d
SEP T
DEC T
Feb T
May P
Bootstrapped coefficients
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
1920-1987
1924-1991
1928-1995
1932-1999
1936-2003
1940-2007
Interval (years)
May T
R² = 0.798*
Coefficients
0.30
0.25
0.20
SEP T
R² = 0.942**
0.0
-0.1
-0.2
-0.3
SEP T
R² = 0.808*
DEC T
R² = 0.916**
Feb T
R² = 0.876**
0.3
0.2
0.1
0.0