Climatic response of Juniperus monticola Martinez, a multi-century alpine shrub from the high mountains of central Mexico

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Abstract

The mountain juniper *Juniperus monticola* Martinez, a decumbent alpine shrub growing at elevations up to 4600 m a.s.l. on the high mountains of central Mexico, reaches an age of nearly a millennium. We conducted a dendrochronological study of this species at Pico de Orizaba volcano, the highest peak in central Mexico, to analyze its dendroclimatic potential and the influence of ocean-atmospheric forcing on the interannual variability of radial growth. A ring-width chronology was developed extending from 1178 to 2016 (839 years). Climate data from a local weather station and from CRU TS version 4.01 were used to determine the climatic response of *J. monticola*. The species is positively correlated to the average maximum temperature of May-June ($r = 0.38$, $p < 0.05$) and negatively to the March-April precipitation ($r = -0.44$, $p < 0.05$) of the local weather station. Gridded drought indices (PDSI, SPEI) were used to analyze the combined effect of rising temperatures and evapotranspiration on ring-width. A significant negative response ($r = -0.354$, $p < 0.01$) was found between the instrumental PDSI records (June, July, August) and the ring-width series; similarly, a negative correlation was obtained for the SPEI from December of the previous year to June of the current year ($r = -0.4$, $p < 0.01$). These negative correlations suggest that higher temperatures occurring in recent decades are favoring increases in radial growth. The ring-width chronology is significantly correlated, although weakly, with the El Niño/Southern Oscillation, the Pacific Decadal Oscillation, and the Atlantic Multi-decadal Oscillation, consistent with the influence of those phenomena on PDSI and SPEI over central Mexico.

Introduction

A great deal of dendrochronological research has been conducted in Mexico over the last three decades (Sánchez-Calderón et al. 2022). Much of that work has focused on conifer species from cold and temperate mixed-conifer forests distributed along the main mountain ranges of northern, central and southern Mexico (Villanueva Díaz et al. 2000; Stahle et al. 2016; Stahle et al. 2020). Annual growth of conifer species mostly responds to seasonal winter-spring precipitation and occasionally to annual rainfall (Biondi 2001; Cleaveland et al. 2003; Villanueva Díaz et al. 2009; Meko et al. 2013; Carlón-Allende et al. 2018), but rarely to temperature (Villanueva-Díaz et al. 2016).

Interannual climate variability in northern Mexico is significantly influenced by the El Niño Southern Oscillation teleconnection (ENSO) favoring above-normal precipitation during the warm phase (El Niño), particularly in the winter-spring months, and dry conditions in the cold phase (La Niña). In contrast, in central and southern Mexico El Niño phase is usually associated to summer droughts and La Niña phase to normal or above-normal precipitation (Magaña Rueda et al. 1999; Méndez and Magaña 2010; Stahle et al. 2012). Other circulatory modes such as the Pacific Decadal Oscillation (PDO) (Biondi et al. 2001) and the Atlantic Multidecadal Oscillation (AMO) (Mendoza et al. 2006; Méndez and Magaña 2010; Stahle et al. 2012; Metcalfe et al. 2015) exert additional influence on the climatic variability of Mexico, but their physical mechanisms are not well understood. Therefore, it is important to analyze the historical impact of these climate forcing modes for a better understanding of the long-term climate variability characterizing different regions of Mexico (Cavazos 1999; Meko et al. 2013; Stahle et al. 2016).

Dendrochronological studies of the high-elevation forests dominated by the Mexican mountain pine or Hartweg's pine (*Pinus hartwegii* Lindl.) present between 2400 m a.s.l. and the treeline (ca. 4000 m a.s.l.) in the mountains of central Mexico, show that the species responds to precipitation at elevations below 4000 m a.s.l. (Biondi 2001; Villanueva Díaz et al. 2015). Correlations between tree ring width and winter-spring precipitation are positive in the range of 0.53 to 0.76 at different mountains (Manzanilla-Quiñonez et al. 2020). Temperatures before and during the growing season are negatively correlated to annual radial growth, but growth response is modulated by microsite conditions (Astudillo-Sánchez et al. 2019; Correa-Diaz et al. 2019; Manzanilla-Quiñones et al. 2020). Even though temperature is considered to be the most limiting factor to determine the extent of the growing season and recruitment rates of this species above the timberline (ca. 4000 m a.s.l.), few studies have been carried out to analyze the influence of rising temperature on tree establishment rates (Astudillo-Sánchez et al. 2017; Quadri et al. 2021).

Above the treeline the presence of the Mexican mountain juniper shrub *Juniperus monticola* Martinez (Martínez 1963; Giménez de Azcárate Cornide and Escamilla Weinmann 2001; Adams 2014; Steinmann et al. 2021) represents a potential option to develop centuries-long chronologies sensitive to temperature variations and potentially to climate warming (Villanueva-Díaz et al. 2016). The value of juniper trees to develop long tree-ring series has been documented both for low elevation (e.g., Derose et al. 2016) and for timberline environments (Lyu et al. 2019; Zhang et al. 2015).

In this research we focus on the Mexican juniper shrub *Juniperus monticola*, an alpine species that grows mainly between the treeline at ca. 4000 m a.s.l. and ca. 4600 m a.s.l., the highest elevation recorded for a woody species in the mountains of Mexico (Fig. 1). It is only surpassed in the American continent by keñua (*Polylepis tarapacana*), a species that reaches elevations above 5200 m a.s.l. in the Andes (Solíz et al. 2009). Previous research on *J. monticola* at Monte Tlaloc (4120 m a.s.l.) in central Mexico indicates that the species is multi-centennial and the derived ring width chronology is positively correlated with temperature (Villanueva-Díaz et al. 2016), but further research is needed to corroborate this finding, particularly on the potential effect of climate warming on the physiological response of the species.

Instrumental climate records from high-elevation sites in Mexico are very scarce, non-representative and often of poor quality. Therefore, to analyze the climatic response of *J. monticola*, we used climate data from climatic stations at lower elevations and from an international climate database. In addition, we used gridded drought indices based on hydrological balances such as the instrumental and reconstructed Palmer Drought Severity Index (PDSI) to estimate relative dryness (Palmer 1965; Alley 1984; Stahle et al. 2016), and the Standardized Precipitation-Evapotranspiration Index (SPEI) (Stahle et al. 2020). The SPEI is a multiscalar drought index based on climatic data involving a hydrological balance that takes into account monthly and seasonal temperature and evapotranspiration (Vicente-Serrano et al. 2010). The SPEI has been used to determine the onset, duration and magnitude of droughts with respect to normal conditions.

The analysis of these drought indices can provide scientific support to investigate the response of woody species to a warming climate and water availability, and to determine their potential physiological behavior on climatic scenarios derived from IPCC models (Seager et al. 2009; Flato et al. 2013). Furthermore, it is important to determine the influence of large-scale modes on the climate variability of alpine ecosystems (Efthymiadis et al. 2007).

The objectives of this study are to develop a centennial ring-width chronology of the alpine woody shrub *Juniperus monticola* found around and above the treeline of Pico the Orizaba volcano, east-central Mexico; to determine its response to climatic variables (precipitation, temperature) and drought indices (PDSI, SPEI); and to analyze the influence of large-scale atmospheric modes (ENSO, PDO, AMO) on the interannual and multiannual climate variability that characterizes sites around 4,000 m a.s.l. in a high mountain of the northern tropics. We hypothesize that *J. monticola* ring width, due to its ecological alpine habitat, is positively correlated with temperature. If so, the analysis of *J. monticola* could provide multi-century temperature proxies that complement the precipitation proxies derived from most other high-elevation mountain conifers in central Mexico.

Methods

Study site

The study was carried out at an elevation range between 3900 and 4650 m a.s.l., i.e. below and above the timberlineof Pico de Orizaba (5650 m a.s.l.), the highest mountain of Mexico, located near the Gulf of Mexico at a latitude of 19°N (Figs. 1 and 2). In central Mexico the elevation of the timberline (ca. 4000 m a.s.l.) corresponds to a mean annual temperature of 5°C (3°C and 7°C for January and August, respectively) and mean annual precipitation around 900 mm (Lauer 1978). The climate is classified as ET (tundra climate). The forest at and below the timberline is almost exclusively formed by *Pinus hartwegii*. Vegetation above the timberline is an alpine grassland, with grasses of the genus *Festuca* and *Calamagrostis*, shrubs of the genus *Ribes*, and alpine herbs of the genus *Lupinus*, *Asplenium*, *Senecio*, among others (Martínez 1963; Giménez de Azcárate Cornide and Escamilla 2001; Farjon 2013; Almeida-Lenero et al. 2007; Steinmann et al. 2021).

Prevalent xeric environmental conditions induced by a high insolation rate occur above the timberline, where strong winds are capable to evaporate over 70% of the annual precipitation. High soil permeability, dominant freezing temperatures and windy conditions limit the expansion of *P. hartwegii* towards higher elevations (Astudillo-Sánchez et al. 2017), although scattered specimens have been located up to ~ 4,400 m a.s.l. on the southern slopes of Pico de Orizaba.

Juniperus monticola is a decumbent shrub with multiple stems growing near to the ground. It is a genetically predetermined *krummholz* or true *krummholz* in the sense of Holtmeier (2009), i.e. a species without a tree form below the timberline (Fig. 1b). The individuals reach 1.20 m in height with a basal diameter of the main stem in general less than 20 cm, and a deep and extended root system (Martínez

1963). The species is found on steep slopes (45^{o} to 90^{o}), on ridges or cliffs of basaltic or andesitic rocks, preferably on southern aspects where the solar energy stored by rocks in daylight hours is preserved and released at night hours for longer periods of time, thus favoring its physiological activity (Beaman 1962; Giménez de Azcárate Cornide and Escamilla Weinmann 2001). Otherwise, the species is also present on gently sloping terrains on rock crevices or small pockets of recently formed volcanic ash soil. *J. monticola* has been present on the highest mountains of the Transmexican Volcanic Belt throughout glacial-interglacial cycles of the Quaternary (Mastretta-Yanez et al. 2018). Three forms of the species have been recognized (Adams 2014). Individuals sampled in this study at elevations between 4130 and 4515 m a.s.l. correspond to the form *Juniperus monticola* f. *orizabensis* Martinez (Víctor Peña, personal communication).

Despite a relatively high precipitation on the high mountains of central Mexico, bare rock surfaces and porous sandy soil textures with high infiltration rates and elevated insolation make this environment xeric. Snowmelt represents a source of slow-release moisture at the start of and during the first stage of the growing season (Farjon 2013). *J. monticola* could be affected by climate change, but currently there is not enough evidence to support this statement (Farjon 2013), even though temperature has increased around 1.4°C over the last few decades at the elevations where the alpine shrub grows (Harris et al. 2014). However, there is concern about the sparse population of this species within the alpine vegetation of the Trans-Mexican Volcanic Belt (SEMARNAT 2015; Almeida-Leñero et al. 2007).

The presence of fire scars on death branches of some individuals of *J. monticola* indicates that the species can resist low-severity fires, which are common around the timberline (Yocom and Fulé 2012). However, severe grassland fires like the one resulting from the strong El Niño event in 1998 produced high mortality rates of *J. monticola* specimens, endangering its presence in alpine environments of most of the volcanic peaks of central Mexico.

Sample collection and processing

Sampling of woody material of *J. monticola* was conducted on the southern slope of Pico de Orizaba volcano at an elevation range of 4130–4515 m a.s.l. from dead specimens distributed on the south- and southeast-facing slopes of a ca. 3,000-year-old lava flow (Alcalá et al. 2018) (Figs. 1 and 2). We found a young specimen growing at 4620 m a.s.l., the maximum elevation for the species in our records. A total of 86 individuals of *J. monticola* with regular growth were selected for sampling based on morphological features of longevity i.e., size of the stems, presence of twisted branches and microhabitat features. The selected specimens were growing on rock crevices and shallow soils with low water holding capacity and limited soil fertility (Myers-Smith et al. 2015). Nearly 95% of the samples were obtained from dead specimens killed by the 1998 fire event (Fig. 1b).

Two to- four cross-sections were obtained with a mechanical chainsaw from each one of the selected individuals to analyze intra-plant growth variability. The first one was collected near the root collar of the stems; the next ones were separated from each other by nearly 10-cm along the main stem (Liang and Eckstein 2009). It was not practical to obtain increment cores due to the presence of multiple small-size

stems (< 15 cm), to irregular growth and to difficulties in handling the borer in small spaces between the stems. Each sampled specimen was georeferenced, the cross-sections labeled, air-dried, and sanded with progressively finer sandpaper grit to enhance the visibility of ring boundaries and cell structures (Stokes and Smiley 1968). In the sanding process, the vessel cell structures became plugged with dust, which was removed with compressed air, a procedure that helped to improve the ring boundary visibility for dating purposes.

One of the problems involved in the development of tree-ring chronologies from *J. monticola* is its irregular growth due to pith eccentricity, the presence of compressed and reaction wood, and the development of multiple stems (Fig. 1b and 3a). Therefore, three to- five radii were selected in different directions in each cross-section, counted and predated, then measured with a Velmex measuring system at 0.001 mm accuracy and the series were integrated into a total ring-width database. The software COFECHA (Holmes 1983; Grissino-Mayer 2001) was used to analyze the quality of dating. Those series accurately dated and with higher inter-series correlation (> 0.3281, $p < 0.01$) were saved to develop a detrended and standardized ring-width chronology using the ARSTAN program (Cook 1987; Cook and Krusic 2005). For the standardization procedure we used a double detrending option, where the first one consisted of a negative exponential curve or regression line with positive or negative slope, whereas the second detrending was a cubic smoothing spline that preserved 50% of the variance contained in the measurement series at a wavelength of 128 years (Cook 1987).

The standardized time series quality was assessed using dendrochronological parameters, i.e., inter-series correlation (a measure of common signal calculated with COFECHA); mean sensitivity (variation in mean ring-width from one year to the next); first-order autocorrelation (degree of the relationship of each value for one year lag); signal-to noise ratio (ring-width variations due to a common factor compared with those attributed to other variables considered as noise) (Fritts 1976); average correlation among all dated radii (RBAR), and the Expressed Population Signal (EPS) (common variability in a chronology which is dependent on sample depth) (Wigley et al.1984; Cook and Krusic 2005; Speer 2010).

We compared the ring-width indices from the *J. monticola* chronology against ring-width indices from a set of *Pinus hartwegii* chronologies previously developed from high mountain areas of the Trans-Mexican Volcanic Belt (Villanueva Díaz et al. 2015). *P. hartwegii* is the treeline species characterizing the high-elevation forests usually growing in pure stands, but in general at lower elevation than *J. monticola* (Farjon et al. 1997).

Climatic response

Climatic information from high-elevation sites in Mexico is scarce, preventing a direct comparison with the physiological development of species growing above 3000 m a.s.l. To analyze the climatic response of the *J. monticola* ring-width chronology, we used information from the Climatic Research Unit gridded Time Series (CRU TS version 4.01) based on a 0.5° latitude by 0.5° longitude grid (Harris et al. 2020). The climatic half-degree grid for Pico de Orizaba included the upper and lower section of this mountain range

with centered coordinates 19.25º N, -97.25º WG. In addition, we used records from the “Tembladeras” climatic station (19º 30’ 44” N, 97º 07’ 05” W; 3100 m a.s.l.) run by the Mexican Meteorological Agency and located 60 km to the NNE of the sampling sites. This station, although relatively distant, has few missing records and may represent the better option to determine the dominant weather conditions characterizing the *J. monticola* habitat. To analyze the combined effect of temperature, precipitation and evapotranspiration rates on radial growth, we used gridded drought indices (PDSI, SPEI) as indicators of climate variability (Stahle et al. 2016; Stahle et al. 2020; Vicente-Serrano et al. 2010).

Pearson correlation values and response function analyses from Dendroclim2002 (Biondi and Waikul 2004) were used to determine the association between ring-width indices and ENSO indices, which includes the Southern Oscillation Index (SOI), a standardized surface pressure difference between Tahiti and Darwin (Trenberth 1984); the Multivariate ENSO Index (MEI), a comprehensive index for monitoring ENSO that combines analysis of multiple meteorological and oceanographic components (Mazzarella et al. 2013); and the Tropical Rainfall Index (TRI), an estimate of ENSO variation using rainfall anomalies in the Tropical Central Pacific (Wrigth 1979). In addition, indices of the Pacific Decadal Oscillation (PDO) and the Atlantic Multidecadal Oscillation (AMO) were compared with the ring-width chronology to determine their potential influence on interannual and multiannual climate variability on high-elevation mountains of central Mexico.

Results

Tree-ring series

Juniperus monticola is a slow-growing species that may contain over 50 microrings per centimeter (Fig. 3b), many of them locally absent or entirely missing due to irregular radial growth and harsh environmental conditions where the species grows (Villanueva-Díaz et al. 2016). As a result, the analysis of the growth rings was extremely difficult and many of the samples could not be dated. From an initial sample size of 86 specimens, only 33 (38%) were dated to the year of formation. To increase sample depth, 3 to- 4 radii from each cross-section were cross-dated, producing a ring-width database of 111 series in total (Fig. 4).

The ring-width chronology extends from 1178 to 2016 (839 years) (Fig. 5) and has an interseries correlation of 0.34 (higher than the critical value of 0.328, $p < 0.01$ from COFECHA for well dated series), a mean sensitivity of 0.327, first-order autocorrelation of 0.442, Rbar of 0.181, and 20% of the common variance explained by the first principal component. An EPS > 0.85 corresponding to a suitable chronology for climate reconstruction purposes includes 13 radii for the period 1350–2016 (Fig. 5). Sample depth was low at the most recent part of the series (years 2014, 2015, and 2016) given that few cross-sections from living trees were included to build this part of the chronology.

Pearson correlation values between the *J. monticola* chronology from Pico de Orizaba and chronologies of *Pinus hartwegii*, *Pseudotsuga menziesii*, and *Abies religiosa* from Pico de Orizaba or nearby volcanic

peaks were non-significant ($p > 0.05$). However, there is a correlation value of 0.2 with a *J. monticola* chronology from Cofre de Perote (located 57 km to the NNE) in the common period 1900–2016.

Response of the tree ring chronology to local climate data

The response of the *J. monticola* ring-width chronology to precipitation data unloaded from the Climate Research Unit was not significant except for the current month of March ($r = -0.198$, $p < 0.05$, 1900–2016). A not significant association ($p > 0.05$) was determined for maximum temperature for any of the previous or current months of the growing season. When comparing the data from the local weather station (Tembladeras) with the ring-with series (Fig. 6), a dominant negative association was found between monthly precipitation and the ring-width index, significant for the current March ($r = -0.41$, $p < 0.01$, 1968–2016) and for the accumulated March-April ($r = -0.44$, $p < 0.01$, 1968–2016). On the other hand, the ring-width series shows a positive and significant correlation with the average maximum temperature of May-June of the current year ($r = 0.38$, $p < 0.05$, 1968–2016) (Fig. 6).

Response of the tree ring chronology to drought indices

The comparison between the standard ring-width chronology of *J. monticola* and the gridded instrumental PDSI June, July, August, period 1920–2012 for the studied area indicated a significant negative correlation between both variables ($r = -0.354$, $p < 0.01$, 1920–2012, $n = 93$), where negative values of instrumental PDSI associated with dry and presumably warmer conditions favored the radial increase of the species in the cold alpine environment (Fig. 7).

The correlation between *J. monticola* ring-width and seasonal June, July, August PDSI increased from 1950 to 2012, as follows: 1950–2012 ($r= -0.397$, $p < 0.01$); 1960–2012 ($r = -0.413$, $p < 0.01$); 1970–2012 ($r = - 0.439$, $p < 0.01$); 1980–2012 ($r = -0.451$, $p < 0.01$); and 1990–2012 ($r = -0.587$, $p < 0.01$). This may reflect an increasing response of the species to PDSI values and therefore to drier conditions.

The response function analysis between the ring-width indices and the SPEI values was computed with the Dendroclim2002 program (Biondi and Waikul 2004). Significant negative correlations ($p < 0.05$) were obtained for January (-0.236), March (-0.258), April (-0.224), and May (-0.32), and the correlation increased to -0.40 ($p < 0.01$, 1966–2015, $n = 50$) for the mean SPEI values when considering the seasonal period from December of the previous year to June of the current year.

Association with ocean-atmosphere phenomena

Very weak correlations were found between the *J. monticola* ring-width chronology and climate forcing mechanisms. The association between the ENSO indices (SOI, MEI, TRI) and the ring-width chronology was significant only for the SOI, with a negative correlation value of -0.188 ($p < 0.05$, 1873–2016, $n = 151$). This suggests that negative values of the SOI indicative of El Niño conditions had a positive effect on the annual radial growth of the species, particularly in the years 1889, 1905, 1912, 1978, 1983, 2000, and 2005. However, La Niña years (positive SOI values) associated with high RWI values were detected in the years 1876, 1890, 1939, 1956, 1967, 1971, 1985, 1989, 2008.

The association of the PDO with the chronology was significant from September to November of the growing year ($r = 0.20$, $p < 0.05$, 1902–2016, $n = 115$), whereas the July-September mean AMO value of the previous year had a significant association ($r = -0.176$, $p < 0.05$, 1857–2015, $n = 159$) with the standard ring-width chronology of *J. monticola*.

The power spectrum analysis of the standard ring-width chronology produced significant peaks at frequencies of 31.0, 17.0. 10.1, 6.7, 4.2, and 2.4 years, indicative of the influence of large-scale modes of atmospheric phenomena (Fig. 8). These spectra indicate some power in the ENSO, decadal, bi-decadal, and multi-decadal time periods, despite the very weak correlations with ENSO, PDO, and AMO.

Discussion

The Mexican mountain juniper present at and above the treeline of Pico de Orizaba volcano shows extremely irregular growth characterized by compressed and released episodes of radial growth, resulting in frequent missing rings in some parts of the stem and above-normal growth in others. Locally absent and missing rings are a common feature of alpine species due to eccentricity of the pith and irregular growth around the stem favored by dominant harsh environmental conditions (Myers-Smith et al. 2015). Similar features have also been observed on old, low-elevation juniper shrubs growing on cliffs (Camarero and Ortega-Martínez 2019). To develop a ring-width series of the multiple stem *Juniperus monticola* requires a high sample depth to reduce the noise produced by irregular growth and to capture dominant climate variability at this elevation, as suggested for other alpine and arctic species (Buchwal et al. 2013).

The krummholz shrub *J. monticola* has been shown to live for several centuries and may reach a millennium of age (Villanueva-Díaz et al. 2016) (Fig. 3). The ring-width series developed for Pico de Orizaba extends over 800 years, only surpassed in Mexico by those of Montezuma bald cypress (*Taxodium mucronatum* Ten.), a riparian tree that reaches and age of nearly two thousand years (Villanueva Díaz et al. 2010; Stahle et al. 2012). Schweingruber and Poschlod (2005) report that the oldest living shrub is a 352-year-old specimen of *Juniperus communis* ssp. Nana, but they point out that individuals at very extreme sites might be older. Juniper shrubs with ages close to a millennium are known from environments with limitations such as cliffs (Larson et al. 2000; Camarero and Ortega-Martínez 2019). Juniper trees in upper treeline environments are also known to reach ages of > 900 years (Zhang et al. 2015). According to Liu et al. (2019) three factors may explain the extremely old ages of *Juniperus przewalskii* trees in the NE Tibetan Plateau of China: low metabolic rates related to cold environments; limited human disturbance at high elevation, remote locations; and reduced impact of wildfire at high elevation sites characterized by little or no understory. The three factors operate at the remote, cold and usually rocky environments of the Mexican volcanoes where *J. monticola* grows.

The Mexican mountain juniper present above the treeline of volcanic peaks in central Mexico is the most promising species to analyze climatic variability and climate warming trends on the mountains of central Mexico during the last millennium (Villanueva-Díaz et al. 2016), including anthropic impacts in the

environment. An increase in temperature around 1.4°C has been reported for the last decades on mountain ranges of central Mexico at elevations over 4,000 m a.s.l. (Harris et al. 2014; Lobato-Sánchez and Altamirano-Del-Carmen 2017).

The *J. monticola* annual radial growth seems to have a different climatic response as compared to the *Pinus hartwegii* trees growing at slightly lower elevations. Annual radial growth of *P. hartwegii* is significantly influenced by seasonal precipitation (Biondi 2001; Manzanilla-Quiñones et al. 2020), but in some sites, particularly at the treeline position, temperature seems to exert a substantial influence in radial growth (Astudillo-Sánchez et al. 2017), in particular late spring temperature (Biondi et al. 2005). On the other hand, *J. monticola* radial growth may be limited by different climatic factors and other abiotic variables, among which temperature could be the most important variable (Villanueva-Díaz et al. 2016).

J. monticola showed a significant response to drought indices PDSI and SPEI, both of them influenced by increased temperatures, greater evapotranspiration rates, and decreased water availability. Although annual precipitation is relatively high at the elevation range of the species (900–1000 mm around 4000 m a.s.l.), < 5% of the total falls during the winter (Almeida-Leñero et al. 2007) and < 13% from November to April. Therefore, the water balance is likely negative during the dry season due to high infiltration rates favored by shallow rocky and sandy soils, high solar radiation and diurnal temperatures, strong winds, and high evapotranspiration rates. The dominant environmental conditions of the spring season at Pico de Orizaba exert a key role in the radial growth of *J. monticola* given the significant and positive response to temperature from April to June, and negative to precipitation from March to April. This may actually be the time when the species undergoes cambial activity and form the annual rings.

The ring width chronology of *J. monticola* at Pico de Orizaba shows negative correlation with instrumental PDSI values in recent decades. This began in the 1950´s and reached the highest correlation value of -0.587 for the subperiod 1990–2012 (Fig. 7). This suggests that warmer temperatures at the studied area are favoring an increase in radial growth and therefore in biomass productivity for temperature-dependent species like *J. monticola*. However, this behavior may involve interactions with other environmental variables such as an increase in water and nutrient availability leading to greater growth and recruitment rates (Silva et al. 2016; Astudillo-Sánchez et al. 2019; Scharnweber et al. 2019).

Favorable ecological conditions are rarely found at alpine environments, where dominant species have particular physiological adaptations that allow them to survive in those harsh environments, such as small size, growth close to the ground or in dense clumps and clonal reproductive capacity, among others (Steinmann et al. 2021). A positive response in biomass production due to rising temperature interacting with other environmental variables has been documented for several arctic an alpine species around the world (Elmendorf et al. 2012; Silva et al. 2016; Vanneste et al. 2017; Milner et al. 2018; Buchwal et al. 2013). One of those species is *Rododendron nivale* on the south-eastern Tibetean Plateau, which has a temperature signal and could be beneficiated by climate warming (Liang and Eckstein 2009). Similarly, the dwarf shrub *Cassiope tetragona* found in artic environments has shown potential for climate reconstructions and to analyze phase changes in large-scale atmospheric circulation modes (Rayback

and Henry 2005). Growth of the arctic *Salix polaris* is mainly controlled by summer temperature and is negatively correlated to summer precipitation, as the latter is linked to lower solar radiation and temperature (Buchwal et al. 2013).

The negative association (-0.4, $p < 0.01$) found between the RWI of *J. monticola* and the SPEI drought index from December of the previous year to June of the current year suggests that warmer temperatures during the growing season favor an increase in radial growth. These results support a warming climate trend taking place on the mountains of central Mexico. Such current warming trend has already been attributed to changes in albedo derived from land-use changes, land urbanization and other human activities affecting the physiological response of woody species and other alpine plants on the highest peaks of central Mexico (Stahle et al. 2009; Beramendi-Orosco et al. 2018; Steinmann et al. 2021).

The SPEI index has been used worldwide to determine the presence and intensity of droughts (Vicente-Serrano et al. 2014; Yu et al. 2014, Brázdil et al. 2015; Nam et al. 2015). In Mexico, this index has been applied to analyze the frequency of droughts on basins of the North Pacific region where dry episodes are frequent (Serrano-Barrios et al. 2016; Cabral-Alemán et al. 2022). However, it is important to take into consideration that droughts do not depend only on precipitation, temperature and evapotranspiration, but other climatic and edaphic variables may be involved (McVicar et al. 2012).

The hydroclimatic variability detected in the ring widths of *J. monticola* may reflect the influence of large-scale circulatory modes. The warm phase of ENSO or El Niño condition is characterized by an anti-phase or a dipole behavior, producing above-normal precipitation in northern Mexico (Therrell et al. 2002; Stahle et al. 2016), but dry conditions in the winter-spring and summer seasons for the central and southern part of the country (Magaña Rueda et al. 1999; Méndez and Magaña 2010).

The influence of ENSO in central Mexico using tree-ring data has been well documented by Stahle et al. (2012, 2016). The influence of ENSO as a main forcing of climate variability at high-elevation sites in central Mexico is supported by the relationship found between negative values of the SOI (El Niño), i.e. dry conditions, and higher radial growth of *J. monticola*. However, it must be noticed that negative SOI values were also found to be associated with a reduction in tree growth, such as in years 1987 to 1988, when the lack of rainfall and higher temperatures resulted in limited radial growth. In addition, several years with positive SOI values (La Niña phase), i.e. largely moist in central Mexico, were associated with high RWI.

Other studies corroborate the influence of annual SOI on radial growth of high-elevation species (Biondi 2001; Astudillo-Sánchez et al. 2017, Manzanilla-Quiñonez et al. 2020). This may be an indication that El Niño conditions could be associated to increased temperatures, thus favoring greater growth rates for species like *J. monticola* (Villanueva-Díaz et al. 2016).

The PDO and AMO indices showed low correlations with the chronology of *J. monticola* and do not seem to have a significant contribution to the understanding of the physiological growth behavior of the species.

The power spectrum analysis of the standard ring-width series shows significant peaks at 31.1, 17.0, 10.1, 6.7, 4.2, and 2.4 years. The frequent peaks of 2.4, 4.2, 6.7, and 10.1 years could be associated to the high frequency variability of ENSO at the 2 to 10 year-period (Kestin et al. 1998; Mann et al. 2000; Bruun et al. 2017), whereas the 17.0 year-frequency could be explained by the PDO that behaves in frequencies of 15 to 25 years and 50 to 70 years (Mantua and Hare 2002; MacDonald and Case 2005). Finally, the highly significant 31.1-year peak could be associated to the AMO influence, given that the AMO behaves in frequencies of 65 to 80 years with cold and warm cycles near 30 years (Enfield et al. 2001; Ting et al. 2009).

The interaction of atmospheric circulatory modes in central Mexico is not well understood and seems to produce different outcomes according to the available climatic information. However, there is a consensus that the ENSO phenomenon is the major circulatory mode influencing climate variability all over Mexico (Seager et al. 2009; Méndez and Magaña 2010; Stahle et al. 2016).

Conclusions

Juniperus monticola, the Mexican mountain juniper, is the highest elevation woody shrub in North America and one of the highest in the world. It is a genetically predetermined *krummholz* found around and above the treeline, at maximum elevations of 4515 m a.s.l. on Pico de Orizaba volcano, although a single young specimen was detected at 4620 m a.s.l.

The species may reach an age close to a millennium, which probably makes it the oldest alpine shrub in the world. Its dendrochronological parameters indicate a significant potential to develop long-term dendroclimatic reconstructions, in particular for temperature and precipitation at high elevation sites in Mexico.

The annual radial growth of the species is significantly related to the PDSI and SPEI droughts indices. Negative values of these indices for the winter-spring season, indicative of a negative water balance resulting from lower precipitation, higher temperatures and evapotranspiration rates had a significant positive effect on annual radial growth. Also, the ring-width of *J. monticola* is positively correlated to May-June temperature and negatively correlated to March-April precipitation from a local weather station. These outcomes suggest that the species may be more limited by temperature than by water availability at the time of the year when annual rings form. It is therefore possible that an increase in temperature may have a positive impact on the biomass production of *J. monticola*.

The growth response of *J. monticola* on the highest volcanic peaks of central Mexico represents an excellent opportunity to deepen our understanding of the dynamics of tropical alpine ecosystems, their conservation in the face of rising temperatures and the impact of human activities on mountain environmental services.

Declarations

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Data availability Data will be made available on request.

Competing interests The authors declare no competing interests

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Figures

Figure 1

a Habitat of the Mexican mountain juniper on the south side of Pico de Orizaba at 4150 m. a.s.l. Scattered individuals of the shrubby *Juniperus monticola* f. *orizabensis* Martinez grow on bare rock surfaces of a young blocky lava flow. A few trees of *Pinus hartwegii* are visible on the skyline. Bunch grasses grow on crevices and depressions filled with volcanic ash. **b** Dead specimen of *J. monticola*at

4130 m a.s.l. Note the pen near the center of the photo for scale (photographs taken on December 11, 2017)

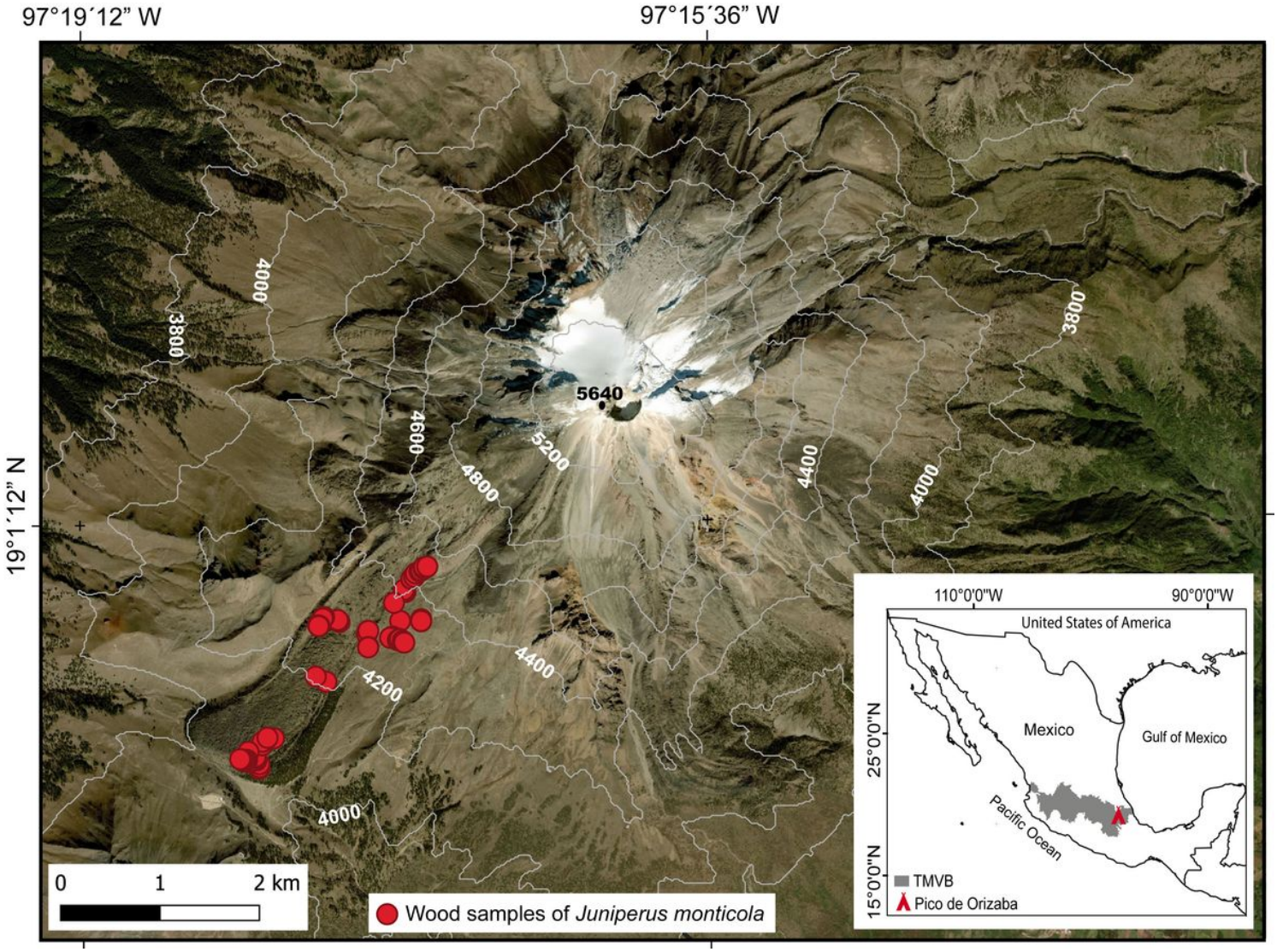

Figure 2

Location of Pico de Orizaba volcano in the eastern portion of the Trans-Mexican Volcanic Belt (TMVB) and sampling sites of *Juniperus monticola*cross-sections

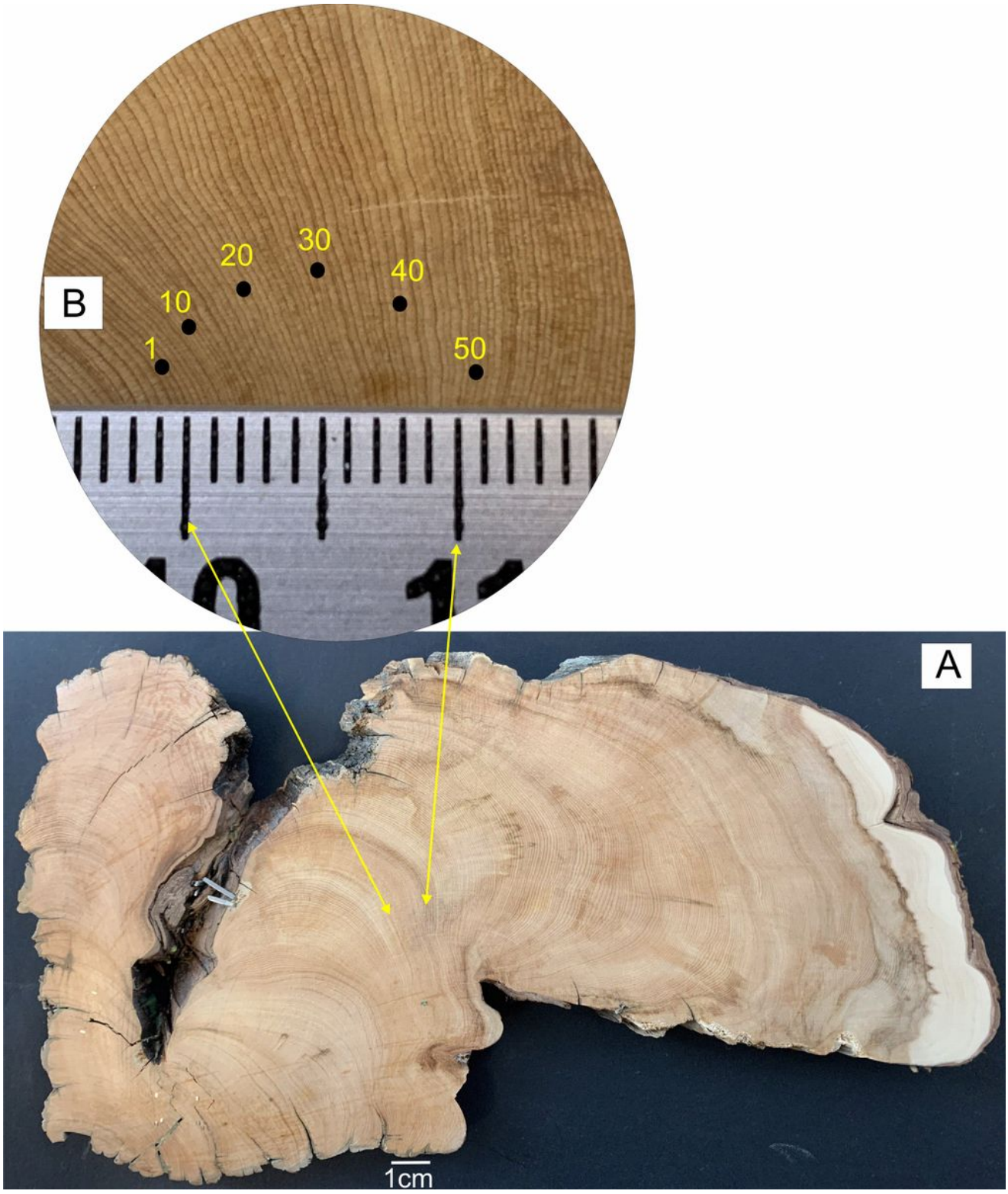

Figure 3

a Cross-section of *Juniperus monticola* Martinez (sample PIJ-08) collected at 4140 m a.s.l near the photo shooting spot of Fig. 1a. The sample has 836 annual rings. **b** Zoom showing ca. 50 microrings cm^{-1}

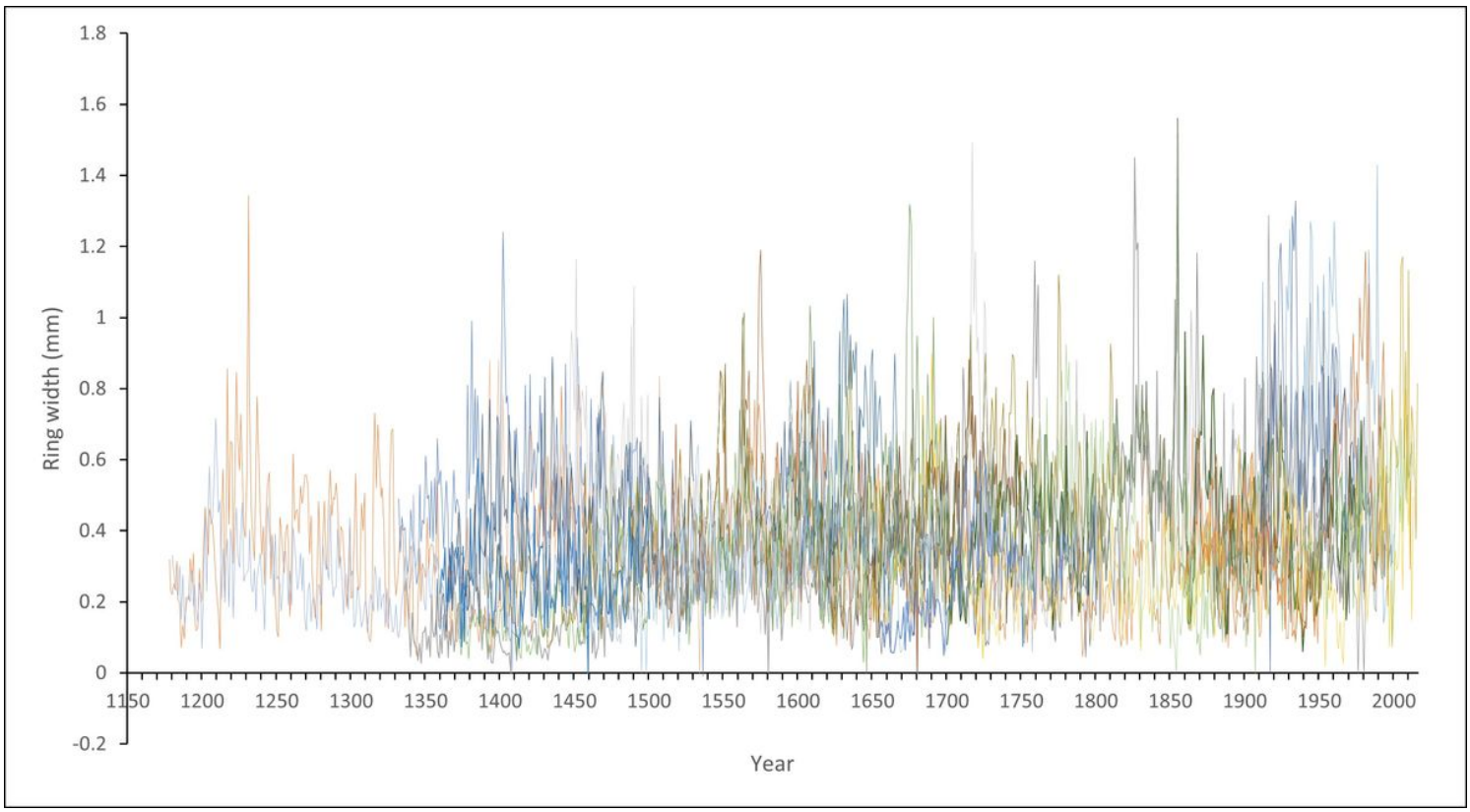

Figure 4

Spaghetti plot of the *Juniperus monticola* dated series indicating similar high and low frequency trends

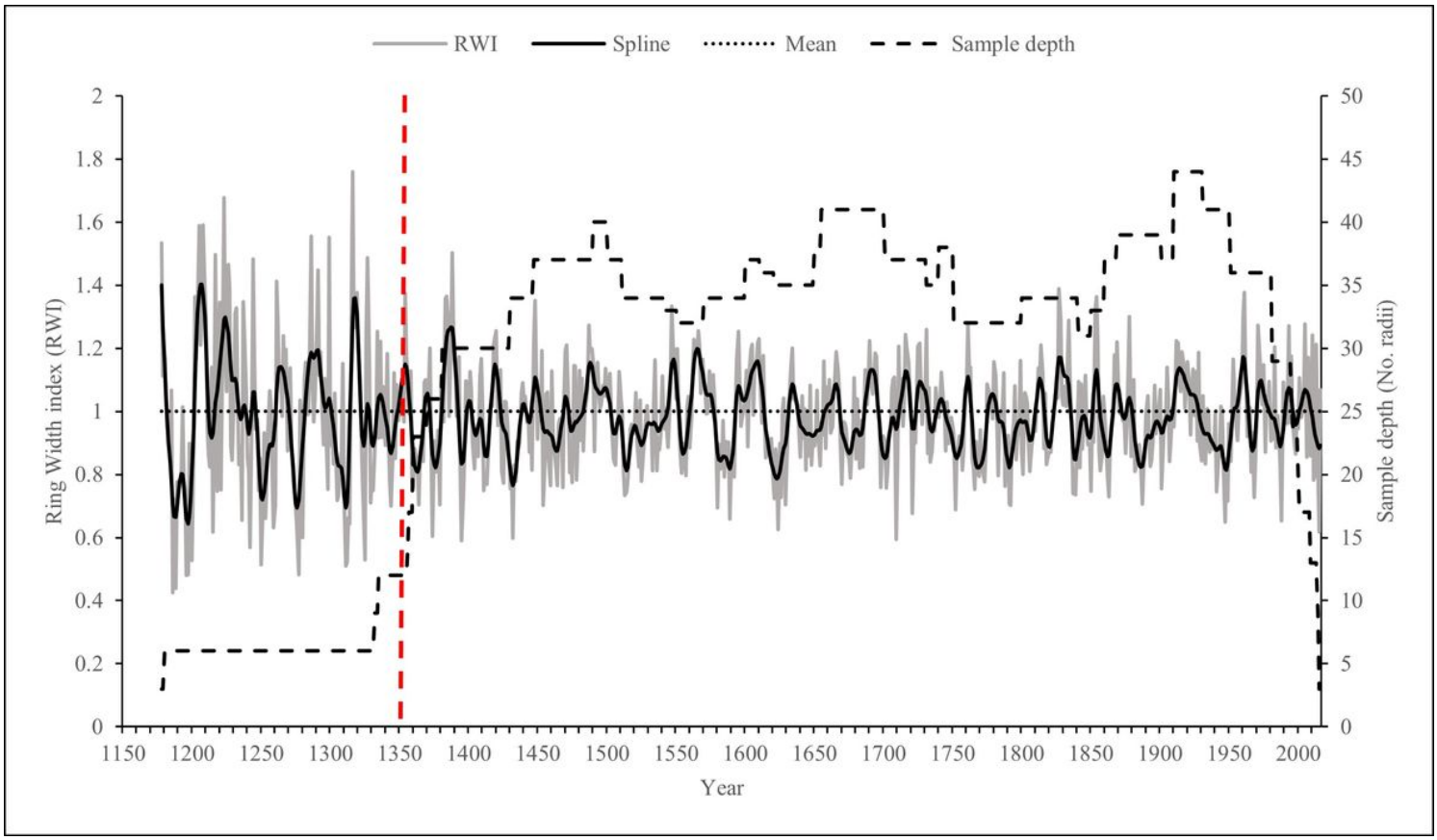

Figure 5

Standard version of the ring-width chronology of *J. monticola*at Pico de Orizaba, Mexico. A decadal spline was fitted to the ring-width annual values to emphasize low frequency variability. The red vertical broken line depicts the first year with an EPS > 0.85 extending from 1350 to 2016, where the chronology is most suitably replicated and correlated among radii

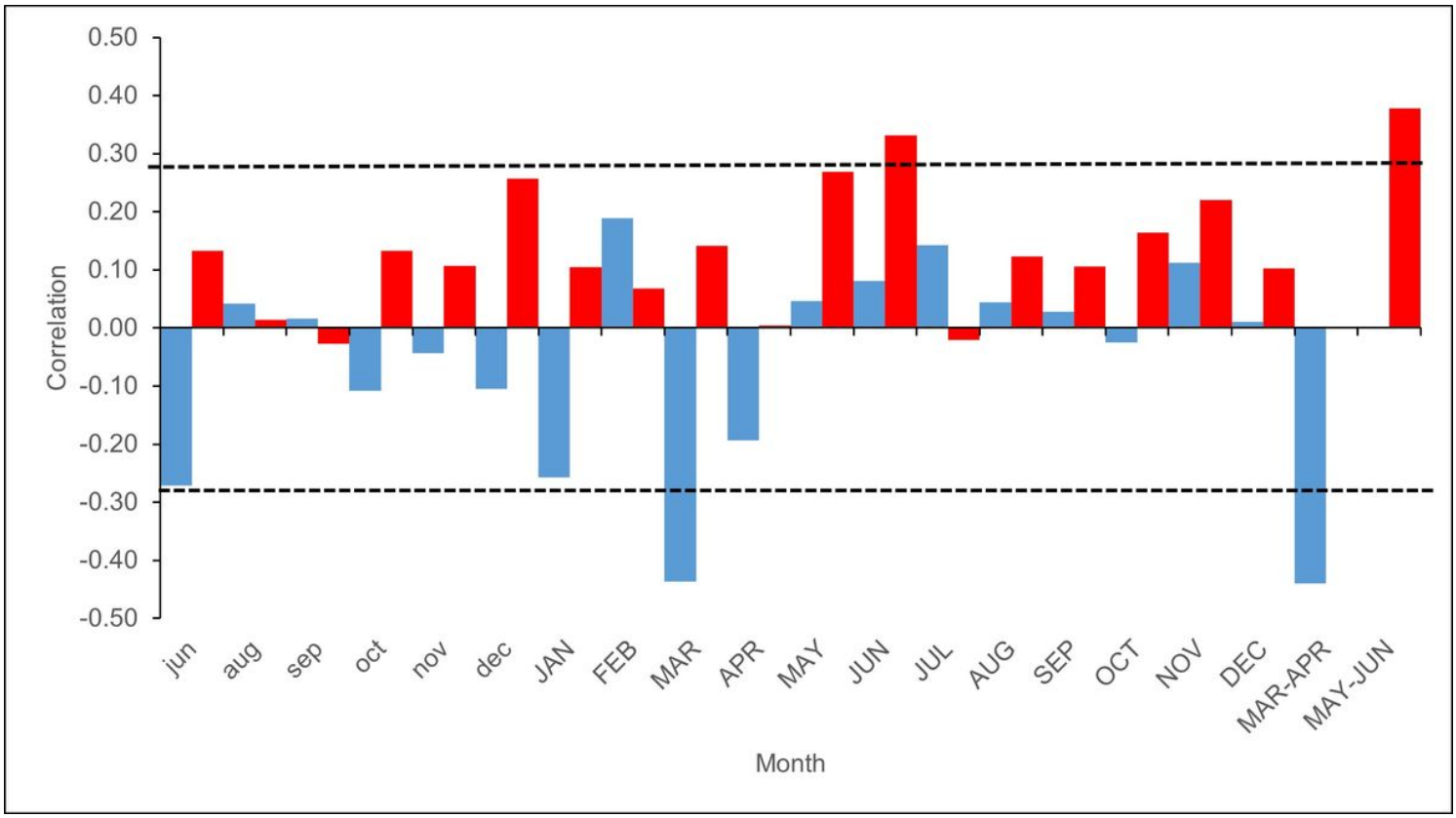

Figure 6

Climatic response function of the *J. monticola* ring-width chronology and climate data (average maximum temperature, precipitation) from the "Tembladeras" weather station for 18 months in total (6 months prior to the growing season and 12 months of the current year). The red bars correspond to monthly average maximum temperature, and the blue bars to accumulated monthly precipitation. Lowercase letters correspond to the previous year and capital letters to the current year. Significant values ($p < 0.05$) are those surpassing the confidence level (horizontal broken lines)

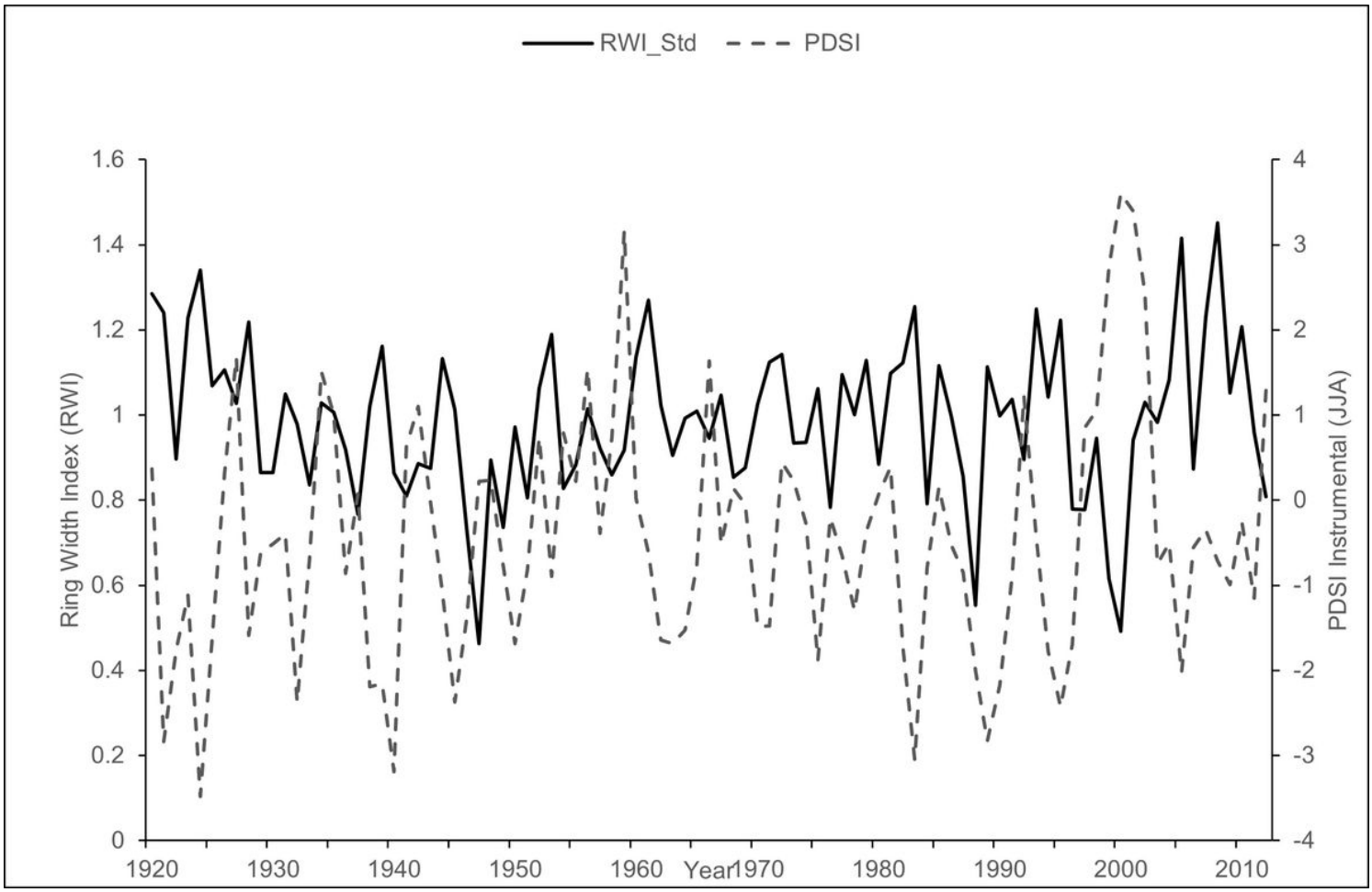

Figure 7

Association between the instrumental PDSI (June, July, August) and the ring-width index of *J. monticola* at Pico de Orizaba. Gridded instrumental PDSI data was obtained from the Mexican Drought Atlas (http://drought.memphis.edu/MXDA/). Low PDSI values indicative of higher temperatures and drier conditions in general favored the radial growth of the species

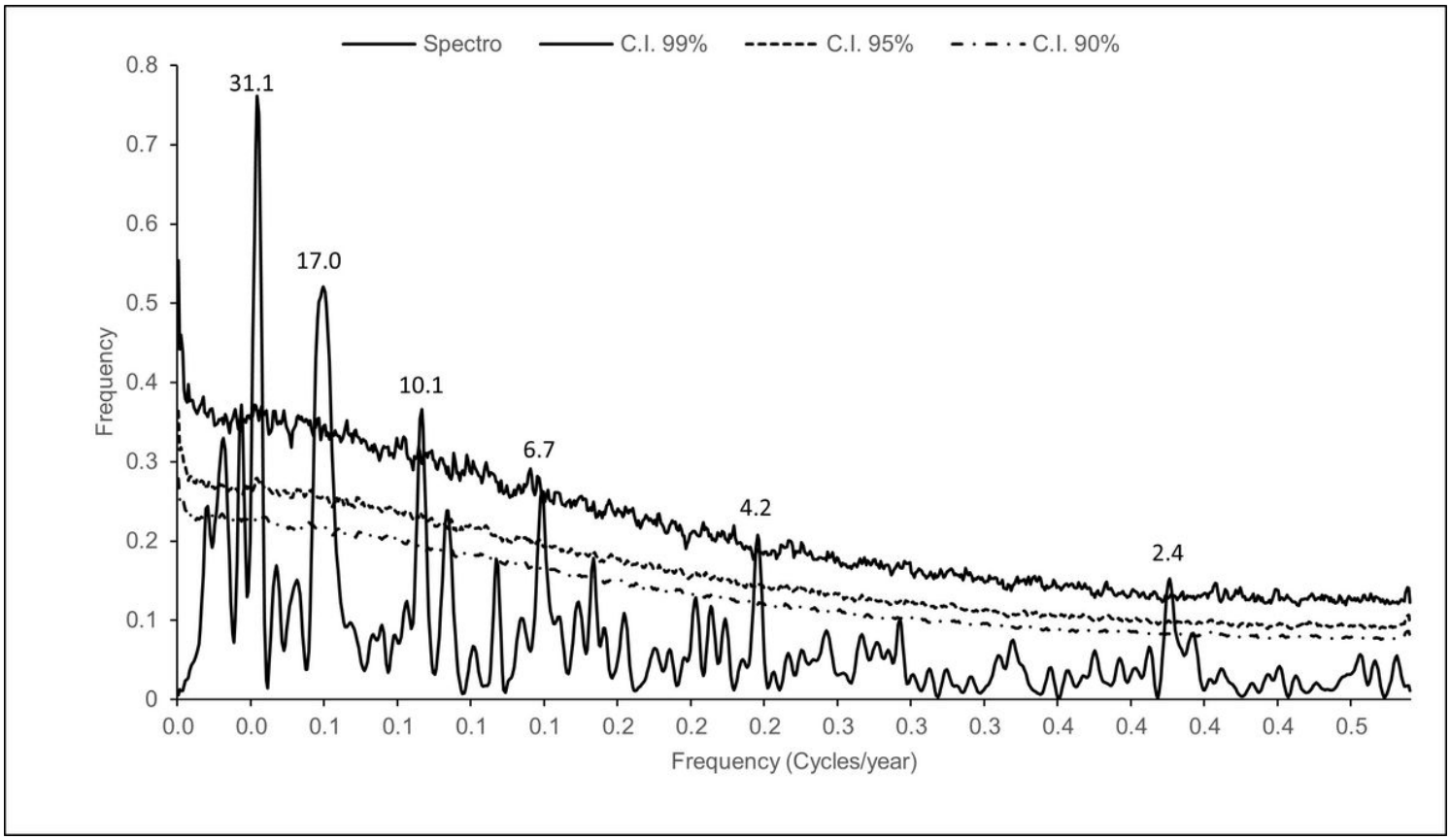

Figure 8

Power spectrum analysis behavior of the standard ring-width series (1178-2016) of *J. monticola* in Pico de Orizaba, Mexico. Significant peaks over 99% of the confidence interval were evident in the ring-width chronology at frequencies of 31.1, 17.0, 10.1, 6.7, 4.2, and 2.4 years