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Contrasting growth trends in *Nothofagus pumilio* upper-elevation forests induced by climate warming in the Southern Andes

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ABSTRACT

The high sensitivity of *Nothofagus pumilio* growth to climate variations at upper treelines provides a unique opportunity to document changes in tree responses to a warmer climate in the Patagonian Andes. In the context of significant recent temperature and precipitation changes across Patagonia, we conducted a study along the precipitation gradient in the Río de las Vueltas basin, southern Patagonian Andes, to: (1) document differences in *N. pumilio* growth trends at upper treelines, (2) determine changes in climate-growth relationships along the precipitation gradient, and (3) estimate future growth responses to simulated 21st century warming. For the past 100 years, mean tree-ring width increases progressively from wet to dry treelines in response to less abundant precipitation and less persistent snow cover into the growing season. Mountain aspect regulates snow cover duration and hence growing season length, thereby also influencing tree-ring width. On interannual scale, temperature directly modulates tree-growth variations in wet and mesic treelines, but is inversely related to growth in dry sites. Growth trends show that the approximate 0.56°C temperature increment since the mid-1970's in the Patagonian Andes dramatically enhanced the recorded long-term increasing growth rates at mesic, but to a lesser extent at humid treelines, suggesting nonlinear interactions between temperature and snow persistence on tree growth. Contrarily, growth rates at dry treelines decreased over the past 100 years. Our predictive statistical models indicate sustained decadal increases in current radial growth rates at wet and mesic sites and decreases at dry treelines towards the end of the 21st century under the simulated future warming scenarios for the southern Andes. However, the nonlinear relationships between warming, snow cover and tree growth, combined with unreliable estimates of precipitation for the region during the 21st century, suggest that these simulated changes in tree growth should be viewed with caution.

1. Introduction

Climate change is affecting the growth and dynamics of forests on global scale (Allen et al., 2015, McDowell et al., 2020). Long-term temperature increase modifies the rate of carbon sequestration through alterations of tree photosynthetic and respiratory processes (McDowell et al., 2008). In addition, the increased frequency of extreme weather events alters the establishment and mortality rates of trees in different size and age classes. Cold and humid forests with energy limitations for growth are expected to respond positively to increases in temperature, whereas dry forests would be negatively affected by increases in temperature and vapor pressure deficit (Babst et al., 2019). These antagonistic processes are occurring globally, so the future of forests is uncertain (McDowell et al., 2020).

Interannual variations in tree growth at high-elevation and high-latitude forests in the Northern Hemisphere have traditionally been associated with seasonal or annual variations in temperature (LaMarche 1974, Jacoby and D'Arrigo 1989, Esper et al., 2016). At humid high-elevation and high-latitude forests, the recent increase in temperature seems to have accelerated the growth rate of trees through an increase in net photosynthesis. In addition, higher temperatures act to reduce snow cover and therefore prolong the growing season (Körner 2007). Thus, recent reported positive responses to temperature in prior fall and early spring suggest that trees in cold and humid areas benefit from longer growing seasons (Babst et al., 2019). In cold environments, higher soil temperatures also favor the assimilation of soil nutrients by plants (Chapin et al., 1995).

Trees from high elevations in the southern Andes are highly sensitive

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to climatic variations. Along the upper treelines in the Patagonian Andes, annual variations in *Nothofagus pumilio* growth have been related to changes in temperature and duration of snow cover (Villalba et al., 1997, 2003; Lara et al., 2005). Most studies indicate that the radial growth of *N. pumilio* in humid sectors of the upper Andean forests is directly influenced by temperature during the growing season. However, as we move towards drier sectors in the upper forests, the radial growth of *N. pumilio* seems to be more strongly regulated by the availability of water during the summer months (Daniels and Veblen 2004). Indeed, recent studies by Rodríguez-Catón et al., (2016, 2019) showed that the growth of *N. pumilio* trees in high altitude dry forests depends on water supply and extreme droughts trigger episodic mortality in the upper sectors of the forest. Taken together, these studies suggest that high-elevation forests are more sensitive than low-elevation forests to climatic changes, as local stand dynamics more often modify growth patterns at lower elevations (Srur et al., 2020).

The climate in the Patagonian Andes has undergone important changes since the mid-twentieth century (Villalba et al., 2003, Masiokas et al., 2008). The change from the negative to positive phase of the Pacific Decadal Oscillation in 1976 was associated with a marked increase in temperatures, particularly in summer, along the Patagonian Andes (Villalba et al., 2003, Vuille et al., 2015). In southern Patagonia, the composite temperature record from Balmaceda (45.9°S) and Cochrane (47.2°S) shows an increase of 0.8°C in summer temperature (October-March) from the early 1960s to present, at a rate of 0.14°C/decade. On the contrary, temperature increases during winter have been moderate with a rate of 0.03°C /decade (Falaschi et al., 2019). In contrast to temperature, the most important changes in precipitation have been recorded in winter. On a seasonal basis, Balmaceda's precipitation decreased from 1954 to the present at a rate of 3.6 mm and 19.8 mm/decade in summer and winter, respectively, with a very steep annual reduction rate of about 25 mm/decade (Falaschi et al., 2019).

In this context of pronounced climatic changes, it is of interest to document the variations in growth rates of high-altitude *Nothofagus pumilio* forests in the southern Patagonian Andes during the last 100 years. The unique environmental setting generated by the Andes in Patagonia and the magnitude of the climatic variations registered in the last century amply justify our objective. During this period, climatic changes in the Andes may have registered the largest magnitude and speed over the last millennium (Caicedo et al., 2020, IPCC 2021). The marked precipitation gradient imposed by the Andes blocking the prevailing winds from the West generates one of the steepest climatic gradients in the world, creating environments with similar thermal conditions, but marked differences in precipitation over short distances (Villalba et al., 2003, Viale et al., 2019).

Century-long chronologies from tree rings have recently been developed in the upper limit of the *N. pumilio* forest in the Río de las Vueltas basin, southern Patagonian Andes. The sampling sites are situated relatively close to each other, but strategically located along the marked precipitation gradient in the watershed (Fig. 1). Therefore, differences in the amount and duration of the snowpack at high-elevation sites facilitate the assessment of variations in growth rates and in tree responses to climate along a moisture gradient. To our knowledge, the role that interactions between temperature and precipitation has on tree growth at the treelines have not been explored in detail in the southern Patagonian Andes. In addition, dendrochronological records provide a long-term perspective of tree growth responses to climate along treelines. In this contribution, we postulate that the steep precipitation gradient in the Patagonian Andes introduces variations in the growth rates and in the responses of upper treelines to climate. It is possible that radial growth at the treelines may not be modulated solely by temperature during the growing season and different responses to climate may emerge along the precipitation gradients (Fajardo and McIntire 2012; Galván et al., 2014). While tree growth in wet locations may be favored by current and simulated 21st

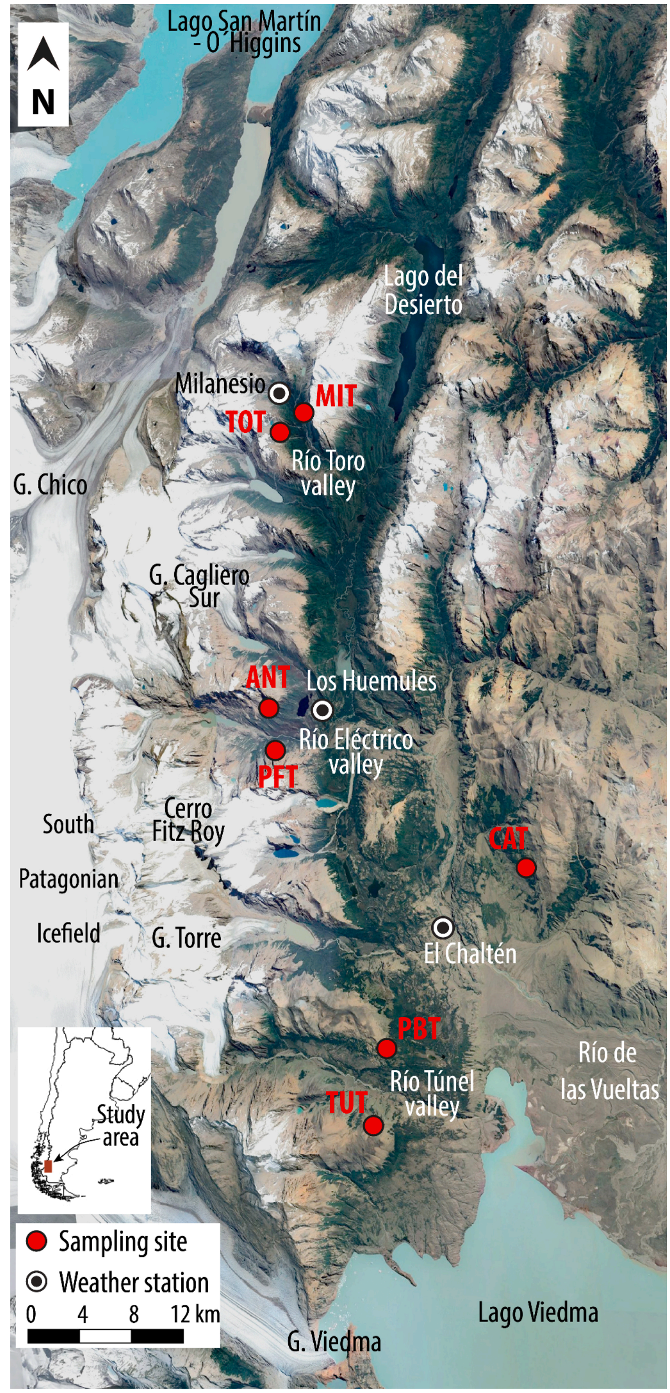

Fig. 1. Sampling sites (red circles) strategically located along the precipitation gradient in the Río de las Vueltas basin. Precipitation decreases in a NW-SE direction, reaching 1450 mm in Milanesio, 980 mm in Los Huemules and approximately 360 mm in the vicinity of El Chaltén. See Table 1 to identify the sites by codes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

century warming, growth could sustain current rates or even decline in drier upper treelines near the forest-steppe ecotones.

2. Materials and methods

2.1. Geographical setting

2.1.1. Climate

The climate of the southern Andes is modulated by the persistent passage of frontal air masses from the Pacific and their interactions with the Andean mountains. Strong westerly winds occur all year-round peaking during the austral summer. The blocking of the Westerlies by the Andes mountains induces a strong west to east precipitation gradient (Villalba et al., 2003, Garreaud et al., 2009, 2013). The north-south movement of the storm tracks in the Southern Hemisphere influences the strength and position of the extratropical Westerlies and consequently drives temperature and precipitation variability across the region (Marshall 2003, Villalba et al., 2012). Mean annual temperature varies from 0°C or less over the Patagonian Ice fields to 6°C on the eastern Andean slopes; precipitation is evenly distributed throughout the year (Villalba et al., 2003, Srur et al., 2018).

2.1.2. The species

Nothofagus pumilio is the dominant tree species in the Río de las Vueltas forests. *N. pumilio* is a deciduous tree widely distributed in the Patagonian Andes of Chile and Argentina between 35° 35′S and 55 °S (Tortorelli 1956, Donoso 1993). In northern Patagonia, *N. pumilio* reaches elevations of up to 2000 m and gradually decreases in altitude throughout its latitudinal range. At 50° S it rarely exceeds 1100 m altitude, while trees barely reach 600 m at the southern ends of its distribution in Tierra del Fuego. North of 41° S, *N. pumilio* occurs in the subalpine zone where it forms the forest upper limit. South of 44-45° S, it occurs throughout the elevational range, descending to sea level in the vicinity of the Strait of Magellan and Tierra del Fuego. Although *N. pumilio* grows on the western slopes of the Cordillera in sites with a total annual precipitation close to 5000 mm, it is also present on the eastern slopes of the Andes at sites with considerably lower precipitation reaching only 400 to 500 mm per year. Throughout the *N. pumilio* geographical range, particularly in the high mountains, precipitation falls in winter in the form of snow (Veblen et al., 1996).

2.2. Study sites

The study area is located in the Río de las Vueltas hydrological basin, Santa Cruz, Argentina, from Lago del Desierto in the north to its discharge into Lago Viedma in the south (Fig. 1). Within the basin, the Andean mountains and the Southern Patagonian ice field create a prominent northwest to southeast precipitation gradient, redirecting the inflow of moist air masses from the Pacific (Villalba et al., 2003). The sampling sites are situated relatively close to each other, but strategically located along the marked precipitation gradient in the watershed (Fig. 1). At the wettest extreme of the precipitation gradient near the Río Toro valley, 52 km north of El Chaltén, the total annual rainfall is above 1500 mm/year. In the mesic sector at Estancia Los Huemules in the Río Eléctrico valley, 27 km north of El Chaltén, total annual precipitation decreases to 1000 mm and eventually to less than 550 mm in El Chaltén, located on the forest-steppe ecotone (Villalba et al., 2003, Srur et al., 2018). During the winter months, much of the precipitation falls in the form of snow, starting as early as May and lasting until mid-November at the upper treelines (1100 m, data from IANIGLA, http://estaciones.ianigla.mendoza-conicet.gob.ar/; Srur et al., 2018).

In the Río de las Vueltas basin, *N. pumilio* occurs from 400–450 m in the ecotone with the Patagonian steppe to 900–1000 m at the treeline. In the lower parts of the valleys, the *N. pumilio* trees form a single stratum between 8 and 20 m in height. During winters, forests above 700–800 m elevation are permanently covered by snow. At the upper limit of the forest, *N. pumilio* appears in a stunted, creeping or krummholz form due to the weight of the snow and the strong winds that deform the branches of the trees. The height of the trees varies according to the snow load, reaching less than 1 m in sectors with high snow accumulation. The band of stunted forest, which forms the ecotone with the high Andean vegetation, varies in extension according to the topography, from a few tens to hundreds of meters. In some dry treelines near the Patagonian steppe, where snow accumulation is lower and the topography offers some protection from strong winds, dense stands of *N. pumilio* with erect trees form the upper limit of the forest.

All treeline sampling sites, except Canigó (CAT), consist of multi-stemmed, closed-canopy krummholz ranging in height from 1–1.5 m in the wet Rio Toro valley (MIT and TOT) to 2.5 m in the dry Río Túnel valley (PBT and TUT). Sampling sites in the Río Toro valley were located on steep west (MIT) and north-east (TOT) facing slopes. In the mesic Río Eléctrico valley, sampling sites were located on similarly steep slopes with south/southeast (ANT) and north/northeast (PFT) aspects. At the driest Río Túnel and Canigó valleys, the sampling sites were located on rolling hills with gentle slopes and variable orientations. In the Canigó valley, erect trees between 4–6 m in height and up to 1m in diameter form the upper limit of the forest in contact with the high Andean vegetation (Fig. 1, Table 1).

2.3. Sampling and tree – ring chronology development

N. pumilio increment cores were collected at seven upper-elevation forest sites along the precipitation gradient in the Río de las Vueltas basin. At each site, between two and three increment cores were taken from a minimum of 30 trees. Tree-ring chronologies were developed following the standard procedures described in Stokes and Smiley (1968). Tree rings were visually dated assigning to the year corresponding to the beginning of ring formation Schulman (1956). Increment core samples with relatively wide rings were scanned at a resolution of 1200 dpi and the digital images imported to CooRecorder where rings were cross-dated and ring width measurements were automatically assigned with an accuracy of 0.001mm Cybis (2020). The remaining samples with micro-rings were visually cross-dated and ring widths measured on a Velmex UniSlide tablet connected to a Metronics Quick-Chek QC-10V digital counter with an accuracy of 0.001 mm. The final collection of all cross-dated ring-width series was exported for further dating-quality verification using the COFECHA program Holmes (1983). Samples with a mean series intercorrelation lower than $r = 0.4$ were removed.

Variations in mean radial growth by site were estimated by chronologically averaging the tree-ring widths from all cross-dated series. Variations in mean annual growth were used to compare the growth rates between sites and to estimate the absolute growth trends before standardization. Differences in mean tree ring widths between sites were tested by ANOVA Zar (1999). For this analysis, ring widths over the period 1900–2010, an interval of good replication in the chronologies, were used. The ring widths were natural logarithm transformed to meet the statistical assumptions required in the ANOVA test. A Tukey post-hoc test Tukey (1949) was performed to determine differences in growth rates between sites.

In order to establish the relationships between interannual variations in climate and radial growth, growth variations not associated with climate (biological trend, endogenous disturbances) were removed by standardization Fritts (1976). Tree-ring measurements were detrended by applying Age-Dependent Spline Standardization using the ARSTAN program (Cook and Holmes 1986). Standard chronologies were generated by combining the standardized tree-ring series with bi-weight robust estimation. Residual chronologies were produced in the same manner as standard chronologies, but in this case the indices were residuals from autoregressive modelling of the standardized series (Cook 1985).

The Rbar and EPS statistics provided a measure of the common signal

Table 1
Characteristics of the sampling sites arranged along the precipitation gradient from the humid Río Toro to the xeric Río Túnel-Canigó valleys.

Valley	Chronology Code	Site	Latitude	Longitude	Elevation (m a.s.l.)	Aspect
Río Toro (humid)	MIT	Milanesio	49°03′26.16"S	72°56′44.93"W	1063m	W
	TOT	Toro	49°04′26.66"S	72°57′52.81"W	1135m	E
Río Eléctrico (mesic)	ANT	Anniversario	49°12′47.97"S	73°00′06.58"W	988m	S-SE
	PFT	Piedra del Fraile	49°14′15.51"S	73°01′10.05"W	1092m	N-NE
Río Túnel (xeric)	PBT	Pliegue Tumbado	49°22′43.33"S	72°56′50.24"W	1068m	E
	TUT	Túnel	49°25′11.90"S	72°56′29.40"W	1075m	N-NE
Canigó (xeric)	CAT	Canigó	49°18′32.24"S	72°49′06.61"W	980m	NW

between the series in a chronology and the representativeness of the sampling replication (Briffa 1995). Rbar is the mean correlation coefficient that results from comparing all possible pairings among the individual standardized tree-ring series that form the chronology, computed for a specified common time interval, in our case a 50-year window with a 45-year overlap (Briffa 1995). The EPS statistic is a measure of the similarity of the total signal between a given tree-ring chronology in relation to a hypothetical, infinitely replicated chronology (Briffa 1995). In this study, the EPS was calculated over a 50-year window with a 45-year overlap. EPS values equal or greater than 0.85 for a given period are considered adequate to reflect a consistent common growth signal in tree-ring series (Wigley et al., 1984).

Pearson correlation and Principal Component Analysis (PCA, Cooley and Lohnes 1971) were used to assess the degree of similarity between the upper-elevation chronologies and identify the dominant patterns in tree growth variability along the Río de las Vueltas precipitation gradient. A PCA was applied to the 7 raw chronologies of *N. pumilio* over the common period 1900–2010 (111 years) showing good replication in most chronologies. Varimax normalized rotation was applied for optimal grouping of the data and Factors, whose associated values (or eigenvalues) were greater than 0.6, were retained in the analysis. Based on these results, composite chronologies were developed for humid, mesic and dry sites to facilitate the analysis between growth and climate.

2.4. Climate records

Climatic records in the southern Patagonian Andes are mostly incomplete and not long enough to adequately evaluate the long-term relationships between climate and tree growth. A regional temperature record was developed based on monthly data from Balmaceda and Punta Arenas weather stations. Both records were standardized using the common period 1975 – 2014, and the normalized deviations from each series used to develop a regional temperature record covering the period 1950-2015. The use of normalized standard deviations ensures that each station has the same weight in the mean regional records, independent of its particular values (Villalba and Veblen 1997).

The larger spatial variability in precipitation than in temperature hinders the use of the few and short (< 15 years) records available in the Río de las Vueltas basin and adjacent areas to develop a representative regional precipitation record. We compared monthly precipitation data from the ERA5 reanalysis for the 49–49.5 ° S and 72.45–73.15 ° W grid box, which encompasses the entire Rio de las Vueltas watershed, with local precipitation records. The ERA5 reanalysis constitutes the combination of vast amounts of historical observations of climate data into global estimates by means of advanced modelling and data assimilation (Hersbach et al., 2020). Precipitation at Estancia Los Huemules, located at the center of our study area, is significantly related ($r = 0.74$, period 2006-2020, $n = 180$, $p < 0.01$) with the ERA5 record. Therefore, the monthly precipitation records from ERA5 starting in January 1979 (over 40 years) was used to compare with tree-ring variations along the treelines.

During the period March 2020 to March 2021, air temperatures at approximately 50 cm above the ground were recorded daily at six treeline sites. Daily temperature records near ground level can be used to estimate the duration of snow cover. Once the sensor is covered by snow, the daily temperature cycle is no longer recorded, and the temperature stabilizes very close to 0°C. The sensor will permanently record the ~0°C value until the snow melts and the sensor is exposed again.

2.5. Climate-tree growth relationships

Correlation function analysis were used to identify the influence of macroclimatic factors on tree growth at upper elevations (Blasing et al., 1984). Since autocorrelation introduces bias in the estimation of the coefficient of correlation (r), residual chronologies instead of raw chronologies were used for comparison with climate data. The correlation functions were determined for the 1950 – 2015 (65 years) and 1979 – 2015 (36 years) intervals for temperature and precipitation, respectively. Because tree rings are influenced by climatic processes occurring over a long period, correlation coefficients between ring-width indices and climate variables were computed over a sequence of 20 months for both temperature and precipitation, commencing in September, at the onset of the previous year's growing season, and lasting until April, the end of the current growing season.

On the basis of the correlation functions estimated over the period 1950–2015, we proceeded to establish the long-term relationships between seasonal variations in temperature and radial growth. Given that results from the response functions emphasize the role of temperature as the dominant factor in the growth of the *N. pumilio* forest in the treelines, we used the Punta Arenas temperature records available since 1920. The Punta Arenas meteorological station has records since the end of the 19th century, however, the data during the first decades are not quality controlled and include many years with absent values. Based on the correlation functions, we estimated the variations in the annual growth for the humid treeline forests using mean December-to-February temperatures, for the mesic treelines using November-to-March temperatures, and finally, for the dry treelines using the period from December of the previous growing season to October of the current growing season.

The predictive capacity of the regressive models relating the *N. pumilio* growth with temperature was validated using the calibration-verification procedures traditionally used in dendrochronology. The regressive models were calibrated over the interval 1920–1969 (50 years) and verified over the remaining interval 1970–2015 (45 years). Subsequently, the process was reversed using the 50 most recent years (1966–2015) for the calibration of the models that were verified over the early period 1920–1965 (45 years). The statistics used to verify the robustness of the models were the correlation coefficient, the determination coefficient, the reduction error (RE) and the coefficient of efficiency (CE; Cook et al., 1994). RE and CE are verification statistics that measure the relative accuracy of the predictions with respect to the observed data (Cook et al., 1994). RE and CE values can range from -∞ to a maximum value of 1.0. Negative values of RE and CE indicate that the predictive models have no skill, while positive values suggest some useful information in the predictions (Fritts, 1976; Cook et al., 1994). Finally, the regressive models relating tree growth with temperature were calculated over the entire study period (1920–2015) between the temperature record and the composite chronologies for the wet, mesic and xeric environments along the precipitation gradient in the Río de las Vueltas basin.

2.6. Projections of radial growth

Based on the long-term regressive models between seasonal temperature and tree growth, we used the regional temperature simulations from general atmospheric circulation models (GCMs) to estimate the potential variations in tree growth at the treelines until the end of the 21st century. We use the results from around 40 GCMs of the CMIP5 subset selected by the IPCC in its 2013 report (IPCC 2013), which provide monthly estimates of temperature variations for the historical period 1850–2005 and the 2006–2100 projections. The monthly simulation data were grouped in seasonal averages according to the season of largest climatic influence on radial growth. The simulations were obtained from the Climate Change Atlas (KNMI/WMO 2020). The simulations corresponding to the emission scenarios RCP 4.5 and RCP 8.5 were obtained for the grid centered on 49° S / 73° W, encompassing our study area.

In a first step, all the historical simulations were compared with the observed temperature records over the common period (1920-2019), to identify those models that best reproduce the climate in the Southern Patagonian Andes. The mean simulation series from the selected models, significantly related to the regional climate, were used as predictors of growth using the previously-developed regressive models derived from the comparison between seasonal temperature and growth during the period 1920-2015. In this way, we were able to estimate the *N. pumilio* radial growth at different treeline environments during the next decades using the emission scenarios RCP 4.5 and RCP 8.5 (IPCC, 2013). The seasonal (NDJF, ONDJFM and DJFMAMJJASO) temperature simulation means resulting from averaging the selected models were re-scaled to have the same means as the instrumental data over the common period 1920-2019.

3. Results

3.1. The chronologies

The upper-elevation chronologies of *N. pumilio* presented in this study ranged between 137 and 243 years in length (Table 2). Starting in 1900, when most chronologies are well replicated, the mean radial growths increase from the wettest to the driest sites (Fig. 2). The mean tree-ring widths for the TOT and MIT sites are 0.33 and 0.47mm/year, less than half that in the TUT and CAT dry sites with mean radial growths of 1.06 and 1.00 mm/year, respectively. In the intermediate mesic sites (ANT, PFT and PBT), the mean radial growth oscillates between 0.50 and 0.64 mm/year. Although somewhat higher than those recorded in the more humid sites, the growth at the mesic sites is significantly lower than in the dry treelines nearby the ecotone with the Patagonian steppe (Table 2 and Fig. 2).

Most treelines in humid and mesic sites show an overall increase in radial growth associated with larger interannual variability since mid-20th century (Fig. 2). Despite the overall increase trend in radial growth, most of these sites show few short periods of declining ring widths and decreased interannual variability. Most notably, radial growth at TUT, CAT and PFT show a marked and sustained decline from the early 1980's, whereas ANT and PBT show the most pronounced positive growth trends until the end of the record period (Fig. 2).

3.2. Spatial tree-growth patterns in the upper forests

A correlation matrix between the seven raw chronologies shows grouping primarily according to latitude, which in the Río de las Vueltas basin reflect changes in total precipitation. The sites MIT and TOT in the northwestern part of the basin receive larger amount of precipitation than those in the southeastern sector. The correlation coefficients are significant between the upper tree-line chronologies located on the humid and mesic sites. In contrast, they are not related to the drier sites TUT and CAT, which are significantly correlated to each other (Fig. 3a).

The Principal Component Analysis of the raw *N. pumilio* chronologies indicated that the first three principal components account for 49.2%, 23.6% and 9.4% (i.e., 82.2 % cumulatively), of the total variance in tree-ring growth over the 111-year common period (1900-2010). The upper tree-line chronologies in the intermediate (mesic) sites had the highest loadings in PC1. PC2 is associated with drier sites (TUT and CAT) chronologies, whereas PC3 joins the MIT and TOT chronologies in the wetter Río Toro sites (Fig. 3b). The PCA results are consistent with the correlation pattern between chronologies shown in Fig. 3a.

Based on the correlation and PCA analyses, the seven high elevation chronologies were grouped into three main clusters that reflect differences in tree growth along the moisture gradient along the Río de las Vueltas basin. Subsequently, composite chronologies were developed using the individual sites included in each cluster. The composite chronology for the wet valley (mean of MIT and TOT chronologies) shows an increase in radial growth from around 0.28 mm/year during the first decade of the 20th century to 0.48 mm/year in the last 10 years, resulting in a mean radial increase of 0.014 mm/decade during the last 116 years (Fig. 4). Comparatively, the mean radial growth for the composite mesic chronology (including ANT, PFT and PBT records) was larger, varying on average from 0.35 mm/year during the 1900's to 0.87 mm in the last 10 years. The mean growth rate for mesic sites was 0.047 mm/decade, three times larger than in the humid sites (Fig. 4). Unlike the increases recorded in humid and mesic sites, the composite chronology of the TUT and CAT sites near the Patagonian steppe show a reduction in radial growth from the beginning of the 20th century (1.20

Table 2
Characteristics of raw tree-ring width chronologies from upper-elevation *N. pumilio* forests along the precipitation gradient in the Río de las Vueltas basin. Sites are arranged from the humid Río Toro to the xeric Río Túnel valleys. Statistics are estimated for the full chronology lengths. Values in brackets for mean growth are from the well-replicated period 1900-2010, used for the ANOVA. Different letters show statistically significant differences at $P \leq 0.05$.

Valley	Code	Record Period	No. of Trees	No. of Radii	Length of Series (mean)	Mean tree-ring width (mm)	Mean sensitivity	Standard Deviation	1st Order Autocorrelation
Río Toro	MIT	1850 - 2015	27	47	166 years (92 years)	0.542 (0.47a)	0.328	0.302	0.696
	TOT	1822 - 2016	26	51	195 years (100 years)	0.382 (0.33b)	0.386	0.236	0.632
Río Eléctrico	ANT	1879 - 2016	29	55	138 years (76 years)	0.635 (0.50a)	0.407	0.410	0.676
	PFT	1880 - 2016	21	39	137 years (83 years)	0.783 (0.64c)	0.359	0.441	0.667
Río Túnel	PBT	1877 - 2017	27	46	141 years (75 years)	0.793 (0.61c)	0.331	0.397	0.666
	TUT	1841 - 2017	28	53	177 years (77 years)	1.141 (1.06d)	0.305	0.487	0.563
Canigó	CAT	1768 - 2010	49	83	243 years (112 years)	1.086 (1.00d)	0.354	0.483	0.533

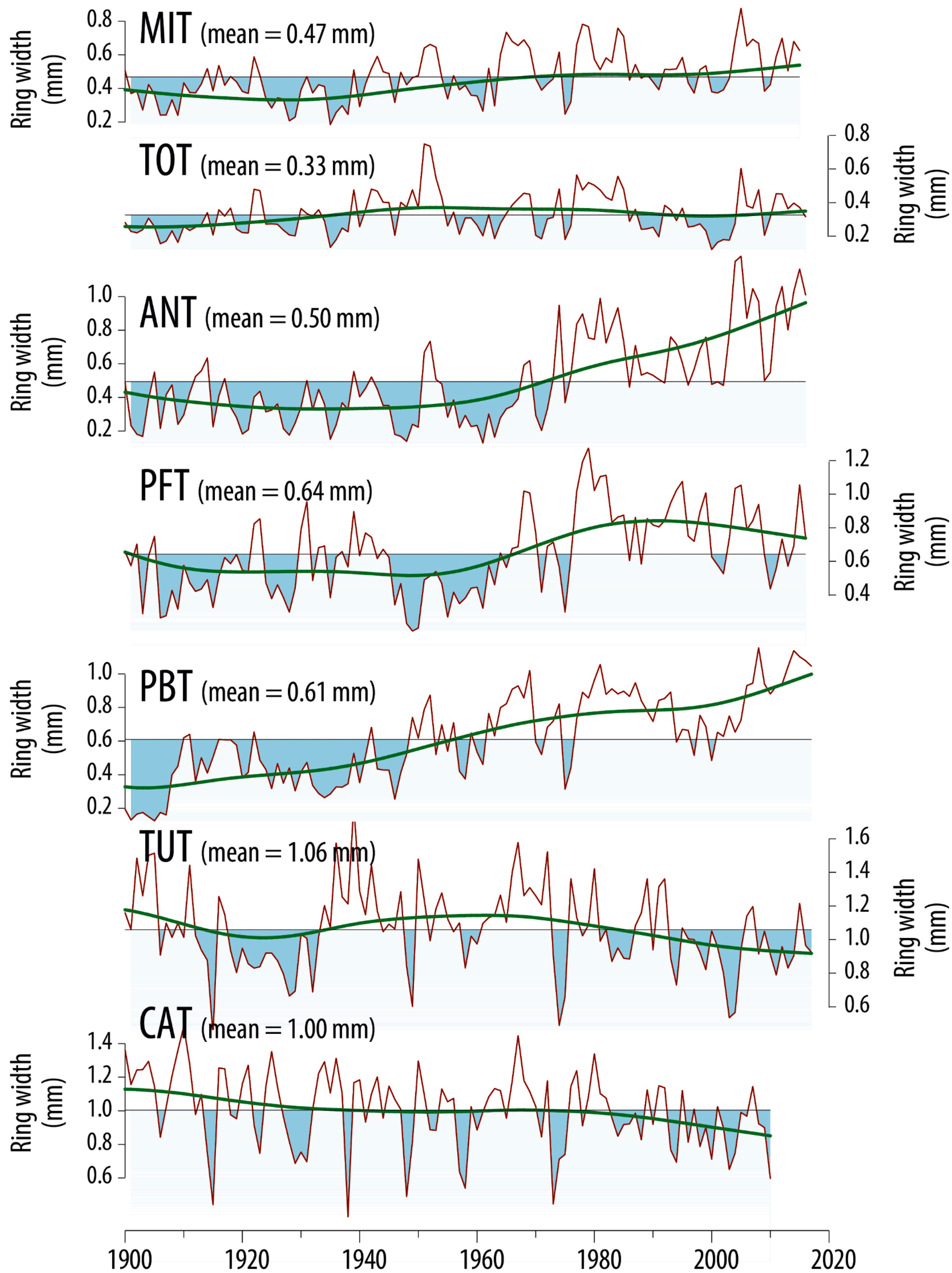

Fig. 2. Raw chronologies for the high-elevation *N. pumilio* forests in the Río de las Vueltas valley arranged from the wettest (MIT and TOT) in the Río Toro valley to the driest sites in the vicinity of the Patagonian steppe (TUT and CAT). The mean radial increments since the early 1900's is indicated for each chronology.

mm for the 1900's) to present (0.95 mm in the last decade) at a negative radial growth trend of -0.015 mm/decade over the last 120 years. The positive and negative trends in tree growth have not been constant over time. A marked increase, both in the humid and mesic sites, is observed since the mid-1970's, while the observed reduction in mean growth in the drier sites is more accentuated for the past 20 years (Fig. 4).

3.3. Climate-growth relationships

Given the relatively-high autocorrelations in the raw chronologies, composite chronologies were created for each environment (humid, mesic, xeric) averaging the individual site residual chronologies (Table 3). The relationships between temperature and tree growth were evaluated over the common period 1950-2015 (66 years). Variations in radial growth at high-elevation forests in the humid and mesic sectors are positively related to temperature, but inversely in the driest sites near the Patagonian steppe (Fig. 5). Although the response-to-climate patterns are similar between humid and mesic sites, in the humid sites the temperature modulation of growth is notably concentrated in the months of November, December and January. Interannual variations in tree growth at MIT and TOT are particularly influenced by the temperature in December (r = 0.62, n = 65 years). In mesic sites, the

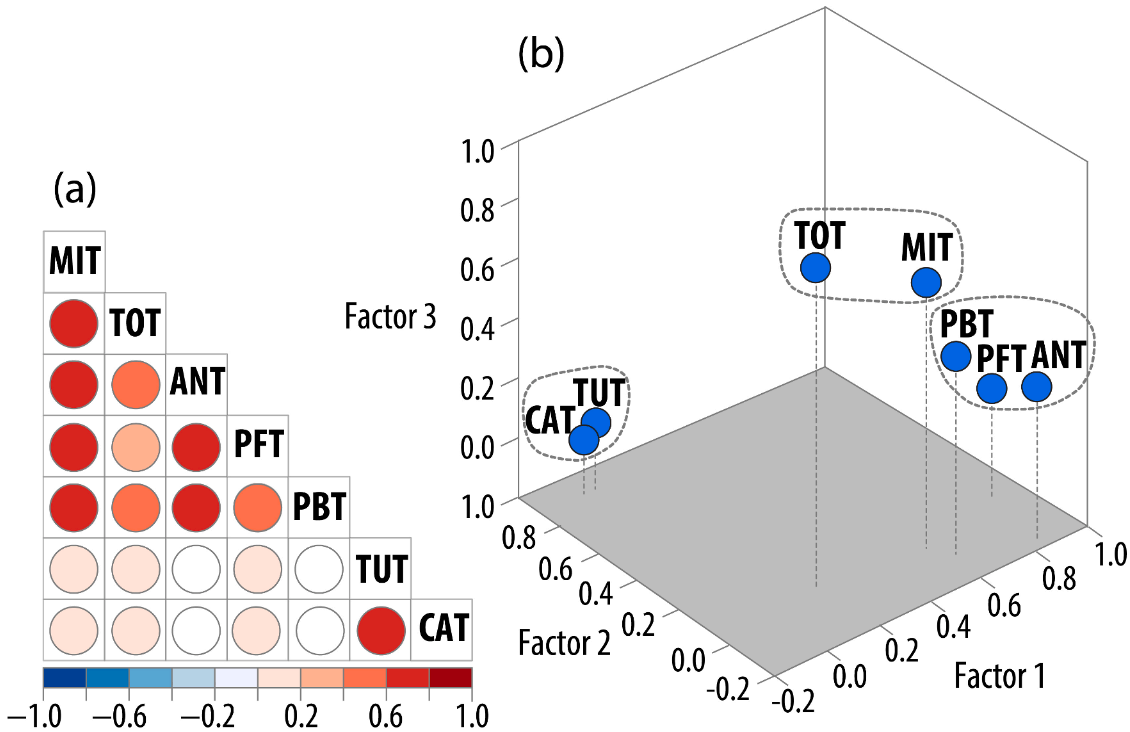

Fig. 3. Relationships between radial growth patterns during the 1900-2010 period between the chronologies from the seven sampling sites based on the analysis of (a) linear correlation (r values) and (b) principal components (PCA). Both analyses show two well-defined groups, one corresponding to the chronologies coming from the humid-mesic high elevation forests (MIT, TOT, ANT, PFT and PBT) and the other to the high elevation forests in drier sites (TUT and CAT) bordering the Patagonian steppe. Additionally, the PCA analysis differentiates chronologies of wet sites (TOT and MIT) from mesic sites (PBT, PFT and ANT). In (a), correlation coefficient $r \geq 0.2$ are statistically significant at 0.01 confidence level.

response is seasonally more extended starting in October, reaching the strongest relationships in December and January and prolonging until March. All months between November and March show significant correlations with the regional temperature (Fig. 5). On the contrary, tree growth in the TUT and CAT sites is negatively related to temperature during most of the year with significant relationships in December and March of the previous growing season and in August during winter. The relationships between growth and precipitation were evaluated for the 1979-2015 period common between the ERA5 precipitation record and the chronologies. No consistent patterns of correlation between precipitation and growth were observed, even at the TUT and CAT sites where growth-temperature relationships are inversed and possibly influenced by changes in precipitation.

Taking into account the relationships between climate and radial growth based on residual chronologies (Figs. 5a and 5b), seasonal (November to January) temperature variations were used to predict the radial growth at the humid MIT and TOT treelines since 1920 ($r = 0.61$, $n = 96$ years, Fig. 6). For the mesic sites, variations in late spring-summer temperature (November to March) were also significantly related to radial growth at the ANT, PFT and PBT treelines ($r = 0.65$, $n = 96$ years). On the contrary, temperatures from December during the prior growing season to October at the onset of the current growth cycle are inversely and weakly related to growth at the xeric high elevation forests ($r = -0.24$, $n = 96$ years, Fig. 6).

3.4. Variations in snow cover and tree growth at the treelines

The duration of snow cover, inferred as the number of days that continuously show near ground temperatures close to 0°C, decreases from the wettest to the driest sites. While at the TOT and MIT sites, located at the wetter end of the precipitation gradient, snow cover extended from June to early November 2020, at the mesic sites snow cover starts on average in July, a month later, and culminates a few days earlier than at the wet sites (Fig. 7a). Consistently, the temperature sensor at the dry TUT site remained exposed throughout the year suggesting no snow accumulation, or below to 50 cm, during the winter of 2020. Our temperature records at 50 cm elevation not only provide useful indicator for estimating differences in snow cover duration between wet and drier treelines, but also shown marked differences in snow duration relative to site exposure. Sites exposed to the north (i.e., on north-facing slopes) receive greater amounts of solar radiation, which accelerate snowmelt, and thus substantially reduce the period of snow cover. Indeed, for the mesic treelines located on opposite slopes of Río Eléctrico valley, snow cover on the ANT south-facing slope lasted about 40 days longer than on the PTF north-facing slope during the winter of 2020 (Fig. 7a). These exposure-induced differences in snow cover duration are remarkable given the lower elevation of ANT (988 m) relative to PTF (1092 m) sites.

The large differences in radial growth rates recorded between the wet, mesic and dry treeline environments in the Río de las Vueltas basin seem to be related to the duration of snow cover (Fig. 7b). In the forest ecotone with the Patagonian steppe, growth at the treelines during the last 100 years was about 1 mm/yr, which is more than double the growth recorded in the wet sites with only 0.40 mm/yr (Fig. 7b). At these wet sites, the snow load is higher and persists well into spring-early summer. Meanwhile, mean radial growth rates of 0.58 mm/yr were recorded at mesic sites with intermediate snow cover durations (Fig. 7b).

3.5. Future projections of radial growth

The CMIP5 temperature simulations most strongly related to instrumental records in southern Patagonia are shown in Table SM1. Although the mean of all CMIP5 models is significantly related with observed temperature, the relationships are stronger when the subset of models is reduced to those showing significant relationships ($p < 0.05$)

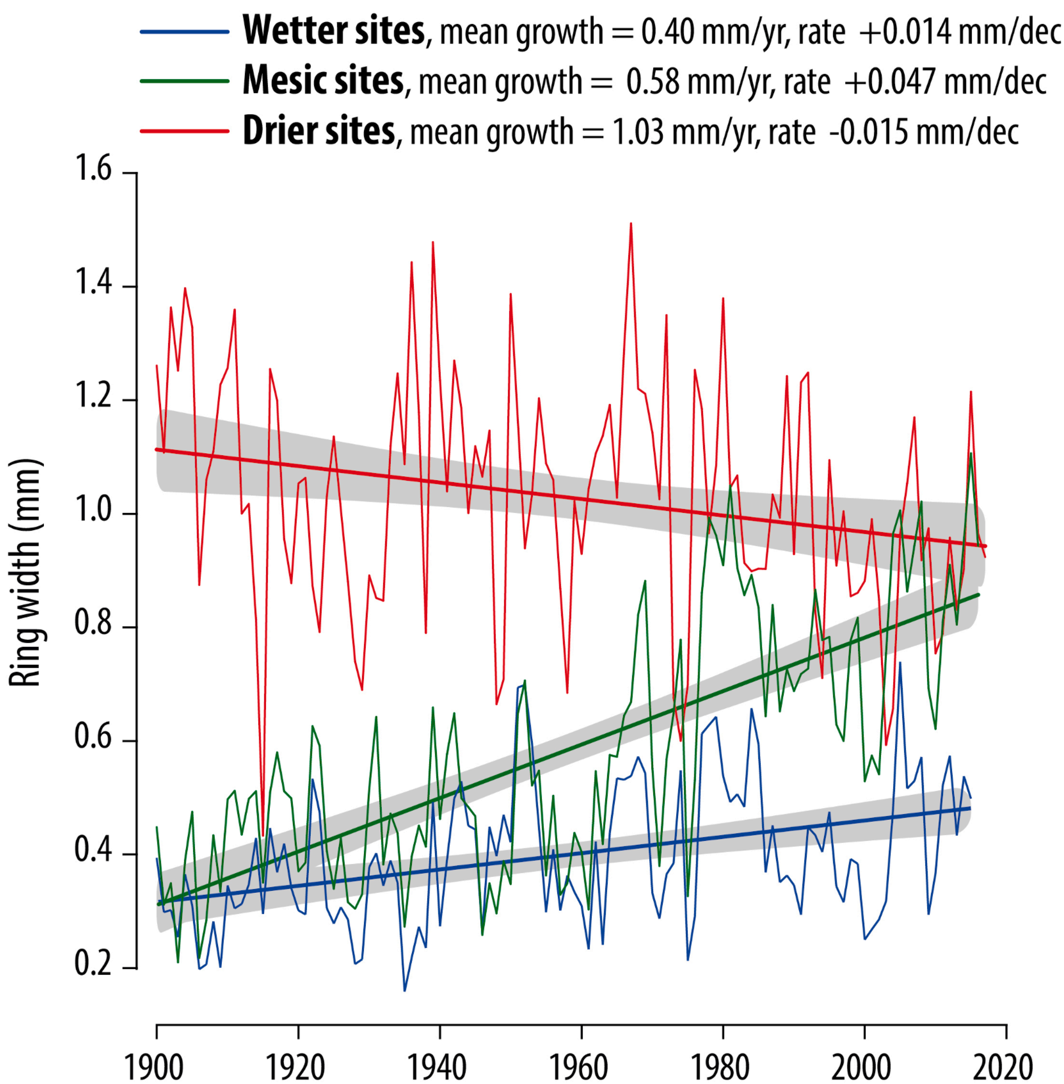

Fig. 4. Dominant trends in radial growth since the 1900s for high-elevation *N. pumilio* forests located in wet (blue), mesic (green) and xeric (red) sites in the Rio de las Vueltas watershed. For each environment, linear growth trends are shown with their regression confidence intervals (p <0.05). All trends are statistically significant. Mean growth and growth rate since 1900 (above) are also shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Characteristics of residual chronologies from *N. pumilio* along the precipitation gradient in the Río de las Vueltas basin. Sites are arranged from the humid Río Toro to the xeric Río Túnel valleys.

Valley	Code	Record period	No. of Trees	No. of Radii	Mean sensitivity	Standard Deviation	1st Order Autocorrel ation	EPS > 0.85(year)	Rbar
Río Toro	MIT	1850 - 2015	27	47	0,412	0,384	-0,024	1910	0,336
	TOT	1822 - 2016	26	51	0,472	0,447	-0,043	1880	0,447
Río Eléctrico	ANT	1879 - 2016	29	55	0,480	0,459	0,016	1904	0,379
	PFT	1880 - 2016	21	39	0,443	0,400	-0,053	1918	0,323
Río Túnel	PBT	1877 - 2017	27	46	0,400	0,361	-0,007	1940	0,234
	TUT	1841 - 2017	28	53	0,370	0,350	-0,031	1900	0,286
Canigó	CAT	1768 - 2010	49	83	0,412	0,373	-0,015	1870	0,305

with the instrumental temperature (Table SM1). The models most strongly correlated with the instrumental temperature records are also those showing the most consistent relationships with radial growth at the treelines (Table SM2, Supplementary Material). For example, the four temperature simulations most strongly related to tree growth at the humid treelines are also included in the six model simulations significantly related to the instrumental temperatures during November, December and January, the period of larger influence of temperature on *N. pumilio* growth at humid treelines (Fig. 5).

The regressions linking seasonal temperatures with *N. pumilio* radial growth in humid, mesic, and xeric environments over the period 1920-2015 (Fig. 6) were used to project tree growth during the 21st century. Positive RE and CE verification statistics indicate some ability of regional temperature variations to predict tree growth in the wet and mesic treelines, whereas negative RE and CE at dry sites are consistent with the poor relationship (r = -0.24) between seasonal temperature and tree growth in the dry treelines (Table 4). However, the comparatively better calibration-verification statistics for the recent period suggest that

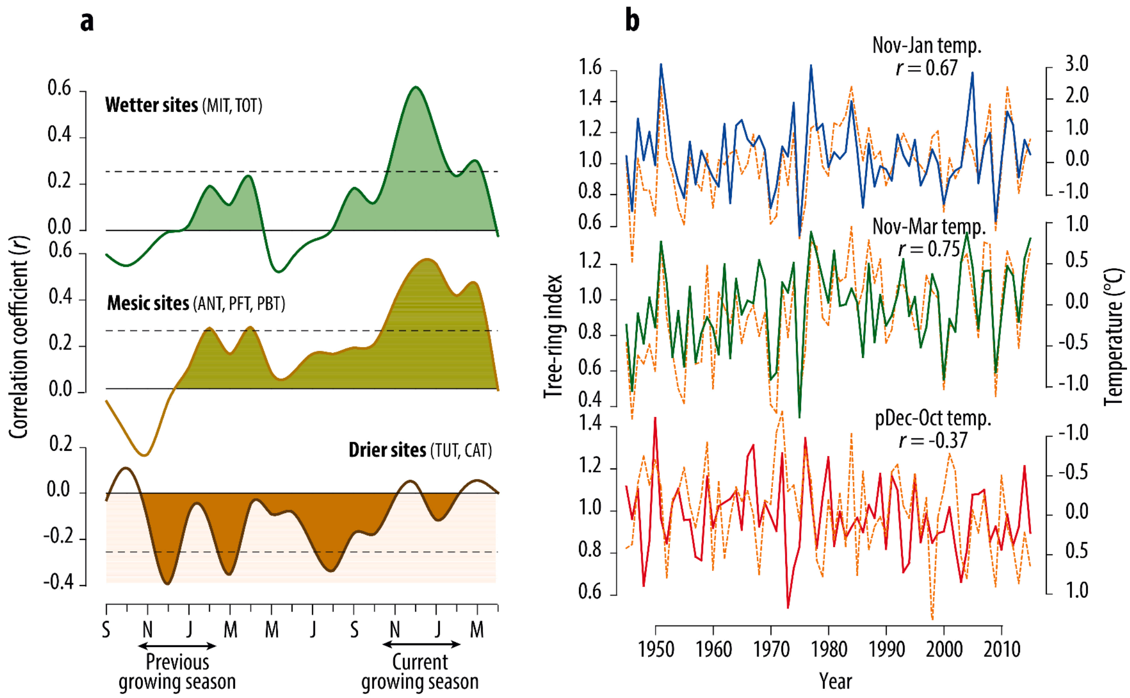

Fig. 5. (a) Temperature-radial growth correlation functions based on composite residual chronologies for wet, mesic, and xeric sites. (b) Comparison between temporal variations in temperature, grouped by seasons based on response functions, and radial growth in humid, mesic and xeric high elevation forests. In (a) and (b), the correlation coefficients greater than $r = 0.25$ are statistically significant at a confidence level of $p < 0.05$.

the negative influence of temperature on tree growth at dry treelines has been more pronounced during the warmer period beginning in the mid-1970s (Table 4). The temperature-simulated mean best related to instrumental temperature (Table SM1) were re-scaled to mean regional temperature to increase the consistency in tree-growth projections.

Fig. 8 shows the mean decadal variations for observed radial growth in wet, mesic, and xeric treelines, together with simulated tree growths over the historical 1850-2020 and projected 2021-2100 periods based on regressions using the CMIP5 temperature simulations for the RCP 4.5 and RCP 8.5 scenarios. The seasonal temperature record (late spring-early summer; NDJ), resulting from averaging the 12 simulations significantly related to regional temperature (Table SM1), was used as a predictor of radial growth for the humid treelines during the historical and projected periods. Given an observed mean radial growth for the last decade of the 20th century (1990) of 0.47 mm/yr, the RCP4.5- and RCP8.5-based simulations predict increases in tree growth of 32% and 74% for the last decade of the 21st century, respectively. These increases in tree growth would be associated with increases in mean NDJ temperature of 1.3°C and 2.9°C during the 21st century for the RCP4.5 and RCP8.5 scenarios, respectively. For an observed increase of 0.8°C between the years 1920 and 2010, the increase in mean growth was about 0.2 mm, equivalent to a ring-width increase of 0.25 mm per 1°C. This observed increase in tree growth is consistent with simulated decadal increases of 0.15 mm and 0.35 mm in response to seasonal temperature increases (NDJ) of 1.3° and 2.9°C through the end of the 21st century under the RCP4.5 and RCP8.5 scenarios, respectively.

A similar analysis for the mesic treeline sites (ANT, PFT, PBT) suggests simulated-growth increases greater than those projected for the humid sites (Fig. 8). Considering that the observed mean growth for the 1990's was 0.73 mm/year, the growths predicted for the end of the 21st century (2090's) represent increases of 42% and close to 100% under the RCP4.5 and RCP8.5 scenarios, respectively. These simulated growth increases for the late 21st century are associated with seasonal NDJFM temperature increases of 1.4°C and 3.1°C, respectively. The observed mean growth increase of 0.37 mm between the 1920's and 2010's was associated with a NDJFM temperature increase of 0.8°C, equivalent to 0.46 mm per 1°C. This increase in growth during the 20th century is somewhat higher than those simulated for the 21st century of 0.31 mm and 0.76 mm associated with increases in the NDJFM temperature of 1.4 ° and 3.1°C based on RCP4.5 and RCP8.5 scenarios, respectively.

Contrary to humid and mesic treelines, the simulated radial growth in the xeric sites would decrease throughout the 21st century (Fig. 8). This simulation is, to some extent, consistent with observed data, which shows a growth decline since the mid-20th century. Based on CMIP5-simulated DJFMAMJJASO temperatures, radial growth would decrease from 0.96mm/yr at the beginning of the 21st century to 0.82 mm/yr and 0.63 mm/yr in the 2090's according to RCP4.5 and RCP 8.5 scenarios, respectively. These ring-width reductions of 15% and 35% would be associated with increases in seasonal (DJFMAMJJASO) temperatures of 1.9°C and 2.8°C during the 21st century according to RCP4.5 and RCP8.5 scenarios. Comparatively, the mean radial growth decreased from 1.03 mm/year to 0.93 mm/year (0.1 mm in 80 years) from the 1930's to the 2010's was concurrent with a seasonal temperature increase of approximately 0.5°C. It is important to note that the largest reduction in simulated growth occurs during the last four to five decades of the 21st century (Fig. 8), however, the long-term growth projections are associated with large uncertainties due to the poor skill of the regression models (Table 4).

4. Discussion

Three dominant patterns of radial growth in the upper treeline have been identified across the Río de las Vueltas watershed over the past 100 years. The first pattern represents the MIT and TOT sites in the most humid sector of the basin. With some tree growth similarities with this wet pattern, the ANT, PFT and PBT sites, located in the intermediate mesic sectors of the basin, integrate the second pattern (Fig. 4). At these sites, precipitation is comparatively less than in the northwestern, humid sector of the basin. Finally, the TUT and CAT sites compose the third pattern that represents the treelines located in the vicinity of the ecotone with the Patagonian steppe with less precipitation and greater continentality than the mesic and humid sites of the Río de las Vueltas

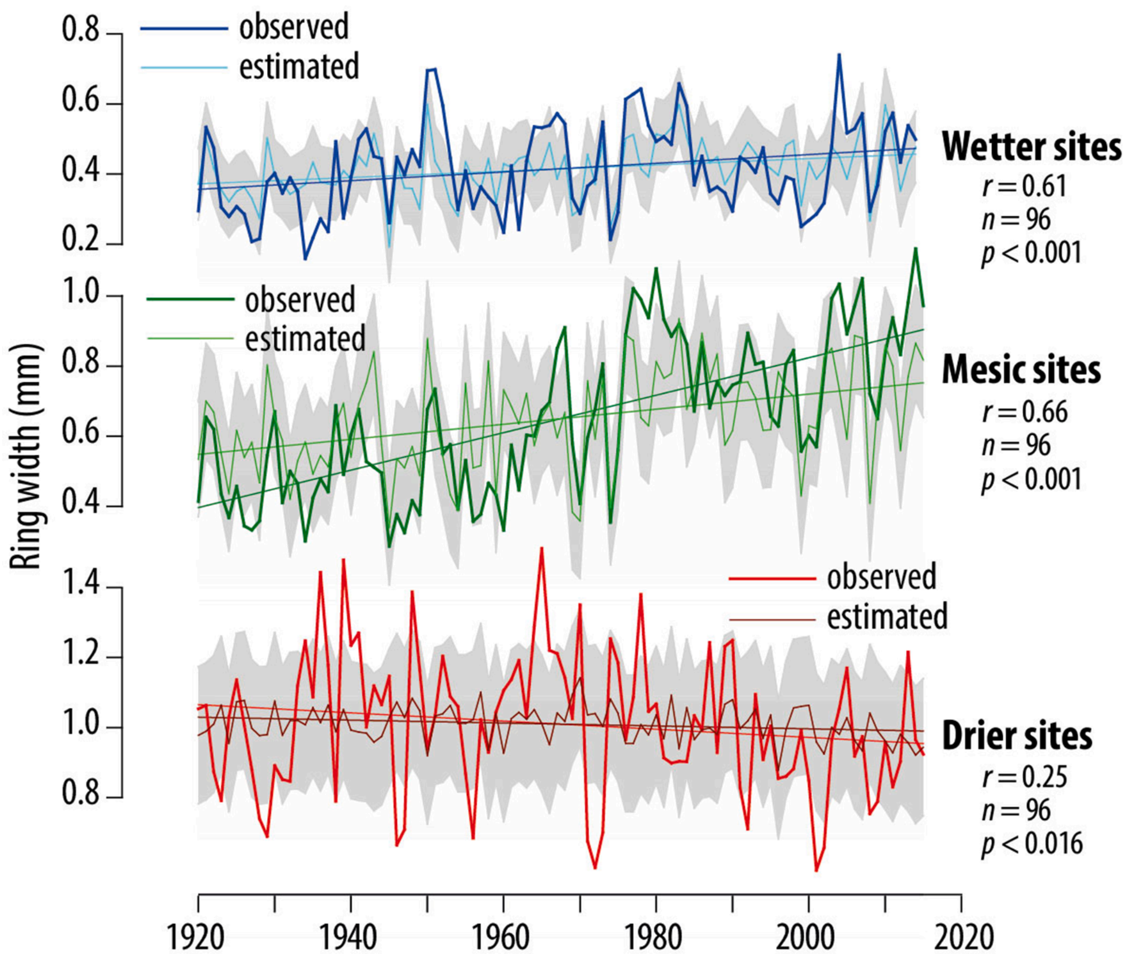

Fig. 6. Comparison between the temporal variations of the radial growth observed in humid, mesic and xeric high elevation forests and estimated growth from the temperature of November to January, November to March and December of the year prior to October of the current year, respectively. For the common period 1920-2015, the correlation coefficients (r) between the observed and estimated values and the corresponding probability levels are indicated. The gray area corresponds to the standard error of the estimate that is wider for the dry forest where the predictive capacity of temperature is substantially lower. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

basin (Villalba et al., 2003).

Given the permanent exposure of high-elevation Patagonian forests to adverse growth conditions including low temperatures, heavy snow cover in winter, high solar radiation during summer and strong winds throughout the year, the growth of the trees in the upper limit of the forest are particularly sensitive to environmental fluctuations. Traditionally, variations in tree growth in the upper treeline have been directly associated with changes in temperature during the growth period (Körner and Paulsen 2004, Babst et al., 2019). Most *N. pumilio* tree-ring records at high elevations in north of Patagonia forests show direct relationships with November-December-January temperatures and inverse with precipitation during the same period (Villalba et al., 1997, Lara et al., 2005). However, in some extremely dry forests in northern Patagonia (Lara et al., 2001, Daniels and Veblen 2004) or in the Patagonian forest-steppe ecotone east of the Andes (Rodriguez-Catón et al., 2016), the radial growth of *N. pumilio* is positively influenced by variations in summer precipitation. Although these studies have been conducted on erect trees (except in Cerro Bayo, Argentina; Daniels and Veblen, 2004), they show that the growth of *N. pumilio* can also be constrained by reduced soil moisture content in dry summers. Radial growth in humid and mesic treelines in the Río de las Vueltas watershed shows a strong and direct dependence on late spring-early summer temperatures, however, growth in dry sites is negatively associated, although weaker, with the temperature throughout the year (Figs. 5 and 6). In these dry high-altitude environments, high temperatures in combination with persistent winds are likely to increase evapotranspiration and reduce the water available for growth. However, local precipitation records show no significant relationships with tree growth, adding further complexity to the relationships between climate and tree growth in dry treelines.

Additional factors should be invoked to explain the weaker relationships between climatic and growth variations in dry treelines compared to wet and mesic treelines. Numerous recent studies question the temporal stability of the relationships between climatic variations and tree growth, a process known as divergence (D'Arrigo et al., 2008) or non-stationarity (Wilmking et al., 2020). It is possible that prior to the recent warm period that began in the mid-1970's, growth in dry sites was alternatively modulated by temperature during cool-wet springs and summers, but by precipitation during dry-warm growing seasons. This alternating climatic pattern limits the establishment of robust relationships between a specific climatic variable (i.e., temperature or precipitation) and radial growth (Allen et al., 2018), limiting the establishment of a clear relationship between climate and radial growth. On the other hand, the *N. pumilio* forests in the ecotone with the steppe have been the most severely affected by caterpillar (*Ormiscoides sp.*) defoliations inducing strong reductions in ring widths (Paritsis and Veblen 2011). In particular, the extreme low growth in the TUT site during the year 2003 coincides with a documented outbreak of *Ormiscoides* in the region (Morales and Villalba 2009). The lack of stability in the climate-growth relationships combined with frequent caterpillar

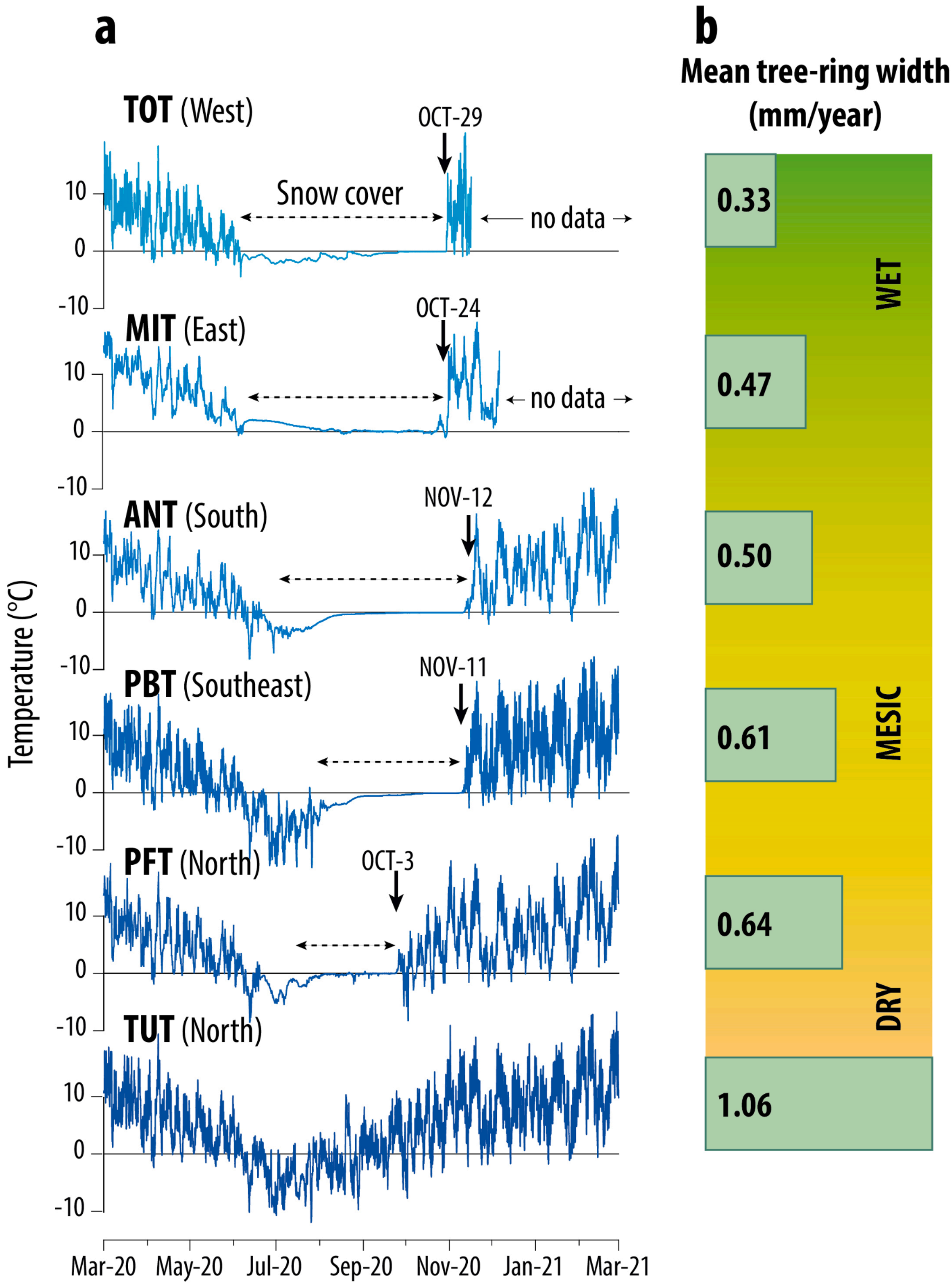

Fig. 7. Variations in temperature close to ground level (50 cm) at six of the sampling sites during the period March 2020-March 2021 and their relationships with radial growth. (a) The lack of a well-pronounced cycle in daily temperature records is considered an indicator of snow cover. For each of the sites, arranged from humid to dry environments in the treelines across the Río de las Vueltas basin, the approximate duration of the snow cover and the date with snow heights < 50 cm are indicated (vertical arrows). The sites are identified by their codes and the dominant aspect is indicated in parentheses. In the driest site TUT, there is no attenuation in the daily temperature cycle with temperature stabilization close to 0°C, suggesting the lack of snow coverage in that place throughout the year. (b) The variations in the mean radial growth per sites during the interval 1900–2010 show a persistent increase trend from the most humid environments (thinner rings) to the driest (widest rings) at treelines in the Rio de las Vueltas basin.

Table 4
Calibration and verification statistics for regressive models predicting tree-ring width from seasonal temperature. For description of statistical tests and the required values for successful model verification are stated in the methodology.

Tree growth		Calibration (1920–1969)	Verification (1970–2014)	Calibration (1965–2014)	Verification (1920–1964)	Final model (1920–2014)
Humid treelines against NDJ temperature	r	0.51	0.66	0.64	0.5	0.61
	r^2	0.27	0.44	0.41	0.25	0.37
	R^2_{adj}	0.25	0.42	0.4	0.23	0.36
	F	17.34	33.3	32.83	14.69	54.12
	P	<0.001	<0.001	<0.001	<0.001	<0.001
	RE		0.396		0.386	
	CE		0.403		0.391	
Mesic treelines against NDJFM temperature	r	0.43	0.59	0.67	0.51	0.66
	r^2	0.19	0.34	0.45	0.26	0.44
	R^2_{adj}	0.17	0.33	0.44	0.24	0.43
	F	11.27	22.41	40.15	15.09	73.46
	P	0.002	<0.001	<0.001	<0.001	<0.001
	RE		0.337		0.43	
	CE		0.381		0.47	
Dry treelines against DJFMAMJJASO temperature	r	0.13	0.32	0.3	0.15	0.25
	r^2	0.02	0.1	0.08	0.02	0.06
	R^2_{adj}	0	0.08	0.07	0	0.05
	F	0.75	5.09	4.97	0.92	6.05
	P	0.389	0.028	0.03	0.341	0.016
	RE		-0.55		-0.566	
	CE		-0.544		-0.562	

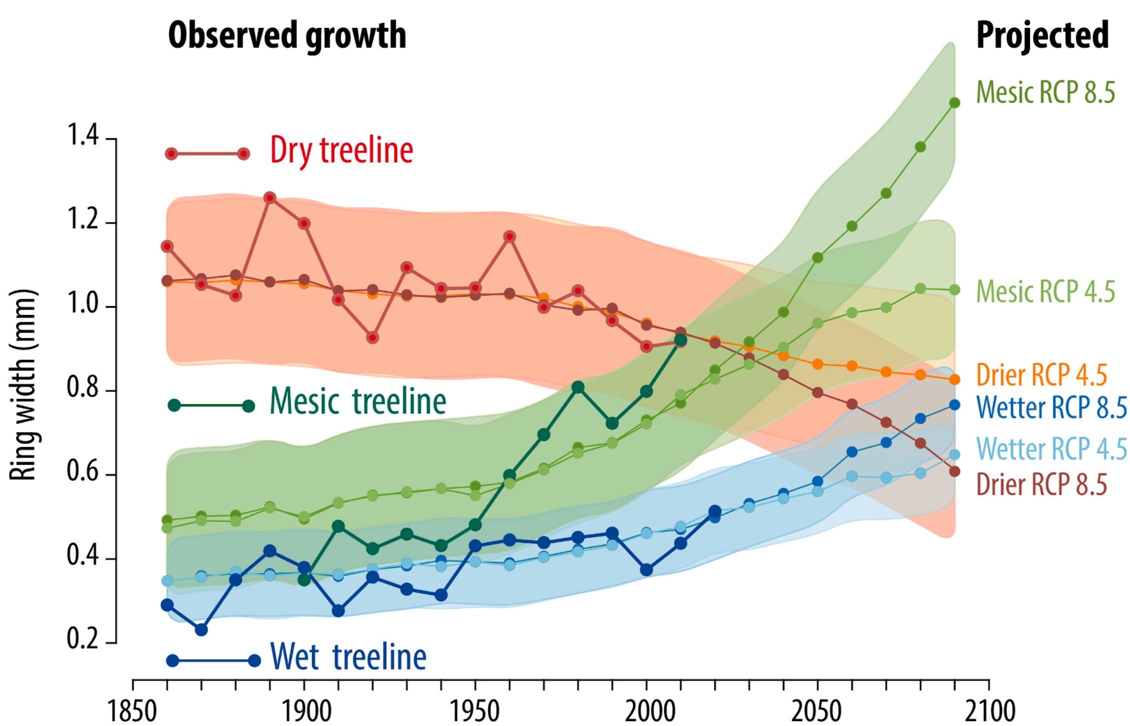

Fig. 8. Decadal mean radial growth observed (1850-2015, thick line) and simulated (thinner line) for the historical (1850-2020) and projected (2020-2100) periods based on CMIP5 models for treelines in humid (Wetter RCP 4.5 and Wetter RCP 8.5), mesic (Mesic RCP 4.5 and Mesic RCP8.5) and xeric (Drier RCP 4.5 and Drier RCP 8.5) environments. Simulated tree-growth is shown with the Standard error prediction bands.

outbreaks could have introduced important variations in the growth of the high-elevation treelines in the dry sector of the Río de las Vueltas basin, and thus limiting the determination of clear relationships between climate and tree growth.

An interesting aspect to highlight is the marked seasonality in tree growth responses to temperature (Fig. 5a). At the humid treelines, positive and significant relationships with temperature occur during three months (November to January inclusive). On the contrary, temperature from the previous summer to the current spring appears as an important indirect regulator of growth in dry sites (Fig. 5a). These observations are consistent with global studies reporting that responses to water availability in dry sites integrate climate over several months during previous and current growth seasons, rather than centered on a few months as observed for temperature (Babst et al., 2019). These differences in the seasonality of *N. pumilio* growth responses to climate between wet and dry treelines in the Rio de las Vueltas valley suggest variations in temperature influence on tree growth across different treeline environments. The geographic arrangement of the southern Andes forests across steep environmental gradients facilitated to characterize the influence that snow cover and its persistence has on tree growth in the treelines. Our observations indicate that abundant precipitation and prolonged snow cover in wet locations significantly shorten the length of the growing season, and consequently the radial growth is comparatively lower relative to mesic and dry sites (Fig. 7). In turn, consistent with the shorter duration of snow cover in north-northwest facing slopes, the radial growth is larger on these orientations (Fig. 7). Tree growth at both mesic sites in the Río Eléctrico valley shows a clear positive trend over the last century (Fig. 2), however, the mean radial growth at the northern exposure PFT site was 0.64 mm/yr, comparatively higher than at the southern exposure ANT site where the mean rate was 0.50 mm/yr since 1900. Comparing our indirect records of snow cover duration with the rates of growth at the treelines, we noted a relationship between the onset of the snow-free period in the forests, associated with the beginning of growing season, and tree-ring widths. At the humid sites, or those located on south-facing slopes, radial growth is comparatively lower than in dry sites and/or located on north-facing slopes (Fig. 7). Previous work has suggested a strong relationship between interannual variations in snow cover and radial growth of *N. pumilio* (Villalba et al., 1997). In the humid sites of northern Patagonia, the radial growth of *N. pumilio* is favored by the reduced duration of the snow accumulation in winter previous to the growing season, whereas abundant snowfall years were detrimental to growth (Villalba et al., 1997). While we acknowledge the short period of snow cover observations, this is the first time that relationships between *N. pumilio* growth and the duration of snow cover at high altitudes have been reported.

Long-term trends in growth over the last century differ among the various treeline environments in the Río de las Vueltas basin. While humid and mesic sites show a sustained increase in growth during the 20th and early 21st centuries, growth in dry sites shows a slight negative trend, accentuated since the mid-1970s (Fig. 3). Long-term growth trends are largely modulated by rising temperatures since the early 20th century (Fig. 6), however, the relationships between temperature variations and tree growth appear not to be straightforward and linear. Although both wet and mesic sites show positive growth trends, their increases since the early 20th century are statistically different (0.014 and 0.047 mm/decade in wet and mesic, respectively), suggesting interactions between temperature increases, snow load and other site forcings (exposure) on radial growth. Regional temperature during the growing season (November to March), strongly related to radial increments of growth at wet and mesic sites, increased 0.56°C between the periods 1920–1977 and 1978-2019. Over these same periods, the mean growth in humid sites went from 0.39 mm/year to 0.45 mm/year, representing a mean increase of 14% between periods. On the other hand, radial growth in mesic sites increased from 0.49 mm/year to 0.80 mm/year, equivalent to a 64% increment in radial growth between periods. On the contrary, in dry sites there was a decrease of 8% (1.05 mm/year in 1920–1977 to 0.96 mm/year from 1978 to present) between the same intervals. The observed changes suggest the occurrence of non-linear relationships between temperature and *N. pumilio* growth. With a regional temperature increase of 0.56°C, the mean growth increases were significantly higher in mesic than in humid sites and with opposite trends in dry treelines (Figs. 2 and 3).

While observed and temperature-estimated *N. pumilio* growth trends are relatively similar in humid environments, they are comparatively different in mesic environments, with observed increases since the mid-1970s higher than those estimated by temperature (Fig. 6). The growth rates in mesic sites during the last decades have reached similar levels to those observed in ecotonal treelines with a longer growing season than in mesic and wet sites (Fig. 7). It is possible that the warmer temperatures of recent decades, combined with a still abundant water content in the soils, are responsible for the large growth rates recorded since the beginning of the 21st century at mesic treelines. Conditions similar to those found today in mesic sites may have been common in dry treelines when cooler temperatures than today prevailed during the first half of the 20th century. Since the mid-1970's, the high evapotranspiration induced by warmer summer temperatures reduces soil moisture below a critical threshold that contributes to the negative, albeit very gradual trend in growth at dry treelines. If these trends continue during the 21st century, it is very likely that the mean annual growth rates in mesic sites will exceed that observed at dry ecotonal treelines. On the other hand, present snow cover in humid areas is still high and would remain as the dominant factor influencing the rate of growth in humid treelines at least during next decades. Although moist treelines have been favored by the warmer spring-summer temperatures during recent decades, associated with a lengthening of the growing season, the prolonged duration of snow cover on stunted trees has prevented them from achieving growth rates similar to those currently observed in mesic treelines. Growth rates during the cold interval prior to mid-1970's was comparatively similar between humid and mesic treelines (0.39 and 0.49 mm/year, respectively); however, the radial growth rate at mesic sites under present warmer conditions almost double that in the humid treelines (0.80 and 0.45 mm/year, respectively). Our observations suggest strong interactions between temperature increases and snow load in regulating the growth at treelines in the southern Patagonian Andes.

In a context of increasing regional temperatures, it is of interest to estimate changes in future growth rates in different treeline environments. Taking advantage of CMIP5 simulations that provide temperature changes from the mid-19th century to the end of the 21st century, we use those simulations that best reproduce local temperature variations during the instrumental period 1920-2015 to infer potential variations in radial growth at the treelines over the next decades. In using this methodological approach, it is important to highlight the constraints and caveats associated with the use of statistical linear regression techniques to predict future *N. pumilio* growth rates in the region. Although the regressive models are comparatively robust to estimate the radial growth during the instrumental period in humid and mesic treelines (Fig. 6 and Table 4), extrapolations outside the observed 1920–2015 temperature range could be risky and should be taken with great caution. Our observations show that the regional 0.56°C temperature increase in the 1970's induced different changes in growth rates between humid and mesic forests most likely mediated by differences in snow cover duration. It is imperative to have physiologically based dynamic models to predict changes in radial growth as a function of climate fluctuations in the southern Andes.

Given the aforementioned caveats in regression models as a tool for predicting growth rates through the 21st century, we only consider decadal rather than annual variations in tree growth paying attention to the growth trends over the next few decades when the statistics models, by including prediction ranges similar to those employed in the calibration period, show better predictive ability. At the treeline environments in Río de las Vueltas basin, the growth trends observed over the past 150 years will persist, but intensify in magnitude during the 21st century, particularly when considering RCP8.5 temperature projections (Fig. 8). For the next decades, growth in mesic treelines will exceed that of dry treelines in the 2030 and 2050 decades based on RCP8.5 and RCP4.5 simulations, respectively. On the contrary, the simulated mean decadal growths in the humid treelines will remain lower than in mesic upper forests throughout the 21st century, and could be equated with that of the dry forests approximately in the period 2080-2090 under emission conditions associated with the RCP8.5 scenario. Despite the projected growth reduction in the dry ecotonal treelines during the 21st century, the radial growth of the humid sites would remain lower than in the dry forests under the emission conditions established in the RCP4.5 scenario (Fig. 8). Considering these projections, however, we cannot rule out that trees in humid treelines surpass, due to the warming during the 21st century, the threshold imposed by the current snow cover duration, accelerating the radial growth as it was observed in the mesic treelines in response to an approximately 0.5°C increase in the mid-1970s. Similarly, simulated temperature increases during the 21st century for the Patagonian Andes, particularly under the conditions of the RCP8.5 scenario, could potentially induce a water deficit at mesic treelines, stabilizing or even reversing the persistent positive trend observed in radial growth over the last 100 years. It is important to mention that given the strong interactions between temperature, snow cover and tree growth recorded in the past 100 years, simulated changes based on statistical models for the second part of the 21st century should be viewed with caution.

5. Conclusions

The recorded regional temperature increase during the 20th century has induced changes in *N. pumilio* growth rates that differs between treelines along the precipitation gradient in the Río de las Vueltas basin, southern Patagonian Andes, Argentina. There are marked differences in the seasonality in which temperature most strongly influences radial growth at wet, mesic and dry treelines. Overall, the recorded regional warming has enhanced the growth rates at wet and mesic sites, but affected negatively the growth at dry treelines. However, our findings suggest that these climate-tree growth relationships are not direct and linear, but rather strongly regulated by the interactions between temperature increase and variations in snow cover duration related to precipitation amount and site exposure. The differences in growth rates under recent warming between humid and mesic treelines have largely been influenced by differences in amounts of winter snowfall and its persistence into the growing season. On the other hand, increased temperatures and a large summer water deficit have resulted in declining radial growth rates at dry ecotonal treelines. However, the absence of significant relationships with precipitation also proves the complexity and questions the temporal stability of climate-growth relationships at dry treelines within our study area.

The strong positive relationship between temperature and *N. pumilio* radial growth in the humid and mesic treelines during the 20th century, in comparison with the weaker relationships recorded with precipitation, suggest the dominant role that temperature increases during the next decades will have on the *N. pumilio* growth in these environments. The linear regression models indicate sustained decadal increases of current radial growth rates at humid and mesic sites and a decrease in dry sites towards the end of the 21st century under temperature increases in both RCP4.5 and RCP8.5 scenarios. Although these statistical growth models at humid and mesic sites showed adequate predictive skills with similar rates of variability during the 21st century to those recorded during the calibration period, the nonlinear relationships between climate and tree growth emphasize the need of dynamic physiologically-based models for developing solid projections of tree growth variations from deciduous species in the Southern Hemisphere.

The interactions between warming, snow cover, and tree growth observed over the last 100 years suggest the need to include snow parameters in models used to predict tree growth at treelines. According to CMIP5 precipitation simulations (IPCC, 2013), our study region is located in the transition between significant reductions in northern Patagonia and gradual increases in precipitation at higher latitudes, with no clear trends for precipitation evolution during the 21st century in the Rio de las Vueltas basin. Consequently, the unreliability of current precipitation projections in the region also adds uncertainties about the potential role of snow cover in the evolution of tree growth at high-altitude forests in the Southern Patagonian Andes during the 21st century.

Author contributions

R.V. and R.B. designed the study. R.B. and A.S. developed the tree ring chronologies. RV secured funding. All authors performed the data analysis and drafted the manuscript.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2022.109083.

References

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6 (8), 1–55. https://doi.org/10.1890/ES15-00203.1.

Allen, K.J., Villalba, R., Lavergne, A., Palmer, J.G., Cook, E.C., Fenwick, P., et al., 2018. A comparison of some simple methods used to detect unstable temperature responses in tree-ring chronologies. Dendrochronologia 48, 52–73. https://doi.org/10.1016/j.dendro.2018.02.002.

Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M.P., Frank, D.C., 2019. Twentieth century redistribution in climatic drivers of global tree growth. Sci. adv. 5 (1), eaat4313. https://doi.org/10.1126/sciadv.aat4313.

Blasing, T.J., Solomon, A.S., Duvick, D.N., 1984. Response functions revisited. Tree-ring Bull 44, 1–17.

Briffa, K.R., 1995. Interpreting high-resolution proxy climate data: the example of dendroclimatology. In: von Storch, H., Navarra, A. (Eds.), Analysis of Climate Variability, Applications of Statistical Techniques. Springer, Berlin, Heidelberg, New York, pp. 77–94.

Pabón-Caicedo, J.D., Arias, P.A., Carril, A.F., Espinoza, J.C., Borrel, L.F., Goubanova, K., et al., 2020. Observed and projected hydroclimate changes in the Andes. Front. Earth Sci. 8, 61. https://doi.org/10.3389/feart.2020.00061.

Chapin III, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J., Laundre, J.A, 1995. Responses of arctic tundra to experimental and observed changes in climate. Ecology 76 (3), 694–711. https://doi.org/10.2307/1939337.

Cook, E.R., 1985. Doctoral dissertation [. University of Arizona, School of Renewable Natural Resources, Tucson, Arizona (ARI).

Cook, E.R., Briffa, K.R., Jones, P.D., 1994. Spatial regression methods in dendroclimatology: a review and comparison of two techniques. Int. J. Climatol. 14 (4), 379–402. https://doi.org/10.1002/joc.3370140404.

Cook, E.R., Holmes, R.L., 1986. Users manual for program ARSTAN. In: Holmes, R.L., Adams, R.K., Fritts, H.C. (Eds.), Tree-Ring Chronologies of Western North America: California, eastern Oregon and the northern Great Basin Holmes. University of Arizona, Tucson, pp. 50–65.

Cooley, W.W., Lohnes, P.R., 1971. Multivariate Data Analysis. John Wiley & Sons, Inc, New York.

Cybis, 2020. CooRecorder basics. http://www.cybis.se/forfun/dendro/helpcoorecorder7/index.htm [Accessed July 18, 2020].

D'Arrigo, R., Wilson, R., Liepert, B., Cherubini, P., 2008. On the 'divergence problem' in northern forests: a review of the tree-ring evidence and possible causes. Glob. Planet. Change. 60 (3-4), 289–305. https://doi.org/10.1016/j.gloplacha.2007.03.004.

Daniels, L.D., Veblen, T.T., 2004. Spatio-temporal influences of climate on altitudinal treeline in northern Patagonia. Ecology 85, 1284–1296. https://doi.org/10.1890/03-0092.

Donoso, C, 1993. Bosques templados de Chile y Argentina. Editorial Universitaria, Santiago Chile, p. 484.

Esper, J., Krusic, P.J., Ljungqvist, F.C., Luterbacher, J., Carrer, M., Cook, E., et al., 2016. Ranking of tree-ring based temperature reconstructions of the past millennium. Quat. Sci. Rev. 145, 134–151. https://doi.org/10.1016/j.quascirev.2016.05.009.

Falaschi, D., Lenzano, M.G., Villalba, R., Bolch, T., Rivera, A., Lo Vecchio, A., 2019. Six decades (1958–2018) of geodetic glacier mass balance in Monte san Lorenzo.

Patagonian Andes. Front. Earth Sci. 7, 326. https://doi.org/10.3389/feart.2019.00326.
Fajardo, A., McIntire, E.J., 2012. Reversal of multicentury tree growth improvements and loss of synchrony at mountain tree lines point to changes in key drivers. J. Ecol. 100 (3), 782–794. https://doi.org/10.1111/j.1365-2745.2012.01955.x.
Fritts, H., 1976. Tree Rings and Climate. Academic Press, London.
Galván, J.D., Camarero, J.J., Gutiérrez, E., 2014. Seeing the trees for the forest: drivers of individual growth responses to climate in *Pinus unicata* mountain forests. J. Ecol. 102 (5), 1244–1257. https://doi.org/10.1111/1365-2745.12268.
Garreaud, R.D., Vuille, M., Compagnucci, R., Marengo, J., 2009. Present-day South American climate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 281, 180–195. https://doi.org/10.1016/j.palaeo.2007.10.032.
Garreaud, R.D., Lopez, P., Minvielle, M., Rojas, M., 2013. Large-scale control on the Patagonian climate. J. Clim. 26, 215–230. https://doi.org/10.1175/JCLI-D-12-00001.1.
Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., et al., 2020. The ERA5 global reanalysis. Q. J. R. Meteorol. Soc. 146 (730), 1999–2049. https://doi.org/10.1002/qj.3803.
Holmes, R., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull 43, 69–75.
IPCC, 2013. Climate CHANGe 2013: the physical science basis. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, p. 1535. https://doi.org/10.1017/CB09781107415324.
IPCC, 2021. Climate change 2021: the physical science basis. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R., Zhou, B. (Eds.), Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press. In press.
Jacoby, G.C., D'Arrigo, R, 1989. Reconstructed Northern Hemisphere annual temperature since 1671 based on high-latitude tree-ring data from North America. Clim. Change 14 (1), 39–59. https://doi.org/10.1007/BF00140174.
KNMI Climate Change Atlas/WMO. (2020). https://climexp.knmi.nl/plot_atlas_form.py?id=someone@somewhere [Accessed May 10, 2021).
Körner, C., 2007. The use of 'altitude' in ecological research. Trends Ecol. Evol. 22 (11), 569–574. https://doi.org/10.1016/j.tree.2007.09.006.
Körner, C., Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. J. Biogeogr. 31 (5), 713–732. https://doi.org/10.1111/j.1365-2699.2003.01043.x.
LaMarche Jr., V.C., 1974. Paleoclimatic Inferences from Long Tree-Ring Records: intersite comparison shows climatic anomalies that may be linked to features of the general circulation. Science 183 (4129), 1043–1048. https://doi.org/10.1126/science.183.4129.1043.
Lara, A., Aravena, J.C., Villalba, R., Wolodarsky-Franke, A., Luckman, B., Wilson, R, 2001. Dendroclimatology of high-elevation Nothofagus pumilio forests at their northern distribution limit in the central Andes of Chile. Can. J. For. Res. 31 (6), 925–936. https://doi.org/10.1139/x00-208.
Lara, A., Villalba, R., Wolodarsky-Franke, A., Aravena, J.C., Luckman, B.H., Cuq, E., 2005. Spatial and temporal variation in *Nothofagus pumilio* growth at tree line along its latitudinal range (35°40''–55° S) in the Chilean Andes. J. Biogeogr. 32 (5), 879–893. https://doi.org/10.1111/j.1365-2699.2005.01191.x.
Marshall, G.J., 2003. Trends in the Southern annular mode from observations and reanalysis. J. Clim. 16, 4134–4143, 10.1175/1520-0442(2003)016%3C4134:TITSAM%3E2.0.CO;2.
Masiokas, M.H., Villalba, R., Luckman, B.H., Lascano, M.E., Delgado, S., Stepanek, P., 2008. 20th-century glacier recession and regional hydroclimatic changes in northwestern Patagonia. Glob. Planet. Change. 60 (1-2), 85–100. https://doi.org/10.1016/j.gloplacha.2006.07.031.
McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., et al., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol 178 (4), 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x.
McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., et al., 2020. Pervasive shifts in forest dynamics in a changing world. Science 368, 6494. https://doi.org/10.1126/science.aaz9463.
Morales, M.S., Villalba, R., 2009. Anillos de árboles como evidencias de ataques de insectos defoliadores en la Patagonia. Bol. Soc. Ent. Argentina 20, 13–14.
Paritsis, J., Veblen, T.T., 2011. Dendroecological analysis of defoliator outbreaks on *Nothofagus pumilio* and their relation to climate variability in the Patagonian Andes. Glob. Chang. Biol. 17, 239–253. https://doi.org/10.1111/j.1365-2486.2010.02255.x.
Rodríguez-Catón, M., Villalba, R., Morales, M., Srur, A.M., 2016. Influence of droughts on *Nothofagus pumilio* forest decline across northern Patagonia. Argentina. Ecosphere 7 (7), e01390. https://doi.org/10.1002/ecs2.1390.
Rodríguez-Catón, M., Villalba, R., Srur, A., Williams, A.P., 2019. Radial growth patterns associated with tree mortality in *Nothofagus pumilio* forest. Forests 10 (6), 489. https://doi.org/10.3390/f10060489.
Schulman, E., 1956. Dendroclimatic Changes in Semiarid America. University of Arizona Press, Tucson.
Srur, A.M., Villalba, R., Rodríguez-Catón, M., Amoroso, M.M., Marcotti, E., 2018. Climate and *Nothofagus pumilio* Establishment at Upper Treelines in the Patagonian Andes. Front. Earth Sci. 6, 57. https://doi.org/10.3389/feart.2018.00057.
Srur, A.M., Amoroso, M.M., Mundo, I., Morales, M.S., Rodriguez-Catón, M., Aschero, V., et al., 2020. Forest dynamics in the Argentinean Patagonian Andes: lessons learned from dendroecology. In: Pompa-García, M., Camarero, J.J. (Eds.), Latin American Dendroecology. Sringer Nature Switzerland AG, Gewerbestrasse, Switzerland, pp. 171–202. https://doi.org/10.1007/978-3-030-36930-9.
Stokes, M.A., Smiley, T.L., 1968. An Introduction to Tree-Ring Dating. University of Chicago Press, Chicago, Illinois.
Tortorelli, L.A., 1956. Argentine Forests and Timbers. Argentine forests and timbers.
Tukey, J.W., 1949. Comparing individual means in the analysis of variance. Biometrics 5 (2), 99–114. https://doi.org/10.2307/3001913.
Veblen, T.T., Donoso, C., Kitzberger, T., and Rebertus, A.J. (1996). "Ecology of Southern Chilean *Nothofagus* Forests" in The Ecology and Biogeography of *Nothofagus* forests. 10, 93-353.
Viale, M., Bianchi, E., Cara, L., Ruiz, E.L., Villalba, R., Pitte, P., et al., 2019. Contrasting climates at both sides of the Andes in Argentina and Chile. Front. Environ. Sci. 7, 69. https://doi.org/10.3389/fenvs.2019.00069.
Villalba, R., Veblen, T.T., 1997. Spatial and temporal variation in *Austrocedrus* growth along the forest – steppe ecotone in northern Patagonia. Can. J. For. Res. 27, 580–597. https://doi.org/10.1139/x96-209.
Villalba, R., Boninsegna, J., Veblen, T.T., Schmelter, A., Rubulis, S., 1997. Recent trends in tree-rings records from high elevation sites in the Andes of Northern Patagonia. Climatic Change at High Elevation Sites. Springer, Dordrecht, pp. 193–222. https://doi.org/10.1007/978-94-015-8905-5_11.
Villalba, R., Lara, A., Boninsegna, J.A., Masiokas, M., Delgado, S., Aravena, J.C., et al., 2003. Large-scale temperature changes across the southern Andes: 20th-century variations in the context of the past 400 years. Climate Variability and Change in High Elevation Regions: Past, Present and Future. Springer, Dordrecht, pp. 177–232. https://doi.org/10.1007/978-94-015-1252-7_10.
Villalba, R., Lara, A., Masiokas, M.H., Urrutia, R., Luckman, B.H., Marshall, G.J., et al., 2012. Unusual Southern Hemisphere tree growth patterns induced by changes in the Southern Annular Mode. Nat. Geosci. 5 (11), 793–798. https://doi.org/10.1038/ngeo1613.
Vuille, M., Franquist, E., Garreaud, R., Lavado Casimiro, W.S., Cáceres, B., 2015. Impact of the global warming hiatus on Andean temperature. J. Geophys. Res. Atmos. 120 (9), 3745–3757. https://doi.org/10.1002/2015JD023126.
Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Appl. Meteorol. Climatol. 23 (2), 201–213, 10.1175/1520-0450(1984)023%3C0201:OTAVOC%3E2.0.CO;2.
Wilmking, M., van der Maaten-Theunissen, M., van der Maaten, E., Scharnweber, T., Buras, A., Biermann, C., et al., 2020. Global assessment of relationships between climate and tree growth. Glob. Change Biol. 26 (6), 3212–3220. https://doi.org/10.1111/gcb.15057.
Zar, J.H., 1999. Biostatistical Analysis. N.J. Prentice Hall, Upper Saddle River.