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ARTICLE

Climate Ecology

Recent increase in autumn temperature has stabilized tree growth in forests near the tree lines in Chilean Patagonia

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Abstract

It is widely accepted that global warming is affecting forests near the tree line by increasing tree growth in these cold-limited environments. However, since about 1970, a reduction in tree growth near the tree line has been observed in response to warming and increased drought stress. This reduction in tree growth has been mainly reported in forests of the northern hemisphere but less studied in southern forests. In this study, we investigated tree populations of *Nothofagus pumilio* located near the arboreal altitudinal limit in the central Patagonian Andes (45–47° S, Aysén region, Chile). In this region, warming has been accompanied by increased drought conditions since the 2000s. We explored whether this climatic variability has promoted or reduced tree growth at the regional scale in tree lines of these broadleaved temperate forests of central Patagonia. We constructed tree-ring chronologies and determined common growth patterns and trends, and then analyzed the influence of recent climate. We detected a significant change in the slope of regional growth trends between the periods 1955–1985 and 1985–2015. We found that positive growth trends in the period 1955–1985 were associated with warmer and drier springs. However, after 1985, we found a stabilization in *N. pumilio* growth associated with a steady increase in temperature in autumn. Our results support the idea that more frequent warm autumns, with very thin or no snow cover, have stabilized tree growth due to water deficit at the end of the growing season of *N. pumilio*. The predicted climate change scenario of increasing temperatures and drought in central Patagonia may increase competition among trees for water, particularly at the end of the growing season. Consequently, we could expect a decreasing forest growth trend in central Patagonia, potentially impacting forest dynamics of these southern forests.

KEYWORDS
climate change, dendrochronology, drought conditions, *Nothofagus pumilio*, subantarctic forests, tree–climate interactions, tree-growth trends

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INTRODUCTION

Climate change has been accelerated since the 20th century, with an approximate global annual average of +1.0°C compared with the period 1850–1900 (Masson-Delmotte et al., 2019). This warming trend, together with changes in precipitation regimes, has affected the growth and productivity of trees in many forests around the world (Jump et al., 2017; McDowell et al., 2020). Trees growing near the tree line have shown growth responses to global warming, becoming important natural and ecological monitors of climate change (Jobbágy & Jackson, 2000; Lloret & Kitzberger, 2018; Serra-Maluquer et al., 2019). Tree line forests are expected to improve their growth despite warming, as higher temperatures promote early snowmelt at high altitudes, lengthening the growing season and promoting faster growth (Körner & Paulsen, 2004). However, in some forests near the tree line, growth is becoming less sensitive to rising temperatures since around 1970 (Briffa et al., 1998; D'Arrigo et al., 2008), which seems to be explained by drought-stress conditions (Büntgen et al., 2008; Galván et al., 2015; Lloyd & Fastie, 2002). One potential explanation is that warmer autumns increase the water deficit in the growth of trees (Black et al., 2000; Chen et al., 2003; Cramer et al., 2001; Piao et al., 2008; Pourtahmasi et al., 2011). Therefore, it is increasingly necessary to understand the role of autumn temperature as a potential new limiting factor in the growth of trees growing near the tree line in temperate forests.

In southern South America (south of 42° S), instrumental temperature records follow the same global warming trend since the second half of the 20th century (Rosenblüth et al., 1997; Veblen et al., 2011). In central Patagonia (45–47° S), warming has been accompanied by increased drought-stress conditions since the 2000s (Olivares-Contreras et al., 2019). These climatic trends can be attributed to El Niño Southern Oscillation (ENSO) events that occurred recently, and the positive phase of the South Annular Mode (SAM) that has been observed in recent decades (Morales et al., 2020). In central Patagonia, forests at altitudinal tree lines are dominated by *Nothofagus pumilio* (Poepp. Et Endl.) Krasser (Nothofagaceae), an endemic broadleaved tree species found in a wide latitudinal range in the Andes mountains (35–55° S). There is still no consensus in the scientific community on the growth response to climate change of *N. pumilio* forests located near the tree line in Patagonia. Early studies have shown that the radial growth of *N. pumilio* was positively related to temperature (e.g., annual minimum temperature, mean temperatures in winter, spring, and summer [June–March]) (Aravena et al., 2002; Magnin et al., 2014; Srur et al., 2008). Therefore, the intensification of the effects of global warming would be expected to generate an increase in radial growth. This was corroborated for the second half of the 20th century in *N. pumilio* populations (e.g., Villalba et al., 2003). However, a marked decline in tree growth has been documented since 1980 potentially because of the increase in drought (e.g., Fajardo et al., 2019; Rodríguez-Catón & Villalba, 2018).

In this study, we analyzed the tree growth of *N. pumilio* in the tree lines of the central Chilean Patagonian Andes (Aysén region). We hypothesized that although global warming has promoted the radial growth of *N. pumilio* in the tree line during the 20th century (e.g., Villalba et al., 2003), *N. pumilio* trees fail to follow warming trends due to the recent impact of the drought in the Aysén region (Fajardo et al., 2019; Olivares-Contreras et al., 2019). We explored this hypothesis at the regional scale of central Patagonia and locally at the stand scale by (1) developing the tree-ring chronologies of three sites of *N. pumilio* close to the tree line distributed in the Aysén region and (2) analyzing the growth trends of *N. pumilio* as a function of climatic variability in the last century.

MATERIALS AND METHODS

Study sites

We studied three sites near the tree line (between 995 and 1145 m above sea level) in the geographical distribution of the *N. pumilio* forests in central Patagonian Andes, Aysén region (between 45–47° S and 71–73° W, Figure 1 and Table 1). The forests were dominated by *N. pumilio*, a deciduous species that can reach 37 m in height, up to 1.86 m in diameter, and 451 years old (Gutiérrez, 2016). The sites are within public protected areas, in the Trapananda National Reserve (TRAP), Cerro Castillo National Park (RCAS), and Patagonia National Park (LARG). These sites were selected for their accessibility and because they present little evidence of anthropic activities, which facilitates the characterization of climate variability (Aravena et al., 2002). The forests of *N. pumilio* are one of the last areas with little human intervention in the world, where large areas of intact forests still remain (Potapov et al., 2009; Watson et al., 2018). The climate of the study area is humid cold oceanic (Donoso, 2015; Villalba et al., 2003), with a marked seasonality (Appendix S1: Figure S1) where rainfall is concentrated in the cold months (May–August) and declines in the warmer months (October–March). All the sites are located on volcanic ash soils (Gerding & Thiers, 2002; Hildebrand-Vogel et al., 1990), with soil depth <15.5 cm, <14.1% of organic matter, acidic, and poor in nutrients

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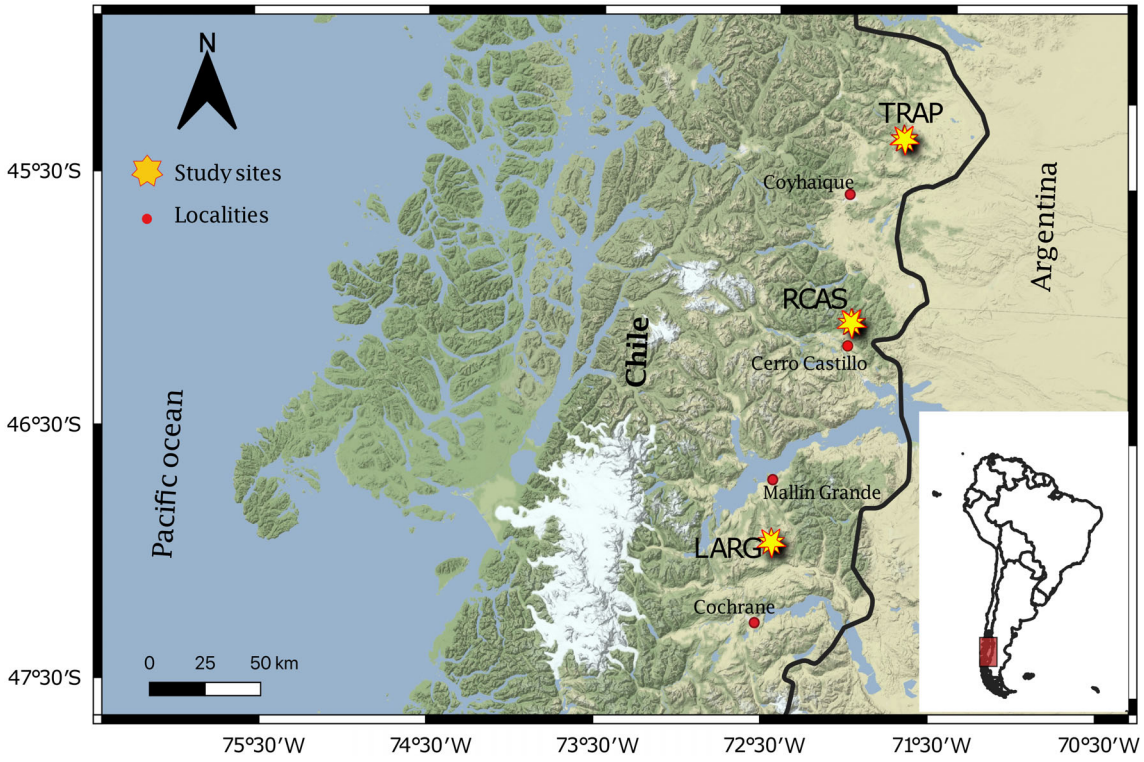

FIGURE 1 Location of the studied forests. Study sites located from north to south respectively: Trapananda National Reserve (TRAP), Cerro Castillo National Park (RCAS), and Patagonia National Park (LARG).

(Table 1). Soils also have a high pore volume and a high infiltration rate, resulting in a structure with little water retention capacity (Hildebrand-Vogel et al., 1990).

Climatic data

Climate data were obtained from the KNMI global climate platform (https://climexp.knmi.nl/). Total monthly precipitation (PP) data and mean, maximum, and minimum temperatures (Tmean, Tmax, and Tmin, respectively) were used for each study site with a spatial resolution of 0.5° latitude–longitude (~60 km) from the CRU-TS4.03 Climate Research Unit for the period 1955–2015 (Appendix S1: Figure S1). In addition, to explore the effect of drought on tree growth, we downloaded the self-calibrating Palmer Drought Severity Index (scPDSI) with spatial resolution of 0.5° from KNMI and the same period. The scPDSI is an index based on water supply and demand, which is calculated using a rather complex water-budget system involving local soil characteristics and historical records of precipitation, potential evapotranspiration, and seasonal snowpack dynamics (van der Schrier et al., 2013). Additionally, it considers previous drought conditions (prior month), allowing the detection of the "memory" effect of trees in response to such events (Dai, 2011). scPDSI has been extensively used to study the influence of droughts and wet spells on tree growth in South America (Morales et al., 2020). The regional climate was calculated by averaging the local climate data at each site to obtain a representative climate signal of the *N. pumilio* forests growing near the arboreal limit in the Aysén region. The trends of the mean temperatures, precipitation, and scPDSI were calculated for season and/or months, to evaluate the changes in the regional climate during the growing season (see also below).

Dendrochronological analysis and age estimation

In January 2017, we collected two increment cores at 1.3 m stem height from all living trees with DBH > 15 cm, inside a circular plot of radius 12.6 m (500 m^2). In total, six plots, that is, 1000 m^2 per site, were sampled to obtain a balanced representation of forest structure. We processed the cores and dated them following the methods of Stokes and Smiley (1968). We measured ring width of all the collected samples using a Lintab 6 measuring table and the TSAP-WIN software (Rinntech, Heidelberg, Germany). Samples were cross-dated to identify

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TABLE 1 Description of the study sites.

Variable	TRAP	RCAS	LARG
Elevation (masl)	1104	1145	995
Latitude (°)	−45.34	−46.07	−46.95
Longitude (°)	−71.77	−72.03	−72.46
Mean DBH ± SE (cm)	$44.5 \pm 1.5_a$	$34.3 \pm 1.5_b$	$32.5 \pm 1.9_b$
Mean age ± SE (year)	$196 \pm 6_a$	$176 \pm 5_b$	$184 \pm 6_b$
Dominant canopy height (m)	14.3	16.3	15.7
Density (trees/ha)	580	1140	1190
Basal area ± SE (m^2/ha)	$142.2 \pm 0.1_a$	$67.8 \pm 0.1_b$	$80.6 \pm 0.1_b$
Canopy cover (%)	85	85	80
Soil depth (cm)	14.5	9.5	15.5
Soil phosphorous content (mg/kg)	9	99	12
Soil potassium content (mg/kg)	89	220	164
Soil inorganic nitrogen (mg/kg)	8	6	16
Organic matter (%)	7.3	10.8	14.1

Note: Subscripts *a* and *b* indicate significant difference between sites with a confidence level of 95%.
Abbreviations: LARG, Patagonia National Park; asl, above sea level; Mean DBH, diameter at 1.3 m breast height; RCAS, Cerro Castillo National Park; TRAP, Trapananda National Reserve.

errors in the dating and the measurement of tree rings by calculating the moving correlations between the individual tree-ring series and an average master series using the program COFECHA (Holmes, 1983). We estimated the ages of sampled trees by counting the dated rings of each core. When more than one core was present, the age was assigned according to the core with more rings. For all those samples that did not reach the pith, due to central rot, the number of tree rings absent from the pith was estimated using the geometric methods described by Rozas (2003). For those cores that did not present pith or arches of the internal rings, the tree age was estimated with a quadratic regression model with DBH as an independent variable, due to its high correlation with the observed ages (Pearson $r > 0.5$; $p < 0.05$, Appendix S1: Figure S2). We used both complete and estimated tree ages to obtain the age structure of the studied *N. pumilio* populations. We determined whether there were differences in the distribution of tree sizes (DBH) and ages between the populations using the Kruskal–Wallis test (Hollander & Wolfe, 1973), with Dunn's test and Bonferroni's method (Dunn, 1961).

Common growth patterns and trends

In order to identify a common signal expressed in the radial growth of trees (regional signal), we conducted a principal components analysis including all ring width series of sampled trees using a common growth period (1900–2015). The above left us with three groups of trees. The first group included all the trees sampled (All trees). The second group included the series of trees with the highest Pearson correlation (i.e., $r \geq 0.45$), with the first principal components (PC1) (Rodríguez-Catón et al., 2016). While the third group resulted from the remaining trees (Other trees). To remove bias in the calculation of tree-ring indices, we logarithmically transformed the series before detrending (Cook & Peters, 1997). Then, we fitted a spline function with a 50% frequency response, and we calculated the ring width indices (RWI) by subtraction, because our series have been subject to variance stabilization (Cook & Peters, 1997). Finally, a stabilized chronology was calculated that considers the temporal changes in the correlation between series (Frank et al., 2007), adopting a robust estimate of the Tukey mean value function that improves the common signal, reducing the effects of outliers (Cook, 1985).

To analyze tree growth patterns, we transformed ring width without standardizing (RWL) into the annual basal area increment (BAI) (Biondi, 1999; Biondi & Qeadan, 2008). According to Bowman et al. (2013), BAI is a biological variable representative of the growth trend as it depends less on the size of the tree, which is considered more suitable than RWL. Changes in growth patterns (BAI and RWL) of trees of all sizes, small (DBH < 53 cm) and large (DBH ≥ 53 cm), were evaluated for the last 60 and 100 years. The procedure consisted of fitting a segmented linear regression model between the BAI (RWL; response variables) and the respective calendar years (explanatory variable). The segmented regression uses a step-by-step method to calibrate the model parameters (i.e., piecewise linear), to identify one or more threshold values that maximized the fit of the curves, that is, allowing to identify sudden changes in tree growth throughout the series. Once the threshold was identified, the growth trends of the trees 30 years before and 30 years after the detected break point were evaluated, using the slopes of the linear regressions between the BAI and RWL series and the calendar years. We used the result to evaluate whether tree growth significantly increased or decreased after the break point using a Kruskal–Wallis test (Hollander & Wolfe, 1973). For data processing and analysis, we used the dplR dendrochronological functions package (Bunn, 2008, 2010) and the segmented trend analysis package (Muggeo, 2003, 2008), both available in R (R Core Team, 2021).

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Dendroclimatic and trend analysis in tree growth

We used BAI and RWI chronologies to examine the relationships with the monthly climatic variables pre- and post-break point detected through a Pearson correlation. To estimate the magnitude of the correlations between growth and climatic series and ensure the robustness of the analysis, an initial resampling or bootstrapping was used to evaluate the stationarity of the correlations with the help of the treeclim package (Zang & Biondi, 2015) available in R. Because tree growth in any specific year is influenced by the climate of the current year (t) and the previous year ($t - 1$) (Fritts, 1976), we performed correlation analyses for a 21-month period, from June (austral winter) of the previous growing season through May (austral autumn) of the current growing season. It should be noted that statistical significance in the correlation between the ring width and climatic variables does not necessarily mean that one variable is the cause of the other (Houlahan et al., 2017). As *N. pumilio* is a deciduous species, a correlation between a climate variable and radial growth in the months of dormancy should not be used to explain growth response. Therefore, in our analysis, we choose climatic variable and/or seasons that we expect to have the greatest influence on the radial growth of *N. pumilio* (Rusch, 1993; Soliani & Aparicio, 2020).

Finally, to elucidate which factors influenced tree growth after the detected break point, we fitted multiple linear mixed models (Chambers & Hastie, 1992; Wilkinson & Rogers, 1973) to quantify the influence of tree size (DBH), climatic variables (temperature, precipitation, and drought), and the site (stand; Table 1) on individual growth (BAI) and growth trends (i.e., slope). In these analyses, we did not include age because (1) for some trees it was impossible to determine age due to rotten tree centers; (2) the error in age estimation increases in larger trees due to missing piths; and (3) we found a strong correlation between DBH and age, which produces collinearity (Appendix S1: Figure S2). We modeled BAI as the response variable logarithmically transformed to ensure the normality of the residues. As explanatory variables, we used DBH and climatic variables pooled by seasons. Seasons were calculated by averaging the months March, April, and May (autumn); June, July, and August (winter); September, October, and November (spring); and December (t), January, and February ($t + 1$; summer). The climatic variables used were precipitation and mean, and minimum and maximum temperatures. In addition, we included the trees nested in the sites as a random factor to consider the variation in growth due to abiotic characteristics, and to avoid autocorrelation between series, we used autoregressive process order 1 (i.e., correlation = corAR1[]). Then, we model growth trends using the slope as response variable. As explanatory variables, we used seasonal and annual climatic variables and stand characteristics (as three-level factors, equivalent to the value of each site). We included trees in the model as random factor. All models were run on R 3.6.1 (R Core Team, 2021) using the lme function of the nlme package following a model building approach (Pinheiro & Bates, 2000). Statistical inference was performed using likelihood ratio tests, and the assumptions of the model were verified with classic graphical diagnoses.

RESULTS

Tree-ring chronologies and common trends in growth

The *N. pumilio* forests presented size distributions (DBH) close to normal, but with negative asymmetry and a certain degree of kurtosis, with a greater number of trees among the age classes between 176 and 196 years (Table 1). One third of the trees sampled (33%) were <164 years old and only 1% were >300 years old. The northernmost site (TRAP) differed from the others in terms of its size and age distribution (Kruskal–Wallis test, $p < 0.01$). The RCAS and LARG sites did not show significant differences in their size and age distributions. From 360 samples collected from 180 trees, we cross-dated 252 cores from 157 trees (70% and 87.2%, respectively; Pearson $r^2 > 0.5$, Table 2). The trees included in the regional chronology had a significant common growth signal from 1816 (EPS > 0.85). The northernmost site (TRAP, Appendix S1: Figure S3) showed above-average radial growth in the first half of the 20th century, which later began to fluctuate around the mean. The same behavior was observed in the radial growth of the central site, but more centered on the mean (RCAS, Appendix S1: Figure S3). By contrast, the southernmost site (LARG, Appendix S1: Figure S3) exhibited growth with greater oscillations every 30 years in the covered period (1900–2015). Overall, the ring-width chronologies for the three study sites (Appendix S1: Figure S3) showed abrupt increases and decreases in radial growth since the mid-20th century, highlighting an above-average growth period between 1975 and 1980. Since 1980, radial growth declined rapidly, returning in 2015 to values near the mean.

The principal component 1 (PC1) grouped 81.5% of the sampled trees (128 trees) and contributed 36.2% of data variability, that is, the regional signal was predominantly

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TABLE 2 Descriptive statistics of the residual chronologies of the studied *Nothofagus pumilio* forests.

Metric	TRAP	RCAS	LARG	Regional chronology
No. cores	82	96	74	252
No. trees	55	57	45	157
Intercorrelation	0.55	0.6	0.62	0.52
Entire length	1698–2015	1762–2015	1750–2015	1736–2015
EPS > 0.85	1816–2013	1835–2014	1856–2015	1816–2015
Mean Rbar	0.31	0.28	0.25	0.32

Abbreviations: EPS, expressed population signal; LARG, Patagonia National Park; Mean Rbar, average correlation between all series; RCAS, Cerro Castillo National Park; TRAP, Trapananda National Reserve.

PC1, grouping trees with a common radial growth variability. Since *N. pumilio* has intermediate shade tolerance, the effect of disturbances in the studied closed canopy forests would not be driving the explained variability in radial growth. The regional chronology obtained from trees of the PC1 confirmed the increase over the mean RWI in the mid-1970s and its subsequent decline since 1985 to the present (2015). Moreover, the trees belonging to PC1 tend to return to the mean, while the rest diverge and tend to decrease. Ratifying the above, basal area increment chronology (BAI) coincided with the increase and subsequent decline around the 1980s, but starting from the 21st century, it exhibits a stabilization in growth (Appendix S1: Figure S4).

The piecewise analysis regression detected a break point in 1985 in the regional chronology of both RWL and BAI (Figure 2). BAI increased steadily during the period prior to 1985 (Figure 2c and Appendix S1: Figure S5). Particularly for the slope of RWL, a change of sign was observed in its slope after 1985 (Figure 2b), whereas the slope of BAI declined, and after 1985 the slope was near zero (Figure 2c). These results were consistent during the last 60 and 100 years (Figure 2 and Appendix S1: Figure S5, respectively). The coefficients of the linear regression model between BAI and RWL, and the calendar years 30 years before and 30 years after the detected break (1985), confirmed these trends (Figure 2b,d, respectively) with statistically significant differences ($p < 0.001$) between the coefficients before and after 1985. The exception were 29 trees that did not correlate with PC1 (red dotted line, Appendix S1: Figure S3) and showed a growth below the mean for the last period (2010–2015). When separating trees by size, we found that for both small and large trees, there was a significant difference ($p < 0.001$) before and after the break point in the BAI slope (Table 3). After 1985, the BAI showed a slightly positive trend in small trees (DBH < 53 cm) and almost no trend in large trees with DBH ≥ 53 cm (mean age = 245 years; Table 3).

Climatic forcing of tree growth and trends in basal area increment (BAI)

Climatic conditions, especially during spring and autumn, and partially during summer, had the strongest correlation with *N. pumilio* growth, for both BAI and ring width (Figure 3 and Appendix S1: Figure S6, respectively). It is worth mentioning that the vegetative growth period for this species begins in September (austral spring), with the budding of the leaves, and ends in May (austral autumn), with their fall (Rusch, 1993; Soliani & Aparicio, 2020). For the period 1955–1985, we found that precipitation had a positive correlation with growth mainly in spring and a negative correlation in winter (Figure 3). During the same period, mean temperature of summer had a positive correlation with tree growth. Tree growth had a positive correlation with minimum temperature (Tmin) during the whole growing season (spring to autumn), whereas maximum temperatures (Tmax) the previous spring were negatively correlated. For the period 1985–2015, we found a change in the growth response to climatic variables. In spring, during this period, tree growth was negatively correlated with precipitation and positively correlated with Tmean and Tmax (Figure 3). In autumn, tree growth was negatively correlated with all temperature variables (Figure 3). This change in the correlation patterns with tree growth could be related to the decreasing trend in precipitation during winter (Figure 4a) and a trend stabilization in precipitation and Tmax of spring since 1985 (Figure 4b). Moreover, both autumn minimum and maximum temperatures showed a significant increase since 1985 (Figure 4d,e), but maximum temperature of autumn showed a change in its slope in relation to the previous period (Figure 4f).

The results of the best multiple linear mixed models showed that tree growth after 1985 was mainly determined by tree size (DBH) and maximum temperature of autumn (TmaxAut). This was consistent when fitting the model for All trees and the trees that correlated with

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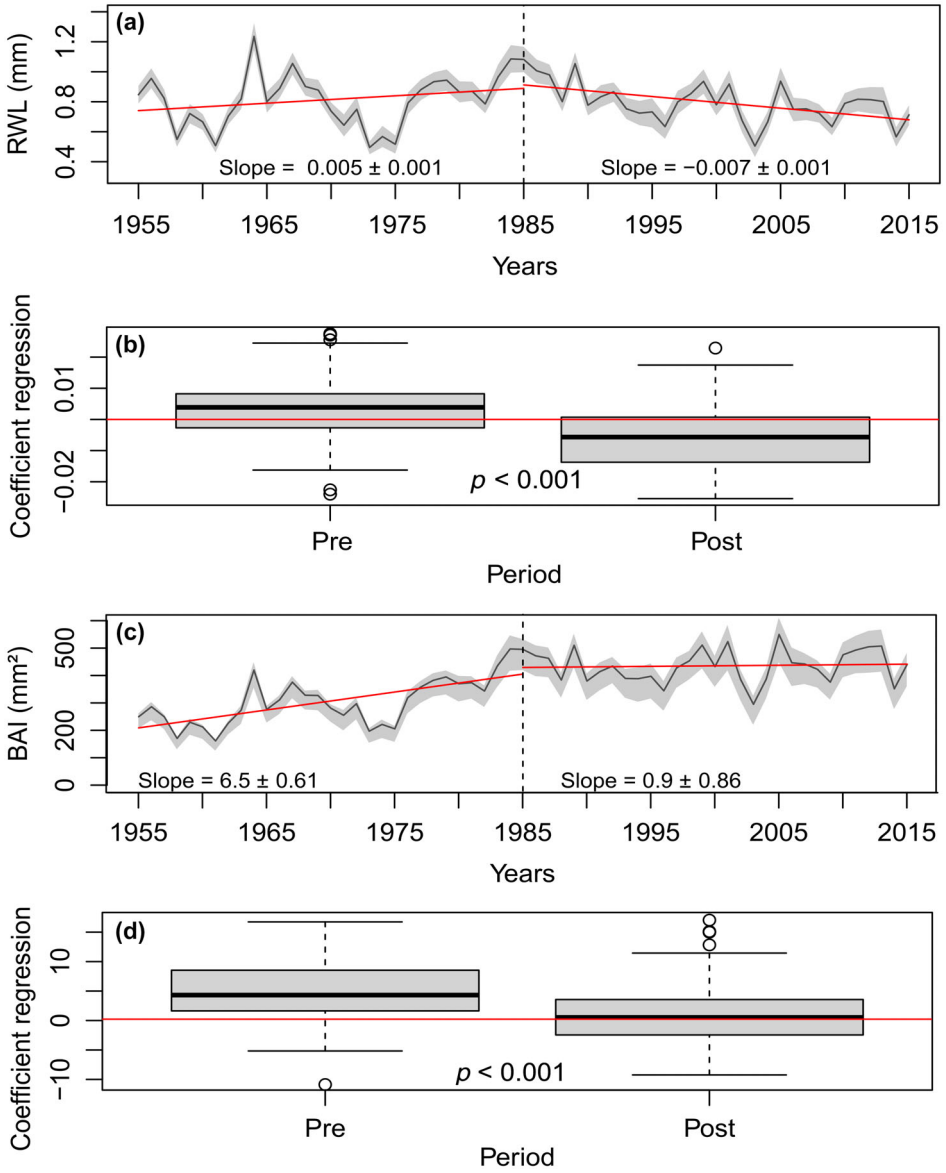

FIGURE 2 Regional growth pattern of *Nothofagus pumilio* including the tree-ring series of trees that correlated ($r \geq 0.45$) with principal component 1 (128, black curve): mean ring width (RWL; a) and mean basal area increment (BAI; c) and 95% CIs of significance (gray background). Red lines are growth trends and the black vertical lines are break points. (b, d) Coefficients (slope) of the linear regression models between RWL (b), BAI (d), and the calendar year 30 years before (pre) and 30 years after (post) the detected break point (1985).

TABLE 3 Coefficients (slope) of the linear regression models between basal area increment and the calendar year 30 years before and 30 years after the detected break point (1985), for all trees, small trees (DBH < 53 cm), and large trees (DBH ≥ 53 cm).

		Slope		
Trees	***N***	**Before 1985**	**After 1985**	***p***
All	157	6.54 ± 0.61	0.91 ± 0.86	1.20E-13
Small	135	6.01 ± 0.53	1.00 ± 0.84	1.74E-12
Large	22	9.23 ± 1.84	−0.02 ± 1.72	0.001104

Note: The *p* value is the significance of a Kruskal–Wallis test between slopes after and before the break point.

PC1 (i.e., All trees and Trees in PC1). The coefficients of the best models indicated that DBH had a positive influence, while TmaxAut had a negative influence on BAI (All trees and Trees in PC1, Table 4). Most of the total variation for each variable was explained by random effects, with conditional R^2 mean values of 0.68 and marginal R^2 values ≤0.27 (Table 4). Trees that did not correlate with PC1 (i.e., Other trees) had lower marginal R^2 values (R^2m = 0.06, Table 4). Regarding the models fitted for BAI slopes, the best model that explained the slope variation after 1985 included only stand density (Den), which had a negative influence (All trees and

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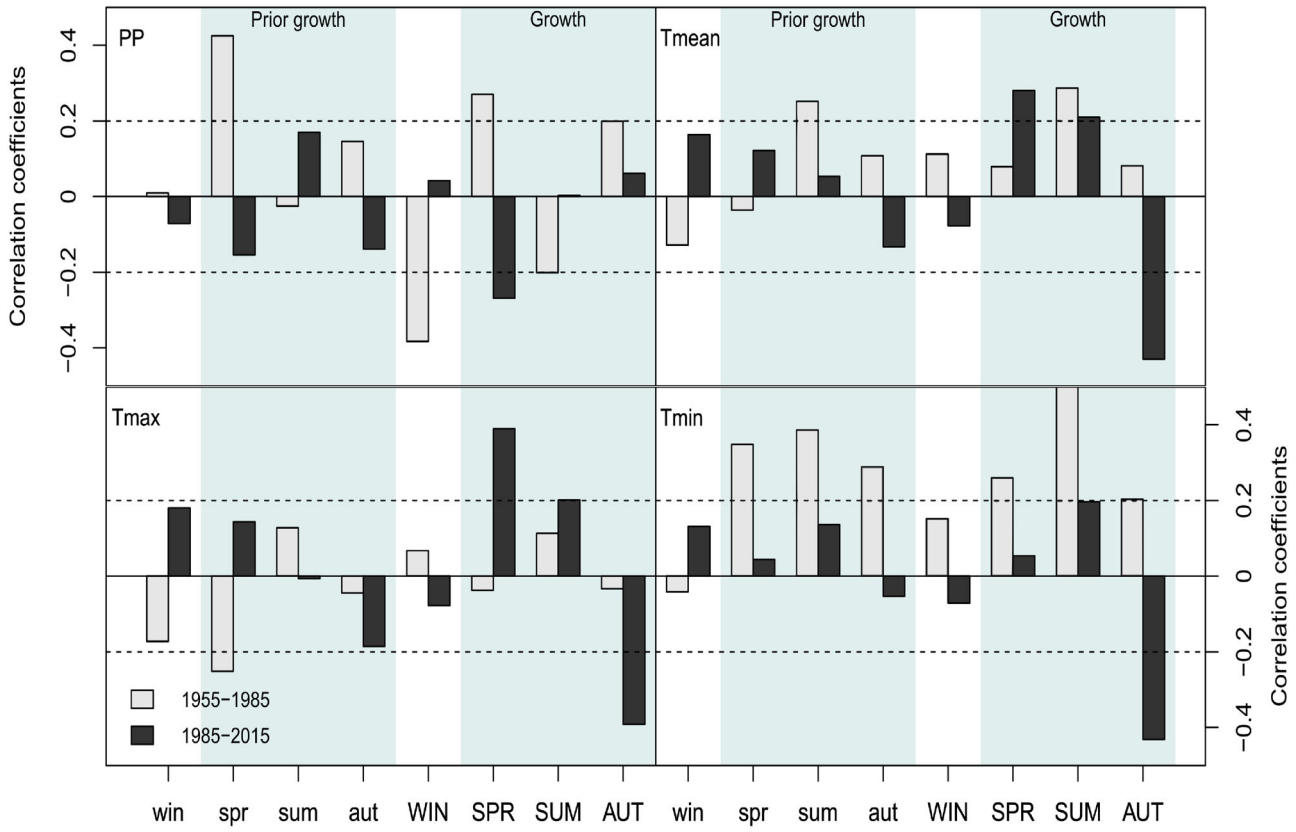

FIGURE 3 Correlation functions between basal area increment chronology and climatic variables for two periods, 1955–1985 (light gray) and 1985–1955 (dark gray). On the abscissa axis, letters represent seasons of the year, winter (win), spring (spr), summer (sum), and autumn (aut), and the shaded area (light blue) represents the previous ($t - 1$) and current (t) growing season. Segmented lines indicate a significant correlation coefficient ($p < 0.05$) with 95% CI. PP, monthly precipitation; Tmean, mean temperature; Tmax, maximum temperature; Tmin, minimum temperature.

Trees in PC1, Table 4). Finally, for those trees that did not correlate with PC1, the best model for BAI growth included autumn mean temperature (TmeanAut) and spring maximum temperature (TmaxSpr), with negative and positive influences, respectively (Other trees in Table 4a). For the slope models of these trees, only latitude (Lat) was included, and it had a positive influence (Other trees in Table 4b).

DISCUSSION

Overall, our results demonstrate that *N. pumilio* populations growing near the tree line are sensitive to regional warming, especially to heat conditions during the beginning (positively) and ending (negatively) growing seasons (i.e., spring and autumn, Figure 3). This sensitivity was expressed in increased tree growth until 1985, but since the mid-1980s, *N. pumilio* growth trend has stabilized due to a significant increase in autumn temperature in central Patagonia (Figure 2c; Figure 4d–f). We propose that the increase in temperature at the end of the growing season would be the main limiting factor on tree growth at tree lines in central Patagonia since the mid-1980s, counteracting the expected increase in tree growth due to global warming.

The ring-width chronologies developed in this study had similar growth patterns and climatic relationships between the studied sites (Appendix S1: Figure S3), suggesting a common growth pattern of *N. pumilio* at the regional scale in central Patagonia (Appendix S1: Figure S4). The growth patterns of *N. pumilio* had periods of slow growth around the 1925s–1930s, 1950s, and mid-1970s. Subsequently, an evident increase in radial growth was observed between 1975 and 1985, coinciding with an increased change in temperatures on the surface of the tropical Pacific sea (Garreaud et al., 2009; Villalba et al., 2012). Our regional chronology (Figure 2c) is consistent with the positive growth trends in other Andean forest sites of *N. pumilio* until 1985 (Aravena et al., 2002; Lara et al., 2005; Villalba et al., 2003). However, our finding of tree growth stabilization after 1985, with slopes close to zero (Figure 2c,d), due to the sustained increase in temperatures at the end of the

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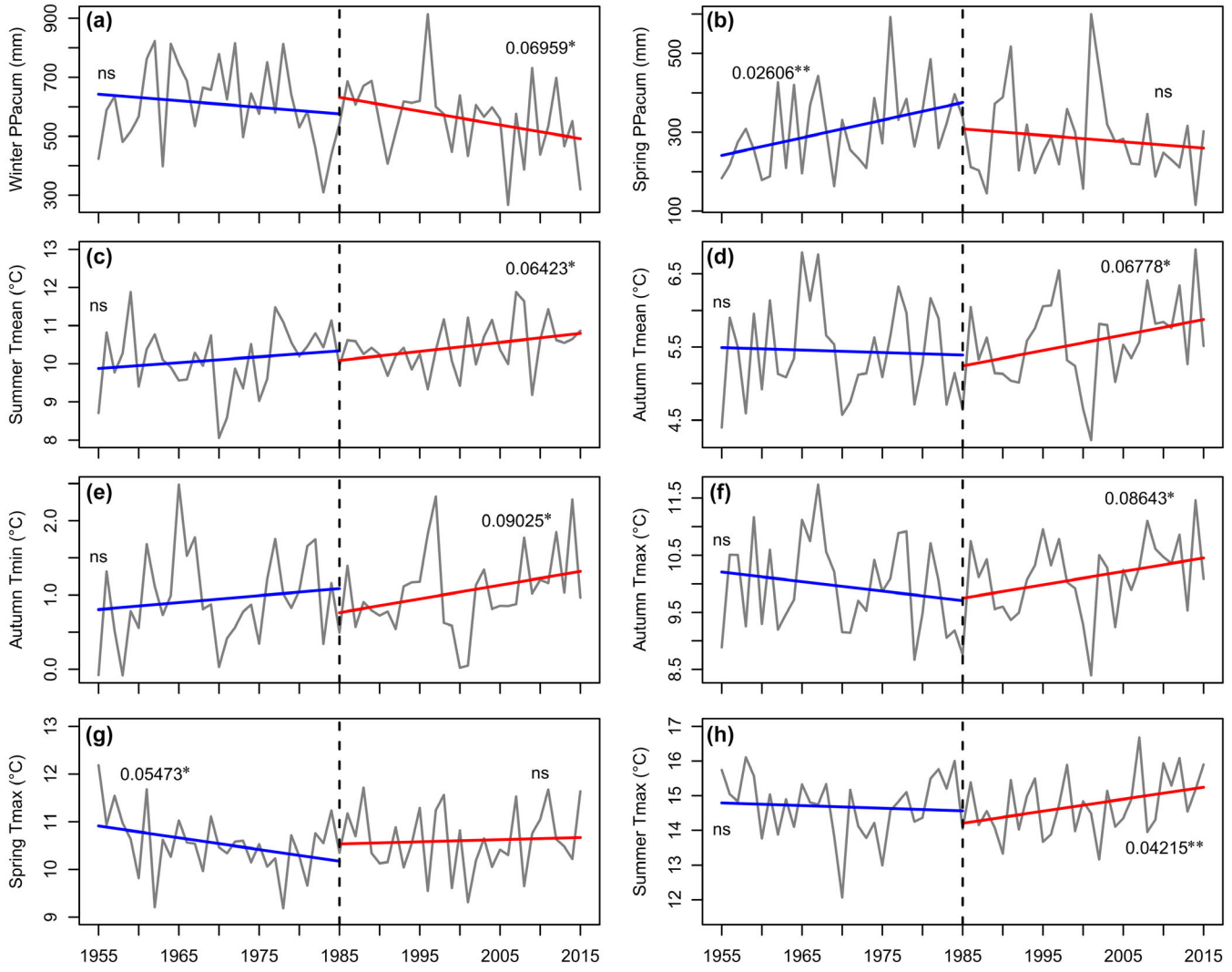

FIGURE 4 Climatic time series showing a significant relationship with tree growth. Seasonal climatic time series from 1955 to 2015 (gray curve). The blue and red lines represent trends in the linear regressions between the climatic variables with respect to the calendar year, for the period 1955–1985 and 1985–2015, respectively. Statistical significance of slope changes in climatic time series is indicated with *p* value (*$p < 0.1$ and **$p < 0.05$) and its absence with nonsignificant (ns). PPacum, accumulated precipitation; Tmax, maximum temperature; Tmean, mean temperature; Tmin, minimum temperature.

growing season (austral autumn), contrasts with the marked growth decline in *N. pumilio* forests in northern Patagonia (36–40° S) and in the eastern Andes Patagonia, in response to recent (after 1980) increased drought conditions (e.g., Álvarez et al., 2015; Fajardo et al., 2019; Lavergne et al., 2015; Rodríguez-Catón et al., 2016, 2019; Villalba et al., 2012). For *N. pumilio* populations growing in the western slope of the Andes and in the north of Patagonia (40° S), the growth decline to the warmer and drier conditions of the summer has been attributed to the persistent, positive phase of the SAM and El Niño events (Álvarez et al., 2015). During the last century, a decrease in the common signal of radial growth patterns has been found in other *N. pumilio* populations growing at lower elevations (rear edge) potentially due to the increase in arid conditions in northern Patagonia (40° S, Serrano-León & Christie, 2020).

In our climate–growth correlation analysis, the positive growth trends of *N. pumilio* between 1955 and 1985 were related to warm springs and summers (Figure 3) that can promote early thaw by lengthening the growing season (Körner & Paulsen, 2004; Lloret & Kitzberger, 2018; Villalba & Veblen, 1997). Similar to Álvarez et al. (2015), we found that after 1985, *N. pumilio* growth was related to warm and dry springs. In addition to the positive relationship between warm springs and radial growth, in our study, we found that *N. pumilio* growth was also strongly related to the end of the growing season, with a negative relationship to autumn temperature (Figure 3, $r < -0.40$, $p < 0.05$). In the same

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TABLE 4 Coefficients of the multiple linear regression models with the best fit to explain the variation in (a) basal area increment (BAI) and (b) changes in BAI trend (slope) after 1985, with a 0.95% confidence level for the intervals (lower and upper).

		All trees[a]			Trees in PC1[b]			Other trees[c]		
Model	**Predictor**	**Lower**	**Estimate**	**Upper**	**Lower**	**Estimate**	**Upper**	**Lower**	**Estimate**	**Upper**
(a) log(BAI + 1)	Intercept	5.654	5.949	6.244	5.559	5.887	6.214	5.1	5.66	6.22
R^2m = 0.18[a], 0.27[b] and 0.06[c]	DBH	0.01	0.016	0.022	0.012	0.019	0.026	...	...	...
	TmeanAut	...	...	...	...	...	...	−0.17	−0.125	−0.08
R^2c = 0.71[a], 0.73[b] and 0.61[c]	TmaxAut	−0.093	−0.075	−0.058	−0.096	−0.077	−0.058	...	...	...
	TmaxSpr	...	...	...	...	...	...	0.029	0.071	0.113
(b) log(slope)										
R^2m = 0.07[a,c] and 0.12[b]	Intercept	3.653	8.297	12.94	6.635	12.03	17.425	−338.16	−140.024	58.112
	Den	−0.013	−0.008	−0.003	−0.017	−0.011	−0.006	...	...	...
R^2c = 0.89[a,b,c]	Lat	...	...	...	...	...	...	−1.277	3.047	7.37

Note: R^2m and R^2c are marginal and conditional coefficient of determination, respectively; the superscripts a, b, and c refer to the number of samples used according to All trees[a] (157), the Trees in PC1[b] (128), and the Other trees[c] (29).
Abbreviations: DBH, diameter at 1.3 m breast height; Den, stand density; Lat, latitude; PC1, first principal component; TmaxAut, autumn maximum temperature; TmaxSpr, spring maximum temperature; TmeanAut, autumn mean temperature.

period, we found a stabilization in *N. pumilio* growth after the climate change that occurred in 1985 in central Patagonia (Figure 4), contrasting with the positive growth trend expected in response to global warming in the tree lines (Jobbágy & Jackson, 2000; Lloret & Kitzberger, 2018). Therefore, although warm and dry springs favor tree growth to some extent, warm autumns impair *N. pumilio* growth in forests near the tree line in our study area. Fajardo et al. (2019) proposed that the recent negative growth trends of *N. pumilio* in Aysén could be due to stomatal closure induced by drought. However, our regional climate–growth correlation analysis did not show a significant relationship with drought (i.e., scPDSI, $r^2 = 0.02$ and $p = 0.10$; results not shown) despite the significant increase in dry conditions since 1985 in central Patagonia (Appendix S1: Figure S7). Therefore, we propose that *N. pumilio* growth stabilization after 1985 represents a response to the increase in autumn temperature that has prevailed in the last decades in the region (Figure 4d–f). We suggest that more frequent warm autumns can produce an early melting of snow cover (Körner & Paulsen, 2004; Wu et al., 2012) producing a water deficit at the end of the growing season of *N. pumilio*. It is likely that this water deficit accelerates leaf fall of trees, reducing earlier the tree growth, as observed in other deciduous species during drought/heat stress events (Decuyper et al., 2020).

Our results are consistent with growth trends in tree lines in the northern hemisphere, in which trees have failed to track the recent warming trend after 1970 and instead have shown a general sensitivity loss of tree growth to temperature or instability in association with climate, that is, the direct correlations between growth and temperature cease to exist or are reversed (e.g., Büntgen et al., 2008; Driscoll et al., 2005; Galván et al., 2015; Lloyd & Fastie, 2002; Wilmking, 2005). For example, tree growth of *Fagus orientalis* is negatively correlated with above-average warm summer and autumn seasons (Pourtahmasi et al., 2011). In modeling studies, an equivocal decrease in ecosystem production was found in warmer autumns; that is, the higher temperature in autumn would reduce tree growth (e.g., Black et al., 2000; Chen et al., 2003; Cramer et al., 2001; Piao et al., 2008). In the subalpine forests in the Rocky Mountains of Colorado, a longer growing season, that is, warmer springs and autumns, was associated with shallower snowpack, resulting in a lower annual absorption of CO_2 (Hu et al., 2010). *N. pumilio* develops on soils with a high volume of pores and a high infiltration rate, which results in a soil structure with little water retention capacity (Hildebrand-Vogel et al., 1990). In addition, warm temperatures (spring and summer) accelerate the early melting of snow (Wu et al., 2012), reducing the availability of water at the end of the growing season (autumn). Therefore, if the current warming conditions continue to accelerate, *N. pumilio* growth in central Patagonia could slow down. To better understand the linkage between a longer growing season and *N. pumilio* growth at tree lines, future research can explore other biophysical mechanisms such as soil moisture and snowmelt dynamics that could result in a stabilization trend (Carrer et al., 2007).

The multiple linear mixed models helped us understand the tree growth response to climate change after the 1985s at local (stand) scales. The tree growth response was mainly explained by tree size and maximum

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temperature in autumn, and growth trend (i.e., BAI slope) by stand density. Specifically, the sites with large and old trees maintained radial growth under the average after the climate change of the 1985s (TRAP, Table 1, Appendix S1: Figure 3), while the sites with small and young trees showed relatively stable radial growth (Figure 2, RCAS and LARG). Based on the fact that young trees could take better advantage of resource availability (Konter et al., 2016), we propose that young-lived and small individuals of *N. pumilio* populations in the tree line are less affected than larger trees by the recent climate change in central Patagonian (Aysén study region). These ideas are consistent with Rodríguez-Catón et al. (2016, 2019) who found that large individuals of *N. pumilio* on the eastern side of the Andes were the most affected by drought episodes, showing negative growth trends. As trees grow less, they reduce energy expenditure, which implies lower respiration rates and water demand, favoring the efficient use of available resources (Manion, 2003), especially water use efficiency (Fajardo et al., 2019). Additionally, forest stand structure, particularly stand density, also played a role in explaining the stabilization of growth trends after the 1985 break point at the local scale (Table 4). Evaporation and soil infiltration are reduced in dense stands, influencing the rate of depletion of the stored water during the growing season (Butcher, 1977; Butcher & Havel, 1976). Consequently, in dense stand, trees tend to compete for soil water (Bréda & Granier, 1996; Laurent et al., 2003; Martín-Benito et al., 2010; Sucoff & Hong, 1974), and potentially soil moisture would not be sufficient to meet the demand for All trees, especially at the end of the growing season (autumn). Therefore, the positive growth response could be limited if droughts and warming continue and certain thresholds are exceeded (e.g., Martín-Benito et al., 2010; Misson et al., 2005). These results complement the generalized stabilization in the growth of the trees in the study region.

Forecasting climate models for central Patagonia (Aysén region) shows an increase in the periodicity and intensity of drought events by 2100, with a decrease in rainfall between 10% and 20% and an increase in temperatures above 1.6°C (Masson-Delmotte et al., 2019). Based on the *N. pumilio* climatic variability detected in our study, future drought and warming conditions could generate a forest decline of *N. pumilio* populations in central Patagonia, concurring with predictions from other authors (e.g., Álvarez et al., 2015; Fajardo et al., 2019; Lavergne et al., 2015; Rodríguez-Catón et al., 2016, 2019; Villalba et al., 2012). Therefore, we expect that the change in the growth trend of *N. pumilio* evidenced in our study (after 1985), which was expressed as greater sensitivity to autumn temperature and tree density, should be more notorious in the coming decades.

In the central Patagonian Andes, massive outbreaks of native insect defoliators have increased in frequency in *N. pumilio* forests since 2000, potentially triggered by regional warming (Estay et al., 2019; Gutiérrez et al., 2020). However, note that the tree line sites we considered in this study were not affected by insect outbreaks. The impacts of biotic drivers of such insect defoliators may increase due to warming in tree lines and require attention in the near future. Additionally, a further understanding is needed on potential impacts of warming and drought on other demographic rates (tree recruitment and mortality rates) of *N. pumilio* populations, as well as permanent monitoring of cell growth and the use of dendrometers to determine the response of *N. pumilio* growth to microclimate. Advances in this direction will contribute to developing robust models of forest dynamics to predict the vulnerability of *N. pumilio* to climate change. Our results showed differences in the studied sites despite climate warming in central Patagonia and suggest a local adaptability of the species to different environmental conditions that should be studied in greater detail. This would help identify refuges of high biological value that could be used as germplasm to buffer the response of these forests to future climate change.

CONCLUSIONS

Our results document an increase in tree growth in the *N. pumilio* tree line on a regional scale in Aysén (central Patagonia, 45–47° S) in response to global warming until 1985, corroborating the sensitivity of this species to temperature variability during the growing season. However, since 1985, a breaking point has been observed in this tree growth trend caused by the increase in autumn temperature in the central Patagonia of Chile. In contrast to the strong decrease in growth observed in other studies in the tree line of Andean Patagonia, we found a stabilization in the growth of *N. pumilio* on a regional scale since 1985. This change in the tree growth trend (slope) is mainly explained by intraspecific competition among trees for resources and by rising temperatures at the end of the growing season. Our results show that, currently, the maximum autumn temperature is becoming the dominant limitation of tree growth in tree lines of temperate forests in central Patagonia. The local variations found in our study, such as stand density and soil, suggest potential refuges in the distribution of *N. pumilio* that can buffer the negative effects of extreme climatic events, in central Patagonia.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Gibson-Carpintero, 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.c.5827211.

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