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Radial growth decline in a tropical Andean treeline in Bolivia

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Abstract. Relative to research efforts in higher latitiudes, the impact of climate shifts in the tropical treeline remains understudied. Little is known about the tree growth dynamics and climate response at this treeline over the past few centuries, and at present under a rapidly changing environment. Here we provide information on recent changes in tree-ring patterns of *Polylepis pepei* BB.Simpson, a tropical tree species that grows in a monospecific forest at the elevational treeline in the Andes-Amazon ecotone of Bolivia and identify factors that limit its radial growth. We first developed a ring width (RW) chronology spanning 1867-2018 C.E. using dendrochronological methods and independently verified annual periodicity with radiocarbon dating. The RW chronology indicates a significant ($p < 0.01$) radial growth decline in *P. pepei* since 1997, a trend that mirrors a decrease reported in other *Polylepis* species from the drier central Andes of South America. *P. pepei* tree-ring width (RW) was mostly limited by mean, minimum, and maximum temperature and precipitation–during austral summer (November-January). Over the instrumental period (1981-2019) prior-year temperatures negatively affected current-year tree growth ($p < 0.05$), while prior-year wet conditions were associated with higher growth ($p<0.05$). Gridded temperature records (1901-2019) showed a significant increase in minimum temperatures and a decline in the diurnal temperature range since 1967, which may reduce orographic convection and water availability at higher elevations where our forest is located. In situ daily measurements from dataloggers in the forest recorded higher temperatures and lower relative humidity values when data was available. Our results suggest less moisture availability associated with warming conditions was related to the observed tree-growth decline. If temperature continues to rise at current rates, one of the highest-elevation tree species on the globe, *P. pepei*, could face severe consequences. This work provides insights into the past and historical trends of a tropical Andean treeline, which shows a recent decline also observed in other high-elevation forests (4657-4800 m.a.s.l.) of tropical South America (> 17°S).

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1 Introduction

Temperature-limited treelines have been well studied in dendrochronology. In the Northern Hemisphere (NH), shifts in latitudinal and elevational treeline have been associated with the effects of global warming (Flynn et al., 2025). For instance, shifts in tree-ring width (RW) have been linked to upward recruitment and ecotonal shifts in forests in the Pyrenees (Batllori and Gutiérrez, 2008). In the European Alps (Paulsen et al., 2000) treeline advances may be associated with radial growth response to minimum temperature thresholds and interannual climate variations overall. A tree-ring network of dominant conifer species from the French Alps found a common radial growth signal since 1930, which may be attributed to a mix of land-use changes, minimum temperature increases and nitrogen deposition (Rolland et al., 1998). At latitudinal treeline in the Ural mountains, forest expansion and species densification was linked to summertime (May-June) warming (Devi et al., 2020). Overall, several studies across Eurasia found increases in growth in agreement with warming, although models predict that this positive relationship between growth and temperature will diverge in the future (Camarero et al., 2020). Conversely, some treeline sites in boreal North America have exhibited a negative growth response and decoupling of RW to recent warming trends, likely due to temperature-induced drought stress (e.g. (D'Arrigo et al., 2008, 2004; Jacoby and D'Arrigo, 1995; Wilmking et al., 2005) and references therein).

By comparison to the northern latitudes, there has been little work at treeline and high mountain locations in South America, where tree-ring studies, in general, have been notably scarce (Andreu-Hayles et al., 2023; Groenendijk et al., 2025; Quesada-Román et al., 2022). The stability of tropical treelines and high-mountain communities under global warming has become of great concern in recent decades (Cuesta et al., 2020; Feeley et al., 2012, 2011; Macek et al., 2009; Young and León, 2006). A recent report for the IPCC (Hock et al., 2019) stated with high confidence that runoff from tropical glacier-melt has already reached its peak in some regions of the Andes and has led to decreases in agricultural yield in high mountain areas due to decreasing water availability (medium confidence). As for vegetation structure, climate change is projected to affect the extent and composition of Andean biomes, with greater effects at high-elevation areas in the tropical regions due to a consistent increase in temperature, while precipitation is projected to be highly variable with clear differences between eastern and western slopes along the Andes (Tovar et al., 2022).

In South America, forests found near the mountain peaks in the Andes Mountains are often referred to as 'treeline' or high mountain areas in literature (Hock et al., 2019; Körner, 2012; Young and León, 2006) and the term used herein is used to describe the upper range limits of the tree species found in the region. Plot studies in the Peruvian Andes-Amazon found that the position of Andean timberline is limited by seed dispersal (Rehm and Feeley, 2013). Tree-ring studies have been critical to understanding the climate response of high elevation forests in South America. A study from the Peruvian puna (upper Andes) presented the first tree-ring chronology of *Escallonia myrtilloides* L.phil. (Requena-Rojas et al., 2021), a species often found at treeline in the tropical Andes (Zapata, 2013), in which the authors showed radial growth is positively related to

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precipitation, and negatively correlated to temperature variability in this region. Also in the central Andes of Peru, *Requena-Rojas* et al. (2020) analyzed the tree rings from three *Polylepis* species, a genus that dominates the treeline forests of South America, and found these trees are slow-growing and sensitive to both current-year temperature and prior year precipitation changes. In subtropical regions, *Morales* et al. (2004) reported that changes in precipitation may be limiting growth in *Polylepis tarapacana* Phil. treelines in Argentina. On the other hand, in tropical montane forests in northern Argentina, the growth of different species appears to be regulated by temperature at the upper elevations of an altitudinal gradient (Ferrero et al., 2013). In the temperate *Nothofagus pumilio* (Poepp. & Endl.) Cuatrec. Andean treeline, temperature variability facilitates tree recruitment in northern and southern Patagonia, while the rate of seedling establishment can be strongly modulated by the interaction between temperature and precipitation driven by the Pacific Decadal Oscillation and the Southern Annular Mode, respectively (Srur et al., 2018, 2016). Yet, there was a radial growth decline in *Nothofagus pumilio* at a Chilean treeline site, where precipitation had increased (Álvarez et al., 2015), possibly suggesting a non-linear growth response of these forests to climate.

Here we describe a tropical treeline site for the species *Polylepis pepei* BB.Simpson (Simpson, 1979), growing high elevations (3700 m.a.s.l-4000 m.a.s.l.) in the Andes-Amazon corridor of Bolivia in South America. This site is located at upper forested limit of Bolivia's Madidi National Park (MNP), a hotspot for biodiversity within the vast Amazon forest, located just east of the Cordillera Real in tropical Andes. The hydroclimate of the Amazon-Andes ecotone in the MNP and broader region is primarily influenced by the South American Summer Monsoon (SASM), which peaks in the tropics during austral summer (December-February). Interannual to decadal sea surface temperature (SST) conditions in the Pacific and Atlantic Oceans (Paegle and Mo, 2002; Vuille et al., 2000) also impact climate in the region. Originating in the tropical Pacific, the El Niño Southern Oscillation (ENSO) system is the dominant mode of annual to decadal hydroclimate variability in South America and indeed the globe (e.g. Garreaud, 2009; Vera et al., 2006; Vuille et al., 2000). ENSO varies between warmer (El Niño) and cooler (La Niña) phases (Ropelewski and Halpert, 1987), and both extremes substantially impact precipitation and temperature conditions over tropical South America. The Atlantic sector also plays a major role in South American climate, as defined, for example, by tropical North Atlantic (TNA) and tropical South Atlantic (TSA) indices, which supply zonal moisture transport across tropical South America (Enfield et al., 1999; Good et al., 2008).

Complex topography in the Andean foothills contributes to a variety of microclimatic conditions and variable controls on tree growth, complicating efforts to directly compare large-scale patterns of climate and tree-ring variability (typically RW) within or between species in a stand. This complexity, and the forest dynamics of the humid Amazon Basin drive gradients in temperature and humidity, shaping patterns of vegetation (Fuentes, 2005), *e.g.* between the lower, drier forests near the Tuichi River (~850 m.a.s.l.) and the upper Andean treeline (~4400 m.a.s.l). At present, only two tree-ring studies have been published for the MNP: one for *Juglans boliviana* (C.DC.) Dode (14°40' S, 68°41' W; 1300 m.a.s.l.) in *Oelkers* et al. (2023) and another by *Andreu-Hayles* et al. (2015), the latter confirming the formation of annual rings in a *Pseudomedia rigida* (Klotzsch &

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H.Karst.) Cuatrec. cross-section (14°33′S, 68°49′W; 1000 m.a.s.l). There is thus much need for additional dendrochronological research in this area, particularly at treeline and the greater forested ecotone between the Andes and Amazon Basin.

In the MNP, mid-elevation woody species typically endure greater annual temperature and elevational ranges than lowland or highland species, based on monitoring studies (Montaño-Centellas et al., 2024). Species composition in the tropical Andes is often related to latitude and elevation as well (Malizia et al., 2020). Despite temperature-driven increases in tree mortality and species migration between 500-3600 m.a.s.l., above-ground biomass increased between 2003-2014 in eastern Andean forests (Duque et al., 2021). This increase was largely driven by intact old-growth forests, for which 30% of the regrowth was attributed to large-sized trees after disturbances. These studies provide information about spatial features of species distribution and abundance and carbon storage in the Andes-Amazon and specifically the MNP. The results herein add an additional, complementary dataset on annual radial growth patterns and climate sensitivity of an Andean treeline site not previously available.

The geographic range of *Polylepis pepei* (family Rosaceae; common name “Kenua” or “Queñoa”) spans from central Bolivia to northern Peru (Simpson, 1979) between 3550-4800 m a.s.l. (Espinoza and Kessler, 2022). The genus name *Polylepis* is derived from the Greek words ‘many layers’, describing multiple layers of compressed thin-bark sheets, a functional trait that allows these trees to adapt to cold temperatures at high elevation. The wide dispersion of leaves along the branches in *P. pepei* and its long fruit distinguish this species from other *Polylepis* types. *P. pepei* can reach significant age (>135 years) and the RW can be sensitive to prior and current-year climate (Jomelli et al., 2012; Roig et al., 2001).

The *Polylepis pepei* site investigated for this study is found between 3700~4400 m.a.s.l. in the western MNP (14°40′-14°43′S; 69°04′-69°06′W). Located near the small settlement of Keara, vegetation is characterized as Alto-Andino Yungueño (Upper Andean Yungas) forest (Navarro et al., 2010) with a seasonally humid climate. This study area was chosen in part because inventory plots already exist at this location, established by botanists from the National Herbarium in La Paz (Bolivia) and the Missouri Botanical Garden (USA). In the following sections we: i.) generate a new RW chronology for *P. pepei*, ii.) identify those climate variables (*e.g.* mean temperature or precipitation) that are the most limiting for annual growth and related trends and iii.) assess the impacts of extreme climate events on the RW variations. In so doing we demonstrate, through dendrochronological methods, the potential for this species to improve our understanding of growth trends and climate response of a tropical treeline in South America for dendrochronological studies.

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2 Materials and methods

2.1 Climate data

Climatic Research Unit (CRU) station-based monthly temperature data V4.07 (Harris et al., 2020) and ground and satellite-derived rainfall data from the Climate Hazards Infrared Precipitation with Station group V2.0 (CHIRPS, accessed 2023; Funk et al., 2015) were used to extract monthly climatology and computing monthly and seasonal correlations with RW. The CHIRPS v2.0 (0.05°) dataset was used due to its higher spatial resolution relative to the CRU precipitation (0.5°) dataset. CHIRPS does, however, cover a shorter period (1981-2025) than the CRU record (1901- 2023). Monthly and seasonal climate data were based on the nearest gridpoint to each of the sites: for CRU average, minimum, and maximum temperature (0.5°) the gridpoint 14.75°S, 69.5°W and for the CHIRPS precipitation gridpoints (0.05°) we used 14.725°S, 69.12501°W.

2.2 Site description and climatology

Fig. 1 shows the location of the study sites in Keara and the landscape and vegetation patches of the high elevation *P. pepei.* Climatology plots for the period 1981-2019 show that the wet season spans from ~October-April, with dry conditions (mean of 36-55 mm per month) from ~June-August (Fig. 1B). The monthly temperature data, limited by the spatial resolution of the CRU 4.07 gridpoint (0.5°×0.5°), shows mean temperature ranged from -8.2 to 14.5°C for the 1981-2019 period while mean annual precipitation (CHIRPS) was 1233 mm per year in Keara. Based on field sampling observations, the foliage of *P. pepei* may be considered evergreen.

Core samples of *P. pepei* were extracted in October 2012 and July 2019. The 2012 collection was from an open-canopy south-facing forest west of the small community in Keara (3795~4000 m.a.s.l.; Fig. 1C), which was originally surveyed during an exploratory expedition. The 2019 collection was made southeast of Keara in a remote, closed-canopy west-facing stand in a high-elevation valley called Waca-cocha (after a lagoon near the sampling site) (4000-4400 m.a.s.l.; Fig. 1D). Both sites feature seasonally humid, upper-montane forests, with persistent mist that evaporates during the day. These sites are largely monospecific, dominated by fragmented patches of *P. pepei* and small amounts of *Gynoxys compressissima* Cuatrec. trees. As noted, the bark of *P. pepei* consists of thick layers of compressed flakes that are red and brown in color, characteristic of the genus (Fig. 2A). The trees are shrublike, with twisted (and at times, multiple) stems.

Core samples were extracted from living trees using 2-threaded increment borers (5 mm in diameter). Cross sections of dead trees were sliced using a gas-powered chainsaw or standard saw-tooth blade. Stem diameter was measured at the same level that core samples were extracted (at breast height ~1.2 m). HOBO® temperature and relative humidity data loggers (https://www.onsetcomp.com/) were installed near the *P. pepei* trees at 14°40'S 69°06'W (4158 m.a.s.l.) during the 2012 visit to Keara and data was recorded hourly from 1 September 2011 to 2 September 2014. New HOBO sensors were installed in the 2021 and collected during fieldwork in 2023. Unfortunately, the system batteries failed within 9 months of the launch, and

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data was limited to only 20 September 2021 to 23 May 2022. Daily minimum, maximum and mean temperature and relative humidity were calculated from 20 September to 23 May (245 days) for the 2011-2012, 2012- 2013, 2013-2014 and 2021-2022 periods. Kernel density estimates were used to generate and compare probability distributions among the daily time series and nonparametric Kolmogorov-Smirnov (KS) tests (Kolmogorov, 1933; Smirnov, 1948) were conducted to determine the significance of the difference between the timeseries. Kernel density and KS tests were conducted using seaborn (Waskom, 2021) and SciPy (Virtanen et al., 2020) packages in *python*.

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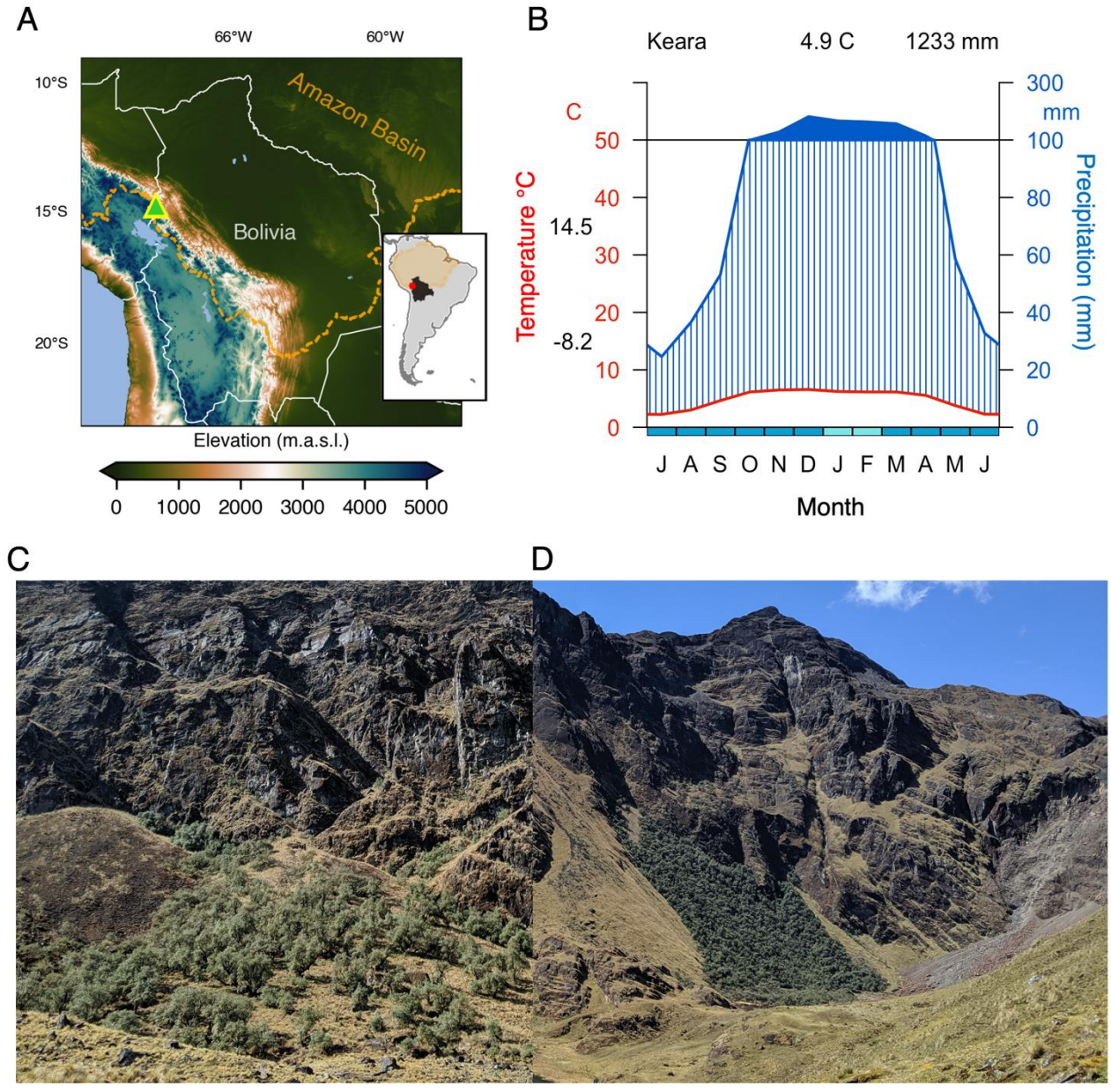

Figure 1: (A) Location of *Polylepis* site near Keara in the Eastern Cordillera of the Andes-Amazon ecotone. (B) Monthly climatology (1981-2019) for Keara based on minimum and maximum temperature from CRU 4.07 and precipitation from CHIRPS gridpoint data. Photos of open-canopy (KEPP; C) and closed canopy (SP; D) forest patches which were sampled at altitudinal treeline in Bolivia's MNP (~3700-4300 m.a.s.l).

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2.3 Wood processing and anatomical analyses

Wood samples were shipped to the Lamont-Doherty Earth Observatory (LDEO) in NY, USA for dendrochronological analysis. Cores and cross sections were finely sanded up to 1000 grit using an orbital sander and manually polished with microfiber paper. Most samples had surficial color differences within the stem, mainly reflecting variable transitions between the heartwood (darker color, middle to interior of the stem) and sapwood (the active, lighter wood, beyond the cambium layer towards the outside of the stem). The lighter sapwood made ring characteristics difficult to visualize.

To aid in identifying anatomical properties in the wood, histological (micro) cuts were performed according to techniques described in *von Arx* et al. (2016) using a WSL Core microtome (https://www.wsl.ch/en/services-produkte/microtomes/). *P. pepei* is an angiosperm with diffuse porous wood anatomy, which is typically harder to date than 'ring porous' wood, due to less distinct boundaries between the latewood of the prior year and the earlywood of the current year. *P. pepei* tree rings feature large, semicircular vessel elements in the earlywood that taper tangentially in size towards the transition to latewood, which has thicker, fiber-like tracheid cells (Fig. 2B; Roig et al. 2001).

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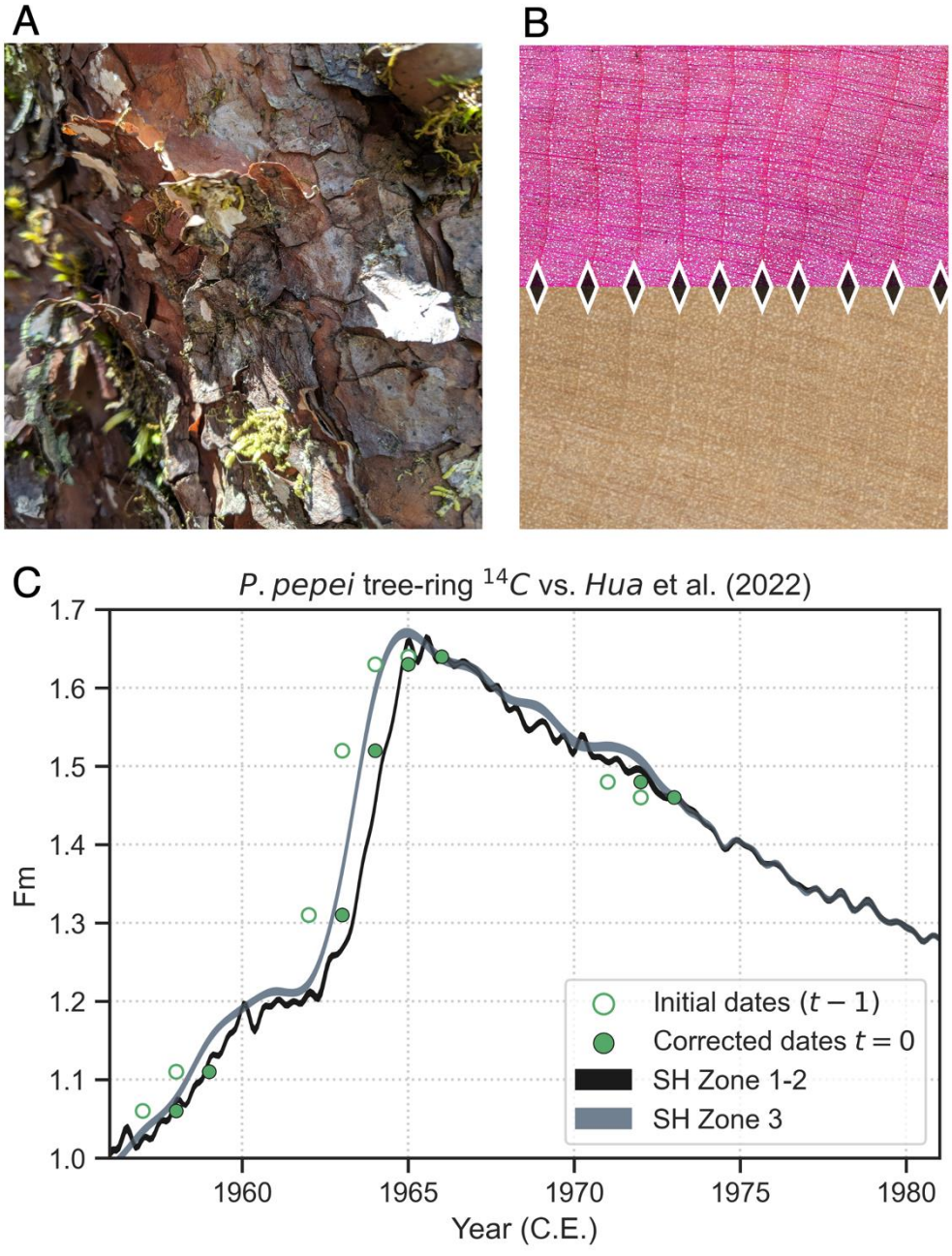

Figure 2: Tree stem (A) and ring anatomy (B) of *P. pepei samples.* The direction of growth for the core and anatomical images is from left to right (pith to bark) while black diamonds indicate the latewood/earlywood boundary between annual rings. (C) Radiocarbon data measured in alpha cellulose from selected rings of the *P. pepei* tree-ring chronology (green circles) plotted with the Hua et al. (2022) reference curves SH Zone 1-2 and SH Zone 3.

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2.4 Tree-ring chronology development

Tree rings were measured and dated visually using standard dendrochronological techniques (Stokes and Smiley, 1968). RW was measured digitally using the *CooRecorder* image analysis program (Cybis Elektronik, 2010). Before completion of the RW chronology, radiocarbon was conducted on a cross-section sample (SP20X; Figure 2C) collected in 2019 in the closed-canopy forest. This sample was chosen due to high correlation between the RW timeseries (1909-2018; r= 0.51) and 11 trees, named 'KEPP' from the 2012 expedition measured previously (1881-2012; overall correlation among samples: r= 0.50). Individual growth rings associated with the years 1957, 1958, 1962, 1963, 1964, 1965, 1971, and 1972 were sliced, extracted for cellulose, and processed for modern radiocarbon analyses to independently confirm annual resolution of the rings. All radiocarbon measurements were compared to the monthly SH $\Delta^{14}C$ radiocarbon curve (1950-2019 C.E.) from the designated atmospheric Zones 1-2 and 3 (SH Zone 1-2; Hua at. 2022).

Initial radiocarbon results (Fig. 2C) showed that ^{14}C measurements of SP20X were offset by 1 year in relation to the SH Zone ^{14}C curves. In the original *P. pepei* RW data generated with material collected in October 2012, the last ring (assigned as 2012) was not measured as it was considered an incomplete growth year. Upon a recent inspection of these samples, we observed that the final ring behind the bark did not always correspond to a partial ring as some trees had not yet started wood formation in 2012 (at least for the side of the stem where the core was sampled). Therefore, the calendar year assigned to the last complete ring for the KEPP RW samples were measured and corrected to 2011. This date-adjustment on the most recently formed ring behind the bark was confirmed after cross-dating RW from additional living trees collected in 2019 from the Waca-cocha forest. The updated KEPP RW chronology (n= 13 trees) showed high correlation with the newly developed SP RW chronology (n=15; 2019 collection) indicating good agreement among all RW series for the Keara *P. pepei* network (combined mean correlation, r= 0.46).

Once final calendar dates were assigned to the tree-ring samples, the Schulman convention (Schulman, 1956), which assigns each ring date to the year growth began, was applied. Individual RW time series from the 2012 and 2019 collection were detrended conservatively with age-dependent cubic splines (initial spline stiffness of 60 yrs) (Cook and Peters, 1981; Melvin, 2004) and RBAR variance stabilization to account for changes in sample size through time (Frank et al., 2006). So-called "standardized" chronologies, which were compared to the climate data, were constructed by taking the ratio of the fitted and observed RW values of detrended time series and combined using a robust Tukey bi-weight mean to produce a dimensionless 'standard' RW chronology (Cook et al., 1990). The so-called "residual" RW is the prewhitened chronology for the Keara samples (i.e. autocorrelation is removed) determined by the Akaike information criterion with autoregressive modelling on the individual time series (Akaike, 1974). The residual chronology was used for i.) identification of small or large outliers in the chronology (top 5 and 95 percentiles) and ii.) for analyses of the growth response of *P. pepei* to extreme ENSO events (see section 2.6).

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The subsample signal strength (SSS) was used to estimate the minimum sample size required to maintain a common signal (Wigley et al., 1984). SSS considers the declining population-size through time and is often used for climate reconstruction purposes (see discussions *Buras* et al., (2017) and *Wigley* et al. (1984)). The Pettit's (1979) changepoint detection test was used on the raw and standard RW to detect the timing and significance ($p < 0.05$) of recent trends in growth. Significance of the growth shifts was determined using a Mann-Kendall test. Changepoint analysis was conducted using the 'trend' package in *R* (Pohlert, 2016).

2.5 Temperature and precipitation signal in *P. pepei* growth rings

To determine the relationships between the RW timeseries, temperature, and precipitation, monthly and seasonal Pearson correlations (*r*) were computed via bootstrapped correlations using the 'treeclim' package in *R* (Zang and Biondi, 2015). Due to the covariance between temperature and precipitation in this region, we used the 'seascorr' function (Meko et al., 2011) to evaluate the significance of the correlation of temperature without the covariance with precipitation, and the other way around. Following methods of *Meko* et al. (2011), partial correlation coefficients with temperature are obtained by: i.) first performing a linear regression between RW and precipitation ii.) calculating bootstrapped, partial correlations between temperature and the residuals from this regression, which represent the portion of RW variability not explained by precipitation. Thus, partial correlations show the relationship between tree-growth and temperatures without the influence of precipitation. Spatial correlations (significance $p< 0.05$) were also computed to assess the extent of the temperature and precipitation signals of the RW records across space for the most significant season for each tree species.

2.6 Superposed Epoch Analysis

To investigate the effects of extreme climate events, including the potential impact of ENSO on tree growth, Superposed Epoch Analysis (SEA) was performed on the residual RW timeseries (Fig. 3B using the method originally described by *Haurwitz and Brier* (1981) and modified by *Rao* et al. (2019). SEA is widely used to statistically determine whether the effects of episodic events (e.g. ENSO events) on a response variable (in this case RW) are statistically significant or due to random noise. The *Rao* method uses 1000 random-sample double bootstrapping to quantify the RW response at the time of the event ($t= 0$) and several years after (in this case 4 years). Table 1 lists the years of known precipitation anomalies in tropical South America connected to El Niño (warmer) or La Niña (cooler) conditions in the Pacific Ocean.

The twelve top-ranked El Niño and La Niña years listed by the National Oceanic and Atmospheric Administration's Physical Science Laboratory (NOAA-PSL: https://psl.noaa.gov/enso/) based on the extended multivariate ENSO index (MEI.ext) (1871-2005) and MEIv2.ext (1979-2024) were used. This bimonthly dataset is based on the dominant modes, or principal components, of the entire tropical Pacific ENSO domain (30°N-30°S, 100E°-70°W) rather than any one region (e.g. Niño 3.4) and integrates observations of sea level pressure (SLP), sea surface temperature (SST), meridional (north-south) wind, and outgoing longwave radiation (MEIv2.ext) (see Wolter and Timlin, 2011). The ranking of extreme ENSO years is mainly

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defined by SST anomalies during DJF, coincidently when ENSO is phase locked with the peak monsoon season (Rasmusson and Carpenter, 1982).

El Niño		La Niña	
1983	1987	1974	2008
1998	1942	1917	1943
1973	1988	1956	1954
1931	1941	1976	1904
1992	1995	2011	1999
1966	1915	1989	1911
1919	2003	1910	1950
1926	1903	1971	1922
1958	1900	1951	1909
1897	1906	2000	2012
2010	2007	1974	1925
1983	1978	1917	1939
1998	1980	1918	1962

Table 1: Years of climate events selected for SEA. The two left columns show the 24 top ranked DJF El Niño or La Niña years based on the PSL Multivariate Extended ENSO index (1895-2015) (https://psl.noaa.gov/enso/past_events.html).

3 Results

3.1 Growth decline in a *P. pepei* tree-ring chronology

The *P. pepei RW* chronology from northern Bolivia (max elevation 4400 m.a.s.l.) spans from 1868-2018 is shown in Figure 3. Wood anatomy confirmed the earlywood and latewood diffuse-porous features of the rings (Fig. 2B) and radiocarbon measurements (Fig. 2C) in selected years before and after the radiocarbon bomb-peak confirmed that the growth periodicity is annual.

Due to extreme suppression in radial growth (Fig. 3B), only one or two cores per tree (out of 3-4 total) were able to be cross-dated and used for the final RW chronology. Nevertheless, the individual trees shared a common coherency in the RW patterns

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with a mean inter-series correlation of r= 0.46 (n= 28). The SSS metric indicated that *P. pepei* RW maintained a common signal especially between 1909-2018 (average age of the samples 92 yrs) with 22 samples needed to reach such a threshold (SSS > 0.85; Wigley et al. 1984). These trees were slow-growing with stem diameters (DBH) ranging from 10 cm to 54 cm (mean DBH 33 cm) with an average radial growth of 0.9 mm yr^{-1}.

Notable growth years since 1909 are denoted as triangles in the residual RW timeseries (Fig. 3D). The plot indicates extremely narrow or wide RW anomalies, mainly during the mid 20th century. Tree-ring values for 1957 and 1972 were in the 5th percentile for *P. pepei*, indicating unfavorable environmental conditions for growth, while the year 1999 showed common above-average growth. Raw RW has been declining steadily since the 1960s (Fig. 3A), especially after 1996 (p= 0.01 determined by the Mann-Kendall and Sen's slope tests), with a less pronounced trend in the standard RW series (Fig. 3C).

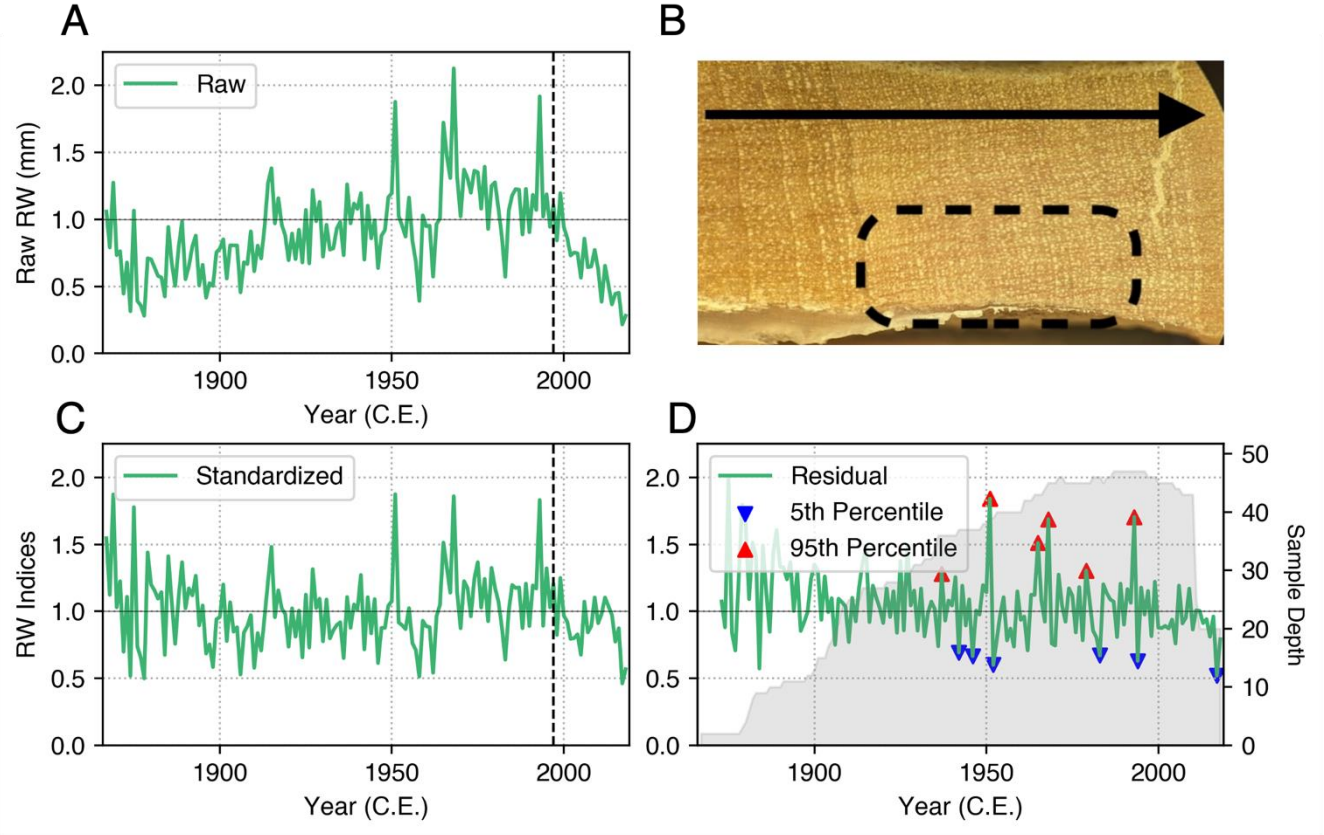

Figure 3: Raw (A), Standard (B), and Residual (C) RW chronologies compiled using *P. pepei* trees from Keara. (A) The raw data shows a decreasing RW trend since 1996/97 (black-dotted line). (B) An image depicts tight growth observed in a core sample where several rings are suppressed within a 4 mm distance (dashed circle). The black arrow indicates the direction of growth for this image (from left to right). The residual chronology is plotted with changing mean sample size (shaded color) for the site through time (D). Triangles on the residual timeseries denote the years within the top 5th (smallest growth rings; Blue color) and 95th (largest growth rings; red color) percentiles between 1909-2018.

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3.1 Monthly climate-growth relationships

Monthly correlation analysis for the period from July 1981 to June 2018 shows negative correlations with temperature and positive correlations with precipitation during growing seasons. *P. pepei* RW shows significant positive correlations with December-January precipitation from the prior wet season (Fig. 4A), with established strong and consistent negative relationships with mean temperatures for an extended season from November to March during the prior wet season (Fig. 4B). Negative, significant correlations were found between *P. pepei* RW and prior season November, January, and February minimum temperatures (Fig. 4C), as well as with December and January maximum temperatures (Fig. 4D). Partial correlations indicate the relationship between temperature and RW was more significant independent of precipitation variability (i.e. the negative mean and minimum temperature signal persists even when the covariance with precipitation is removed).

A robust, negative, temperature relationship with tree growth between 1981-2019 occurs during a period when minimum temperatures have continuously increased since (Fig. 4E). Further, the diurnal temperature range (i.e. difference between maximum and minimum temperature) depicts a significant negative trend in this region since 1967 which means the rate of increase for minimum temperatures has surpassed that of maximum temperature (Fig. 4F). It is interesting to note an extreme cold period observed in annual temperature data the late 1950s (Fig 4E) also corresponds with a growth suppression observed in *P. pepei* RW in Figure 3A and C.

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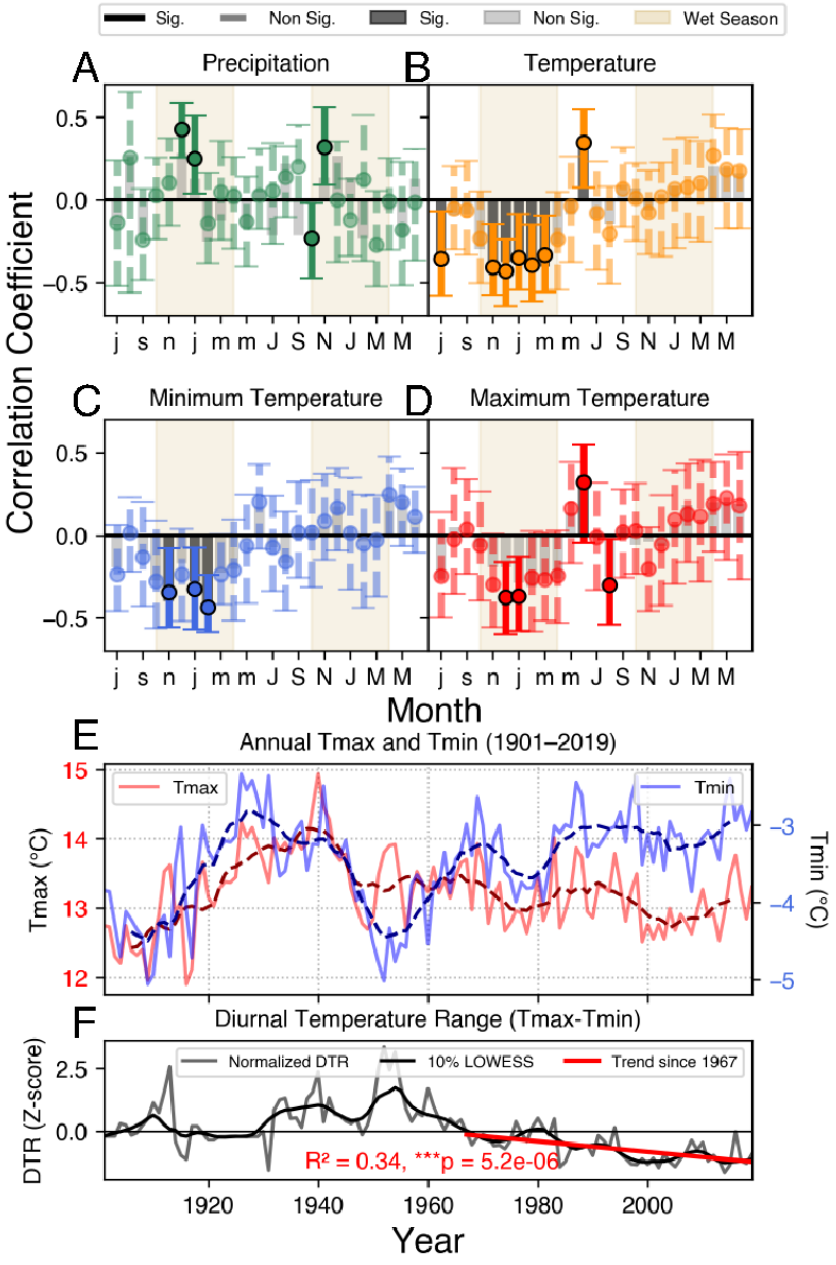

Figure 4: Monthly RW-climate correlations (1981-2019). Pearson correlations ($p < 0.05$) between precipitation from CHIRPS (A) and mean, minimum, and maximum temperatures from CRU (B-D) for grid points closest to the sites. The x-axis represents months beginning in July of the prior-year (t-1, lowercase letters) and extending to June of the current year (t=0, uppercase letters). Tan shading indicates the extended wet period (October- April) for this region of the MNP. Significant correlations are represented by solid lines. Solid gray bars show partial correlations with a given variable. (E) Annual minimum (blue line) and maximum (red line) temperatures between 1901-2019 for the nearest CRU gridpoint. (F) The normalized diurnal temperature range, calculated as the difference between Tmax and Tmin, is plotted with a 10-yr smoothing spline and linear trend line since 1967. The R^2 -value and significance of the 1967-2019 trend are included as red text.

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3.3 Seasonal and spatial climate sensitivity in *P. pepei* RW

The prior-year climate signal in *P. pepei* RW at treeline is even more robust when compared to seasonal-averages of climate averaged for 2-months or more between 1981-2019 (Fig. 5). Correlations for 2-6 month averages reveal significant relationships ($p < 0.05$) between RW and precipitation (Fig. 5A) or temperature (Fig. 5B). The standard RW chronology correlates the strongest with the 3 and 4-month averages of climate, particularly for prior-year OND and NDJ for both temperature and precipitation. Correlations include a positive relationship to precipitation with OND r=.41 and NDJ r= 0.40 and temperature OND $r = -0.45$; NDJ r= -0.47 respectively. Because the highest correlation with climate included the negative NDJ relationship to temperature, this season was selected for illustrating regional correlations in Fig. 5C, D.

Spatial correlations reveal the broader, regional extent of the climate signal recorded in the *P. pepei* RW record between 1981 and 2019 (Fig. 5C, D). Regarding precipitation, *P. pepei* RW is positively correlated to seasonal precipitation in most of tropical South America (Fig. 5C). The strongest precipitation signal (indicated by black dots) is observed locally, extending to the eastern flanks of the central Andes in Bolivia and drier regions in the Southern Altiplano. Spatial patterns of correlation between *P. pepei* RW and gridded temperatures show significant and negative ($r > -0.50$) correlations between 1981 and 2018 across most of tropical South America during November to January (Fig. 5D). Note because the gridpoint data for the site confirmed temperature and precipitation are negatively correlated during the summer season (November-January; r= -0.40, $p < 0.05$), the negative correlations with temperature would reflect the indirect effect of temperature on water availability. The spatial variability of RW to precipitation account in figure 5D reflects heterogeneity of precipitation data in mountain areas, whereas the temperature fields are more uniform.

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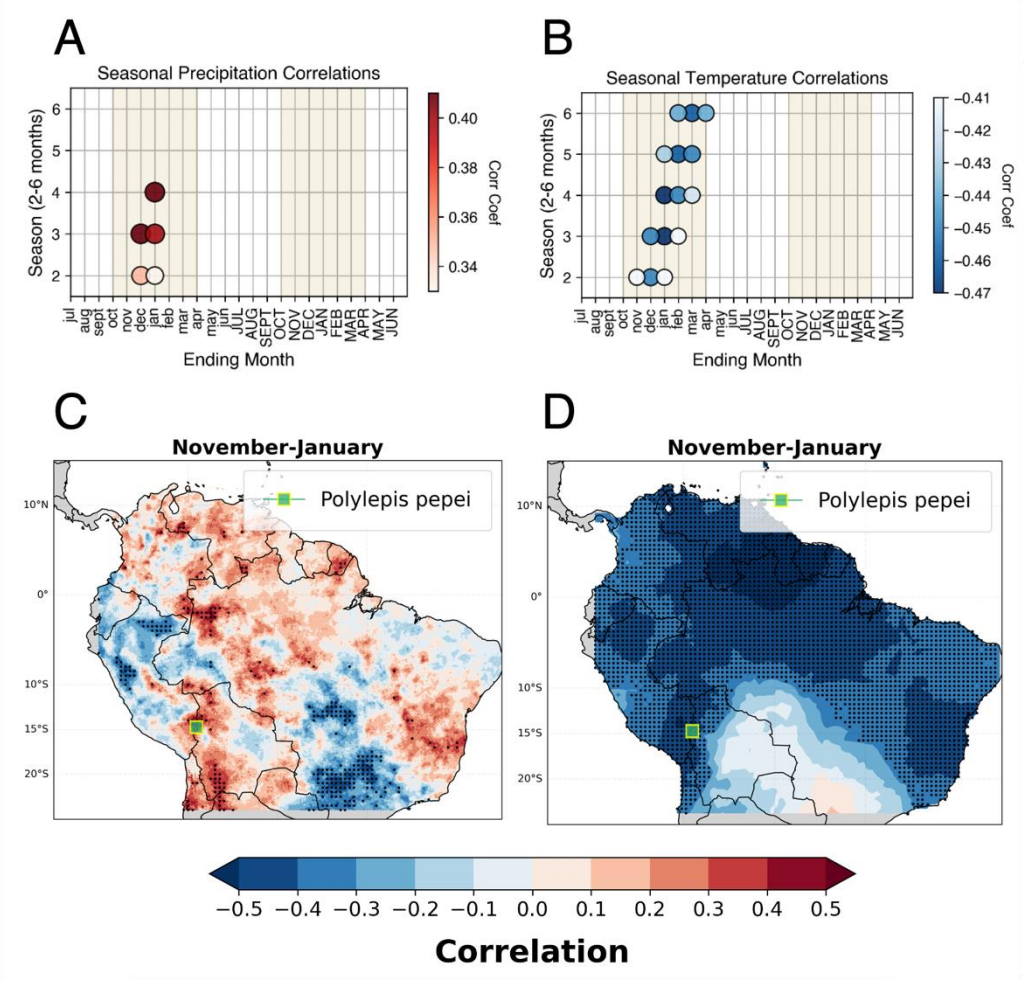

Figure 5. Precipitation (A) and temperature (B) seasonal correlations are shown. The color of the circles represents the value and sign (+ or -) of Pearson correlations (see right-side color bars for r values' reference). The x-axis represents the months in which the averaged seasons end (e.g. if the circle is in January, the season is November-January. The prior-year period of months is represented as lowercase letters and the current period is represented as uppercase letters. The yellow shading represents the wetter period between October-April based on the monthly climatology. Spatial correlations between RW- NDJ precipitation (C) and temperature (D) for the period 1981-2019. Black dots represent the areas where there are significant correlations ($p< 0.05$). RW is lagged t-1 to account for the seasonality of the prior-year growing season. The NDJ season was selected based on moving bootstrapped seasonal correlations with gridpoint data in (A,B).

3.4 Daily temperature and relative humidity recorded near the *P. pepei* treeline

Probability density functions showed changes in the distribution of daily relative humidity and temperatures and among three years between September 20-May 23. Minimum, maximum and mean relative humidity (RH) in 2021-22 was significantly lower ($p<0.0001$) than in 2011-12, 2012-13, and 2013-14. A significant increase in minimum temperature range was reported between the 2021-22 wet season as well as the three other wet seasons ($p< 0.0001$), while non- significant differences were observed between the 2021-2022 dataset and maximum temperatures in 2011-12 ($p= 0.78$), and the mean temperatures in

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2012-13 (p= 0.33) and 2013-14 (p= 0.16). Interestingly, daily maximum temperature in the 2021-2022 year is significantly lower than the 2012-13 and 2013-14 seasons (p< 0.0001). Although 2011-2012 was considered a major La Nina year (Table 1), the distribution of daily relative humidity values of 2012-13, 2013-14 are similar to the 2011-12 period, and all three seasons had higher values than of (min, max, mean) RH than in 2021-22. Conversely, the range of minimum and maximum temperatures were higher overall than the other three years.

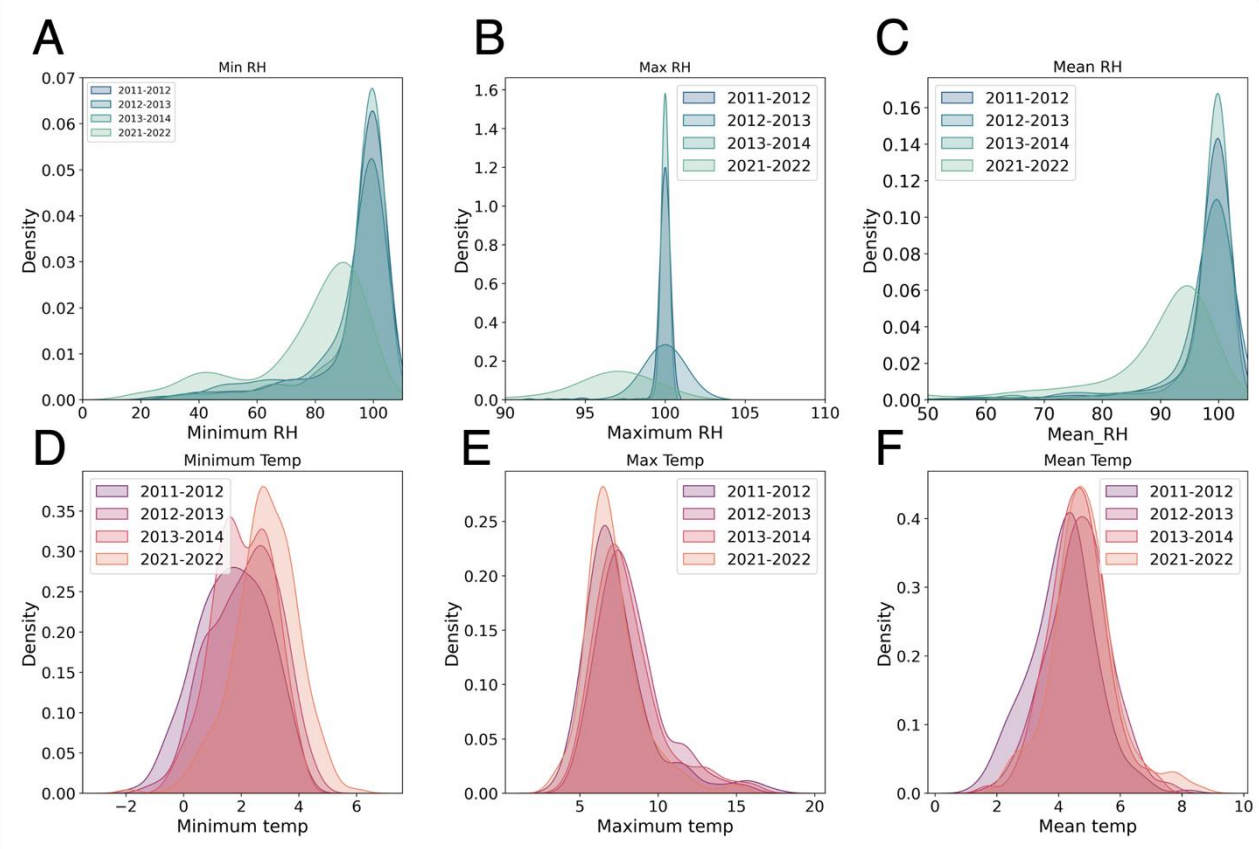

Figure 6: Probably density plots of daily relative minimum, maximum and mean relative humidity (RH) (A-C) and temperature (D-F) recorded for the wet season (September-May) of the years 2011-2012, 2012-2013, 2013-2014 and 2021-2022.

3.5 Growth response of treeline *P. pepei* to extreme climate events

The impact of extreme DJF-ENSO events (Table 1) on residual RW (Fig. 3B) were conducted using SEA methods (Fig. 7A, B). Normalized growth anomalies (Z-scores) are shown for the four years before and after the event (t=0) to assess the timing and significance of the RW anomaly. The impact of drought during El Niño years shows a lagged (t+1) and negative growth response (p< 0.10; Fig. 7A), which means that one year after the event, *P. pepei* decreased radial growth. There are also significant 3-year lagged negative responses during the extreme DJF-La Niña years, respectively (Fig. 7B).

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Figure 7C shows boxplots of mean annual precipitation from the CHIRPS (1981-2022; ~5 km resolution) and CRU (1901-2022; ~55 km resolution) products for the top 24 years of extreme DJF-ENSO events (Table 1), while Fig. 7D includes annual mean temperature from the CRU gridpoint. Regardless of the time span and spatial resolution, both precipitation datasets show that the 24 El Niño extremes during the peak wet-season (DJF) are linked to drier conditions in the study region, and DJF-La Niña events were associated with wetter annual precipitation overall. CRU temperature data showed El Niño conditions were also warmer (Figure 7D). Overall, warmer and drier DJF ENSO events were associated with a smaller growth ring in the following year for *P. pepei*.

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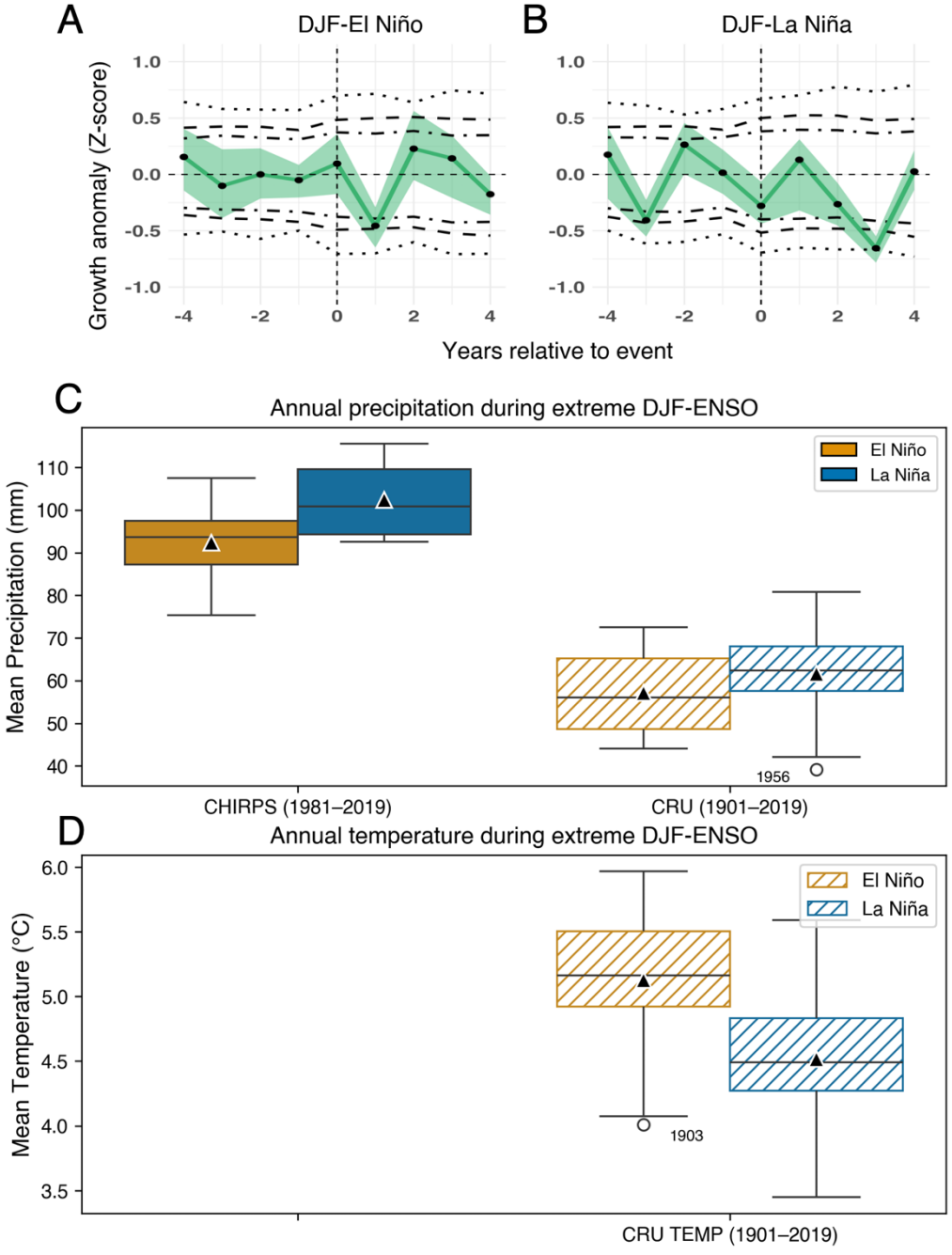

Figure 7: Superposed epoch analysis of the residual RW response before (*t*- 4), during (*t*=0), and after (*t*+4) years of known to the top 12 DJF-El Nino (A) and DJF- La Niña events (B). Dashed black lines represent confidence intervals (two-tailed significance thresholds: 90%, 95% 99%) based on double bootstrapping while the uncertainty of the response is depicted as green shading. (C) Annual precipitation boxplots using the CHIRPS (left) and CRU gridpoints for the (top 24) years of extreme DJF-ENSO. using the nearest. El Niño-related events are represented in orange colors, while La Niña is shown blue. (D) Annual temperature during these events using CRU gridpoint data.

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4. Discussion

4.1. Radial growth decline and climate sensitivity of a tropical treeline site in Bolivia

Annual RW chronologies of *P. pepei* from a high Andean, seasonally humid forest in northwestern Bolivia have been presented and analyzed. A new annually-dated tree-ring chronology for the MNP provides novel and robust information about tree growth at the tropical treeline (4000-4400 m.a.s.l). in an understudied biodiversity hotspot in South America. There is a decline in mean radial growth that is particularly pronounced since 1997 (Fig 3C). This decline can also be seen visually in some samples from the drier (talus-slope) site in Keara (Fig 1C). The potential human influence on RW for trees in Andes-Amazon forests should be considered when evaluating the growth patterns of these Andean forests. For the *P. pepei* near Keara, the lower elevation open-canopy subset (~3700-4000 m.a.s.l.; north and west of the talus slope site) showed possible fire scars in the 1940s and clear forest fragmentation related to cattle ranching. This subpopulation is likely more threatened by human activities than the closed canopy site between 4000-4400 m.a.s.l. (Figure 1C). Nevertheless, dendrochronological approaches made it possible to explore the climate signal recorded in the annual rings.

We found that *P. pepei* RW is limited by prior-year temperature variability and precipitation during the wet season, with larger RW in the subsequent growth year when it was wetter and colder. Although RW-precipitation correlations were robust, our results suggest that this *P. pepei* network is likely more affected by temperature-related moisture-stress changes, as would be expected particularly at elevational treeline (Fritts, 1976). Extreme El Niño and La Niña events during the peak summer monsoon bring dry/warm and wet/cool conditions may amplify or reduce the effect of precipitation and temperature variability on *P. pepei* growth. Overall DJF-El Niño events had a significant negative impact on radial growth of *P. pepei* at our study site. Although La Niña SEA were-inconclusive, the lagged 3-year negative effect may be related to the occurrence of El Niño events in years after La Niña. DJF events were selected for analyses because it is the mature phase of the summer monsoon where the tropical Andes receives 70% of annual rainfall, but annual or NDJ related ENSO events may show larger impacts on trees studied herein.

Future advances of this treeline (Fig 1C) are unlikely due to local geomorphologic constraints (Macias-Fauria and Johnson, 2013) and thermal niches (Kessler et al., 2014; Körner and Hoch, 2023) that are requirements for subalpine recruitment. Studies of *P. pepei* sites between 3800~4300 m.a.s.l. in Peru (Kessler et al., 2014) and Bolivia (Hoch and Körner, 2005) recorded soil temperatures (> 5cm) ranging from 3-5°C during the wet season, highlighting the cold-adapted conditions of this species in the eastern tropical Andes. Despite local soil conditions and human activities that impact the shape of Andean treelines like those for *Polylepis* (Bader et al., 2007), the optimal thermal niche for woody plants is the leading abiotic factor that defines the spatial extent of such forests across the globe (Hertel and Wesche, 2008; Hoch and Körner, 2005; Körner and Hoch, 2023). In addition to the existing constraints for treeline advances, we report on the adverse influence of increased temperature on tree growth. We also report a growth decline that could be the result of these constraints. Although the future extent of the *P.*

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pepei forest under is uncertain, our study provides insight into the limiting factors to radial growth at a tropical Andean treeline in Bolivia since 1981.

4.2. Changes in minimum temperatures and relative humidity at the *P. pepei* treeline in Bolivia

Increases in minimum temperature may be reducing moisture availability in high-elevation Andean tropical sites. Although the shortness of the high-resolution CHIRPS dataset limits our interpretation of the role of climate before 1981 on observed growth trends, the long-term CRU temperature datasets show a significant decline in the diurnal temperature range (Fig. 4F), driven by rising minimum temperatures (Fig. 4 E).

In agreement, daily climate recorded in the data loggers in the *Polylepis* forests (Fig. 6) confirmed September-May in 2021-2022 as having significantly warmer nighttime/early morning conditions (reflected by minimum temperatures) in comparison to the period 2011-2012 ($p < 0.0001$). Despite the fact that higher temperatures increase the capacity of the air to hold more water vapor (i.e. "Clausius-Clapeyron" relation), if the moisture supply does not increase proportionally the humidity will decrease. This is indeed what was observed from the RH data recorded *in situ* that showed significant decreases in minimum, maximum and mean RH at our study forests. In short, a decrease in RH alongside an increase in temperature suggests that the capacity of air to hold moisture has outpaced the actual moisture content, making the air drier despite higher temperatures. Further, analyses of gridded CRU temperature and local CHIRPS precipitation data near the *P. pepei* site are inversely correlated during the extended wet season (October-April). For example, if there is less cloud cover (and less precipitation) there is higher solar irradiance and temperatures, which may limit the photosynthetic capacity of these trees at higher elevations (García-Núñez et al., 2004; Hoch and Körner, 2005; Jaramillo, 2015). Although it is possible the timing of the mechanisms controlling primary (photosynthesis) and secondary growth (wood formation) may not occur at the same time, the RW-climate correlations show there is less radial growth if is warmer and drier than when it is cooler and wetter (Figs. 4 and 5).

Minimum temperatures influence convection, as rainfall in the Andes-Amazon ecotone largely occurs in the afternoon/night as radiative cooling drives cold air downslope and converges with rising warm moist air from the tropical lowlands (Garreaud, 1999; Junquas et al., 2018; Romatschke and Houze, 2010). Known as 'orographic precipitation', this process is key for rainfall distribution across elevations in the Andean foothills like our study area (Arias et al., 2021; Chavez and Takahashi, 2017). A study on southern Peruvian rainfall hotspots (which included our study area in MNP) used radar-based precipitation data to analyses the relationship between rainfall and terrain elevation from 1998 to 2012. Maximum precipitation was found to peak annually between 1000-1300 m.a.s.l., with a vertical decrease in moisture distribution above 3000 m.a.s.l. (Chavez and Takahashi, 2017). However, if minimum temperatures are warmer, the radiative cooling effect is weaker, which means that warm, moist air may converge at lower elevations (Romatschke and Houze, 2010), below our treeline *P. pepei* site.

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Therefore, the increase in annual minimum temperatures since the late 20th century in addition to an observed weakening of upper-level easterlies towards the Andes (Segura et al., 2022) may have contributed to reduced orographic convection, and thus moisture availability at high elevations, potentially limiting growth of *P. pepei*. Although our dataloggers covered a short-term window, the results provide *in situ* evidence of significant increases in minimum temperature and reductions in RH between the 2011-2014 and 2021-2022 seasons (September-May).

4.3. Growth declines related to changes in local environmental conditions

Besides inhibiting moisture convergence and transport from lower elevations, warmer minimum temperatures could also affect the local soil-water balance by increasing transpiration, respiration rates and overall water loss in this forest (Sierra et al., 2022). From an ecophysiological perspective, respiration rates increase with rising temperatures. Without photosynthesis at night, this condition increases the amount of carbon (and water) released to the atmosphere and could negatively impact the life cycle and carbon sink capacity of the forest. A global analysis of tropical tree longevity using tree-ring and other data found that tree mortality is increasing in all tropical biomes due to heat-related water stress, with increased evaporative demand at the leaf level (Locosselli et al., 2020). The loss of smaller trees at the mid-high elevations has also been observed in a forest-biomass plot study across the Andes-Amazon (Duque et al. 2021).

It is important to note that the MNP and vicinity is not strictly undisturbed. In fact, illegal mining and logging activities have deteriorated forest structure and health, with increasing loss of forest cover in recent years (Finer and Mamani, 2023). Prior to the designation of Madidi as a National Park in 1995, large swaths of economically-valuable trees along riverbanks (e.g. *Amburana cearensis* Smith) were harvested for timber (Macía, 2008). Today, *P. pepei* studied herein, is at great risk of endangerment due to habitat loss related to fires and land conversion for cattle ranching (Espinoza and Kessler, 2022; Kessler et al., 2014). These losses of primary forests have severe implications for carbon storage capacity, ecosystem function, and land stability, all critical factors for the survival of native inhabitants. Herein, efforts were made to minimize potential impacts of land use and disturbance in field sampling, but ecosystem disturbances in certain regions of the MNP were nevertheless observed.

Overall, the negative correlations with temperature may reflect the indirect effect of temperature on water availability. High temperatures increase forest evapotranspiration as well as direct evaporation from the soil, thus reducing the amount of water available for growth. Furthermore, due to the observed increase in minimum temperature the high elevation *P. pepei* forest may be experiencing higher respiration rates at the same time receiving less moisture due to a reduction in orographic precipitation to higher-elevations. This may be resulting in the observed growth decline in most of the sampled trees. Although the changepoint tests detected increases in the long-term minimum temperature (e.g. 1967) that occurred earlier than the *P. pepei* RW significant decline (e.g. 1997), we may consider first that the statistics are just detecting a turning point in the data, and second that biological processes do not always occur at the same time as changes in environmental variables. In other

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words, *P. pepei* response to changes in minimum temperatures and RH do not have to be linear and can be determined by thresholds. Nevertheless, the correlations with climate are robust and as described below, the timing of the decline may signify a response to regional shifts in hydroclimate patterns observed in the greater tropics of South America.

4.4. Large-scale climate variability impacting tree growth in tropical Andean treelines

The recent decline observed at our *P. pepei* site in MNP (14°S) near the southwestern Amazon Basin aside from factors described above may be also influenced by broader scale hydroclimate changes. Negative growth at Andean treelines has been reported by *Morales* et al. (2023) of *P. tarapacana* tree rings from southern Peru and Chile (>17°S; 4657-4800 m.a.s.l.). The authors developed a NDJ precipitation reconstruction from these trees noting a drying trend since 1997 that is unprecedented within the time span from 1625 to 2013 CE covered by this 389-year chronology, and which was attributed to drought conditions that have increased in frequency and severity since the 1970s. Studies of *P. tarapacana* conducted in other areas of the Altiplano suggest that the species germination and distribution is projected to decrease as vapor pressure deficits, temperatures, and overall aridity increases (Cuyckens et al., 2016, 2016; López et al., 2022). Southwest of our *P. pepei* site, in the central Andes of southern Peru ice proxy data indicated recent surface warming in the tropics that appears unprecedented in 5000 years (Thompson et al., 2006). In November 2009 near Keara, temperatures were so warm that a catastrophic glacial lake outburst flood eliminated roads, livestock, and structures in the small community (< 3800 m.a.s.l; Hoffmann and Weggenmann, 2013).

Several observational climate studies have reported a delay in the onset of the wet season in the tropical Andes and southern Amazon Basin (> ~15°S), especially since the 1990s (Espinoza et al., 2016; Fu et al., 2013; Marengo et al., 2011). One possible explanation is that an intensification of the atmospheric Hadley circulation, related to warming in the (northern) tropical Atlantic Ocean, has led to an interruption of upward flow from the Amazon during the dry-to-wet period (Beveridge et al., 2024; Espinoza et al., 2021, 2019; Yoon and Zeng, 2010). In particular, *Ronchail* et al. (2018) and *Espinoza* et al. (2019) found a significant increase in dry-day frequency between September-November (austral spring) which marks a delay in the timing of the wet season in Peru and Bolivia since the late 1990s. All these studies, which are based on *in situ* station and gridded climate records, argue that warming of the Atlantic, land-surface changes in the Amazon, and wind anomalies are the primary factors contributing to decreased specific humidity in the central tropical Andes. However, these mechanisms are complex, and their impacts are spatially variable.

Overall, the recent negative trend of *P. pepei* RW studied here may be related to temperature-driven moisture trends observed on both local and regional scales. This study herein has demonstrated the dendroclimatic potential of this species at a treeline from the most biodiverse region of the world (Muller, 2017) and provided insight into the growth response of a tropical forest in South America to climatic change. High mountain paleoclimate proxies, like our *P. pepei* site, independently show how temperature-driven humidity changes modify natural environments in tropical South America.

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5. Conclusions

We reported a significant decline in radial growth in a tropical treeline in Bolivia composed by *P. pepei,* in contrast to growth increases that have been observed in mid-elevation species from the same area of MNP (e.g. *Juglans boliviana*, Oelkers et al. 2023). Several studies have reported on the observed increased dry season length in the southern Amazon and central tropical Andes, while lowland areas such as the northern Amazon and Andes-Amazon basin (< 2000 m.a.s.l.) are becoming wetter in the wet-dry season (Arias et al., 2021; Espinoza et al., 2021, 2019; Malhi et al., 2008; Zanin and Satyamurty, 2020). Our results show that the observed decline in *P. pepei* treeline may be associated with increases in minimum temperatures driven a reduction of available moisture through different mechanisms resulting in drought stress. Climate-growth correlations showed *P. pepei* RW was smaller if the prior-year wet season was warmer and drier at the Keara treeline. By expanding the *P. pepei* network in Keara and the tropical Andes, there is the potential for reconstructions of precipitation and temperature, and thus drought, for the Central Andes. This would be the first of its kind for northern Bolivia, extending the limited station records (~30 years in length on average) back to at least the 1800s. The results presented herein have provided insights into the response of a tropical Andean treeline in an era of global warming, increasing climate extremes, and human activities, and support the use of dendrochronology in future research of tropical forests.

Code and Data Availability

R and python codes will be deposited on a Zenodo Archive. The final RW chronology from Keara will be made available on the NOAA International Tree-ring Database.

Author contribution

Co-authors LAH, DRC, MRC, MEF, RO, ET collected tree samples in Keara. Tree-ring dating, measuring, and analyses was conducted by corresponding other RO. Site images for figure 1 were taken by RO.

Competing interests

The authors declare that they have no conflict of interest

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