# Radial growth decline in a tropical Andean treeline in Bolivia

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**Abstract.** The ~~impacts~~impact of rising temperatures ~~in~~on tropical treeline ecosystems remains understudied. Here we report on ~~a remarkable decline in~~ the ~~radial~~ growth history of *Polylepis pepei* BB.Simpson trees growing in Madidi National Park, a tropical ~~tree species that grows in a monospecific~~ forest setting at ~~the~~ elevational treeline in the Andes-Amazon ecotone of Bolivia. Using dendrochronological methods, we developed an annually ~~-~~resolved tree-ring width chronology spanning from 1850 to 2018 C.E. To our knowledge this is the longest tree-ring record ~~of annual tree growth (169~~(168 yrs) for this species. ~~This~~ The standardized ring-width chronology revealed a significant ~~(p= 0.01)~~ radial growth decline ~~in *P. pepei*~~ after ~~1997, which was also observed in other high-elevation *Polylepis* forests of tropical South America (> 17° S; 4600 m a.s.l.). Between~~the 1962-1963 growth ring (i.e. 1963-2018). From 1960-2015, ~~*P. pepei* RW was mostly regulated by prior year minimum temperature and mean precipitation variability during the wet season (~November-March). RW-climate correlations suggest the observed growth decline at this tropical treeline is likely due to temperature driven moisture stresses. Smaller ring-width was~~smaller ring-widths were associated with drier and warmer conditions ~~in the forest~~during the previous wet season (~November-March), while wetter and cooler conditions led to enhanced growth in the following year. ~~Between~~*P. pepei* radial growth decline occurred at the same time a significant increase in minimum temperature and decrease in precipitation and diurnal temperatures was observed both locally and regionally across tropical South America between 1960-2015~~, minimum temperature significantly increased during the wet season, while precipitation decreased.~~ These climate trends ~~observed in our~~



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~~study region in the Madidi National Park~~ at treeline may indicate a reduction in moisture convergence and transport to such higher ~~elevations where our forest is located.~~elevation settings in the Andes. If temperature ~~continues~~continue to rise at current rates, one of the highest-elevation tree species on the globe, *P. ~~pepei~~, ~~could face severe consequences~~pepei*, may continue to decline leading to forest mortality and jeopardizing the survival of treeline ecosystems.

## 1 Introduction

South American treelines or 'high montane' forests refer to the upper range limit of tree growth within the Andes Mountains, and are the longest, most biodiverse ecotone in the tropical latitudes (Körner, 2012; Young and León, 2006; Zelazowski et al., 2023). Whether or not such tropical treelines will remain stable under global warming is a topic of great concern due to increasing anthropogenic and climate-related pressures that threaten South American forest dynamics. In recent decades, land-use change and warming temperatures have led to observed shifts in species composition, distribution and increased tree mortality in the tropical Andes treelines (Cuesta et al., 2020; Feeley et al., 2012, 2011; Macek et al., 2009; Young and León, 2006). In southern Peru, ice core records indicated that recent surface warming in the central Andes has been unprecedented in the past 5000 years, and land-atmosphere models suggest the net primary production of upper montane forests in South America will decrease as temperatures increase(Fajardo et al., 2019; Nagy et al., 2023; Thompson et al., 2006). Despite the value of these modeling and plot-based studies of tropical South American treelines, our knowledge of forest age, annual growth patterns, and historical response to climate trends remains limited.

Dendrochronological studies in tropical South America are generally scarce (~8°N-24°S) but have been key in reconstructing long-term tree-growth and climate variability in the Andes (Andreu-Hayles et al., 2023; Groenendijk et al., 2025; Quesada-Román et al., 2022). ~~The stability of tropical Andean treeline communities under global warming has become of great concern due to observed shifts in forest composition, distribution and increased tree mortality in recent decades (Cuesta et al., 2020; Feeley et al., 2012, 2011; Macek et al., 2009; Young and León, 2006).~~ Tree-ring studies have reported that several Andean treeline species form annual growth rings and that the width of the rings (i.e. RW) are sensitive to precipitation and/or ~~temperature (Fajardo et al., 2019; Nagy et al., 2023; Thompson et al., 2006). Despite the value of these modeling and plot-based studies of tropical South American treelines, our knowledge of forest age, annual growth patterns, and historical response to climate trends remains limited.~~

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~~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 tropical treeline (Zapata, 2013), in which the authors showed radial growth is positively correlated to precipitation, and negatively correlated to~~ temperature variability ~~in this region. In the central Andes of Peru, *Requena-Rojas* et al. (2020) analyzed the tree rings from three *Polylepis* species, and found these trees are slow-growing and sensitive to both current-year temperature and prior year precipitation changes. In subtropical regions, prior-year moisture availability was the dominant limiting factor for~~e.g. *Escallonia myrtilloides, Polylepis tarapacana* ~~Phil. treelines in Argentina, based on RW-climate correlations spanning 1934-1980 (~~, *Polylepis reticulata* (Alvites et al., 2019; Argollo et al., 2004; Morales et al~~. 2004) On the other hand, the growth of several tropical montane species in northern Argentina appears to be regulated only by temperature at the upper elevations of an altitudinal gradient (Ferrero et al., 2013). Although seedling recruitment of *Northfagus pomillo* is driven by temperature~~ ., 2004; Requena-Rojas et al., 2021, 2020). The relationship between annual RW in treeline species and local climate variability~~, the rate of seedling establishment was limited by overall moisture conditions in Patagonia (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 of~~ in the tropics can vary depending on the latitudinal and elevational position of the forest along the Andes (e.g. Polylepis pepei ~~BB.Simpson (Simpson, 1979), growing high elevations (3800–4000 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 just east of the Cordillera Real in the Andes Temperature and humidity gradients shape unique ecotones in the *MNP* including diverse seasonally dry forests near the Tuichi River (~ 850 m.a.s.l.) and humid monospecific forests at Andean treeline (~ 4400 m.a.s.l.). The hydroclimate of the MNP (and Andes-Amazon) is primarily~~in northern vs. Southern Bolivia)(Jomelli et al., 2012; Roig et al., 2001). Hydroclimate conditions in South America are largely influenced by the ~~South American Summer Monsoon (SASM), which peaks in the tropics during austral summer (December-February). Inter-annual to decadal sea surface temperature sea-surface temperature (SST) conditions in the Pacific and Atlantic Oceans also impact climate in the region (Paegle and Mo, 2002; Vuille et al., 2000). 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.~~). In addition to inter-annual and decadal fluctuations in temperature and precipitation, circulation patterns related to the timing and strength of the South American Summer monsoon, are modulated by ENSO as well (Garreaud, 2009; Vera et al., 2006; Vuille et al., 2000). ~~-~~ENSO-related ~~anomalies~~ SST anomalies have contributed to extreme weather events in South America such as seasonal drought, flooding, and other geohazards (Vera et al., 2006; Vuille et al., 2000). ~~Tree~~At the central tropical Andes treeline, *Polylepis tarapacana* tree-ring width (RW) and oxygen isotopes have recorded these ~~extreme~~extreme events ~~at treeline *P. tarapacana* in the central tropical Andes~~ and provided year-to-year to centennial records of ENSO variability ~~overall(Christie et al., 2009; Crispín-DelaCruz et al., 2022; Rodriguez-Caton~~

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et al., 2022) Currently there is no information on the impacts of such ENSO-related climate extremes on *Polylepis pepei* tree-rings, or for treeline sites within the MNP.

*Polylepis* is the dominant genus for tropical Andes treelines and represent the highest elevation tree species in South America (Pyre et al. 2025; Simpson 1979). The name *Polylepis* is derived from the Greek word 'many layers', which refers to the multiple sheets of thin, compressed of bark useful for thermal insulation at high elevations (Rada et al. 2001; Rodriguez-et al. 2021 However, as the climate warms, frost tolerance may no longer be an advantageous trait, and some studies predict that the germination and spatial distribution of *Polylepis* at the treeline will decrease as vapor pressure deficits, temperatures, and overall aridity increase in the Andes (Cuyckens et al., 2016; López et al., 2022). The geographic range of *Polylepis*To date, it is not known whether such projected decline has already occurred in treeline *Polylepis* populations.

Here we describe a new tree-ring record of *Polylepis pepei* from a treeline site at the Madidi National Park (MNP) in Bolivia, a hotspot for biodiversity in the southwestern Andes-Amazon region in Bolivia (BB.Simpson)(Simpson, 1979). The geographic range of *P. 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 wide dispersion of leaves and long fruit distinigushes *P. pepei* from other *Polylepis* species. Tree-ring studies in Bolivian and Peru have shown *P. pepei* can reach significant age (>135 years) and the RWring-width can be sensitive to both prior and current-year climate variability (Jomelli et al., 2012; Roig et al., 2001).The wide dispersion of leaves along the branches in *P. pepei* and its long fruit distinguish this species from other *Polylepis* spp. 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 survive freezing air temperatures. This species is also adapted to cold soil temperatures in the eastern cordillera of the Andes. Ecological 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 (> 5cm)shallow soil temperatures ranging from 3-5°C during the wet season.

(Kessler et al. 2014; Hoch and Körner, 2005). Like much of the treeline species across the Andes-Amazon, *P. pepei* is under threat of shifting temperature regimes and human impacts on the ecosystem. Some studies predict the germination and spatial distribution of treeline *Polylepis spp* in the Andes is projected to decrease as vapor pressure deficits, temperatures, and overall aridity increase (Cuyckens et al.,

In the small community of Keara Bolivia where this study is located,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 temperatures were so warm that a catastrophic glacial lake outburst flood eliminated roads, livestock, and structures in the small community of Keara Bolivia (< November 2009 (~3800 m.a.s.l.; Hoffmann and Weggenmann, 2013). In the MNP, there is evidence of a temperature-inducedA recent forest-monitoring study

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in the MNP observed an upslope migration ~~(i.e. thermophilization)~~ of mid-elevation tree species ~~towards Andes ecotones caused by~~ due to increased ~~of~~ temperatures and tree mortality ~~near~~in the ~~treeline~~Upper Andes vegetation (Farfan-Rios et al. 2025).

~~Humans also play a role in modifying the forested landscape near the MNP. Ilegal mining and logging activities in low-elevation forests (<1200 m.a.s.l.) 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 (e.g. *Amburana cearensis*; Macía, 2008). ~~Today~~In recent years, illegal mining and logging activities have deteriorated forest structure and health, with increasing loss of forest cover at lower-elevations (below 2000 m.a.s.l; Finer and Mamani, 2023). At treeline, *P. pepei* is at ~~great~~ risk of endangerment due to habitat loss related to fires and land conversion for cattle ranching or religious practices (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. Since this ecotone~~Since the MNP is facing a rapidly changing environment due to climate and human-related disturbances, high resolution tree-ring records ~~at this treeline~~ may offer valuable insight on the past and current ~~growth responses.~~

response of this treeline to rising temperatures. At present, only two tree-ring studies have been published for the MNP: one for *Juglans boliviana* ~~(C.DC.) Dode~~in *Oelkers* et al. (2023) (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 & H.Karst.) Cuatrec.~~ cross-section (14°33′S, 68°49′W; 1000 m.a.s.l). The ~~*Polylepis pepei* site investigated~~objectives for this study ~~is found between ~ 3800-4400 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, the 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). Our specific objective~~ are~~:~~ i.) to generate ~~a new~~the first RW chronology for *P. ~~pepei~~,pepei* in the MNP and assess radial growth patterns; ii.) to identify the primary climate variables (e.g. ~~mean~~ temperature~~,~~ or precipitation~~, drought), that are the most limiting for annual~~) modulating tree growth variability, and iii.) to assess the impacts of extreme climate events ~~on the RW variations.~~ at this treeline.

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## 2 Materials and Methods

### ~~2.1 Site description and climatology~~

### ~~Our~~ 2.1 Climate data

The network of *Polylepis pepei* for this study ~~site~~ is located ~~in northwestern Bolivia (Fig. 1A), where two locations were visited in October 2012 and July 2019 to extract samples of *P. pepei* trees~~ at ~~altitudinal~~ treeline in ~~Keara (Fig. 1C, D). Two to four core samples were extracted from living trees using 2-threaded increment borers (5 mm in diameter). Cross sections of recently dead trees were sliced using a gas-powered chainsaw or a standard saw-tooth blade. In 2019, diameter at breast height (DBH; ~1.2 m) was measured for the trees at the same level that core samples were extracted.~~

~~The 2012 collection was from an open-canopy south-facing forest (~~the MNP near the small community of Keara, Bolivia (14°42S, 69°05W; 3795~~ 4100 m.a.s.l.), while the 2019 collection was primarily focused in a closed-canopy west-facing stand in a high-elevation valley called Waca-cocha (named after a nearby lagoon; 4000~~,4400 m.a.s.l.~~;~~ ). Local~~Fig. 1D). Both sites feature seasonally humid, upper-montane forests, with persistent mist that evaporates during the day. The sites were largely monospecific, dominated by fragmented patches of *P. pepei* and small numbners of *Gynoxys compressissima* Cuatrec. trees. Based on field observations in July 2019, the foliage of *P. pepei* may be considered evergreen and the bark consists of thick layers of compressed flakes that are red and brown in color, characteristic of the genus (Appendix A: Fig. A2A). The trees are shrublike, with twisted (and at times, multiple) stems.~~

~~The climatology of the study site (1960-2015 Figs. 1B, A1) shows a distinct wet season from October-April and a dry season from June-August (1960-2015; Fig. 1B). The wet season is defined by heavy rainfall (~1900 mm in January; Pre), and warmer mean (6°; Tavg) and maximum temperatures (Tmax; 12-14.7°C). In contrast, the dry season is characterized by low precipitation (65 to 115 mm per month) and extremely cold temperatures (minimum temperature range -7.1 to -8.3°C; Fig. A1). Consistent with these patterns the mean diurnal temperature range (the difference between Tmax and Tmin, DTR; Fig A1 B.) is smallest during the peak wet season (12.1 to 16.9°C) due to warmer minimum temperatures (~0°C), and highest during the drier months. Wet-season precipitation and temperature (Oct-Apr) was significantly and negatively correlated between 1960-2015 ($r$=-0.27, p=0.05) indicating wetter months at this site are typically associated with cooler temperatures, while no significant correlations were found during the dry season.~~

### ~~2.2 Climate data~~

~~In this study, we used local~~ precipitation data~~,~~ and gridded temperature products were used to generate monthly climate indices ~~near Keara (1960-2015; Fig. 1B).~~ for the site between 1960 and 2015. This period was selected for the site climatology and climate-growth analyses due to the limited availability of continuous precipitation data for this region of Bolivia. Daily precipitation from the Italaque station in Bolivia (15.48°S, 69.03°W~~,~~; 3500 m.a.s.l.) was gap filled ~~and homogenized~~ with



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nearby station data to generate a continuous monthly timeseries ~~(Pre) from 1960-2015 following procedures described in *Huerta* et al. (2025a) and~~ using the 'redprecc' package in *R* (Huerta et al~~. 2025b). Raw (daily)~~., 2026).Nearest-neighbor interpolation was constrained to precipitation stations above 3000 m.a.s.l. Raw precipitation data for Italaque (1978-2005) and nearby stations (~1945-2015, non-continuous) ~~can be~~were obtained from the DECADE dataset ~~(Hunziker et al. 2018),~~ which were originally sourced from the National Meteorology and Hydrology Service of Boliva (Hunziker et al., 2018)(SENAMHI~~; https://senamhi.gob.bo/index.php~~https://senamhi.gob.bo/index.php~~). Monthly mean (Tavg), minimum (Tmin), maximum (Tmax) temperature data was obtained from the Climatic research Unit TS 4.08 (CRU; 0.5° resolution; Harris et al. 2020). In addition, we also used CRU monthly diurnal temperature range (DTR; 0.5° resolution; 1901-2015), which represents the difference between Tmax and Tmin, to evaluate temperature variability in the region. The monthly climatology (1960-2015) and long-term variability of DTR (and Tmax and Tmin; 1901-2015) can be found in Appendix A Figs. A1 and A4 (see section 2.5 for more details).~~ Satellite-derived rainfall data from the Climate Hazards Infrared Precipitation with Station group V2.0 (CHIRPS, accessed 2025~~; ;~~(Funk et al., 2015~~)))~~ was used for spatial precipitation analyses (see Section 2.~~5).~~6). Precipitation and temperature from the Climatic research Unit TS 4.08 was used to determine the average climate during years of known ENSO-DJF events between 1901-2018 (see section 2.7; nearest grid point 14.75°S, 69.25°W;(Harris et al., 2020)). Precipitation values from the nearby station were also evaluated for climate during extreme ENSO years, but the timeseries is limited to the period of 1960-2015. Although CHIRPS v2.0 is limited to observations after 1981, it has a higher spatial resolution (0.05°) than ~~CRU~~Climatic research Unit TS 4.08 precipitation (0.5°), which can be more effective for spatial climate-growth analyses in regions with complex topography such as our site in the Andes-Amazon.

Monthly mean, minimum, maximum temperature data (Tavg, Tmin, Tmax) from the nearest CRU grid point were used for local temperature-growth analyses (1960-2015; 14.75°S, 69.25°W). CRU minimum and maximum temperatures for tropical south America region (15°N~24°S, 82°W~39°W) were used for spatial correlation analyses with the *Polylepis pepei* ring-width chronology (see section 2.6 for more details). In addition to the 1960-2015 climate-growth analysis period, we also used CRU monthly diurnal temperature range (i.e. DTR; the difference between Tmax and Tmin) to evaluate long-term annual temperature variability at the site between 1901-2015, as well as seasonally for the wet (October to April) and dry (June to August) seasons.

In situ high-resolution climate data was also obtained for this study. In August 2011 ~~(one year before the 2012 sampling campaign),~~ 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.) and data was recorded hourly from 1 September 2011 to 2 September 2014. New HOBO sensors were installed in 2021 and collected during fieldwork in 2023. Unfortunately, the 2021 system batteries failed within 9 months of the launch, and data was limited to only 20 September 2021 to 23 May 2022. ~~Daily~~ To compare the in-situ records of wet-season climate with the long-term DTR data, daily minimum, maximum and mean temperature and relative humidity ~~were~~was calculated from ~~20 September~~1 October to ~~23 May (245~~30 April (~212 days) for

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the 2011-2012, 2012- 2013, 2013-2014 and 2021-2022 ~~periods (see Appendix A Fig. A3. Kernel density estimates were used to generate and compare probability~~seasons. Daily climate distributions were visualized using ridgeline density curves generated with the 'ggridges' package in *R* (Wilke and Wilke, 2022). Differences among the ~~daily time series. Nonparametric~~four seasonal distributions for temperature and humidity were evaluated using the nonparametric Kolmogorov-Smirnov (KS) ~~tests~~statistic and implemented via the 'stats' package in *R* (Kolmogorov, 1933; Smirnov, 1948~~) were conducted to determine the significance of the mean difference between the~~). To account for serial dependence in daily ~~timeseries. Kernel density and KS tests were conducted using seaborn (Waskom, 2021) and SciPy (Virtanen et al., 2020) packages in *python*.~~observations, p-values were estimated using a moving-block bootstrap (e.g. contiguous 7-day blocks resampled 5000 times; (Kunsch, 1989)).

## 2.2 Site description and climatology

Two populations of *Polylepis pepei* were sampled at the MNP treeline in October 2012 and July 2019 (3795-4400 m.a.s.l. 14°40′-14°43′S; 69°04′-69°06′W; Fig. 1A, C, D). The 2012 campaign took place within an open-canopy south-facing forest (3795-4100 m.a.s.l.), while the 2019 collection was primarily located within a closed-canopy west-facing forest called Waca-cocha (named after a nearby lagoon; 4000-4400 m.a.s.l. Fig. 1D). The forests were largely monospecific, dominated by fragmented patches of *P. pepei*, and a small number of *Gynoxys compressissima* trees. This treeline is characterized as Alto-Andino Yungueño vegetation (Upper Andean Yungas) with a seasonally humid climate illustrated by the monthly climatology (Fig. 1B)

There is a distinct wet season from October-April and dry season from June-August at this site (Fig. 1B). 90% of annual rainfall occurs during the wet season with an average of 1045 mm per month and a mean temperature range between 5-7 °C. In contrast, the dry season is characterized by mean precipitation totals of 95 mm and cooler average temperatures between 2.2-3.1 °C (June-August). October and November are the warmest months of year with maximum temperatures around 14.5 °C (austral spring), but precipitation totals peak in January with an average of ~1900 mm (austral summer). The coldest and driest month of the year is July when minimum temperatures and precipitation are as low as -8.3 °C and 65 mm, respectively (Fig. 1, A1, austral winter). There is a marked seasonality in diurnal temperature range with smaller differences in minimum and maximum temperatures during the peak wet -season (~14.5 °C, December-March; Fig. A1).

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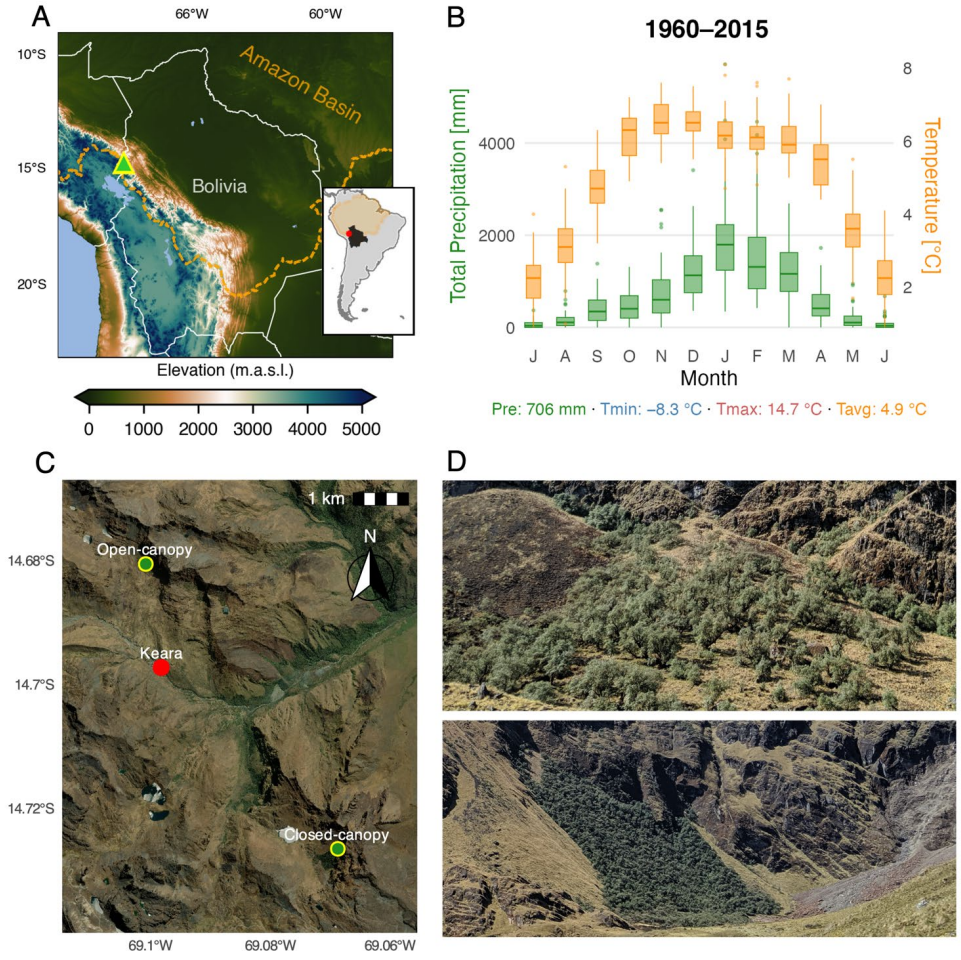


Specifically, minimum temperatures range from -2.2 °C to 0 °C and maximum temperatures from 12 °C to 14.5 °C during the wetter months of October-April. Diurnal temperature differences are largest between June-August (~20°C) with minimum temperatures ranging from -7 °C to -8.3 °C and maximum temperatures between 12.5 °C to 13.3 °C.

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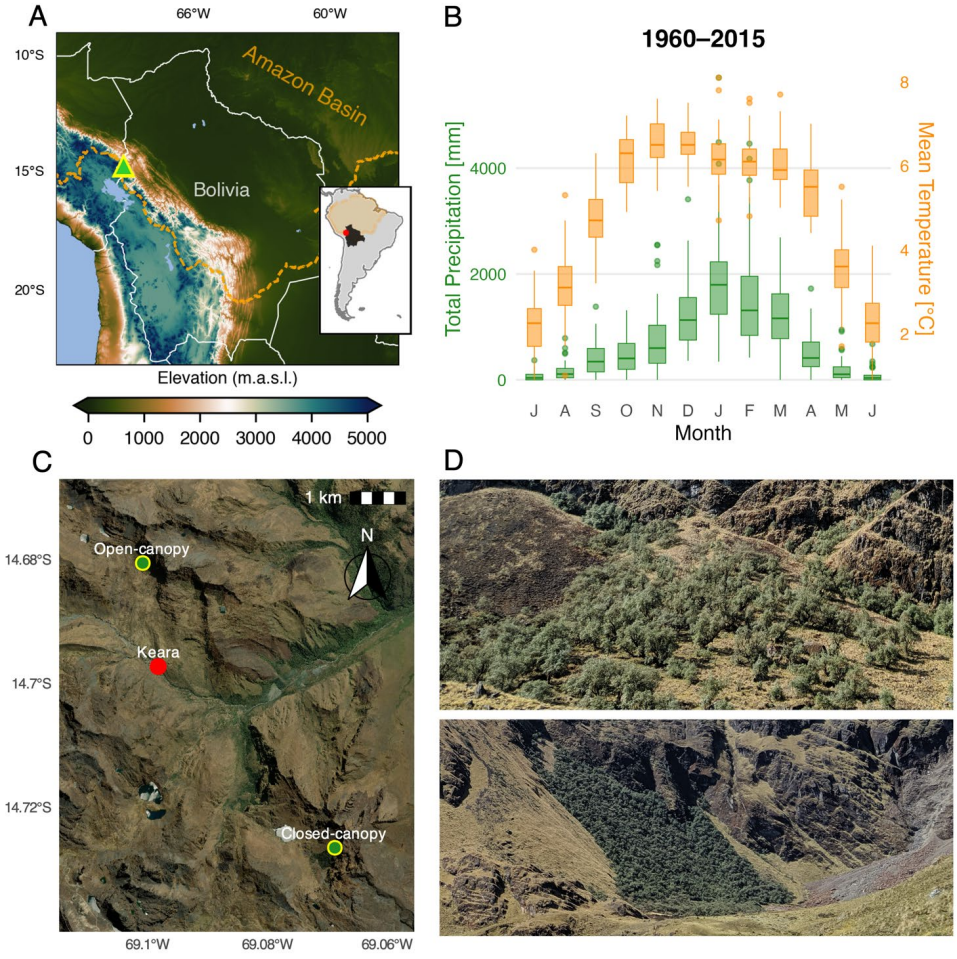


**Figure 1: (A) Location of *Polylepis* site in the Eastern Cordillera of the Andes-Amazon ecotone in Bolivia. The orange dotted line (and orange shading in the inset map) represent the spatial limits of the Amazon Basin. The elevation map was generated using the "ETOPO-1" model ~~(https://www.ncei.noaa.gov/products/etopo-global-relief-modelhttps://www.ncei.noaa.gov/products/etopo-global-relief-model~~; ~~(~~(B) The monthly climatology for the region of Keara between 1960-2015. Monthly distribution of mean temperature ~~and total precipitation (1960-2015) in Keara~~ was generated using ~~the~~ the nearest temperature CRU gridpoint (14.75°S, 69.5°W) and total precipitation is reconstructed ~~precipitation from~~for the Italaque station (15.48°S, 69.03°W). ~~The average temperature (Tavg), mean precipitation (Pre), and range of minimum and maximum temperatures (Tmin, Tmax) for the study period are included.~~ (C) Aerial**



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**view of the sampling locations near the community of Keara, and the MNP treeline (D) photos of open-canopy (top) and closed canopy (bottom) forest patches sampled at altitudinal treeline in Bolivia's MNP (~3700~~3800~~-4400 m.a.s.l.). The basemap in (C) was obtained through opensource ESRI images.**

### 2.3 Wood processing and anatomical analyses

Tree-ring samples from at least 30 living *P. pepei* were collected using a 2-threaded 16-inch increment borer (5 mm in diameter) in October 2012 and July 2019. Two to four cores were extracted from varying directions within the stem (north, south, east, and/or west radii) in an effort sample an accurate representation of radial growth. Trees were cored at breast height (1.2 meters), or near the base of the largest stem for multi-stemmed trees (~30 cm). During the 2019 field campaign, tree-diameter was also measured at the height core samples were sampled (1.2 meters on average). Tree-ring cross sections from 3 recently dead trees were sliced using a gas-powered chainsaw or a standard saw-tooth blade.

Wood samples were shipped from the National Herbarium of Bolivia in La Paz 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 transitions between the heartwood (functional xylem near the pith, darker color) and sapwood (the active xylem beyond the cambium layer, lighter color).

*P. pepei* is an angiosperm with diffuse porous wood anatomy, which is ~~typically~~particularly harder to cross-date ~~than 'ring porous' wood,~~ due to less distinct boundaries between the latewood of the prior year growth ring and the earlywood of the ~~current~~next year (Fig. A2). To aid in identifying ~~anatomical properties~~ ring-boundaries in the wood, histological (micro) cuts were performed ~~according to~~on a single cross-section following the techniques described in von Arx et al. (2016) using a WSL Core microtome (https://www.wsl.ch/en/services-produkte/microtomes/). ~~*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. A2 B).~~High-resolution images of the thin sections were captured using an Echo Revolve R-4 microscope camera, with a magnification of 40X. Further information regarding the wood anatomy of this species is included in the Appendix (Fig. A2).

### 2.4 Tree-ring width chronology development

Tree rings from ~~51 *P. pepei* samples from 28 living and 3 dead trees (~~31 trees ~~total~~(51 radii) were dated visually using standard dendrochronological techniques (Stokes and Smiley, 1968). Each wood sample was scanned using an Epson Expression 11000XL scanner at 3200 dpi resolution. RW was measured digitally using the *CooRecorder* image analysis program (Cybis Elektronik, 2010) and statistically crossdated using the program COFECHA (Holmes, 1983) and dplR package in R (Bunn, 2008). To independently confirm annual periodicity of the growth rings, radiocarbon dating was conducted on a cross-section sample (SP20X; Fig. A2) collected in 2019 in the closed-canopy forest. Individual growth rings associated with the years 1957,

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1958, 1962, 1963, 1964, 1965, 1971, and 1972 were sliced, extracted for cellulose, and processed for modern radiocarbon analyses. 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). Further details on the radiocarbon analyses and earlier iterations of the Keara RW chronology can be found in the Appendix (Fig. ~~A2 C~~A2C).

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 were detrended conservatively with age-dependent cubic splines using the 'dplR' package in *R* (initial spline stiffness of 60 yrs) (Bunn et al. 2008; Cook and Peters, 1981; Melvin, 2004). Standardized indices were generated 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). For the residual chronology, autocorrelation was removed from the series using autoregressive modelling determined by the Akaike Information Criterion (Akaike, 1974). A third chronology of average (raw) RW was also generated to review the absolute growth of these trees at treeline. The final ~~RW~~ chronologies (raw, standard ~~and,~~ residual) represent the RW for entire *P. pepei* ~~RW~~ network (2012 and 2019 tree samples) and thus variance stabilization was applied to account for temporal changes in sample depth (Frank et al., 2006). ~~-~~The standard RW chronology was primarily used for changepoint and RW-climate correlation analyses~~,~~ (section 2.5), and the residual chronology was used for i.) identification of small or large outliers in the chronology (top 5th and 95th percentiles) and ii.) analyses of the growth response of *P. pepei* to detrended monthly and residual climate and extreme ENSO events (see section 2.6).

The subsample signal strength (SSS) calculation was used to ~~estimate the minimum sample size required to maintain a growth~~ determine how well the available tree-ring samples represent the common growth signal ~~(Wigley et al., 1984).~~of the P. pepei population (i.e. site)(Cook and Pederson, 2011). SSS ~~considers~~quantifies the strength of the shared variance through time by incorporating the number of cores per tree, the number of individual trees, and the mean interseries correlation among RW series ~~to determine how well the available samples reflect the growth signal of the population (i.e. site).~~ An SSS ~~value~~threshold of 0.85 (or better) is ~~a common threshold~~ commonly used in dendrochronology and ~~represents~~signifies the ~~period~~years when sample ~~size~~replication is adequate and the ~~common RW signal~~chronology is considered robust (see discussions *Buras* et al., (2017) and *Wigley* et al. (1984) for more details). An annual SSS Index was generated using the 'dplR' package in *R* (Bunn, 2008).

## 2.5 Changepoint detection

The period in which SSS was greater than 0.85 was used for changepoint analyses of the raw and standard RW chronologies to detect abrupt shifts in radial growth before and after low-frequency is removed (i.e. detrending). The Pettit's (1979) changepoint ~~detection~~ test was applied ~~to the raw (radial)~~ using the 'trend' package in *R* (Pohlert, 2016) which identifies a single year when the median tendency of the RW chronology ~~to detect the timing of recent trends in growth.~~is significantly

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higher or lower after the changepoint. Significance of the RW trend ~~after~~for the post-changepoint ~~(p < 0.05)~~period was ~~determined by~~evaluated using the non-parametric Mann-Kendall test on ~~the~~an estimated Sen's slope (Sen, 1968~~). Changepoint analyses was conducted using the 'trend' package in *R* (Pohlert, 2016~~).

### 2.~~5~~6 Climate-growth analyses

To explore the climate sensitivity of *Polylepis pepei* ~~at the treeline~~, we correlated annual RW ~~to~~with local monthly and seasonal precipitation, and minimum, maximum, and mean temperature ~~and precipitation for the period 1960-2015. Monthly~~ (1960-2015; see Section 2.2). Correlations were evaluated using a 24-month window spanning from prior July to current June to account for lagged climate effects on *P. pepei* RW. Long-term and inter-annual growth response was assessed by correlating i.) standard RW with mean (raw) climate, and ii) residual RW with linearly detrended climate respectively. 3-and 4-month seasonal climate correlations (standard and residual) were calculated to determine whether growth at this site is influenced by cumulative rather than monthly temperature ~~data (Tavg, Tmin, Tmax) was from the nearest CRU gridpoint to our site:14.75°S, 69.25°W, while monthly~~ and precipitation ~~(Pre) was obtained from local station data (see section 2.2). Monthly~~ conditions.

Pearson correlations (*r*) were ~~computed with the~~estimated using stationary ~~bootstrap method~~block-bootstrapping methods and implemented with the ~~boot~~'boot' package in *R*. (Canty and Ripley, 2017). This technique resamples contiguous, randomly-sized blocks of data ~~(n = 1000) at varying block size~~ times to preserve autocorrelation and quantify the uncertainty of the RW-climate relationship (see Politis & Romano 1994). Significance ~~of the climate-growth relationship~~ was inferred from the two-tailed 95% confidence intervals of the median bootstrapped correlation (i.e., 95% CI excludes zero).~~–~~ Due to the covariance between temperature and precipitation in this region, we used bootstrapped partial correlations ($r_p$) to evaluate the independent effect of one variable on RW (*e.g.* temperature), while controlling for the other (*e.g.* precipitation). Following methods of *Meko* et al. (2011), partial correlation coefficients for RW-temperature were obtained by: i.) first performing a linear regression between RW and precipitation and ii.) calculating bootstrapped correlations between temperature and the residuals from this regression. ~~The results~~ After removing the influence of precipitation, partial correlations represent the distinct portion of RW variability ~~not~~that is explained by ~~precipitation. Thus, partial correlations show the distinct relationship between RW and~~monthly temperature ~~while controlling for the influence of precipitation.~~.

Spatial RW-Climate correlations across tropical south America were used to ~~assess~~test the ~~extent~~magnitude of the climate sensitivity of the standard RW chronology to regional temperature (Tmax and Tmin) and precipitation ~~signals of the RW within tropical south America. Seasonal climate windows selected~~variability. The seasonal window for ~~the spatial analyses were~~ each climate variable was inferred from the significant monthly climate-growth relationships~~. Spatial~~ and the results from 3-to-4-month standard and residual correlations ~~with precipitation.~~ Precipitation correlations were conducted using the gridded CHIRPS ~~between~~dataset for the 1981-2015 period (see section 2.2). Otherwise, ~~all monthly and (seasonal) spatial~~local climate-growth analyses which used reconstructed station data and spatial temperature (gridded CRU data) correlation analyses ~~(RW~~

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~~vs. climate) were~~was between 1960-2015. Field significance was assessed using a binomial test (e.g. ~~-~~the probability that *n* number of grid-cell correlations were significant by chance (raw p<0.05) due to the high number of comparisons; see: Livezey & Chen, 1983).

Linear trends in the ~~local (~~seasonal~~)~~ climate (1960-2015) were assessed using the Sen's slope estimator (section 2.4), and significance was evaluated using Mann Kendall tests. Slopes were reported as the average change in climate in units per decade ~~(Fig. A4).~~ Annual and seasonal (October-April; June-August) trends of diurnal temperature anomalies (DTR) were also evaluated for the same period. Additionally, monthly anomalies of ~~Tmin,~~minimum and ~~Tmax~~maximum temperature were calculated relative to the 1901-2015 CRU baseline (full temporal extent of CRU data) to illustrate long-term temperature variability during the wet and dry season ~~(Fig. A5 BC).~~ .

### 2.~~6~~7 Superposed Epoch Analysis

ENSO varies between warmer (El Niño) and cooler (La Niña) SST phases (Ropelewski and Halpert, 1987) in the Pacific Ocean, and both extremes substantially impact precipitation and temperature conditions over tropical South America. To investigate the effects of extreme ENSO events on tree-growth, Superposed Epoch Analysis (SEA) was performed on the residual RW timeseries ~~(Fig. 2D)~~ 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.* extreme climate 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 (lag= 0) and several years after (in this case four years).

We analyzed twenty-six years of RW based on the top-ranked December-February (DJF) El Niño and La Niña events (*n*=13 each) listed by the National Oceanic and Atmospheric Administration's Physical Science Laboratory (NOAA-PSL: https://psl.noaa.gov/enso/). These ranked DJF years are determined by NOAA-PSL with the multivariate ENSO indices (MEI; 1871~2024). MEI reflects the principal components, or dominant modes, 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), SSTs, meridional (north-south) wind, and outgoing longwave radiation (see Wolter and Timlin, 2011). Extreme years are defined by Pacific SST anomalies during DJF, coincidently when ENSO is phase-locked with the peak monsoon season (Rasmusson and Carpenter, 1982). ~~Annual Pre (station data; 1960-2015) and CRU precipitation and Tavg (nearest gridpoint 1901-2018) were plotted to determine the average climate during years of known ENSO-DJF events near Keara.~~ The list of DJF- ENSO-events obtained from NOAA-PSL are included in Appendix Table A1.

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## 3 Results

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

The *P. pepei RW* chronology ~~from~~covers the ~~MNP treeline spans from~~period 1850-2018 and consists of 51 tree-ring samples (31 individual trees) from open and closed-canopy forests near ~~Keara~~ the MNP treeline (Table 1; Fig. 2). Radiocarbon and standard dendrochronological methods confirmed ~~the growth rings are~~these trees form annual rings and ~~reflect high frequency patterns of high and low growth through time~~share a common growth signal in this region (Figs. 2A, C, D). Site metadata and RW chronology statistics for the *P. pepei* network are summarized in Table 1.

**Table 1. Summary of *P. pepei* tree-ring sample location, age, sample size, and mean correlation among RW timeseries. The RW chronologies represent the entire collection of cross-dated *P. pepei* samples in Keara obtained in both 2012 and 2019.**

| Site | Location (elevation) | *n* trees (*n* samples) | Mean age [yrs] | Timespan | Mean ~~RW~~ Correlation [$\bar{r}$] | ~~Mean DBH [cm]~~ |
|---|---|---|---|---|---|---|
| *Open-canopy forest* (south-facing) | 14°40'S 69°06'W (3795-4100 m.a.s.l.) | 16 living 2 dead (33) | 89 | 1850-2018 | 0.53 | ~~24 cm (*n* = 6 trees) *~~ |
| *Closed-canopy forest* (west-facing) | 14°43'S 69°04W (4000-4400 m.a.s.l.) | 12 living 1 dead tree (18) | 101 | 1871-2018 | 0.44 | ~~31 cm~~ |
| **Full network** (mean Raw, standard, residual chronologies) | - | 31 (51) | 93 | 1850-2018 | 0.50 | ~~30 cm~~ |

~~**Table 1. Summary of *P. pepei* tree-ring sample location, age, sample size, and mean correlation of RW timeseries per site. *DBH information is only from the samples collected in 2019 which included 6 trees from the open-canopy forest and 13 trees from the closed-canopy site. The final RW chronologies represent the entire collection of *P. pepei* samples in Keara obtained in both 2012 and 2019.**~~

Due to extreme suppression in radial growth (Fig. 2B), only one or two cores ~~per tree (out of three total) were able to~~from the living trees could be measured and included in the final RW chronologies. Despite the complex anatomy of *P. pepei*, the cross-dated ~~and used for the final RW datasets. A recent decrease in radial growth was observed in samples from both the open-canopy (18 trees) and closed canopy (13 trees) sites (Fig.~~ samples ~~2A). The entire Keara *P. pepei* network (mean raw RW;~~

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~~Fig. 2A) has been declining steadily since the 1960s, especially after 1996 (p= 0.01), with a less pronounced trend in the standard RW series (Fig. 2AC).~~

~~Despite difficulties with crossdating due to suppressed tree rings, the entire network~~ shared a coherency in the RW patterns with a mean inter-series correlation of ~~$\bar{r}$~~ $\bar{r}$ = 0.50 for the 1850-2018 period ~~(n = 51 samples, 31 trees). The SSS metric indicated the common growth signal was particularly robust (SSS > 0.85) between 1900-2018 when the sample size was greater than 17 (Fig. 2C;~~. The oldest living tree sampled was 168 years of age from the open-canopy forest. The average age of the trees was 93 ~~yrs). The~~ years and the average ~~radial~~ growth rate between 1850-2018 was ~ 1.~~04~~40 mm $yr^{-1}$. DBH measurements in 2019 ~~(6 trees in the open canopy and 13 in the closed canopy site),~~ confirmed these trees were slow-growing with stem diameters ranging from 10 cm to 54 cm (mean DBH 30 cm). The sub-sample signal strength indicated the RW chronology is particularly robust between 1900-2018 when sample size exceeds 17 (SSS >0.85 Fig. 2C).

*P. pepei* RW at this treeline has been declining steadily since the 1960s (Fig 2.A, C). A changepoint in the raw RW chronology was detected in 1993 (p=0.0019), with a significant decline of 0.02 mm $yr^{-1}$ after 1994. This trend in absolute growth is evident in both the open-canopy and closed-canopy forests at the site (Fig. 2A). Although a non-significant changepoint in the standard RW chronology was detected in 1962 (p=0.062), two-tailed Mann-Kendall tests determined the negative slope between 1963-2018 was significant (-0.007 units $yr^{-1}$, p<0.001; Fig. 2C). ~~Years with extremely large RW (95$^{th}$ percentile) included the 1951/52 and 1965/66 growth years (Fig. 2D) which occur before and after a visible growth suppression during the mid-to-late 1950s (Fig.2 A, C). Tree rings that began forming in 1906 or 1945 had extremely low values of RW indicating unfavorable growing conditions during the growth year.~~

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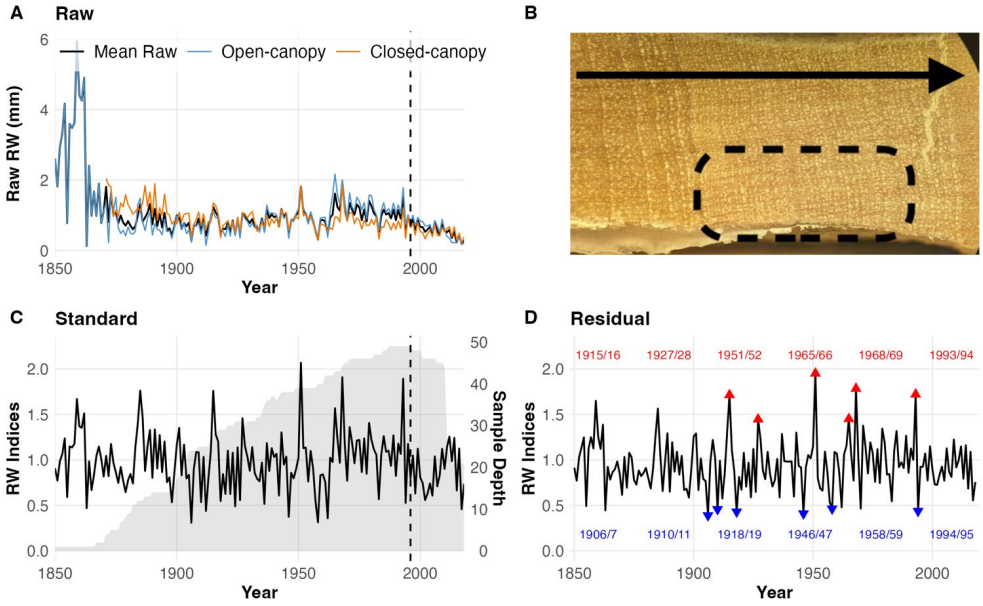


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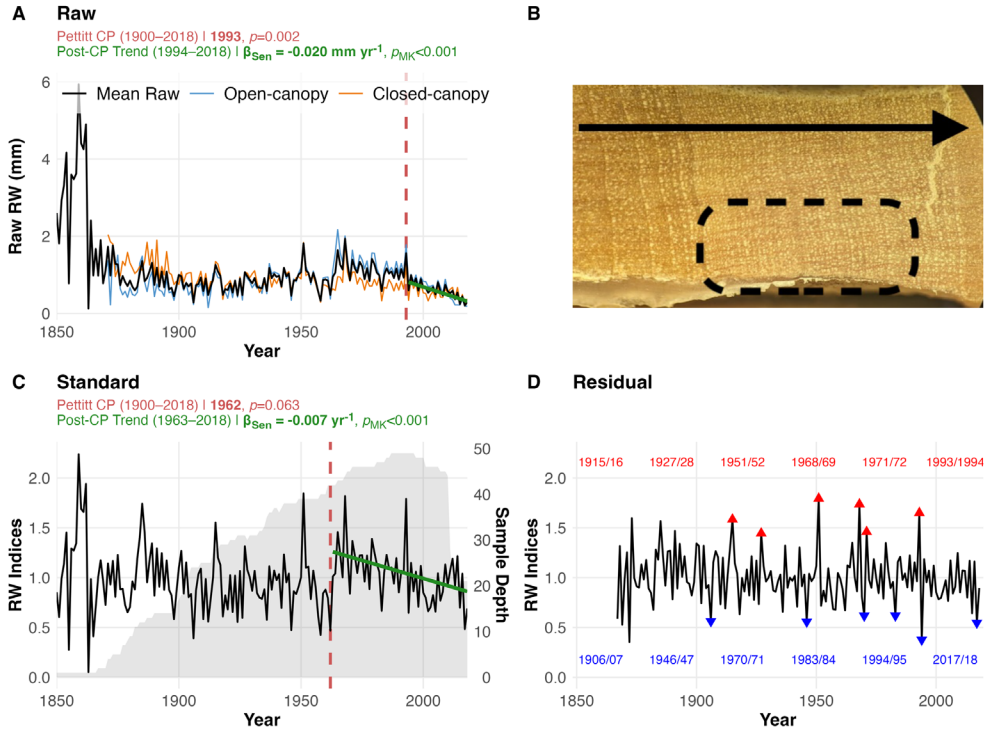


**Figure 2. The (A) Raw (C) Standard and (D) Residual RW chronologies of *P. pepei* in Keara. The chronologies (1850-2018) are plotted using the Schulman convention (*i.e.*, anchored on the year of initial ring formation; see section 2.3).** ~~**(A) There has been a distinct decline in raw (radial) RW since the 1996/1997 growth-year (changepoint is indicated by the black-dotted line. (A) This decline ($p$=0.01) was evident in both the open-canopy (blue line) and closed-canopy (orange line) forests that were sampled.**~~ **(B) An image depicts a core sample where several rings are suppressed within a 4 mm distance (dashed circle). The black arrow indicates the direction of radial growth for this core (from left to right).** ~~**(**~~**C) The standard RW is plotted with the mean sample-depth of the full network through time (grey-shading).** ~~**Triangles**~~**Blue and red triangles on the residual timeseries (D) signify the years within the top 5th** ~~**(six smallest growth rings; Blue color)**~~ **and 95th** ~~**(i.e. largest growth rings; red color)**~~ **percentiles of RW since 1900 (SSS> 0.85). Since the tree rings are estimated to form during the wet season (two- calendar years ~October-April), both years are labeled in the colored text** ~~**(**~~**and ordered chronologically**~~**).** **within the plot (D). Vertical red lines signify the significant changepoints detected in the raw and standardized RW chronologies (1900-2018; SSS >0.85), while the green solid lines represent the trends after the changepoint estimate via Sen's slope. Changepoint and trends statistics for the raw and standard RW chronologies are included in the subtitles for A and C. There was a significant decline in raw (radial) RW after the 1993/94 growth-year (i.e. 1994-2018) and between 1963-2018 in the standard RW chronology.**

### 3.2 Monthly and sesaonal climate-growth relationships at Keara's treeline

The climate sensitivity of *P. pepei* RW ~~to local climate between 1960-2015~~ is illustrated by bootstrapped correlations ~~between~~with monthly ~~Pre, Tavg, Tmin,~~mean precipitation and ~~Tmax in~~temperature timeseries (1960-2015; Fig. 3~~.~~, A3). *P. pepei* RW ~~(standard chronology) positively correlates with Pre~~ benefits from higher rainfall in the months of December-April (Pre lag=1, $r$=0.39 for February; Fig.3A). This forest had a more significant RW response to cumulative rather than monthly precipitation variability ~~during the wet season (Fig.3A). There are significant~~ , with the highest correlations ~~between RW and prior (lag=1)~~observed for the 4-month December-March ~~precipitation ($r$=0.37 for January). Correlations with prior-year December~~ (season (DJFM lag=1, r= 0.~~20) weakened when controlling for Tavg, but current-year November Pre remains robust ($r_p$~~42, $p$=0.~~27). Fig. 008; Figs. A3A,~~ A4A ~~shows December-March (~~-B). DJFM~~)~~ precipitation significantly decreased ~~over the 1960-2015 period~~ at this site at a rate of ~6 mm ~~per decade at the same time there was an observed decline in *P. pepei* RW (Fig. 2A).~~ decade$^{-1}$ after 1960 (Fig. 4A), but residual RW-precipitation correlations remained significant after climate trends were removed (Fig. A4B).

~~RW is~~

In general, wet season precipitation is significantly and negatively correlated ~~to prior-year Tavg DJFM (~~with temperature at this treeline (Oct-April $r$=-0.~~21 in March to $r$=-0.34 in February, p<0.05).~~ 31, $p$=0.02). However, after controlling for precipitation effects~~, partial correlations for Tavg revealed a~~ on RW variability, partial correlations revealed a robust and independent relationship between RW and current-year monthly temperature (*i.e.* the monthly correlations persist after the covariance with precipitation is removed; Lag=0 Fig. 3B-D). *P. pepei* RW correlates positively with current-year mean and maximum temperatures particularly for the months of April (Tavg r=0.37, Tmax=0.38; Fig. 3B, D). The strongest positive~~, robust relationship (p<0.05) with RW current-year~~ correlations with temperature were for the 4-month February ~~to April (FMA) months ($r_p$= 0.25 in February to 0.37 in April). *P. pepei* RW also correlates positively with FMA Tmax (Fig. 2D),~~ May season, emphasizing the importance of late- summer temperature variability for tree-growth at this site (FMAM Tmax, lag=0, r=0.47, Fig. A5H). There was weak evidence of a decreasing trend FMAM maximum temperatures for the analyses period -0.06°C decade$^{-1}$, p=0.17; Fig. 4D).

Monthly residual correlations showed *Polylepis pepei* RW was primarily sensitive to interannual temperature variability at this site (Figs. 3B-C, A3B-C, Tavg, Tmax, Tmin). However, prior-year correlations with monthly Tmax and Tavg decreased after accounting for lagged precipitation effects on RW (Fig. 3B and D lagged partial correlations). Lagged minimum temperature variability, however, had a distinct and significant impact on RW (Tmin lag=1, Figs. 3C, A3C). Negative correlations were found between RW and prior-year wet~~ season temperature variability near our site on current-year RW as well.~~ season minimum temperatures (NDJF lag=1; $r$=-0.40; Fig. A4F). Although there were no significant trends in ~~FMA Tavg between 1960-2015 (Fig. A4 B), there was a significant decrease of Tmax FMA of nearly 0.1°C per decade (Fig. A4 D, p=0.05~~FMAM mean and max temperature for the 1960-2015 period (p > 0.16; Fig. 4B, C), NDJF minimum temperatures significantly

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increased at a rate of 0.15°C decade$^{-1}$ (p=0.02, Fig. 4C). In summary, *Polylepis pepei* RW was limited by minimum and maximum temperatures for distinct seasons (e.g. positive relationship with FMAM Tmax lag=0 vs. negative relationship with NDJF Tmin lag=1).

~~Unlike Tavg, partial correlations indicate RW correlations with prior-year Tmin (Fig. 3C) are significant independent of precipitation variability (i.e. the negative signal persists even when the covariance with precipitation is removed). Negative, significant correlations were found between *P. pepei* RW and prior November- March Tmin (NDJF; $r$= -0.28 in November to $r$= 0.35 in February). It is interesting to note an extreme cold period near Keara during the late 1950s (Tmin. Fig. A5 BC) corresponds with a growth suppression observed in *P. pepei* RW in Fig. 2A and C. Unlike the decrease observed in Tmax near Keara (FMA), NDJF Tmin significantly increased at a rate of 0.1°C per decade (p=0.02). In summary *Polylepis pepei* RW is limited by FMA Tmax (positive, current-year relationship) and NDJF Tmin (negative, lagged relationship) for distinct seasons.~~

Overall *Polylepis pepei* RW is larger under wetter and cooler conditions. However, ~~climate~~this site experienced significant warming and drying trends ~~since~~between 1960~~ (Fig. A4) indicate this~~ ~2015 at the same time a growth decline in the treeline ~~is facing a warmer and drier November-March (Pre, Tmin) and a cooler wet-to-dry 'shoulder season' months between February- April (Tmax). As mentioned in Section 2.1, Tavg and Pre are negatively correlated during the wet season (~October-April, $r$= 0.27) in Keara and thus the robust negative correlations between RW temperature (Tmin, Tmax)~~*P. pepei* was observed (Figs. 2C, 4A, 4C). Residual climate-growth correlations were significant for the same seasons as the standard correlations, despite the linear trends identified in both mean climate and RW (Fig. 2, 4). These results emphasize ~~the indirect effect of temperature~~that both long-term and inter-annual climate variability had significant impacts on ~~water availability and thus~~ *P. pepei* ~~tree growth~~RW at this treeline~~. Seasonal averages of DJFM precipitation, NDJF Tmin and FMA Tmax were selected for spatial correlation analyses for the greater tropical south American region.~~ in the MNP. Further, RW was primarily limited by prior-year wet-season conditions (e.g. ~Nov-March Pre and Tmin lag=1) but was also significantly and positively related to current-year temperature variability (FMAM lag=0).

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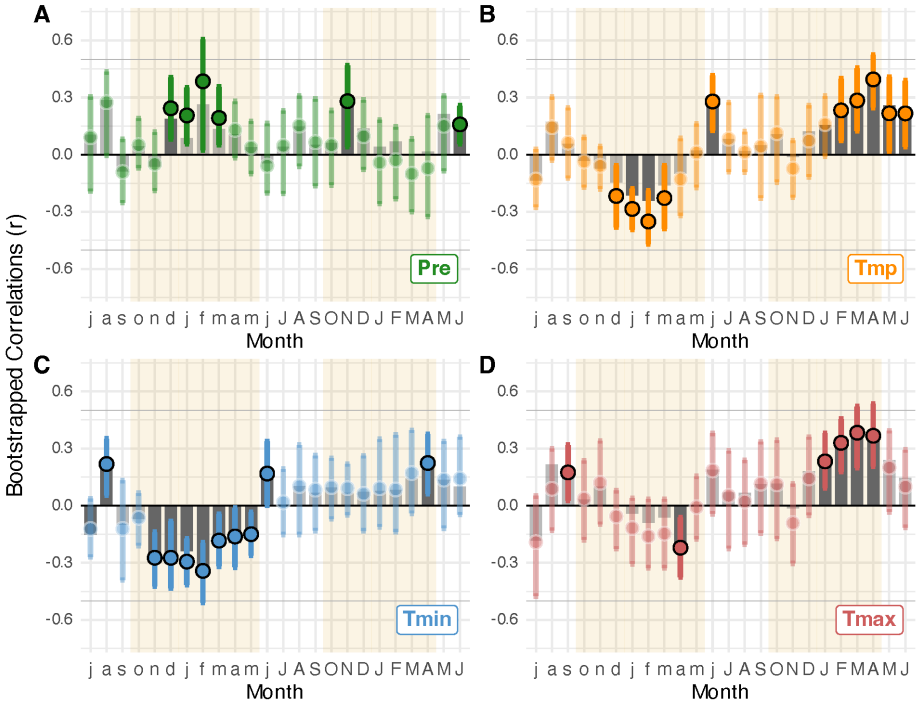


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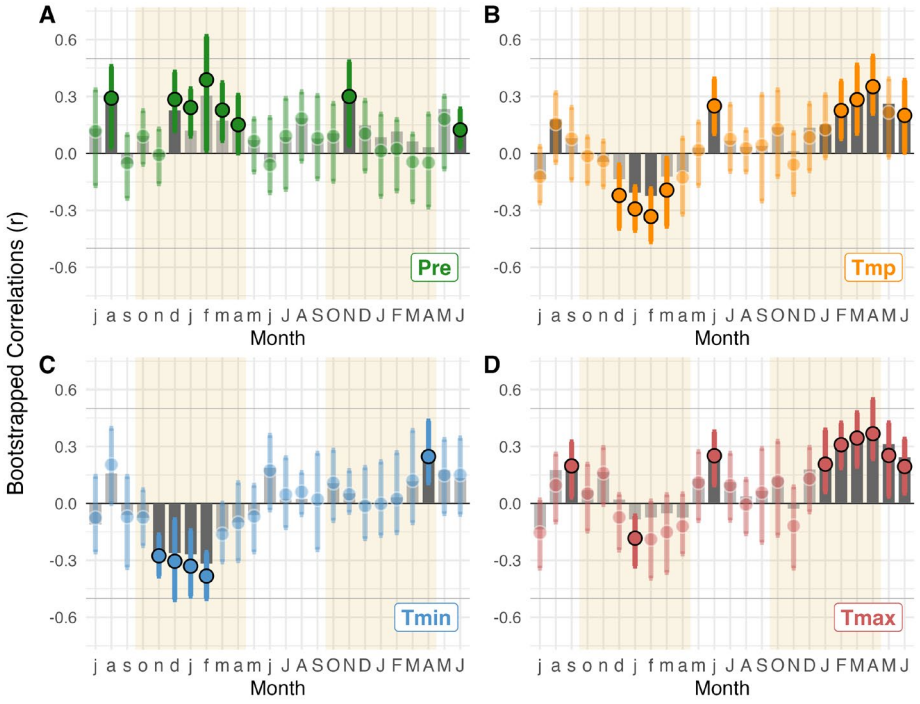


**Figure 3:** ~~Bootstrapped~~Standard bootstrapped **correlations between *P. pepei* RW and** average **monthly climate from 1960-2015.** ~~The x-axis represents months beginning in~~ Monthly temperature data was from the nearest CRU gridpoint for our site: 14.75°S, 69.25°W, while monthly precipitation was obtained from local station data. The x-axis covers the 24-month period between **July of the prior-year (lag=1, lowercase letters) and** ~~extending to~~ **June of the current year (lag=0, uppercase letters). Tan shading indicates the** ~~extended wet period (~ October- April)~~wet-season **for this region of the MNP** (~October-April). (A~~:~~) Monthly RW-precipitation correlations (**green**~~ color, precipitation from local station data.~~ , Pre). (B-D~~:~~) RW **correlations with** ~~CRU~~monthly mean (orange, Tavg), minimum (blue, Tmin), and maximum **temperature** ~~grid points Tavg(orange), Tmin (Blue), Tmax~~**(red**~~). The median Pearson correlation (r) is~~ , Tmax). Significant correlations are **represented by** solid**-colored circles** ~~plotted with upper and lower limits of confidence intervals. Partial correlations ($r_p$) are represented by~~(median pearason *r*) or solid **grey bars.** ~~Solid circles and bars indicate significant~~ (partial **correlations** ~~which are,~~ $r_p$) and **inferred from 95% confidence intervals** ~~from the random bootstrapping.~~ .



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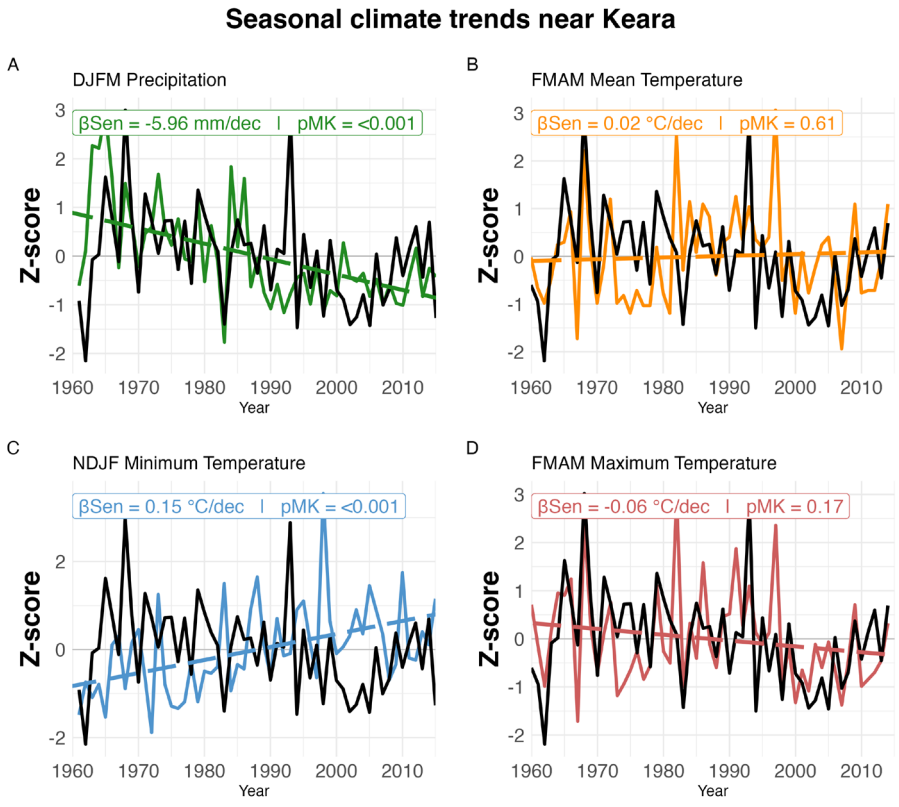


**Figure 4.** Z-scored *P. pepei* RW (black lines) and seasonal climate variables (colored solid lines) between 1960-2015. The selected seasons were based on the highest and most significant correlations between local climate and RW for this period (standard and residual, $p<0.05$). Lagged DJFM Precipitation is in green (A, lag=1), FMAM mean temperature is orange (B, lag=0), lagged NDJF minimum temperature is blue (C, lag=1) and FMAM maximum temperature is in red (D, lag=0). Averaged seasonal trends are reported in units of climate per decade (β, colored dashed lines). Mann-Kendall tests were used to estimate the two-tailed significance of the linear trend (pMK). Precipitation data is reconstructed from nearby station records and temperature data is sourced from the nearest CRU TS 4.08 grid point.

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### 3.3. ~~*Polylepis pepei*~~ RW and climate variability across tropical South ~~American climate variability~~America

~~Spatial correlations reveal the broader,~~ Figure 5 highlights the regional extent of the seasonal climate signal recorded in ~~the~~ P. pepei RW at the ~~Keara~~MNP treeline. ~~(Fig. 4). Binomial field tests indicated the spatial extent of significant correlations (black dots; p<0.05) exceeded what would be expected~~Gridded DJFM precipitation (lag=1), NDJF minimum temperature (lag=1), and FMAM maximum temperature fields for tropical South Americal were used for spatial correlation analyses and were limited by ~~chance (p<0.001 for all variables). *P.*~~the temporal extent of available data (Fig. 5A 1981-2015, Fig. 5B-C 1960-2015). The RW-precipitation correlations reflect the heterogeneity of precipitation variability along the Andes, whereas the temperature fields are more uniform (Fig.5A vs. Fig. 5B, C). *P. pepei* RW is positively correlated to prior-year DJFM ~~precipitation (CHIRPS; 1981-2015)~~rainfall in most of tropical South America for the 1981-2015 period (Fig. ~~4A~~5A). The strongest precipitation signal is observed along the eastern flanks of the Peruvian Andes and the northern Amazon Basin in Brazil~~.~~ (r =0.45 to 0.50). There were significant correlations with wet-season minimum temperature variability for most of tropical South America, especially near southeastern potions of Brazil (NDJF Tmin lag=1, 1960-2015; Fig. 5B). RW is also positively correlated to ~~FMA Tmax~~late austral summer maximum temperature variability in the northern and southern portions of the tropical Andes~~ Amazon with the strongest values ($r$ > 0.50)~~ (FMAM Tmax lag=0, 1960-2015, Fig. 5C). The highest correlations between RW and maximum temperature were centralized both locally to the site and near the Bolivian Altiplano~~.~~ ($r$> 0.50). In summary, the relationship between *P. pepei* RW and large-scale seasonal climate variability was significant for the same seasons identified in the local climate-growth analyses (1960-2015, Figs. 3, A4, A5).

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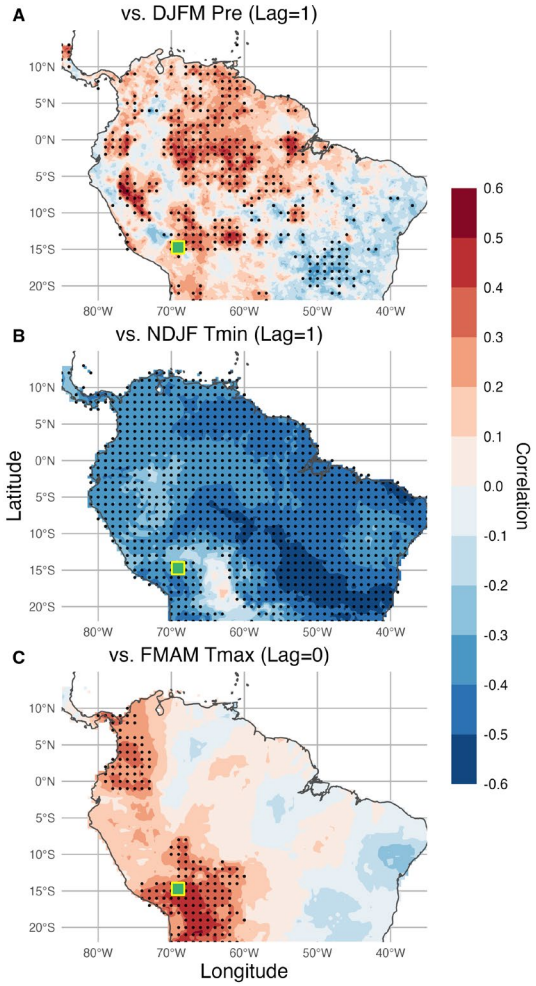


**Figure 5.** **Spatial correlations between *P. pepei* RW and prior-year NDJF Tmin (CRU 1960-2015) showed significant and negative correlations across most of tropical South America (Fig. 4C), especially near southeastern potions of Brazil. The RW-precipitation correlations also reflect the heterogeneity of precipitation data in mountain areas, whereas the temperature fields are more uniform.**

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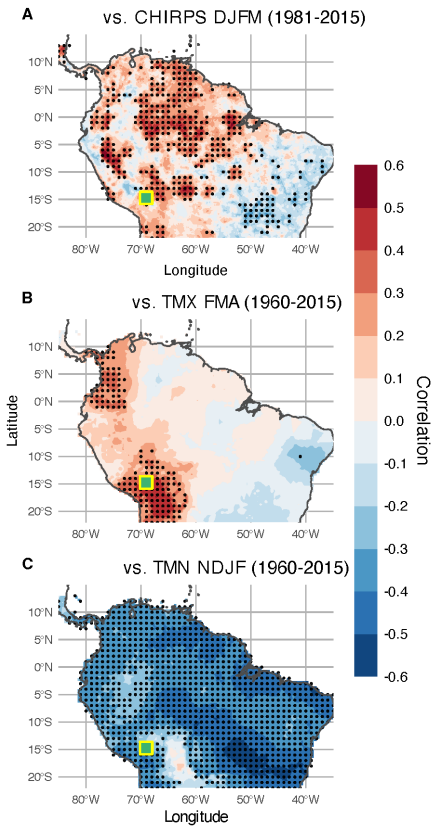


~~Figure 4. Spatial correlations between *P. pepei* RW and (A) CHIRPS DJFM precipitation (1981-2015, lag=1), (B) CRU NDJF Tmin (1960-2015, minimum temperatures (lag=1), and (C) CRU FMA Tmax (1960-2015, FMAM maximum temperatures (lag=0).) in tropical South America. Black dots represent the areas where there are significant correlations (p<0.05). Binomial field tests indicated there~~significant grid points ($p<0.05$). Gridded precipitation analysis was limited to 1981-2015 due to the availability of CHIRPS data (A) while RW-temperature correlations covered the 1960-2015 period (B-C, CRU data). There were more significant cells than expected by chance ~~(p=0.05)~~ for all ~~variables (~~spatiotemporal relationships (binomial field test $\alpha=0.05$, $p<0.001$).

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### 3.4. Long-term changes in diurnal climate conditions at the Keara treeline

In agreement with the decreased DTR trend observed since 1960, in situ daily temperature loggers independently confirmed that minimum temperatures for the October-April season have increased at this site (Fig. A6 A-C). Minimum temperatures for the October-April season in 2011-2014 ranged from 1.9-2.3 °C and increased to 3°C in 2021-22, which is higher than the 0°C average between 1960-2015 (Section 2.2, Tmin Fig. A1). The distribution of daily wet season minimum temperatures in 2021-2022 was significantly higher than the 2011-2014 seasons overall (bootstrap KS test $p<0.001$~~).~~ ; Fig A6).

~~3.4~~

Interestingly, average October-April maximum temperatures recorded by the data loggers ranged 7.2°C-8.2°, which is substantially lower than the 1960-2015 average (Section 2.2, Tmax~13°C; Fig. A1). Daily maximum temperature for the 2021-2022 season was significantly lower than the 2012-13 and 2013-14 seasons ($p< 0.01$), while no significant difference was detected relative to the 2011-2012 season ($p= 0.37$).

The daily data loggers also recorded a significant reduction in relative humidity within the 2011-2022 period (October-April; Fig A6D-F). Relative humidity declined from an average of 98% in 2011-2014 to 90% in 2021-2022, while minimum daily humidity decreased from ~94% to 80% (Fig. A6D, F). Although 2011-12 corresponded to a DJF-La Niña year (Table A1), the distribution of daily relative humidity values during that season was comparable to the 2012-13 and 2013-14 years ($p> 0.05$), and all 3 seasons were more humid than the 2021-22 year (Fig. A6. $p<0.001$). In fact, almost one third of daily relative humidity values for 2021-2022 (63 days) were below 90% for October-April, while less than 25 days were recorded for the same threshold in the 2011-2014 seasons.

In summary, the long-term warming and drying trends observed in precipitation and temperature between 1960-2015 (Figs. 4, A5) are consistent with in situ measurements of higher temperature and lower relative humidity for 4 distinct October-April seasons between 2011-2022 (Fig. A6).

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

~~The impact of extreme DJF-ENSO events on climate and the residual RW chronology is shown in Figure 5.~~ Table A1 lists the years of known ~~moisture~~hydroclimate anomalies in tropical South America connected to El Niño (warmer SST) or La Niña (cooler SST) conditions in the Pacific Ocean. Regardless of the ~~time span and~~ spatial temporal resolution, climate datasets ~~show~~agree that the El Niño-DJF events were linked to drier and warmer conditions at this site, while extreme La Niña-DJF years were wetter and cooler (Fig. 6A, B). SEA of the residual RW response depicts temporal growth anomalies for top 26 ENSO DJF events: 13 El Niño and 13 La Niña (Figs. 6CD). There was a one-year delayed and negative RW response to El

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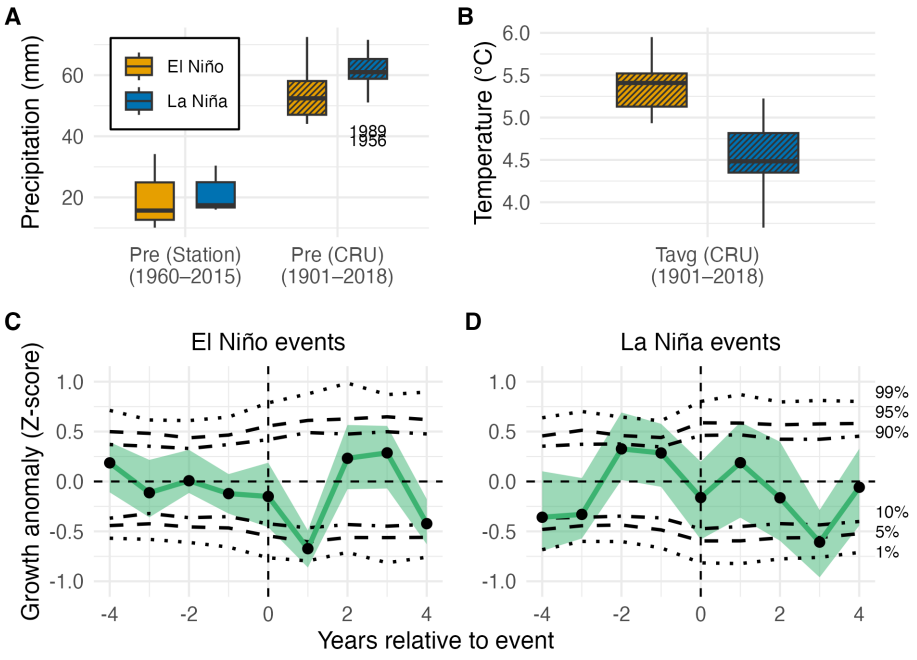
Niño events, i.e., one year after an event, *P.* ~~5AB).~~ *pepei* showed a significant decrease in radial growth (α = 0.1). There was a significant negative response two and three years after an extreme DJF-La Niña.

~~SEA results for El Niño DJF years show there was a one-year delayed and negative~~

Some RW ~~response, i.e., outliers identified in the residual~~~~one year after an event, *P. pepei* showed a decrease in radial growth (α = 0.1). Although there was a non-significant growth increase in~~ RW ~~after a La Niña DJF, there was a significant negative response three years after an extreme DJF La Niña~~ chronology coincide with years of known ENSO events. (Fig. ~~5B). It's interesting to note however, the~~ 2D) The largest ~~growth~~ tree-ring observed in *P. pepei* ~~formed during~~occurred at the ~~1950-1951 wet season and correspond to~~same time than an extreme DJF-La Niña ~~events~~event in ~~DJF~~ 1950 ~~and 1951 (Fig.~~-51 while the~~2C). The~~ smallest ~~(5th percentile)~~ growth ring in ~~1906-07 occurred~~the chronology was formed after a ~~major~~ DJF-El Niño event in 1905~~. In summary, *P.*~~ (Table 1; Fig 2D). Overall, the inter-annual *P. pepei* RW at the Andes-Amazon treeline has a lagged significant response to extreme DJF-ENSO conditions.



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To visualize the significant increase of minimum temperatures near Keara in a long-term context, annual and seasonal diurnal temperature range anomalies were calculated for the full CRU TS 4.08 calibration period 1901-2015 (Fig A5; DTR, Tmin, Tmax). There was a significant decrease in DTR and an increase in minimum temperature anomalies since the mid-20$^{th}$ century at this site. The largest decline in DTR was observed for the October-April season at a rate of -0.197°C decade$^{-1}$, though annual and July-August DTR declined at a similar rate (-0.191°C and -0.194°C decade$^{-1}$ respectively, 1960-2015; Fig. A5).

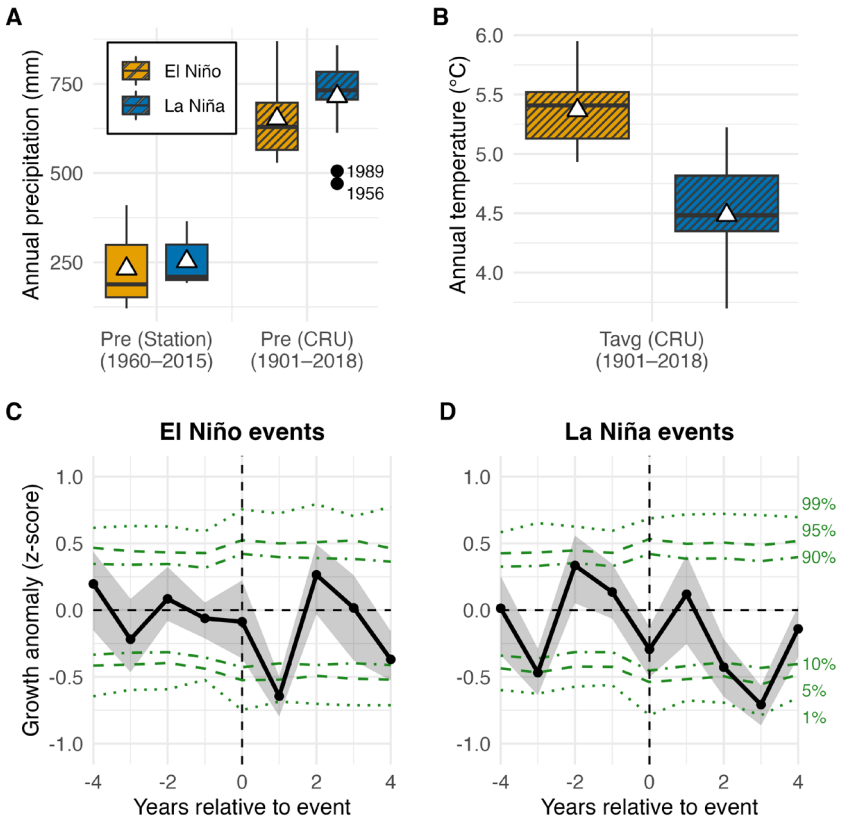

**Figure ~~5~~6: Boxplots ~~showing~~of annual (A) precipitation and (B) temperature for the 26 years of extreme DJF-ENSO events, using both station and CRU data. Outlier years in the CRU precipitation data are ~~labeled in (A).~~represented as black dots (A; 1956, 1989). Annual mean climate during El Nino-DJF is represented as orange colors, while La Niña is shown in blue (*n* = 13 years per event). Superposed epoch analysis of the residual RW response ~~between~~ 4 years before and 4 years after the DJF-ENSO events (C, D; black line). The uncertainty of the growth response is depicted as ~~green~~grey shading. Horizontal ~~black~~ green-lines represent ~~confidence intervals~~ (the two-tailed significance thresholds: (10-90%, 5-95% 1-99%) ~~based on~~derived from stationary bootstrapping.**

## 4 Discussion

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

~~Annual RW chronologies of~~ Here we have generated the first *P. pepei* tree-ring chronology from ~~a high Andean Amazon forest~~the MNP treeline in Bolivia ~~have been presented~~ and ~~analyzed. This is~~ the ~~first tree-ring~~longest annual growth record for this species in South America spanning from 1850 to 2018 CE (3795-4400 m a.sl; 14.75°S). These results provide new information of tree growth and climate dynamics in an understudied biodiversity hotspot in the southwestern Andes-Amazon corridor. We found that *P. pepei* RW is limited by prior-year minimum temperature (negatively) and precipitation (positively) variability during the wet season, leading to larger RW in the subsequent growth year when it was colder and wetter (Figs. 3 and 4). There was also a positive relationship between current-year maximum temperature and RW variability between 1960-2015 at this treeline. The lagged RW-precipitation signal is consistent with one of the two *P. pepei* tree-ring studies (lag=1; 1969-2004; 16°12S, 68°79W; 4130 m.a.s.l; Jomelli et al. 2012) and several *Polylepis tarapacana* investigations that reported prior-year water availability as a useful predictor of RW (Argollo et al. 2004, Morales et al. 2004, Christie et al. 2009, Soliz et al. 2009, Crispín-DelaCruz et al. 2022, Rodriguez-Caton, et a. 2021). The second study of *P. pepei* found that RW was positively correlated to current-year temperature variability (lag=0; 1941-1983; 17°S, 65°39W; 4100 m.a.s.l Roig et al. 2001). However, the dominant and negative relationship between RW and lagged minimum temperature variability has yet to be explored for treeline *P. pepei*.

The pronounced decline of radial growth in *P. pepei* since 1960 coincided with warmer and drier austral summers at this treeline (~November-March, 1960-2015; Figs. 2C & 4AC). There was also a significant step change and subsequent decline in raw RW after the 1993 growth-ring (Fig. 2A). It is possible that this area was affected by an 8.2 magnitude earthquake ~150

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km east of the site was recorded in June 1994 (Myers et al. 1995). Although this region of Bolivia is sparsely populated, landslides were reported in southern Peru and Chile, and thus it is possible that slope failures in 1994 occurred near this treeline in Keara Bolivia (Blodgett et al. 1998). This decline also occurred 1 year before the broader study region of Madidi was designated a National Park ~~and the longest record of *P. pepei* RW chronology in South America (1850-2018). This record provides new information about tree growth and climate~~ in September 1995 due to its extremely high levels of biodiversity and endemism for the Southern Amazon. The results herein verify the sensitivity of *P. pepei* tree-ring width at this site to both local climate and environmental disturbances. An altitudinal advance of this treeline is unlikely due to local geomorphologic constraints (Fig. 1D; Macias-Fauria and Johnson, 2013). Further, species-specific thermal niches that are required for seedling establishment and recruitment may be at risk due to the observed increasing temperature trends in recent decades (Kessler et al., 2014; Körner and Hoch, 2023). ~~in an understudied tropical treeline in South America (~3800-4400 m.a.s.l.). The potential human influence on RW for trees~~Although the spatial extent of this forest under increased warming and environmental change is uncertain, this study has helped clarify the nature of past and current growth variability of *P. pepei* in this region.

Human activity in Andes-Amazon forests should be considered when evaluating the growth patterns at tropical treelines ~~in this region. For the *P. pepei* near Keara.~~. Forest fragmentation was observed in the lower elevation open-canopy forest (3795-4100 m.a.s.l.) and tree-ring samples showed ~~possible~~evidence of fire scars in the 1940s ~~and clear forest fragmentation related to cattle ranching.~~. This subpopulation is likely more threatened by ~~human activities~~ small-scale cattle ranching in Keara than the closed canopy ~~site between~~ forest located at higher elevations (4000-4400 m.a.s.l~~. sampled in 2019 (Fig. 1CD).~~.; Fig. 1C, D). 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 (mostly in areas below 2000 m.a.s.l.). Despite ~~the potential for local environmental effects on growth~~these observations, correlations between *P. pepei* RW and ~~local with climate are~~regional temperature and precipitation variability were robust and may signify a response to ~~regional shifts in~~ larger-scale hydroclimate patterns ~~observed~~seen in tropical South America~~.~~ (Fig. 5).

~~We found that *P. pepei* RW is limited by prior-year temperature and precipitation variability during the wet season, with larger RW in the subsequent growth year when it was wetter and colder (Figs. 3 and 4). This is consistent with previous studies showing *Polylepis* ring-width positively correlated with previous growing-season water availability in the Andes (Argollo et al.~~The MNP treeline ~~2004, Morales et al. 2004, Christie et al. 2009, Soliz et al. 2009, Crispín-DelaCruz et al. 2022, Rodriguez-Caton. et a. 2021). Although the RW-precipitation correlations were robust, our results suggest that this *P. pepei* treeline is likely more affected by temperature-related moisture stress changes (Fig. A4), as would be expected particularly at treeline (Fritts, 1976). A pronounced decline in radial growth since 1997 (Fig. 2A) was observed at the same time this region has endured warmer and drier austral summers (~November-March) in recent decades (Figs. A4, A5). The Keara treeline also~~ revealed an imprint of extreme ENSO-related drought events in *P. pepei* growth rings.



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Hot ~~drought~~ and dry conditions related ~~to~~ DJF-El Niño ~~events~~years had ~~a~~ significant and negative ~~impact~~impacts on radial growth ~~of *P. pepei* at our study site. Although La Niña SEA were inconclusive, the lagged negative effect (*t*-3) may be related to the occurrence of El Niño events in years after La Niña. DJF anomalies were~~ (Fig. 6C). Although simiar RW responses to large-scale drought DJF ENSO events were selected for analyses because ~~it is the~~they occur during mature phase of the summer monsoon (70% of annual rainfall), but the ~~use of annual (instead of seasonal) events may show larger impacts on RW.~~

~~Future advances of this treeline towards higher elevations (Fig. 1C) are unlikely due to local geomorphologic constraints (Macias-Fauria and Johnson, 2013) and thermal niches that are required for subalpine recruitment~~ (impacts of annual or broader seasonal ENSO extremes may be more informative due to the sensitivity of RW to cumulative climate conditions (e.g. seasonal correlations Fig. A4). Overall local and regional climate-growth analyses suggest this treeline is primarily limited by temperature-driven moisture stress during the peak wet season (~November-March Figs 3,4, A3, A4). ~~Kessler et al., 2014; Körner and Hoch, 2023). As mentioned in the Introduction, *Polylepis pepei* in the tropical Andes is adapted to cold soil temperatures (3-5°C). Although the future spatial extent of the *P. pepei* forest under warming is uncertain, our study provides insight into the limiting factors to radial growth at a tropical Andean treeline in Bolivia since 1960.~~ In the following sections we discuss ~~potential local environmental and climate variables~~both site-level and large-scale hydroclimate conditions that may ~~contribute *P.*~~ have contributed to the growth decline of treeline *P. pepei* ~~tree-ring variability in Keara~~since the 1960s.

### 4.2. ~~Changes in temperatures~~Local temperature and humidity changes at the *P. pepei* treeline in Bolivia

Increases in minimum temperature ~~(Tmin)~~ may be reducing moisture availability in high-elevation Andean tropical ~~sites. Hourly~~forests. The mean diurnal temperature range near Keara has significantly and negatively declined since 1960, signifying that the rate of minimum temperature increase has surpassed that of maximum temperature (Fig. A5. CRU TS 4.08 ;1901-2015). Daily climate ~~data recorded by data~~ loggers ~~at our~~within the *P. pepei* site ~~(Fig. A3) showed that the period September~~ indicated the 2021-~~May~~ 2022 ~~had~~wet season was significantly warmer ~~Tmin and lower relative humidity (RH) in comparison to the period~~and drier than in 2011-2014 ($p < 0.0001$ October-April). This decrease in ~~RH~~ relative humidity alongside an increase in ~~temperature~~minimum temperatures suggests that the capacity of air to hold moisture has outpaced the actual moisture content, making the air drier despite higher temperatures. Although ~~these results~~the data logger records cover a short time- window, they provide in situ ~~evidence of~~, high-resolution data over a 10-year period in Keara, and thus they are useful to confirm: i.) the warming ~~and drying~~ trends observed in the long-term climate data ~~of this site (Fig. A4). DTR variability (i.e. difference between Tmax and Tmin) near Keara in Fig. A5 depicts a significant negative trend in this region since 1960, which means the rate of increase for minimum temperatures has surpassed that of maximum temperature. Even though warmer temperatures increase the capacity of the air to hold more water vapor (i.e., the Clausius-Clapeyron relation), if the moisture supply does not increase proportionally, humidity will decrease.~~(Fig. 4, A5), and ii.) that the increase in minimum temperatures coincided with a decrease in humidity at this site (Fig. A6) .



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*P. pepei* ~~had significant negative correlations with increasing~~RW was significantly and negatively impacted by lower wet-season precipitation and higher minimum temperatures ~~on the local and spatial scale (Figs. 3 and 4~~even after linear trends in climate were removed (Fig. A4; residual correlations). Minimum temperatures influence convection, as rainfall in the Andes-Amazon ecotone largely occurs in the afternoon/night when radiative cooling drives cold air downslope and converges with rising warm moist air from the tropical lowlands (Garreaud, ~~1999~~2009; Junquas et al., 2018; Romatschke and Houze, 2010~~).~~; Rosales et al., 2022). Known as 'orographic precipitation', this process is key for rainfall distribution across ~~elevations in~~ the Andean foothills ~~like our site~~ (Arias et al., 2021; Chavez and Takahashi, 2017). According to the hourly in situ data loggers in Keara, daily RH peaked at 3:00 P.M. on average, likely reflecting afternoon cloud formation at this site. In the region of the MNP, maximum precipitation ~~occurred~~totals occur between 1000-1300 m.a.s.l., with a sharp decrease in moisture ~~distribution towards higher elevations >~~transport above 3000 m.a.s.l. (Chavez and Takahashi, 2017). If minimum temperatures increase, the radiative cooling effect ~~is weaker~~weakens, which may result in warm, moist air converging at lower elevations~~,~~ (e.g. below our ~~treeline~~ *P. pepei* site ~~()~~(Romatschke and Houze, 2010). ~~The hourly meteorological data between September-May~~ In terms of tree-growth in ~~2011-14 and 2022-23 shows that RH peaks at 3:00 P.M. in Keara on average, suggesting afternoon cloud formation. It's~~this area, one interesting ~~to note~~ observation is the declining *P. pepei* RW trends observed ~~in *P. pepei* (>3800~~at the MNP treeline (above 4000 m.a.s.l.~~)~~) diverge from the increasing RW trends observed in lower-elevation humid forests ~~from MNP since~~in the ~~1980s~~MNP (e.g. *Juglans boliviana* ~1300 m.a.s.l.~~,~~ ) (Oelkers et al. 2023). ~~It is possible that the increase in Tmin since the late 20th century (Fig. A5) may have contributed to reduced orographic convection and moisture availability, thus potentially limiting the growth of *P. pepei*. Future research needs to be conducted on horizontal moisture transport in the Andes-Amazon and the diverging trends in growth between the lower Amazon and treeline forests.~~

One possible explanation for this pattern is that warmer minimum temperatures alter the local balance between temperature, humidity, and upslope moisture transport in the Andes–Amazon ecotone. Because precipitation at these elevations depends strongly on orographic processes and on the interaction between moist lowland air and cooler mountain conditions, weaker nighttime cooling could reduce the efficiency of moisture convergence at the elevation of the treeline. We cannot demonstrate that mechanism directly here, but the observed increase in minimum temperature, decline in DTR, and reduction in relative humidity in Keara are all consistent with a shift toward locally dry conditions that may limit P. pepei growth (Figs 4, A5, A6). In this sense, the results point to moisture stress amplified by warming, rather than temperature alone, as the most plausible explanation for the long-term decline in ring width at the MNP treeline. Future research needs to be conducted on elevational moisture transport in the Andes-Amazon and these diverging tree growth trends observed within the MNP.

Besides inhibiting moisture convergence and transport from lower elevations, warmer minimum temperatures could also affect the tree water-balance in Keara ~~by increasing transpiration and respiration rates (Sierra et al., 2022).~~ 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 and increased evaporative demand at the leaf level (Locosselli et al., 2020). From an ecophysiological

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perspective, respiration rates increase with ~~rising~~warmer temperatures ~~and~~ . Excessive warming at night (i.e. increased Tmin) without the process of photosynthesis ~~occurring at night. This in turn increases~~may increase the amount of tree-level carbon (respiration) and soil-water~~)~~ content released ~~from the trees~~ to the atmosphere~~.~~ (Körner et al. 2012). Temperature and precipitation near the *P. pepei* site are inversely correlated during ~~the extended~~peak wet season ~~(October-April~~(~November-March, $p<0.05$). ~~If~~Thus, if there is less cloud cover (and ~~rainfall~~precipitation), there is higher solar irradiance and temperatures, which may limit the photosynthetic capacity of trees especially in tropical ~~trees at higher elevations~~moist treelines (García-Núñez et al., 2004; Hoch and Körner, 2005; Jaramillo, 2015). ~~The current-year positive relationship between RW and FMA Tmax (Fig.3C, Fig. 4.B), may also highlight the ecophysiological link between tree-ring size (i.e. xylogenesis) and cooler trends in Tmax at the end of the wet season between 1960-2015 (see discussion in Rodriguez-Caton et al. 2021). Although it is possible that 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. 3, A4).~~ Further research must be conducted to determine the ~~phenology and~~ physiological response of *P. pepei* ~~to micro-climate conditions such as a reduction in orographic precipitation at~~at this treeline ~~or low~~ to diurnal and seasonal changes in orography and soil-water availability.

The positive relationship between *P. pepei* and February-May mean and max temperatures may demonstrate ecophysiological link between tree-ring size (i.e. xylogenesis) and cooling observed at the end of the wet season (lag=0; FMAM Tmax Figs. 3BD, A3BD). Although it is possible the mechanisms controlling primary and secondary growth may not occur at the same time (i.e. photosynthesis vs. wood formation), the RW-climate correlations indicate growth rings are smaller when there are cooler conditions in late austral summer (or vice versa; Figs. 3, 4). It is interesting to note that an extreme cold period observed near Keara during the late 1950s corresponds with a growth suppression observed in raw, standard and residual *P. pepei* RW chronologies, emphasizing the coupled relationship between RW and mean and maximum temperatures during this period (Figs. A5B, C and 2A, C). The exact growing season for *P. pepei* in Keara estimated to be during the wet season (~ October-April), but the phenology of *P. pepei* in the MNP and elsewhere is largely unknown. The use of point-dendrometer bands that record high resolution variations of stem circumference may reduce uncertainty regarding the onset and cessation of tree-growth during the hydrological year and its relationship temperature variability between February to May.

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

~~The~~ In addition to site-level conditions at this treeline, the recent decline in ~~radial~~annual growth may ~~be~~ also ~~influenced by~~ be linked to broader scale hydroclimate ~~changes.~~patterns observed in tropical south America. In the central Andes treeline, ~~(>17°S; 4657-4800 m.a.s.l.). Negative~~negative RW trends in *P. tarapacana* since the 1970s were attributed to increasing drought conditions in southern Peru and northern Chile ~~since the 1970s.~~ (>17°S; 4657-4800 m.a.s.l) (Morales et al. ~~(~~2023~~)~~ ~~developed a NDJ precipitation reconstruction from these trees and discovered that a drying trend since 1997 was unprecedented in the 389-yr reconstruction. Although 1997 was identified as a changepoint in the raw ring-width data of *P. pepei*, our site is~~

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~~in the Amazon basin, a much more humid environment than the *P. tarapacana* in *Morales* et al. (2023). Nonetheless the shared timing of growth decline in these high-Andes forests is interesting.~~

~~).~~ Increasing drought frequency ~~in the tropical Andes and southern Amazon Basin (> ~15°S)~~ has been linked to delayed wet season onset (Espinoza et al., 2016; Fu et al., 2013; Marengo et al., 2011). One possible explanation is ~~an~~that the intensification of the atmospheric Hadley ~~circulation, related to~~Circulation during the 20th century, driven by warming SST in the ~~(northern)~~ tropical Atlantic ~~Ocean, which interrupts upward flows from the Amazon~~, has led to ~~the Andes~~a weakening of zonal moisture transport and in increase in subsidence during ~~the~~transitional dry-to-wet ~~period~~ seasons in the central Andes(Beveridge et al., 2024; Espinoza et al., 2021, 2019; Sierra et al. 2022; 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 in Bolivia and Peru which marks a delay in the timing of austral spring rainfall. Additionally, an observed weakening of upper-level easterlies winds from the Amazon to the Andes (Segura et al. 2022);~~. In that context, the decline observed in *P. pepei* may ~~have contributed to reduced moisture transport potentially affecting tropical~~be part of a wider pattern of increasing hydroclimatic stress at high elevations in the tropical Andes. At the same time, the Keara site differs from drier Polylepis treelines ~~like *P. pepei* in Keara.~~ such as *P. tarapacana* (Morales et al. 2023;), so annual growth-comparisons should be interpreted cautiously.

In contrast to a drier start to the wet-season, a recent increase in precipitation at the end of the wet season ~~< 2000 m.a.s.l.~~ has been observed in lowland regions ~~of~~below 2000 m.a.s.l. in the northern Andes and Amazon ~~and Andes-Amazon~~Basin (Arias et al., 2021; Espinoza et al., 2021, 2019; Malhi et al., 2008; Zanin and Satyamurty, 2020). These studies argue that the warming of the Atlantic Ocean, land-surface changes in the Amazon, and wind anomalies are the primary factors contributing to changes in circulation and specific humidity in tropical south America overall (~~particularly between March-May;~~ see references in (Beveridge et al., 2024)). ~~Within Bolivia, contrasting trends in~~Contrasting precipitation ~~and tree-growth~~ trends have been observed ~~between low~~at various latitudes and ~~highland elevation forests. Tree-~~elevations within Bolivia as well. tree-ring oxygen isotopes ~~(δ$^{18}$O~~(d$^{18}$O) from ~~*C.*~~*Cedrela odorata* in the lowland Bolivian Amazon ~~(10°5′S, 66°18′W; 106 m.a.s.l.)~~ reflected an increase in November-March precipitation ~~(and decrease in δ$^{18}$O)~~ between 1980-2010 ~~(~~(10°5′S, 66°18′W; 106 m.a.s.l.)~~, Baker et al., 2016; Cintra et al., 2025),~~ while treeline *P. tarapacana*~~, in~~d$^{18}$O from the Bolivian Altiplano ~~(22.3°S, 67.23°W; ~4600 m.a.s.l.)~~ recorded a ~~pronounced dry period for~~ decrease in December-March precipitation between 1992-2012 (22.3°S, 67.23°W; ~4600 m.a.s.l.; Baker et al., 2016; Cintra et al., 2025;Rodriguez-Caton et al., 2024). ~~Despite the fact that~~Even though these hydroclimate trends are complex and spatially variable, having *in situ* high-resolution climate proxies at the Andes-Amazon treeline such as this *P. pepei* may be useful in understanding long-term changes in orography.

Overall, growth variability at this *P. pepei* treeline ~~in~~ is modulated by temperatures and moisture available at the site, which may be influence by small-scale climate dynamics driven by orography, but may also reflect broader hydroclimatic changes across the tropical Andes- and adjacent Amazon ~~here may be related~~basin mentioned above. *Rather* than implying a shared



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mechanism across all Andean treelines, our results suggest that distinct Polylepis treelines may be responding to ~~temperature-driven moisture trends observed at local and~~ a common regional ~~scales. This study herein has demonstrated the dendroclimatic potential of this species at a~~ trend toward warmer and, in some cases, effectively drier conditions during the peak wet-season near the Andes-Amazon treeline ~~from the most biodiverse region of the world (MNP; Muller, 2017) and~~ (~November-March). Overall, this newly-generated record has provided ~~insight into the~~in situ evidence of a long-term, and negative growth response of a tropical ~~forest in South America under a warming environment.~~treeline to increased temperature trends in Northwestern Bolivia between 1960-2015 (14°S, 4400 m.a.s.l).

## 5 Conclusions

We ~~reported~~report a significant decline in radial growth in Polylepis pepei at a tropical ~~*P. pepei*~~ treeline in ~~Keara, Bolivia, at~~ the ~~edges of the Andes-~~southwestern Amazon ~~high-elevation forests. Here, grow decreases~~Basin (~4400 m a.s.l.). Our results indicate that this decline is associated with ~~warmer~~increasingly warm and ~~drier~~dry conditions ~~in~~ since the 1960s, particulaly through reduced precipitation and higher minimum temperatures during the ~~prior-year~~ wet season~~, and there is an adverse influence of temperatures, in particular Tmin, on growth. Higher Tmin weakens~~ preceding ring formation. Together, these changes suggest increasing moisture stress at the site. Rising minimum temperatures, especially when not matched by equivalent increases in maximum temperatures, may also reduce moisture availability by lowering relative humidity, altering local moisture transport, and increasing nighttime ~~convection that brings moisture from lower elevations to this site, and in general~~respiratory carbon losses. More broadly, warmer conditions ~~increase~~are likely to enhance evaporative ~~demands~~demand and ~~cause water stresses.~~further constrain tree growth. We also found a tendency ~~of~~for narrower ~~growth~~ rings in the year following warm and dry El Niño events, ~~while~~whereas the ~~role~~influence of La Niña ~~events was inconclusive. This~~ remained less clear, suggesting an asymmetric ~~influence of~~ ENSO ~~on tree growth warrants further investigations. Moving forward, since we found *P. pepei* to develop annual rings~~effect that ~~are climate sensitive, expanding~~deserves further study. Expanding the *P. pepei* network ~~in Keara would enable~~ at Keara could provide the basis for the first tree-ring-based climate reconstructions ~~of precipitation and temperature of the southwestern Amazon-Andes ecotone. This would be the first of its kind~~ for northern Bolivia, extending the ~~limited station records~~short instrumental record back to the mid-~~1800s. Our results~~ nineteenth century. Overall, our findings provide new ~~insights~~insight into the ~~response~~vulnerability of ~~a~~ tropical ~~treeline in an era of global~~treelines to ongoing warming~~, increasing climate extremes,~~ and ~~human activities~~hydroclimatic change, and ~~support~~they highlight the value of *P. pepei* for future dendrochronological and ecophysiological research ~~of *P. pepei* in South America. We recommend pursuing research that~~in the tropical Andes. Future work should thus focus on quantifying leaf respiration ~~and temperature response~~, temperature sensitivity, and the timing of wood formation using ecophysiological measurements and point dendrometers, to better understand the ~~ecophysiology of~~ mechanisms linking climate change and growth decline in this ~~tropical treeline~~ species ~~in Bolivia.~~

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## Author contribution

Co-authors LAH, DRC, MRC, MEF, RO, ET, AF collected tree samples in Keara. CM and AF organized field campaigns and provided essential information regarding Madid National Park. RDD and LAH assisted in initial experimental design and editing. Tree-ring dating, measuring, and analyses was conducted by corresponding other RO. HTTN, aided in correlation analyses and concept. APS assisted in wood anatomical methods. Editorial review provided by all co-authors. Site images for ~~Fig~~Figs. 1 and A2 were taken by RO.

## Competing interests

The authors declare that they have no conflict of interest

## Acknowledgements

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## Data Availability

The *Polylepis pepei* RW chronology from Keara will be made publicly available on the NOAA International Tree-ring Database.

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## Appendix A

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| El Niño DJF | La Niña DJF |
|---|---|
| 1983 | 1974 |
| 1998 | 1917 |
| 1973 | 1956 |
| 1931 | 1976 |
| 1992 | 2011 |
| 1966 | 1989 |
| 1919 | 1910 |
| 1926 | 1971 |
| 1958 | 1951 |
| 1897 | 2000 |
| 2010 | 1918 |

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| | |
|---|---|
| 1987 | 2008 |
| 1942 | 1943 |

**Table A1. NOAA-PSL list of 26 top ranked DJF-ENSO events (13 each) which were selected for SEA analyses of *P. pepei* RW. The years provided for the DJF seasons are centered on January. The remaining 22 top ranked events (48 total) are available on the website (https://psl.noaa.gov/enso/past_events.html).**

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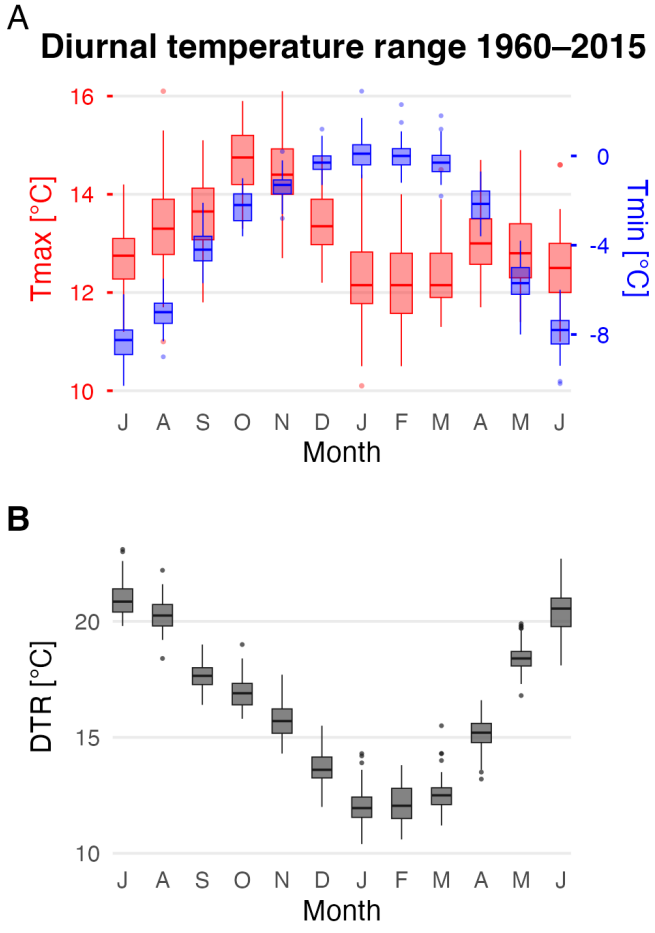


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915 **Figure A1: (A) Boxplots of the mean monthly distribution of maximum and minimum temperatures and (B) the diurnal**
916 **temperature range (grey:DTR) for the study region between 1960-2015 using the nearest CRU 4.08 grid point data**
917 **(14.75,69.25). Boxplots include the temperature median (horizontal line), 1.5x the inter-quartile range (whiskers), and**
918 **outliers (colored dots).**

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## Appendix A2. Photo of *Polylepis pepei*, Wood anatomy and Radiocarbon Analyses

At early stages of RW chronology development for the *Polylepis pepei* network, initial radiocarbon results (Fig. A2.C) 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 timeseries generated with material collected in October 2012, the first ring behind the bar 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 for the 2012 growth year (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 was corrected to 2011. This date-adjustment on the samples from the 2012 campaign was confirmed after cross-dating RW from additional living trees collected in 2019 from the Waca-cocha closed-canopy forest. The final RW chronology shown included 31 trees from 2019 (combined mean correlation, $r$= 0.50). In summary, the traditional dendrochronological crossdating techniques of RW measurements, wood anatomical cuts, and radiocarbon results confirmed *P. pepei* in Keara formed annual rings.

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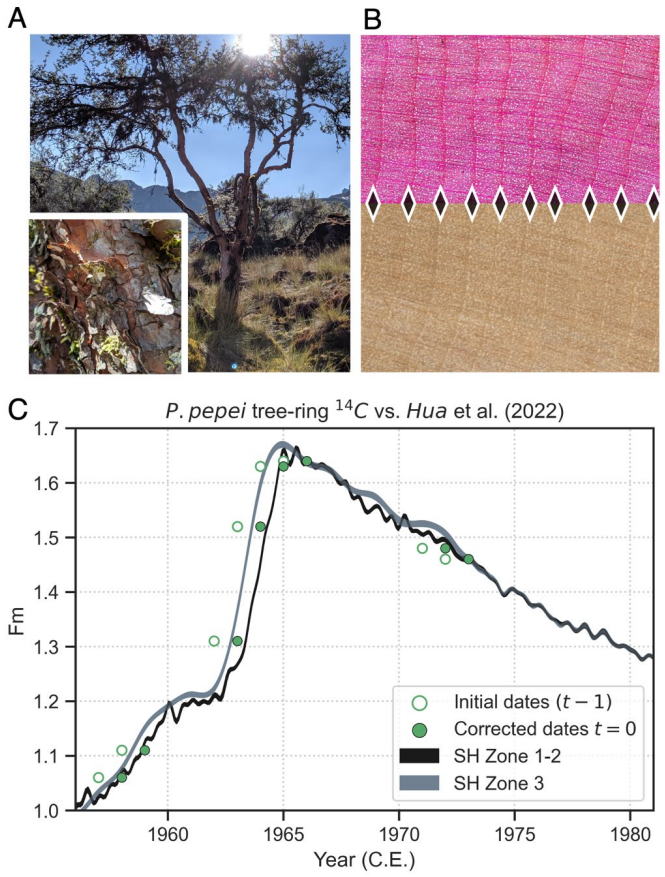


Figure A2. (A) Photo of a P. pepei tree in Keara during the dry season in July 2019. The trees have evergreen foliage, and can appear shrublike, with twisted, and at times multiple, stems. The bark consists of thick layers of compressed flakes that are red and brown in color. (B) P. pepei wood anatomy for a histological slice (40X magnification Echo microscope camera) and scanned image of a tree-core (3200 dpi). The direction of radial growth is from left to right (pith to bark) while diamond shapes indicate the latewood/earlywood boundary between annua tree-rings. P. pepei tree rings feature large, uniformly distributed vessels in the earlywood while the latewood includes both solitary vessels and thicker, fiber-like tracheid cells. The vessel lumen area in the latewood appears to taper tangentially in size before each subsequent growth-ring boundary. (C) Radiocarbon measurements (green circles) from the alpha-cellulose of selected rings in a cross-section is plotted with the Hua et al. (2022) reference curves SH Zone 1-2 and SH Zone 3.

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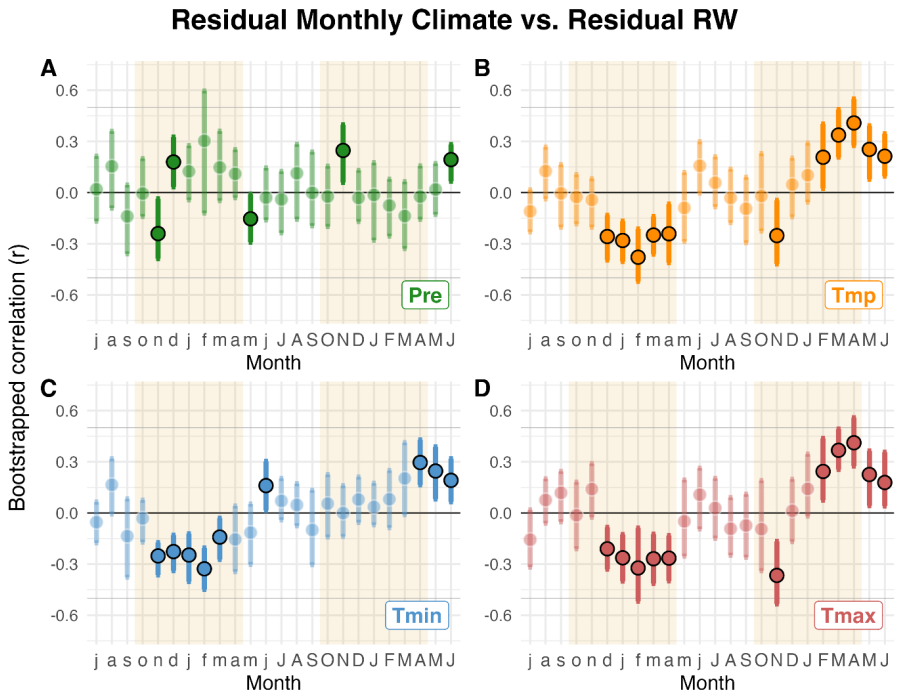


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945 **Figure A3. Residual *P. pepei* RW correlations with Residual monthly climate data 1960-2015. The residuals from a**
946 **linear regression were applied to the local monthly precipitation (A), and mean, minimum, and maximum temperature**
947 **series for the site (B-D) to evaluate the interannual relationships between annual RW and monthly climate variables.**
948 **Lowercase letters on the x-axis represent prior-year climate (lag=1). Correlations are reported as the median *r***
949 **estimated using stationary bootstrapping. Significance was defined from 95% bootstrapped confidence intervals and**
950 **are denoted in solid-colored circles outlined in black. Tan-shading represents the estimated 'wet-season' for the treeline**
951 **site which extends between October-April for this period.**

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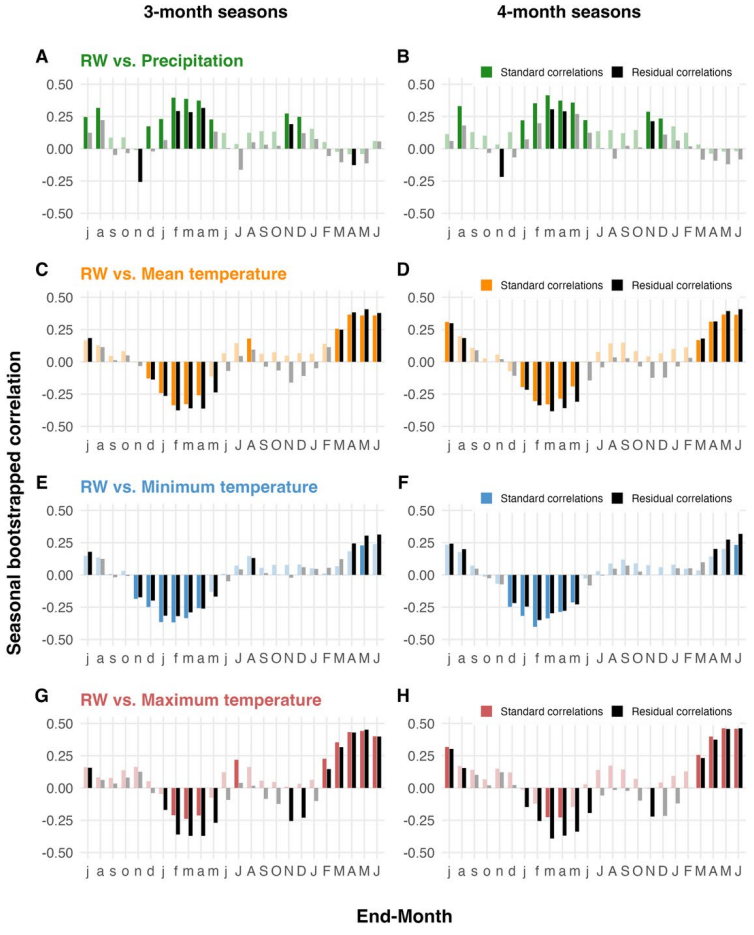


**Figure A4. Running seasonal climate correlations with *P. pepei* RW for 3-month (left column) and 4-month (right column) seasonal averages using local temperature and precipitation data (1960-2015). 'Residual correlations' are represented as black bars (i.e. detrended climate vs. residual RW), while colored bars represent 'standard correlations' (i.e. mean climate vs. standard RW). The x-axis represents the 'end-month' of the season, for example, lowercase 'f' in panel (A) represents correlations between RW and prior-year December-February precipitation (lag=1). Significance was inferred from 95% bootstrapped confidence intervals. Non-significant seasonal correlations are faded, while significant correlations are solid-colored bars.**

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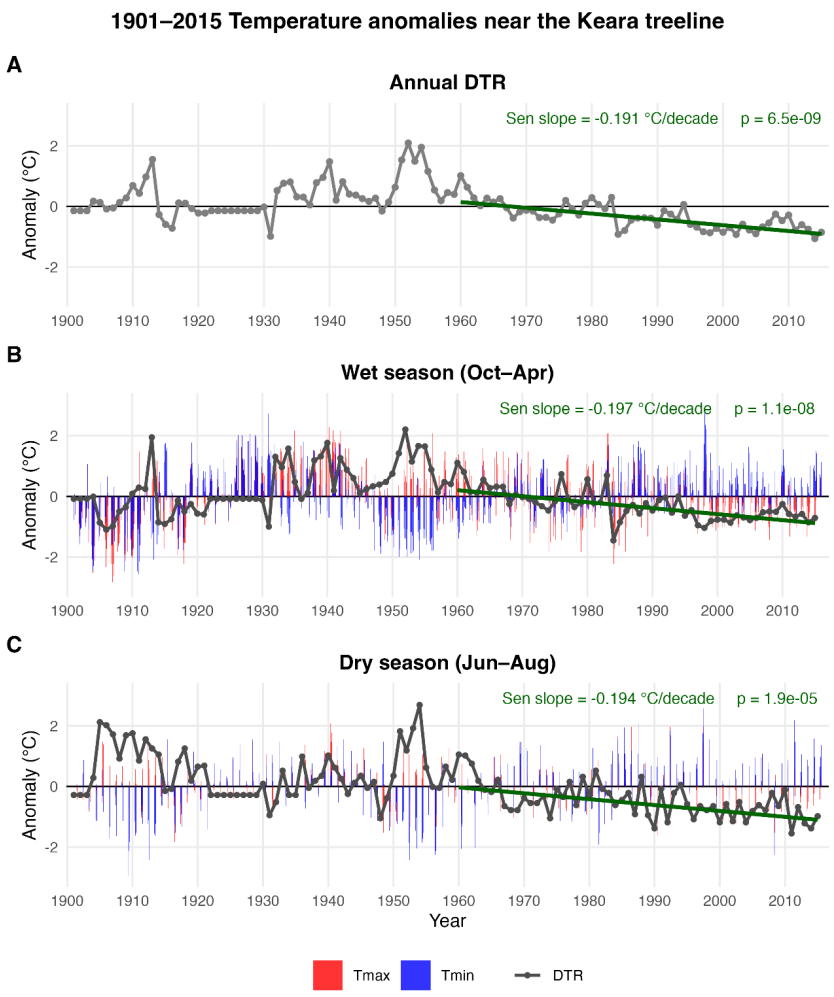


Figure A5. Long-term temperature anomalies for the Keara site (1901-2015). The grey timeseries represents annual (A) and seasonal (B-C) diurnal temperature range for the nearest gridpoint from CRU TS 4.08. 1901 is the earliest year of available data for CRU. Linear trends in DTR anomalies were estimated using Sen's slope. The significance of the 1960-2015 trend was evaluated using a two-tailed Mann-Kendall test. The mean slope is reported as the average change in DTR per decade (°C). Seasonal anomalies for Tmax (red) and Tmin (blue) are represented as vertical bars for the 1901-2015 period (B-C).

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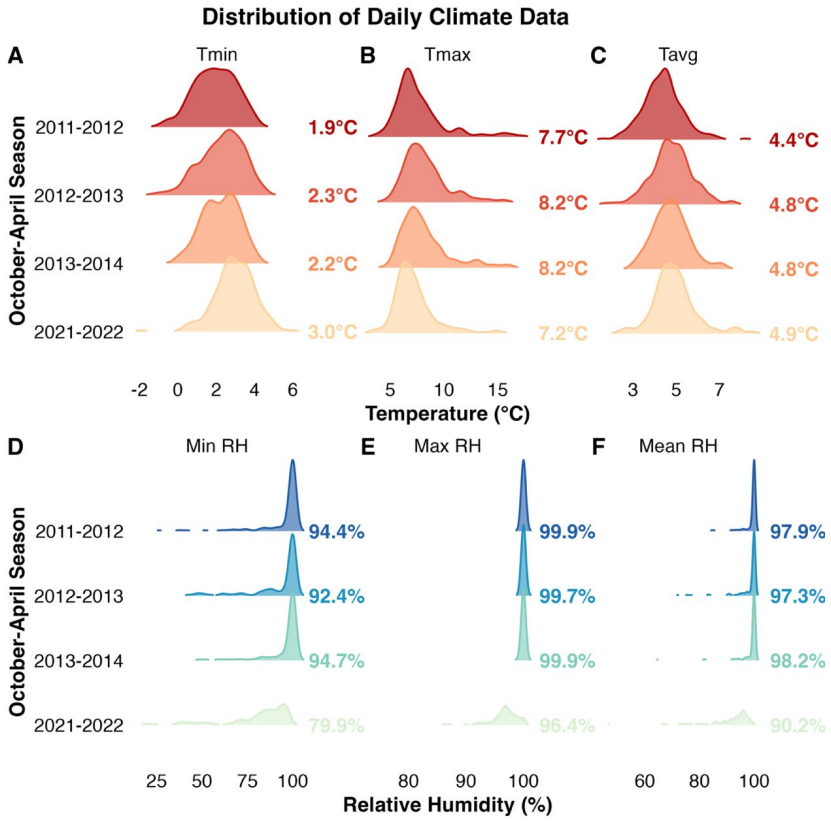


**Figure A6. Ridgeline distributions of daily temperature and relative humidity between October–April for the 2011–2012, 2012–2013, 2013–2014, and 2021–2022 seasons at the site. This data was resampled from hourly measurements recorded *in situ* from dataloggers installed near the Keara open-canopy site in 2011 (see section 2.1). The top row (A-C) represents daily minimum (Tmin), maximum (Tmax), and mean (Tavg) temperature. The bottom row (D-F) displays minimum, maximum, and mean relative humidity (RH; bottom row). Colored ridges represent daily observations within each season, and bold values at the right margin indicate seasonal means for each year.**

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