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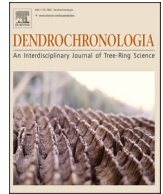Andreu-Hayles, Laia
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Age structure and climate sensitivity of a high Andean relict forest of *Polylepis rodolfo-vasquezii* in central Peru

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ABSTRACT

For a better understanding of forest ecology, tree-ring studies can provide information on climate sensitivity, tree growth patterns and population age structure that can inform about stand dynamics such as recruitment of new individuals, and other interspecific interactions related to competition and facilitation. Little is known about the ecology of the recently identified high Andean tree species *Polylepis rodolfo-vasquezii*. Here, we analyzed the relationship between tree size and age of two *P. rodolfo-vasquezii* forest stands located in the central Peruvian Andes at 11°S in latitude, and compared their growth patterns and climate sensitivity. We measured the height and diameter of each individual tree and collected tree core samples of living trees and cross sections of dead standing trees to generate two centennial tree-ring chronology at Toldopampa (1825–2015 CE) and at Pomamanta (1824–2014 CE) sites. The dendrochronological dates were evaluated by ^{14}C analysis using the bomb-pulse methods analyzing a total of 9 calendar years that confirm the annual periodicity of this tree species. At the Toldopampa stand most trees ranged from 70 to 80 years old, with a 190-year old individual, being an older and better preserve forest than Pomamanta, with younger trees, probably because more human disturbances due to closer village proximity. No significant relationships were found between tree age and size in the oldest stand alerting that tree diameter should not be used as a metric for estimating tree ages as a general rule. The distinct growth patterns and the size-age relationship observed at the two forests may reflect distinct histories regarding human activities such as fire and logging. Nevertheless, both the Toldopampa and the Pomamanta tree-ring width chronologies exhibited common growth patterns and shared a similar positive response to temperature of the current growing season. Overall, our study confirmed the annual radial growth periodicity in *P. rodolfo-vasquezii* trees using an independent method such as ^{14}C analyses and a strong climate sensitivity of this tree species. These findings encourage the development of an extensive *P. rodolfo-vasquezii* tree-ring network for ecological and paleoclimate studies in the tropical Andes in South America.

1. Introduction

The *Polylepis* genus is distributed along the Andes from Venezuela to northern Chile and the 'Sierras de Córdoba' in Argentina in high Andean montane forests ranging between 900 and 5000 m a.s.l (Segovia-Salcedo et al., 2021). These forests have a high biological diversity and are refuge of endemic species of flora and fauna (Fjeldså and Kessler, 2004; Sevillano Ríos et al., 2018). The most recent taxonomic revision of

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Polylepis genus lists a total of 23 species for Peru, 15 of which are endemic (Boza Espinoza and Kessler, 2022). Activities such as logging, grasslands burning and livestock browsing (Kessler, 2006; Jameson and Ramsay, 2007; Renison et al., 2013; Morales, 2017) have directly or indirectly generated a decline of these forests and constrained its distribution. Currently, the *Polylepis* forests exhibit a fragmented distribution often restricted to rocky areas and steep slopes over topographic conditions not optimal for tree growth. This loss of habitat of *Polylepis* forests together with their exposure to extreme environmental conditions and hazards (Azócar et al., 2007; Jameson and Ramsay, 2007; Morales et al., 2018) ranked them as one of the most vulnerable ecosystems in the world (Tejedor Garavito et al., 2012, 2015). In this context, there is a growing awareness, among public and private institutions, of the importance of implementing conservation and restoration strategies for preserving these relict *Polylepis* forests. Therefore, it is important that academic and forestry communities join efforts for a more sustainable management and conservation of these Andean forests (Morales et al., 2018).

Several studies have been conducted to understand the ecology and dynamics of these high-elevation Andean forested ecosystems (Hertel and Wesche, 2008; Kessler et al., 2014; Morales, 2017; Morales et al., 2018). One of the most common approach is related to the measurement of allometric variables in order to describe the structure of the forest (Fernández et al., 2001; Martínez and Villarte, 2009; Castro and Flores, 2015). In particular, forest structure based on allometric data has been used to study environmental changes and human impact (Toivonen et al., 2011; Kessler et al., 2014; Camel et al., 2019), but also to estimate tree ages for restoration studies (Aragundi et al., 2011; Renison et al., 2011; Toivonen et al., 2011). Therefore, an accurate determination of tree ages is very important for a better understanding of forest dynamics (Bormann and Berlyn, 1981; Aakala et al., 2013; De Groote et al., 2018; Hadad et al., 2020). Although it is usually assumed that there is a correspondence between tree size and tree ages, this relationship does not always occur due the heterogeneity of the environmental conditions for tree growth (Abrams, 1985; Suarez et al., 2008; Domic and Capriles, 2009; Gareca et al., 2010; Xing et al., 2012; Castagneri et al., 2013; Arenas-Castro et al., 2015) and/or the complexity in forest structure, particularly in mixed species and/or uneven aged stands. The inclusion of accurate tree ages in the study of forest dynamics allows for providing information on tree recruitment, growth and mortality, which is information that can be very useful for conservation actions (Xing et al., 2012; Brown et al., 2019).

For *Polylepis* genus (Rosaceae) specifically, very few studies have analyzed the relationship between allometric and age structure and they found contrasting findings (Suarez et al., 2008; Domic and Capriles, 2009; Gareca et al., 2010). Yet, the relationship between these age-size variables is not clear and patterns appear to vary between species, and even among forests of the same species located in different sites (Camel et al., 2019). Factors such as geographical location, environmental growing conditions and species response need to be considered case by case before assuming that age and size are related in a certain location. For example, *Polylepis australis,* the southernmost *Polylepis* tree species, is likely to grow under different environmental conditions than *Polylepis tarapacana*, which forms the highest elevation forests in the genus (Azócar et al., 2007). Therefore, extrapolating information based on the results of one tree species to others may not be advisable because the phytogeographical distribution of the *Polylepis* genus covers a wide latitudinal and altitudinal range, and therefore different forests can be living in very distinct environmental conditions (Renison et al., 2018; Segovia-Salcedo et al., 2021).

Studies based on dendrometers, equipment that measure daily growth rates with high precision, have been conducted (Schöngart et al., 2017). These studies are usually limited to a duration of 5–10 years, although in rare occasions there are records from the 1960 s (Sullivan et al., 2020). Tree-ring analyses can provide an estimation of the age of the trees and contribute to interpretations of longevity (life span) and regeneration processes (Boninsegna et al., 1989). A dendroecological approach not only allows for the representation and understanding of the structural patterns of a forest, but also for inferences about the processes behind (Amoroso and Suárez, 2015). Furthermore, the dendrochronological methods require less time in the field than long-term monitoring approaches such as the installation of permanent plots and/or dendrometers.

The *P. rodolfo-vasquezii* (Rosaceae) was described as a new tree species in 2015 (Valenzuela and Villalba, 2015; Boza Espinoza and Kessler, 2022). This endemic tree species is restricted to the central Peruvian Andes and forms monodominant moist forests, where the soils are composed mainly by moss, tree debris and rotten wood, and the individuals are growing over rocky surface or boulder areas. Its altitudinal range was reported to vary between 3600 and 4300 m a.s.l. (Ames-Martínez et al., 2019) and according to more recent investigations from 3700 to 4750 m a.s.l. (Boza Espinoza and Kessler, 2022). *P. rodolfo-vasquezii* trees can reach 10 m of height and diameters of 30 cm (Camel et al., 2019). Considering its endemism in central Peru, *P. rodolfo-vasquezii* is an important new tree species for conservation (Segovia-Salcedo et al., 2018; Boza Espinoza and Kessler, 2022). Furthermore, the fact that is one of the tree species within the genus *Polylepis* that present visible growth layers (i.e., tree rings) with well-defined boundaries pointed out great potential for ecological and paleoclimatic studies in the tropical Andes (Requena-Rojas et al., 2020a).

The study presented here is focused on unravelling ecological insights of *P. rodolfo-vasquezii* forests using the information provided by tree rings and allometric variables. Specifically, we study two relict *P. rodolfo-vasquezii* forests to confirm the annual periodicity of the tree rings using dendrochronological crossdating methods and ^{14}C analyses as a necessary first step to assess (1) the relationship between tree size and age, (2) radial growth patterns, and (3) climate sensitivity.

2. Materials and methods

2.1. Study sites

Our study site is located at 4 km from the Toldopampa village in the district of Pampa Hermosa, province of Satipo, Peru (11.50 ºS; 74.89 ºW) at an altitude range between 3900 and 4170 m a.s.l (Fig. 1A, B) and on a west-facing steep slope with an inclination of 40%, with a 45-cm moss layer covering the rocky basal floor. This relict *P. rodolfo-vasquezii* forest covers approximately 3 ha of extension and it is located at the top part of a hill surrounded by a forest of *Gynoxis sp.* Evidence of anthropogenic activities like moss collection and logging were observed. We also analyzed tree-ring data from another *P. rodolfo-vasquezii* forest located at Pomamanta (11.43 ºS; 75.80 ºW; 4360 m a.s.l.) in the Comas district, province of Concepcion (Fig. 1A, B) that was previously sampled by Requena-Rojas et al. (2020b). The forest is growing on a south-facing slope with 43.6% of inclination. The moss layer covers the forest floor to a lesser extent than at Toldopampa. Anthropogenic activities such as logging, grassland burning and cattle browsing are present facilitated by a topography that facilitates accessibility to the site.

The *P. rodolfo-vasquezii* forests are mainly located in the eastern side of the central Peruvian Andes in the biogeographic terrestrial ecoregion of the Puna (Fig. 1A). According to the nearby meteorological station of Comas, the climate is characterized by a mean annual temperature of 8.9 °C with the lowest values from June to August (Fig. 1E). Annual rainfall is 929.3 mm, with the highest amounts from December to March and the lowest from May to July (Requena-Rojas et al., 2020a). During the rainy season (December to April) high precipitation amount is associated to low minimum daily temperatures (Fig. 1C). Moisture in this region is mostly coming from air masses from the central Amazon (Segura et al., 2020). Our study forests are frequently covered by fog (Fig. 1D).
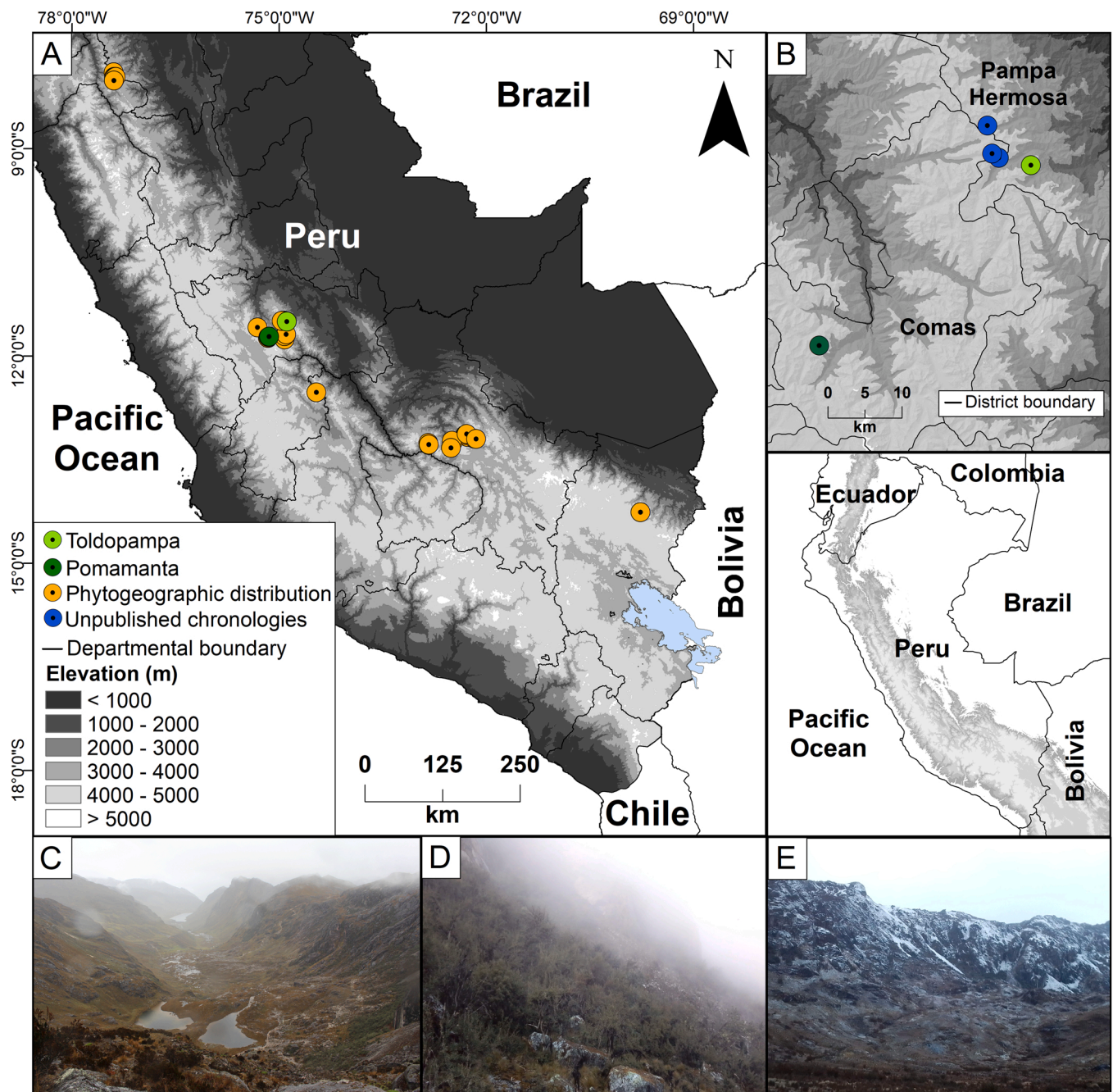
Fig. 1. (A) Location of the sampling sites of *P. rodolfo-vasquezii* in the central Andes in South America. Orange circles represent other field collections and herbarium samples of *P. rodolfo-vasquezii* (Boza Espinoza and Kessler, 2022). (B) Unpublished chronologies of *P. rodolfo-vasquezii* (blue circles) next to the sites of study. (C) Main topographic features characteristic of the areas where forests are commonly found. (D) Humid conditions where fog is frequent. (E) Rainy conditions during the growing season that coincides with the lowest temperatures.

2.2. Sample collection

Fieldwork took place at Toldopampa in April 2017. The Pomamanta site was first sampled in September 2016 by Requena et al., (2020b) and re-visited in May 2018 for this study. Two methodological approaches were followed at both sites. The first approach was focused on obtaining the age structure of the forests using one transect of 10 × 150 m laid on the slope direction (Toldopampa) and two plots of 20 × 20 m (Pomamanta). The Pomamanta forest is placed on a steep hillside and is denser than the Toldopampa forest, which did not allow us to sampling following a transect. Tree size variables such as diameter (measured approximately at breast height between 0.40 and 1.30 cm) and total

height were measured for all the trees sampled in the plots (first methodological approach). Collected samples were excluding trees with less than 5 cm of diameter at breast height and/or with any sign of decay status.

The second approach aimed to generate ring-width chronologies for climatic analyses, and thus the sample collection was focused on the longest-lived trees based on specific morphological features (e.g., whitish bark) that were preferentially growing in non-optimal conditions (e.g., lack of soil and water reserves) following the principle of the limiting factors (Fritts, 1976). From each living trees 2 increment cores of 5 mm diameter were extracted using increment borer (Pressler), while cross sections (slices) were taken from standing dead trees and

stumps.

2.3. Sample preparation and ring-width measurements

At the Tree-Ring laboratory of the Continental University in Huancayo (Peru), the samples were processed following the standard dendrochronological protocols (Stokes and Smiley, 1968). The increment cores were mounted on wooden supports, and together with the cross sections were polished using sandpaper in an ascending grain sequence (120–1200). Only for cross section samples, we used 80 sandpapers with belt sander. The width of each ring was measured with an accuracy of 0.001 mm using a Velmex system (Stokes and Smiley, 1968).

Following the Schulman's convention for the Southern Hemisphere (Schulman, 1956), we assigned to each ring the calendar date of the year when the tree start growing.

Due to the different environmental conditions, each species of *Polyelpis* show distinct length and timing of the growing season (Morales et al., 2004). The growing season of *Polylepis rodolfo-vasquezii* species approximately spans from the austral spring (~November) to the austral early fall (~May) (Requena-Rojas et al., 2020b).

At Toldopampa the fieldwork took place in April 2017 very close to the end of the growing season. Thus, the ring next to the bark finished its formation in the year 2017 and following the Schulman convention was assigned to the year 2016 (i.e. the year when the tree start growing). However, because the growing season at this moment was not finished yet this ring was considered only partly formed. The most recent completely formed ring that was measured to be part of the chronology was the assigned to the year 2015 (Table 1).

At Pomamanta the situation differs since the initial fieldwork took place in September 2016, right before the onset of the growing season. At this moment, even if growing season is assumed to start approximately in November, some trees can exhibit an incipient layer of wood depending of their particular circumstances of insolation, water availability etc (Roig et al., 2001). This seemed to be the case for some trees at Pomamanta that already exhibited an earlywood layer that was assigned to 2016. However, it was not easy to discern which trees exhibited this incipient 2016 ring or the ring corresponding to 2015, new samples were collected in the field in May 2018 and further analysis (see Section 3.3) allowed us to provide an updated version of the original Pomamanta chronology ending in 2015 (Requena-Rojas et al., 2020b).

2.4. Tree-ring width chronologies

The visual crossdating and the quality of the measurements were verified with the COFECHA program (Holmes, 1983), which statistically compares the measurements of each series with a master chronology for the site by correlating 50-year segments with 25-year overlaps. The detrending of the ring-width series was conducted using the RCSigFree software (Cook et al., 2017a), by adjusting each individual growth series to an age-dependent spline with an initial value of 20 years, that applies flexible fits in the early years and stiffer in later years, preserving high-frequency climatic information and removing the non-climatic (Cook and Peters, 1981; Melvin et al., 2007). The signal-free (SSF) chronologies obtained were characterized by the following statistics (Table 1). The mean sensitivity (MS) measures the variability in the ring width timeseries year to year and represents the sensitivity range of the species to the changes of environmental conditions. Mean correlation between time series (R-bar) measures the agreement among tree-growth patterns. The Expressed Population Signal (EPS) is an estimation of how well the signal gather in the chronology with a certain sample depth represent the overall signal of a stand. An arbitrary value of 0.85 is used as a threshold to consider a suffice coherent stand-level signal (Wigley et al., 1984; Speer, 2009). Also, a second chronology were computed by the ARSTAN program (Cook et al., 2017b) using a cubic smoothing spline of 20 years as detrending to generate the residual chronologies.

2.5. Age, diameter and height structure

The tree age was estimated by counting the number of rings on each tree from bark to pith on the samples in which crossdating was successfully validated through a quality control by the COFECHA program (see above). To estimate de number of missing rings of the samples where the pith could not be intercepted or had rotten centers, we used a graphic method (Villalba and Veblen, 1997) that was compared with a geometric method (Duncan, 1989). For both methods a total of 6 cross sections were used to simulate the loss of rings close to the pith. For the selection of the most accurate method, a chi-square test was applied and when no significant differences were found, the geometric method was used. When the estimation of missing rings exceeded 15 years, the samples were discarded. To compute the age and size distributions the data were grouped based on 20-year age classes, 5-cm classes for diameter (Kitzberger et al., 2000) and 1-m classes for height (Martínez and Villarte, 2009). At Toldopampa a total of 59 individuals were analyzed for age and diameter, but only 40 individuals could be included in the height analysis since 12 trees were dead trees. At the Pomamanta site a total of 50 individuals were analyzed for age and both allometric variables.

2.6. Linear models

Relationships between age and allometric parameters (diameter and height) were determined by Spearman correlation coefficients (Gareca et al., 2010) using the program RStudio version 4.1.0. (R Core Team, 2021). The effect of age classes on trees growth rates was evaluated using generalized linear models (GLMM) with a log-linkage and Gamma distribution family using the glmer function in package lme4 that allowed to treat normality and homoscedasticity (Bates et al., 2015). Finally, Spearman correlations between allometric variables, age and mean width tree-ring were conducted.

2.7. The ^{14}C bomb-pulse dating

Since tree-ring identification in the tropics is sometimes challenging, we evaluated the annual periodicity in the Toldopampa and Pomamanta *P. rodolfo-vasquezii* chronologies by measuring the ^{14}C content of tree rings using the 'bomb-pulse dating' method (Hua et al., 1999). Here, we selected rings dated with dendrochronological methods formed before and after the global ^{14}C spike associated to nuclear test (e.g., Andreu--Hayles et al., 2015; Santos et al., 2020). When the ^{14}C content of the selected rings assigned to particular years agrees with the values of the atmospheric ^{14}C curves, it means that the dendrochronological dating was accurate and the tree species studied present annual growth layers (Santos et al., 2020, 2021).

The selected tree rings to measure the ^{14}C content were extracted

Table 1

Statistical characteristics of the tree-ring width chronologies for *P. rodolfo-vasquezii*.

SIGNAL FREE CHRONOLOGIES	Toldopampa	Pomamanta
No. series	116	78
No. trees	73	59
Range	1825–2015	1824–2014
Mean sensitivity	0.35	0.35
Series intercorrelation	0.49	0.52
EPS*	0.83	0.91
R-bar*	0.31	0.41
Mean width tree-ring (mm)†	1.20	0.82

Obtained with COFECHA (Holmes, 1983)

* Values obtained with RCSigFree software (Cook et al., 2017b)

† Obtained by averaging the measurements after to convert from Tucson format to columns using the YUX application (Holmes, 1983)

from three crossections that showed high correlation with the TRW chronology at each site, absence of partially missing rings or multiple consecutive narrow rings. Due to particular features of tree growth at each sample, we selected different rings at each crossection to ensure enough wood material to conduct the ^{14}C analyses. The rings assigned to the years 1962, 1963, 1970, 1975 from one single sample were selected for Toldopampa, while at Pomamanta the selected years were 1940, 1955, 1970, 1985 for one sample and 1963 for a second sample (Table 2). We provide enough wood material to ensure that at least 2 mg of cellulose could be extracted for each single ring. Alpha-cellulose was extracted at the Lamont-Doherty Earth Observatory of Columbia University implementing the proceedings described in Andreu-Hayles et al. (2019) with some modifications described in Santos et al. (2020). Cellulose extracts were processed to filamentous graphite at the University of California, Irvine (KCCAMS/UCI) to undergo high precision radiocarbon (^{14}C) measurements by Accelerator Mass Spectrometry technique (AMS), following the procedures described in Santos et al. (2007). Full sample processing was also applied to well-known ^{14}C woody reference materials (Santos et al., 2020), such as FIRI-J (post-bomb barley mash), FIRI-H (sub-fossil wood) and AVR (wood-blank).

2.8. Growth patterns and climate sensitivity at the study forests

We compared tree-growth variability between the Toldopampa and Pomamanta TRW chronologies to assess the influence of a common regional factor affecting tree growth at both sites. The level of agreement was assessed computing Pearson's correlation coefficients between the two signal-free (SSF) chronologies and the residual chronologies to assess the high-frequency variability, and accounting for the number of pointer years shared at both sites. Performing the zChron analysis using the software R—package pointRes (van der Maaten-Theunissen et al., 2015), we identified the pointer years when at least more than 75% of the series showed indices values exceeding 1 standard deviation from the Z-transformed chronology, generated as the average of the anomalies of all the individual time series (Jetschke et al., 2019).

We assessed the relationship between regional climate and signal-free (SSF) chronologies at Toldopampa and Pomamanta in order to investigate if both *P. rodolfo-vasquezii* sites shared a common climatic signal. We used climatic data for temperature and precipitation from the National Service of Meteorology and Hidrology (SENAMHI) that was

processed into 49-year regional climatic records spanning from 1965 to 2013 by Requena-Rojas et al. (2020b). Response-correlation analysis using the dcc function between the signal-free (SSF) chronologies and monthly regional climatic data from August of the previous year to July of current year were performed in R using the TreeClim package (Zang and Biondi, 2015).

3. Results

3.1. Age, diameter, and height structure

At the Toldopampa site, the average age of individuals was 78 ± 37-year old and 13 trees from a total of 59 individuals were older than 100-year old, while at Pomamanta the average age was 72 ± 34-year old and 12 trees from a total of 50 individuals were older than 100-year old (Fig. 2A). The resulting age structures show that the Pomamanta forest is a younger forest (trees < 130-year old) than the more developed Toldopampa forest with older individuals reaching ages up to 190-year old.

In general, *Polylepis rodolfo-vasquezii* trees have average diameter and height of 14.28 ± 5.21 and 4.35 ± 1.47, respectively. Also, maximum and minimum values ranged from 29.92 to 5.41 cm for diameter and from 8 to 1.65 m for height. Regarding comparison of allometric variables; between forest, the trees were bigger and taller at Toldopampa than Pomamanta. Most of the Toldopampa trees (46 of 59 individuals) had a diameter between 10 and 20 cm, while Pomamanta trees (34 of 50 individuals) had smaller diameter between 5 and 15 cm (Fig. 2B). The mean height of the Toldopampa trees (5 ± 1 m) was greater than Pomamanta trees (4 ± 1 m), with a maximum tree height of 8 m (Fig. 2C). While almost all Toldopampa trees were above 5 m tall, almost all trees in Pomamanta (40 individuals) were below 5 m (Fig. 2C).

No significant relationships between age and the allometric variables were found at the Toldopampa forest. The correlation coefficient between age and diameter was 0.14; (p-values = 0.30; Fig. 2D) and between age and height was 0.30 (p = 0.06, Fig. 2E). As an example, trees with a diameter of ~15 cm were between 39 and 190 years in age. On the other hand, at the Pomamanta forest we found significant relationships between age and diameter (r = 0.77, p values $\leq$ 0.001; Fig. 2D) and between age and height (r = 0.57, p $\leq$ 0.001; Fig. 2E). Both sites presented significant relationship between height and diameter

Table 2

The ^{14}C analysis of the *Polylepis rodolfo-vasquezii* tree-ring samples for selected years. Signatures of Fraction Modern Carbon (F[14]C) are provided, as recommended in Reimer et al. (2004), for a total of nine samples followed by uncertainty ($\pm 1\sigma$) and UCIAMS# reference codes. Dendrochronological calendar dates show the two calendar years when *P. rodolfo-vasquezii* grows. The growing season (GS) starts approximately in November (year t, Schulman convention) and stops around May (year t + 1). A monthly adjustment of 0.1250, corresponding to February 15th representing approximately the middle of the GS, was used to plot the tree-ring F[14]C over the SH[14]C curves (decimals values available in the supplementary material of Hua et al., 2021). The F[14]C values from the SH[14]C curves Zone 1–2 are indicated for mid-February and for the average from November to May (approximate GS).

DENDROCHRONOLOGICAL CALENDAR DATES			RADIOCARBON INFORMATION					
t Year when tree start growing in austral spring -Schulman convention-		t + 1 Year when tree stop growing austral summer- fall.	Monthly adjustment	F[14]C curve values (Hua et al., 2021) SH Zone 1–2		Radiocarbon tree-ring results and sample code.		
Initial calendar dates	Calendar dates corrected			Feb (t + 1)	Average (GS) Nov (t) to May (t + 1)	F[14]C	$\pm 1\sigma$	UCIAMS#
Toldopampa site								
1962		1963	1963.1250	1.2752	1.2795	1.3564	0.0024	234650
1963		1964	1964.1250	1.4859	1.4810	1.5695	0.0026	234651
1970		1971	1971.1250	1.5062	1.5071	1.5101	0.0022	234652
1975		1976	1976.1250	1.3740	1.3714	1.3829	0.0020	234653
Pomamanta site								
1940	1939	1940†		0.9808		0.9812	0.0015	234649
1955	1954	1955	1955.1250	0.9915	0.9881	0.9806	0.0015	234648
1963 *	1962	1963	1963.1250	1.2752	1.2795	1.3054	0.0020	251178
1970	1969	1970	1970.1250	1.5316	1.5279	1.5452	0.0022	234646
1985	1984	1985	1985.1250	1.2188	1.2153	1.2067	0.0016	234647

*The selected tree-ring wood material is the only one from a different sample.
†Validation was done using the sequence of Camanducaia, Minas Gerais, Brazil curve (Santos et al., 2015) whose radiocarbon resolution is annual.
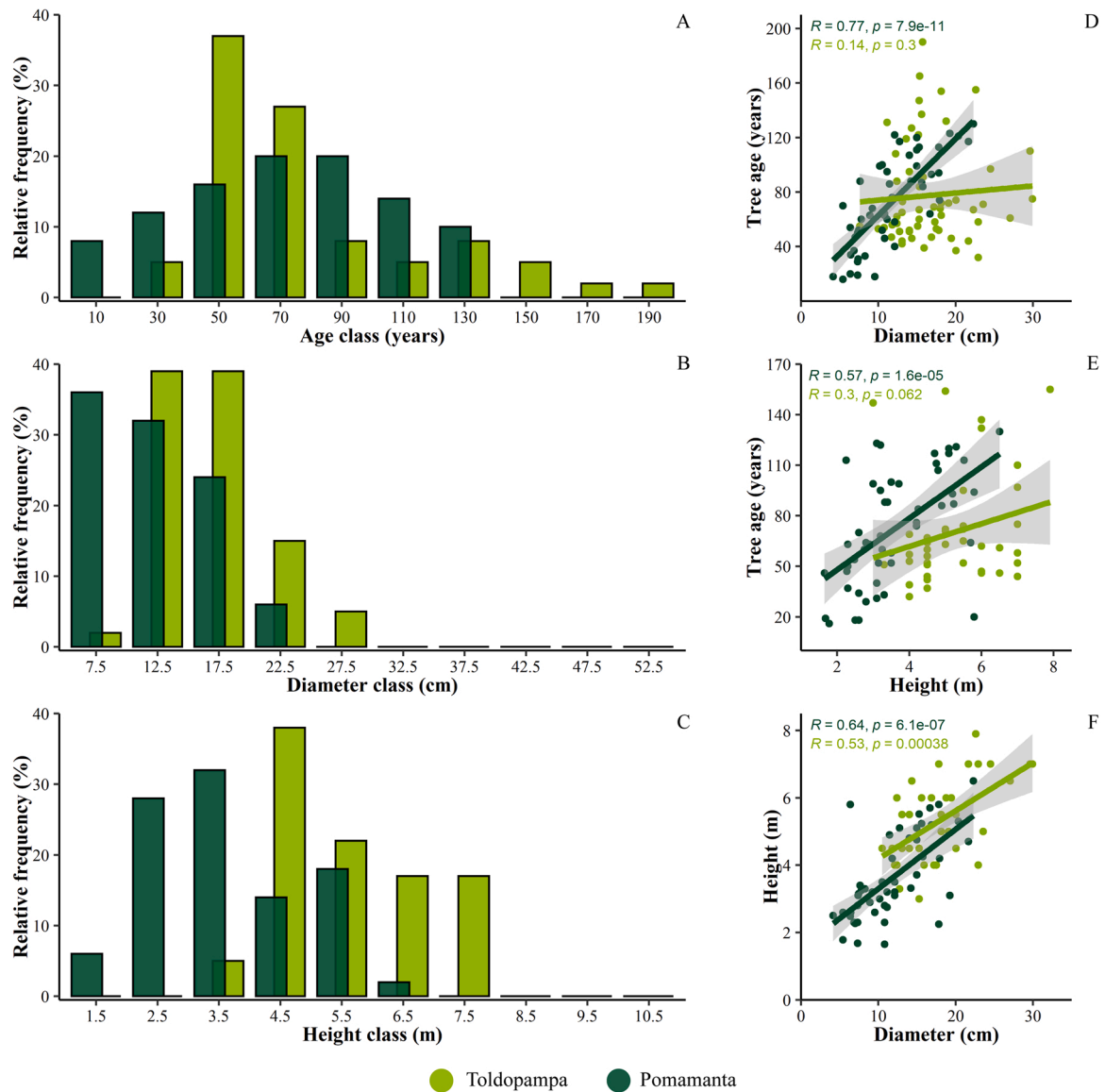
Fig. 2. Histograms of age and size tree distribution and size-age correlation: (A) age classes ranging from 32 to 154 years; (B) diameter classes from 8 to 29.92 cm; (C) height classes from 3 to 7 m. (D) Linear models between age and diameter; (E) Linear models between age and height; (F) Linear models between height and diameter. Each graphic show R values of the Spearman correlation analyses, and p-value number indicate the significance.

(r = 0.53; r = 0.64; p ≤ 0.001) for Toldopampa and Pomamanta, respectively (Fig. 2F).

3.2. Cumulative radial growth by age classes

There are differences of growth pattern between age classes and sites as observed by the lower slope values of the cumulative radial growth for trees in Pomamanta than in Toldopampa (Fig. 3A-F); with the exception of 120–140-year age class, in which both curves overlap (Fig. 3 G). In general, the Toldopampa trees had greater cumulative radial growth than the Pomamanta population, for example, trees at the 20–40-year class grew three times faster at Toldopampa (Fig. 3B). We observed that cumulative radial growth in Pomamanta age classes increases with age unlike to Toldopampa age classes that does not show any clear pattern.

No trees were found in the 140–160-year age classes and older for the Pomamanta population. At the Toldopampa population, the 140–160-year age class (Fig. 3H) showed similar growth pattern with the 120–140-year age class (Fig. 3G). The Pomamanta 120–140-year age

class reached the higher cumulative radial with a little bit more than 150 mm (Fig. 3G). The 160–180-year and the older age class provide some insights on old-growth pattern at Toldopampa site, but caution is requested because only tree was present in each category (Fig. 3I, J). None of the two study population showed a saturation of tree growth pattern, even in the older age classes.

Additional analyses showed a significant high negative correlation between tree age and mean tree-ring width at Toldopampa forest, while at Pomamanta this relationship was not significant (Fig. 3K). Regarding the correlation coefficient between mean tree-ring width and diameter both Toldopampa and Pomamanta sites showed low, but still significant relationship at 95% and 90%, respectively (Fig. 3L). Finally, at both sites no significant correlations were found between mean tree-ring width and height (Fig. 3M).

3.3. Comparison between the dendrochronological and the ^{14}C dates

Fig. 4 shows the $F^{14}C$ results (Table 2) measured for the selected rings at the two study sites in comparison with the SH atmospheric ^{14}C
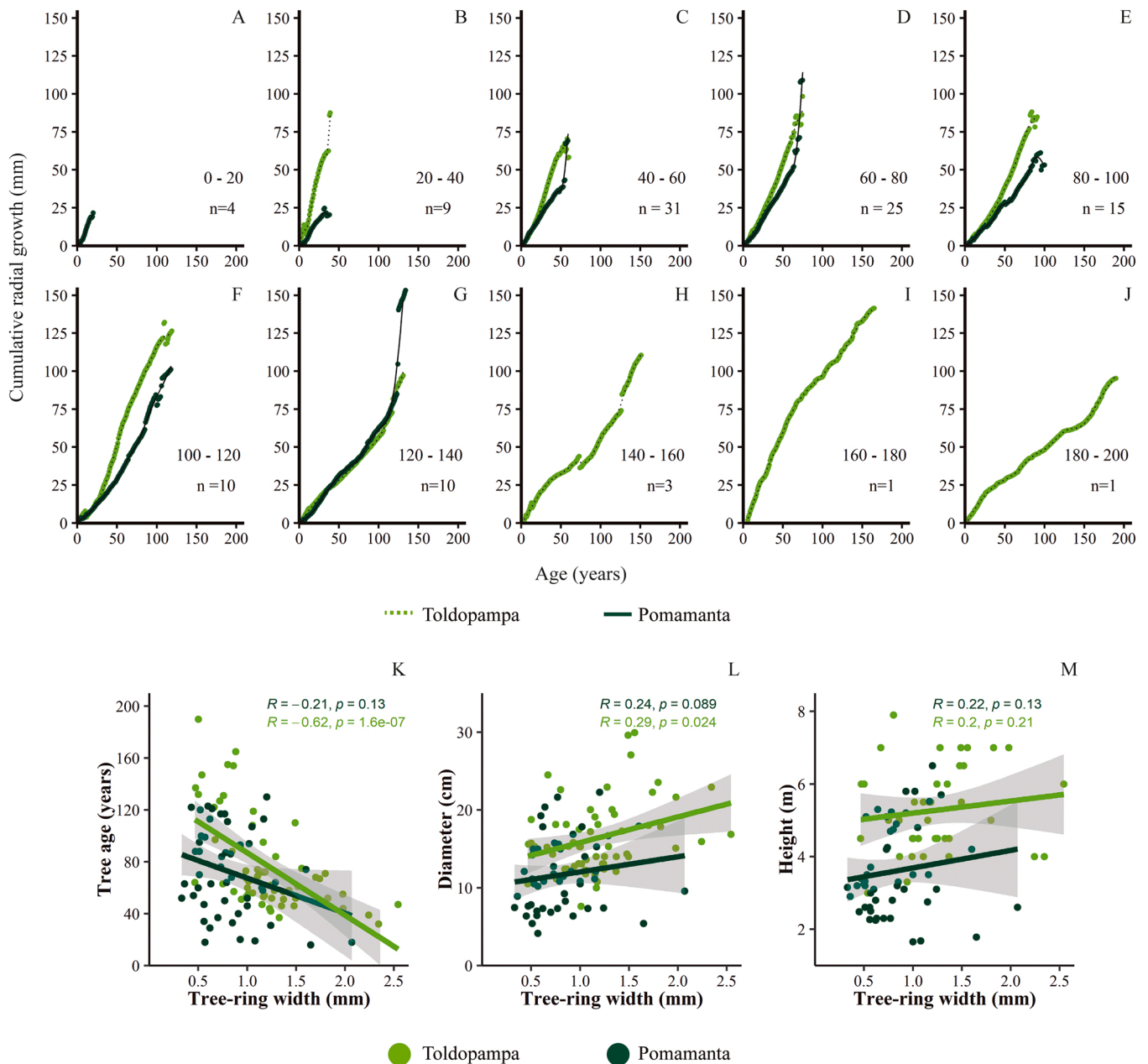
Fig. 3. (From A to J) Comparison between sites and same age class of the cumulative radial growth depending on age for *P. rodolfo-vasquezii*. Solid and dash lines represent the average cumulative radial growth in each age class for Toldopampa and Pomamanta sites. (K) Linear models between age and average ring width; (L) Linear models between diameter and average ring width; (M) Linear models between height and average ring width. Each graphic show R values of the Spearman correlation analyses, and p-value number indicate the significance.

calibration curves (Hua et al., 2021). We plotted the tree-ring ^{14}C values over the month corresponding to February (0.1250, Table 2) for all the years considering that this month is approximate in the middle of the growing season (see Section 2.3). The dendrochronological dates and ^{14}C content measured in the Toldopampa rings show a good match between the SH curve zone 1–2 and zone 3. This confirms the annual periodicity of calendar dates assessed by dendrochronology methods for *P. rodolfo-vasquezii* at this site.

At the Pomamanta site, the dendrochronological initially assigned dates were one-year shift forward in time from the calendar dates indicated by the ^{14}C content (see Fig. 4, initial dates), thus the first complete ring originally assigned to 2015 (Schulman) was re-assigned to 2014. After adjusting the initial dendrochronological dates sent to ^{14}C analysis at Pomamanta site, we found that the ^{14}C content of these Pomamanta tree rings also matched well the SH curves zone 1–2 and

zone 3 (Fig. 4). A re-evaluation of the original dendrochronological dates on the wood collection was done. The reason of this initial mismatched was due to the incorrect assignation of the ring next to the bark to the year 2016 under the assumption that the tree already started growing when the fieldwork took place in September 2016. Therefore, the following consecutive year considered complete and measured was erroneously assigned to 2015. Considering that the tree did not started growing that season, the year next to the bark was re-assigned to calendar year 2015 based on Schulman (i.e. year when the tree start growing) and the complete first year measured also was re-assigned as 2014. This update was confirmed by the significant coherence on the growth patterns between the Pomamanta ring-width chronology and the Toldopampa ring width chronology (r = 0.25; p < 0001), as well as the good visual and statistic agreement with several unpublished *P. rodolfo-vasquezii* chronologies (r = 0.28, r = 0.30 and r = 0.34, all p < 0,01)
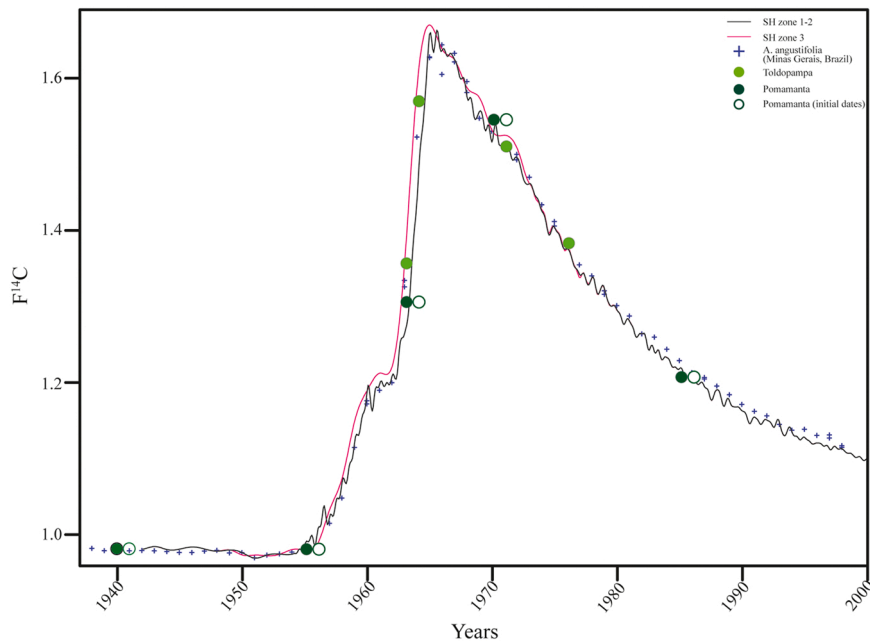
Fig. 4. F^{14}C values from ^{14}C AMS analysis (circles) plotted over the Southern hemisphere (SH) ^{14}C bomb curves compiled by Hua et al. (2021). Filled circles indicate the^{14}C content for the dendrochronological dates, while empty circles indicate the initial dendrochronological dates sent for the Pomamanta site. Crosshead represent the Camanducaia, Minas Gerais, Brazil dataset (Santos et al., 2015).

that our team have been building in the central Andes of Peru (Fig. 1B).

After adjusting the initial dendrochronological dates sent to ^{14}C analysis at Pomamanta site, we found that the ^{14}C content of these Pomamanta tree rings also matched well the SH curves zone 1–2 and zone 3 (Fig. 4). Overall, the two studied *P. rodolfo-vasquezii* chronologies show a good agreement between the dendrochronological dates and ^{14}C content with the SH curve zones (Fig. 4) confirming the annual

periodicity of this Andean tree species.

The ^{14}C results of LDEO alpha-cellulose extracts from reference materials FIRI-J and FIRI-H yielded expected values, i.e., 0.7571 ± 0.0023 (n = 3) and 1.1042 ± 0.0019 (n = 2). Wood-blank AVR used on ^{14}C background corrections yielded in average a F^{14}C value equivalent to 43.7 ± 0.4 kyrs (n = 3), which was slightly better than those reported in Santos et al. (2020) for LDEO extracts.
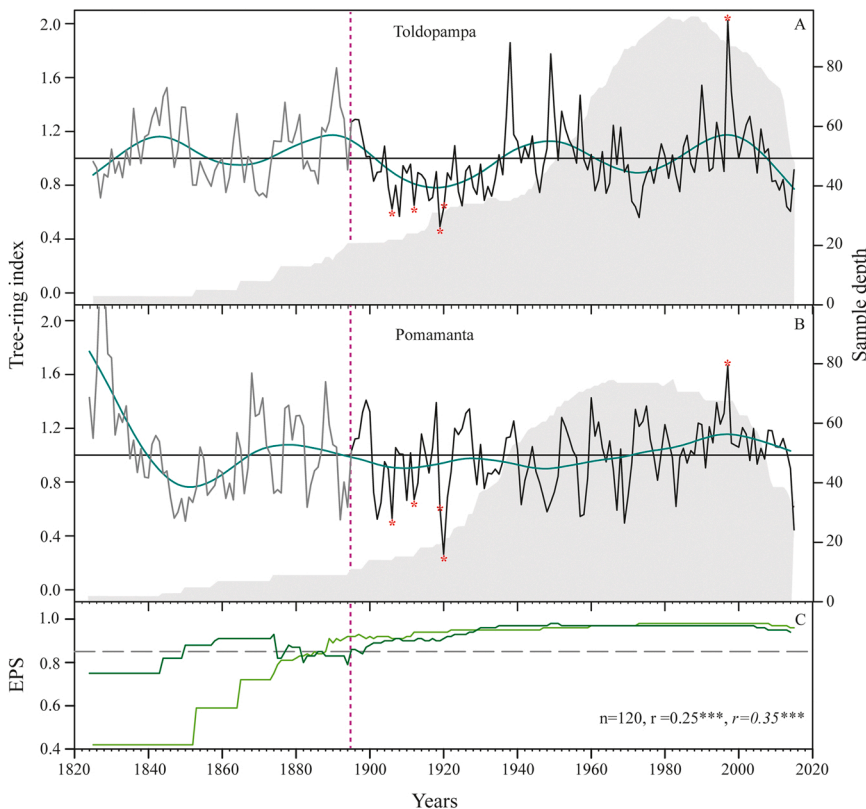

Fig. 5. Synchronicity in medium and high frequency domain of the tree ring width chronologies in Toldopampa (A) and Pomamanta (B) from 1895 year where the EPS matched values above 0.85. Black lines represent Signal Free tree-ring index, green lines represent smoothing of tree-ring index that conserve the 50% of signal variance at 40 years of wavelength, filled area refers the sample depth and red asterisks show pointer years with the most 5 extreme narrow and wide tree-ring values shared by both sites. (C) EPS variation along all time span of chronologies, soft green line for Toldopampa and dark green line for Pomamanta. Pink vertical dashed line indicates the match year where EPS> 0.85 in both sites. Both "r" are Pearson correlation between the signal-free (SSF) chronologies and residual chronologies (italic) with the same number of n variables. Asterisks show significance: * P < 0,05; * * P < 0,01; * ** P < 0001.

3.4. Comparison of the two tree-ring width chronologies

Both chronologies of *P. rodolfo-vasquezii* span 191 years (Fig. 5) and were significantly correlated to each other (r = 0.40, p = 0.001) indicating a common signal among tree growth variability at these two relict forests. The MS of 0.35 indicates that this species records inter-annual variability. The EPS of Toldopampa and Pomamanta tree-ring chronologies exceed the 0.85 cut-off point for the 1895–2014/5 period and the Rbar values were 0.31 and 0.41, respectively, indicating a relatively high common signal within each chronology. Trees at Toldopampa had mean tree-ring width values higher than Pomamanta trees (Table 1).

A significance correlation value of r = 0.35 (p < 0.001) was found between the two chronologies in the high frequency domain when the residual chronologies were compared (Fig. 5). In contrast, lower but still significant correlation values of r = 0.25 (p < 0.001) were found when correlations between the signal-free (SSF) chronologies were computed. The two chronologies shared extreme values in the tree-ring indices in 5 years. For extreme wide rings (i.e. high growth) the year 1997 and for extreme narrow rings (i.e. low growth) the years 1906, 1912, 1919 and 2020.

3.5. Climate sensitivity of the P. rodolfo-vasquezii forests

Fig. 6 shows that the TRW chronologies shared a positive regional temperature signal for the months belonging to the current growing season. For Toldopampa significant correlation coefficients were found in September and from December to June. Similarly, at Pomamanta all the correlation coefficients were positive for the same period, but the coefficients were only significant for January, March, April and May. Regarding regional precipitation, the only significant correlation found was negative between Toldopampa tree growth and January precipitation from the prior growth period.

4. Discussion

4.1. P. rodolfo-vasquezii relict forest structure and growth

We reported an age of 190 years for an individual of *P. rodolfo-vasquezii*, being the oldest tree reported for any species within the *Polylepis* genus after the ancient P. tarapacana trees (Gareca et al., 2010; Moya and Lara, 2011; Roig et al., 2001; Suarez et al., 2008). The age structure
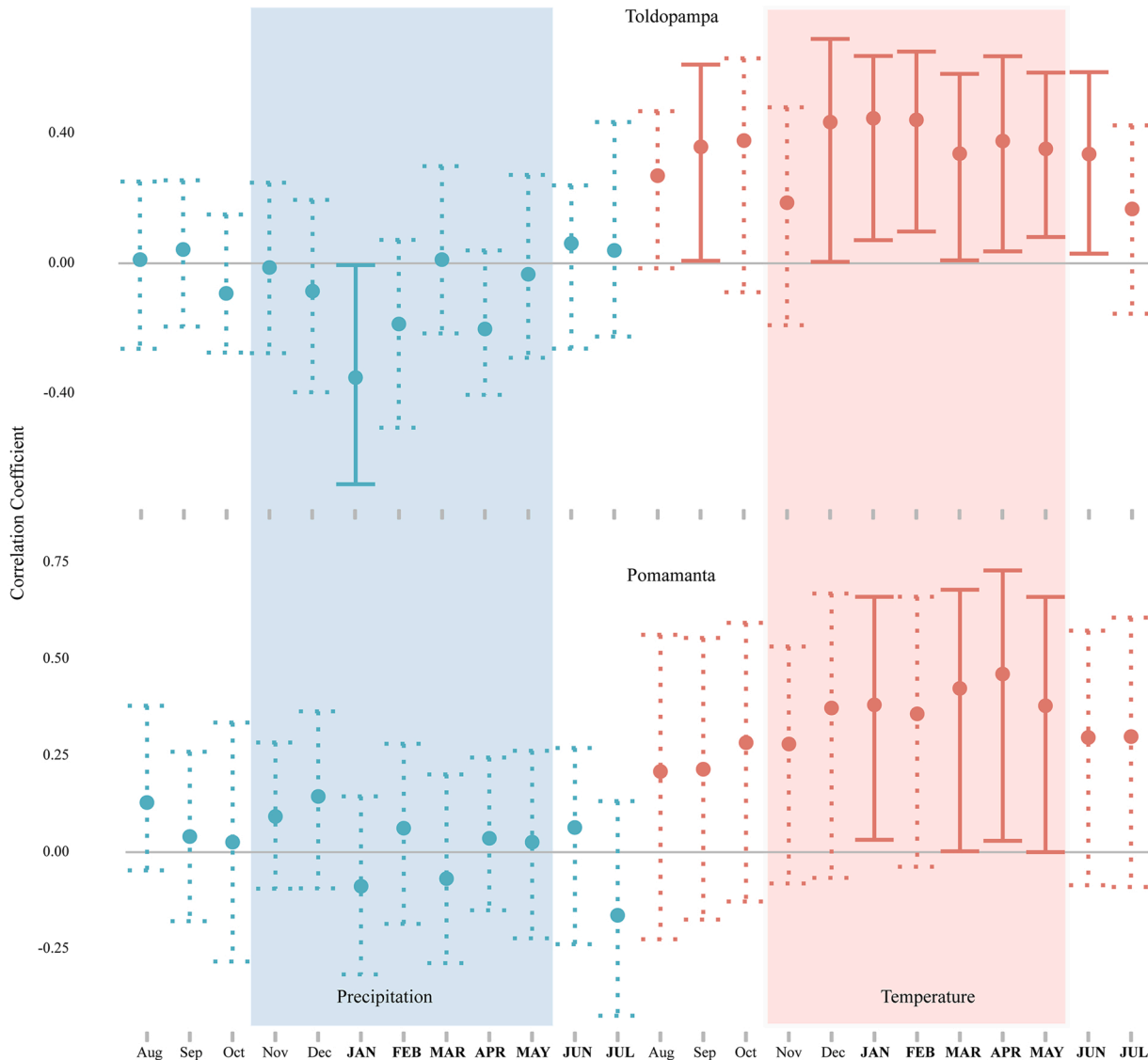

Fig. 6. Correlation analysis between tree-ring index and regional precipitation (left) and temperature (right) from previous August to current July for the Signal Free TRW chronologies of Toldopampa and Pomamanta. Previous-year months are given in lowercase letters and current-year months in uppercase bold letters. The current growth period (November–May) is indicated by shaded boxes being blue for precipitation and red for temperature. The error bars with solid lines indicate significant correlations (P < 0.05).

analyses revealed that the Pomamanta forest is younger than the Toldopampa forest that has an age structure of almost two centuries old. In the Pomamanta forest we found a positive relationship between age and allometric variables very likely because its structure is mostly based on young trees, which exhibit high growth rates associated to large diameters and heights. In contrast, in the Toldopampa site, the population have some ancient trees with lower growth rates. This could be a possible reason for the lack of a significant relationship between age and size variables. In other words, trees of similar sizes may have distinct ages at the Toldopampa site. Therefore, estimating the age based on size variables (i.e. diameter and height) in old stands of *P. rodolfo-vasquezii* can potentially lead to misleading conclusions.

Considering the stem diametric growth, a lower growth rate was observed for the oldest trees at Toldopampa, which supports a more mature stage of development than at Pomamanta. The strong and negative relationship between tree-ring width and age found in Toldopampa (Castagneri et al., 2013) confirms that trees at young stages have accelerated growth rates, but as the trees reach ages older than ~120-year old, growth rates are slowing down as expected in trees beginning a maturity stage. The height growth can sometimes be in synchronicity with the growth rates, but this was not the case for our study site (i.e., no significant correlation). A plausible explanation may be related to the fact that in high elevation environments with extreme harsh conditions associated to strong winds and a wide range between maximum and minimum temperature during day and night, trees can use growth resources to increase more in diameter than in height to better face adverse conditions (Domic and Capriles, 2009).

The diameter and height structures of the trees at each population indicate different historical ecological processes (Camel et al., 2019; Cierjacks et al., 2008). The Toldopampa forest is more inaccessible than the Pomamanta stand, which is under a larger anthropogenic pressure from cattle ranching, recurrent fires and logging (Camel et al., 2019). Thus, the Toldopampa forest hold a better conservation status that is also confirmed by an age structure that preserves the highest number of long-lived individuals. In addition, our findings also reported that the forest with a lower degree of anthropogenic disturbance exhibited higher cumulative radial growth rates within age classes. This highlights the importance of protecting undisturbed natural forests and the need to intervene in disturbed ones by excluding livestock and avoiding logging and fire for facilitating a recovery of forest health.

Our findings do not allow us to determine what is the time span required for *P. rodolfo-vasquezii* to be considered a well-established mature stand, but they reveal that in population structures with individuals older than ~120-year old an ecological-functional stability could be achieved (Requena-Rojas et al., 2020a) since morphometric changes seem to be less noticeable. Therefore, we hypothesize that forests with trees about 120-year old or older may become more resistant to environmental disturbances and the pressure of certain anthropogenic activities, such as fire and livestock, but not to selective logging, which could alter both the allometric and age structure.

Despite that the relationship between diameter and height can be altered when the forests are disturbed by human activities (Domic and Capriles, 2009), our two study forests show significant positive correlations between diameter and height, even at Pomamanta that suffered high human pressure intensity. This may indicate that the allometric structure of these relict forest has a high resilience to disturbances. However, this was not the case for age structures and cumulative growth rates that indicate that tree radial growth can be critically altered by the impact of human activities.

Different relationships between diameter and age in *Polylepis* genus and other trees species have been reported. For example, while *Polylepis australis* exhibits a positive relationship between tree diameter and age (adjusted $R^2 = 0.48$, P = 0.0001) (Suarez et al., 2008), *Polylepis tarapacana* (adjusted R2 = −0.01, P = 0.45) and *Polylepis besseri* (r = 0.16, P = 0.65; r = −0.15, P = 0.65) did not show any significant relationship (Domic and Capriles, 2009; Gareca et al., 2010). These studies pointed

out contrasting results regarding the relationships between allometric variables and age concluding that impacts of internal forest dynamics, as well as anthropogenic activities and environmental conditions can alter these age-size relationships (Arenas-Castro et al., 2015; Domic and Capriles, 2009; Tyrrel, 1994). Other factors associated with tree species, geographic location, microsite conditions and degree of disturbance would have to be further evaluated together to have a comprehensive understanding of the Andean forested ecosystems.

Diameter and height are commonly used as age predictors under the assumption that size always increases with age (Domic and Capriles, 2009). Our results with *P. rodolfo-vasquezii* also show that it is not always reliable to take the allometric structure of these high Andean forests to estimate ages, and thus that allometries cannot be used as an indicator of forest conservation status. Similar results have been found in the Boreal forest from Norway (Castagneri et al., 2013), subtropical forests from China (Xing et al., 2012) and subalpine forests from North America (Veblen, 1986).

4.2. Annual periodicity of tree growth in P. rodolfo-vasquezii

The annual periodicity of tree growth of *P. rodolfo-vasquezii* in two Andean forests in Peru was confirmed by coupling two methods, dendrochronological techniques (Stokes and Smiley, 1968) and bomb pulse ^{14}C analyses of selected calendar years (Santos et al., 2020, 2021). The F^{14}C values of the selected tree rings appear to fall between the two curves, SH 14 C zone 1–2 and zone 3 (Hua et al., 2021) and reproduce the shape of the bomb peak, which validates the annual periodicity of *P. rodolfo-vasquezii* growth pattern. Moreover, the year 1940 corresponding to Pomamanta site also matched well the sequence of Camanducaia, Minas Gerais, Brazil curve (Santos et al., 2015) of the time period before the onset of the thermonuclear bomb test.

Measuring the ^{14}C content in tree rings has proven to be a very useful method for confirming dendrochronological dates and for correcting systematic offsets in our trees in the same way has been done in other regions (Santos et al., 2020). At this regard, while in the Toldopampa site the dendrochronological and ^{14}C dates matched perfectly, for Pomamanta site the situation was different and the 14 C content allowed us to identify a shift in the calendar year. Now we learned that the reason of this initial mismatched was due to the incorrect assignation of the ring next to the bark to the year 2016 under the assumption that the tree already started growing when the fieldwork took place in September 2016. This offset did not imply that the trees at this location are not annual because the tree-ring 14 C data reproduced well the shape of the SH 14 C curves during the bomb peak pulse. After performing additional analysis comparing growth variability in our two study sites with other chronologies nearby of the same tree species, as well as verifying the calendar year of the last ring next to the bark according to the sampling date, the correct calendar years could be assigned to the rings and agreed with the 14 C results. This experience describes some of the challenges related to tropical dendrochronology (e.g the selection of the sampling moment within the growing season), and the potential of combining independent methods such as dendrochronology and radiocarbon.

Notwithstanding, we can conclude that the *P. rodolfo-vasquezii* tree species tested here exhibit annual periodicity based on both dendrochronological and radiocarbon analyses. Our findings highlight the eligibility of this tree species to provide material to generate a complete tree-ring ^{14}C dataset for future global atmospheric^{14}C compilation in lower latitude in South America as have been done with others tree species (e.g., Ancapichún et al., 2021; Santos et al., 2015).

4.3. Shared common tree-width patterns and climate sensitivity

The long time span of our two chronologies starting almost in 1800 CE can only be compared with the time span covered by trees species such as *Polylepis reticulata* and *P. tarapacana* (Alvites et al., 2019; Argollo

et al., 2004). The high mean sensitivity and correlation among time series (e.g., Rbar) in our chronologies are comparable to other species in similar altitude and latitudes (Jomelli et al., 2012; Roig et al., 2001). The mean tree-ring width is in agreement to values reported by other species and are characteristics of ancient trees (Di Filippo et al., 2007; Requena-Rojas et al., 2020a; Rötheli et al., 2012).

We found higher synchronicity in the high-frequency domain than in lower-medium frequency domain between the tree-growth variability of the two study chronologies, which can be attributed to the different degree of impact of anthropogenic disturbances more present in the medium frequencies. Local environmental features such aspect could be influencing the minor synchronicity since in this region differences in site conditions over short distances account for major differences in growth responses to climate variations (Villalba et al., 1998; Solíz et al., 2009). Nevertheless, the two forests show a very similar sensitivity to regional climate variability. For example, both chronologies registered the 1997–98 El Niño event (Vuille et al., 2000) where the warmest temperature produced a pointer year (1997) characterized by positive growth.

P. rodolfo-vasquezii trees were favored by warm temperatures during the current growing season from November to May. Other species of *Polylepis* such as *P. tarapacana, P. subsericans, P. pepei, P. australis, P. besseri* and *P. reticulata*, showed very similar relationships with temperature during the current growing (Roig et al., 2001; Gareca et al., 2010; Jomelli et al., 2012; Lanza et al., 2018; Alvites et al., 2019; Crispín-DelaCruz et al., 2022). The lower temperature sensitive in the Pomamanta forest in comparison to Toldopampa could be related to lower sensitivity of young trees to climate variability than old trees. This could be associated to distinct physiological process and responses to changes depending on age and size (Rozas et al., 2009) or higher noise in the tree growth variability time series with larger human impacts.

Regarding the lack/low sensitivity to precipitation observed in our two sites of *P. rodolfo-vasquezi*, we hypothesize that forest soil may be water saturated in the high-elevation humid eastern Andes cordillera due to abundant moss and recurrent fog blocking solar radiation. Therefore, soil moisture would not depend on precipitation, thus, its variations may not be reflected in the radial growth of (Hertel and Wesche, 2008; Kessler et al., 2007; Körner and Paulsen, 2004).

5. Conclusions

In this work we confirm the annual periodicity of tree growth for *P. rodolfo-vasquezii*, which is the second most equatorially located and high- elevational tree species within the *Polyelpis* genus. An individual tree up to 190-year old found in our study site placed *P. rodolfo-vasquezii* as the second oldest *Polylepis* tree species after *P. tarapacana*. Our findings report that population dynamics in high Andean forests cannot be only based on allometric variables, particularly when there is no correlation between tree age and size potentially due to historical anthropogenic or natural disturbances of the past and/or longevity of the trees. We also alert that age structures cannot be estimated using allometric data such as diameter and height in *Polylepis* Andean forests. Furthermore, our study indicates that this tree species presents greater resilience in the diametric structure than in the age structure based on the existence of significant correlations between diameter and height, but not always between age and these morphological variables.

The agreement between growth patterns between the two study forests and their shared high sensitivity to temperatures pointed out *P. rodolfo-vasquezii* as an important tree species for future paleoclimate reconstructions in lower latitudes of tropical South America from 11° S and below, where *P. tarapacana* is no longer present. Finally, our study provides a better understanding of past environmental history through two unique tree-ring archives in the central tropical Andes in South America.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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