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Forest and shrubland structure of *Polylepis tarapacana* in topographic and substrate gradients across the Argentine Altiplano †

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Abstract

Background: *Polylepis tarapacana* (queñoa) is a species that grow from forests to shrublands in Chile, Argentina, Bolivia and Peru, reaching an elevation range of 4400-5000 m a.s.l. In Argentina, this species occurred in the Altoandina phytogeographic eco-region, which presents scarce vegetation, and where it is the most important tree species for its great socio-economic importance. The structure of these communities and the changes related to environmental gradients are not well described in the literature. The objective was to relate topographic factors with variables of structure of the *P. tarapacana* communities, evaluating the occupation degree (e.g. density and crown cover) of the species.

Methods: We studied *P. tarapacana* forests and shrublands in northern Argentina, sampling 98 plots (50–4000 m^2) to measure diameter at the base (DAB-cm), dominant height (DH-cm), life forms, crown cover (CC-%), and density (DEN-n ha^{-1}). Topographic variables (elevation, slope, aspect) and substrate type were also recorded. Generalized Linear Models (GLM) were used to assess the influence of topography on forest structure, and univariate analyses to evaluate structural changes across life forms with topography.

Results: Great heterogeneity was observed in the structure of open forests or shrublands patches of *P. tarapacana*, at high elevations (<4500 m a.s.l.), gentle slopes (21°) and in north aspect (95% of the plots). Topographic factors influence vegetation structure variables, e.g: elevation has a significant positive effect on DH ($\beta = 0.105$, $p = 0.011$), while slope ($\beta = -0.144$, $p = 0.001$) and eastern aspect ($\beta = -0.083$, $p = 0.040$) have significant negative effects on DH ($F=6.85$, $p <0.001$). Slope was the only significant variable with a positive effect on CC ($\beta = 0.275$, $p = 0.001$). The life forms of *P. tarapacana* are influenced by topographic gradients, and the tallest communities (178.2 cm DH) are found at high elevations and low slopes, mainly in areas with bare soil and understorey vegetation.

Conclusions: *Polylepis tarapacana* structure was associated to the studied topographic gradients. It is crucial to identify changes in the composition and structure of forest and shrubland, considering both the substrate in which they develop, and the different life forms they adopt.

Keywords: Queñoa; niche; environmental factors; aspect; topography; life forms.

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Introduction

The high-elevation Andean regions are characterised by steep environmental gradients (e.g. snow cover, thermal amplitude, solar radiation), and adverse climatic conditions (e.g. cold and dry climate, with strong winds and low rainfall) (Garreaud et al. 2003; Morello et al. 2012). These marked topographic gradients influence at a local scale the availability of soil nutrients, runoff, infiltration capacity, and soil conditions (Cabrera 1968; Körner 2012; Rahbek et al. 2019; Marcora et al. 2021; López et al. 2022). The main stress factors are associated with the water availability, potential evapotranspiration, wind exposure, low soil nutrient contents and the high thermal variation during the day and seasons (Christie et al. 2009; Monteiro et al. 2011). Alpine and subalpine forests and shrublands are sensitive to climatic variations (Kullman 1988), as well as to a range of disturbances caused by various environmental factors, which can affect the population structure of species inhabiting these ecosystems (Kessler et al. 2014). Environmental changes associated with elevation influence the upper limits of tree distribution and the lower limit of the alpine treeline (Körner 2012).

At the world's highest treeline in semi-arid subtropical regions, tree growth is constrained due to low temperatures (Hoch & Körner 2005; Körner 2023), and may exhibit variability due to topographic features and slope exposure (Körner 2012). This limitation arises from the restriction of the annual growth period and the direct impact on growth in both vertical shoots and roots (Hoch & Körner 2005). In open areas, soils are warmer than the air temperature, similar to soils beneath treeless alpine vegetation, facilitating the growth of dwarf shrubs, life forms that are capable of adapting to these environmental conditions (Hoch & Körner 2005; Körner 2023).

The Altoandina phyto-geographic eco-region, together with the Puna, presents the highest proportion of rocky outcrops with low soil development (Morello et al. 2012). The Argentine (Altiplano) highland region is dominated by communities characterised by perennial grasses and scattered low forests and shrubs (Luebert & Gajardo 2005). Under these conditions, the tree genus *Polylepis* (*Rosaceae*: *Sanguisorbeae*) is found at the highest elevation (Kessler & Herzog 1998; Morales et al. 2004; Boza Espinoza & Kessler 2022). Among the different species within the genus, *Polylepis tarapacana* Phil. (commonly known as Queñoa) grows at the highest elevation between 4000 and 5200 m a.s.l. (Boza Espinoza & Kessler 2022) in Peru, Bolivia, Argentina, and Chile, and its distribution can be continuous or in isolated mono-specific patches (Boza Espinoza & Kessler 2022, López et al. 2022) according to slopes and substrates (e.g. rocky areas) (Kessler 1995). *Polylepis tarapacana* is an extraordinary species due to its ability to inhabit higher elevations compared to any other woody species on Earth (Boza Espinoza & Kessler, 2022) being able to grow up to 5200 m a.s.l. and can reach an age of more than 600 years (Argollo et al. 2004; Morales et al. 2012). In Argentina, *P. tarapacana* distribution is primarily confined to the provinces of Jujuy and Salta, within the southernmost limit of its distribution area (Peng et al. 2015; López et al. 2022). *Polylepis tarapacana* can present different life forms across its environmental gradient (López et al. 2023), from small shrubs to trees with a twisted trunk (30-60 cm long) with an elongated or open crown, with a maximum height of 3-5 m (Boza Espinoza & Kessler 2022). It is considered as Near Threatened (IUCN 2020), due to historical human impacts (firewood and rural construction), which resulted in partial habitat degradation (Renison et al. 2013).

The study of forest and shrubland structure of *P. tarapacana* and its relationship with the environment is of great socio-economic and conservation importance, as a result of the species being adapted to very restrictive environmental conditions (Renison et al. 2018). In fact, it is expected a strong climate change impact in this eco-region, with an increase of temperatures and decreased rainfall, creating uncertain conditions for the future of these ecosystems (Cuyckens et al. 2016). The data informed on structure and habitat requirements of *P. tarapacana* is scarce, mainly restricted to grey literature (degree theses and technical reports) (Cuyckens et al. 2024).

Likewise, the influence of elevation gradients, which modify temperature and precipitation, is paramount for the development of forests in mountainous regions, however, variations in slope, aspect, and substrate composition create complex patterns at finer scales (Körner 2012). Different substrate compositions influence many species, reflecting variable amounts of edaphic endemism and acting as local barriers to distributional changes (van de Ven et al. 2007).

This study aims to evaluate *P. tarapacana* forests and shrublands in the Altiplano of Argentina, relating the woody structures (size, life forms, occupation degree) with topographic and substrate features. We set the following research questions: (i) which are the optimal topographic conditions and substrate type for the occurrence of these communities? and (ii) how can topography and substrate type explain forest and shrubland structure? Does a change occur in the presence or predominance of tree life forms with elevation? Our predictions are that: i) presence and development of *P. tarapacana* patches may be associated with intermediate elevations, gentle slopes, north-facing exposures, and rocky substrate; and ii) a gradual shift can be observed in the presence or predominance of single stem life forms as elevation increases, with a higher predominance of these life forms at higher elevations and a gradual decrease at lower elevations. This study could contribute to better understand the influence of topographic variables on the structure of trees and shrubs in these high elevation regions for biodiversity conservation and territorial planning.

Methods

The genus *Polylepis* dominates the montane woody communities from Lara (09°34' NL, Venezuela) to San Luis (32°20' SL, Argentina) (Simpson 1979; Kessler & Schmidt-Lebuhn 2006; Renison et al. 2013; Boza

Espinoza & Kessler 2022). This study was carried out in the High Andean region of northern Argentina (22°04'-23°40' SL to 66°46'-65°49' WL) in the southernmost distribution of *P. tarapacana* (López et al. 2022) (Figure 1). The Argentine Altiplano has a cold and dry climate with very strong winds, where annual temperature varies from 0 to 4°, with monthly temperatures below zero more than half of the year (Morello et al. 2012). Solar radiation is higher due to the elevation, and annual precipitation reaches on average 190 mm yr^{-1} mostly during summer (>80% of the total) (Wawrzyk & Vilá 2013; Cuyckens et al. 2016). Its vegetation combines species with traits linked to xerophytes, extremely low temperatures and wind, where 80-90% of the surface is bare (Morello et al. 2012).

Sampling measurements

A total of 98 *P. tarapacana* patches were selected across their full distribution in Argentina, considering: (a) a patch size >1 ha, (b) homogeneous cover, where the distance between individuals was nearly constant; and (c) accessibility. The plots were located at each patch and varied in the area (25 to 4000 m^2) according to the individual density. Each plot was composed of two rectangular subunits (of variable width and length). Each subunit was adjusted to a minimum of 20 individuals of each size class, one subunit with individuals with a height of ≥20 cm to <1.3 m and another subunit with a height ≥1.3 m. The diameter at the base (DAB - cm) and height (H - cm) of each individual were measured, considering the tallest trunk in the case of multi-stem plants. The crown area was measured in two axis to calculate the area covered by each individual.

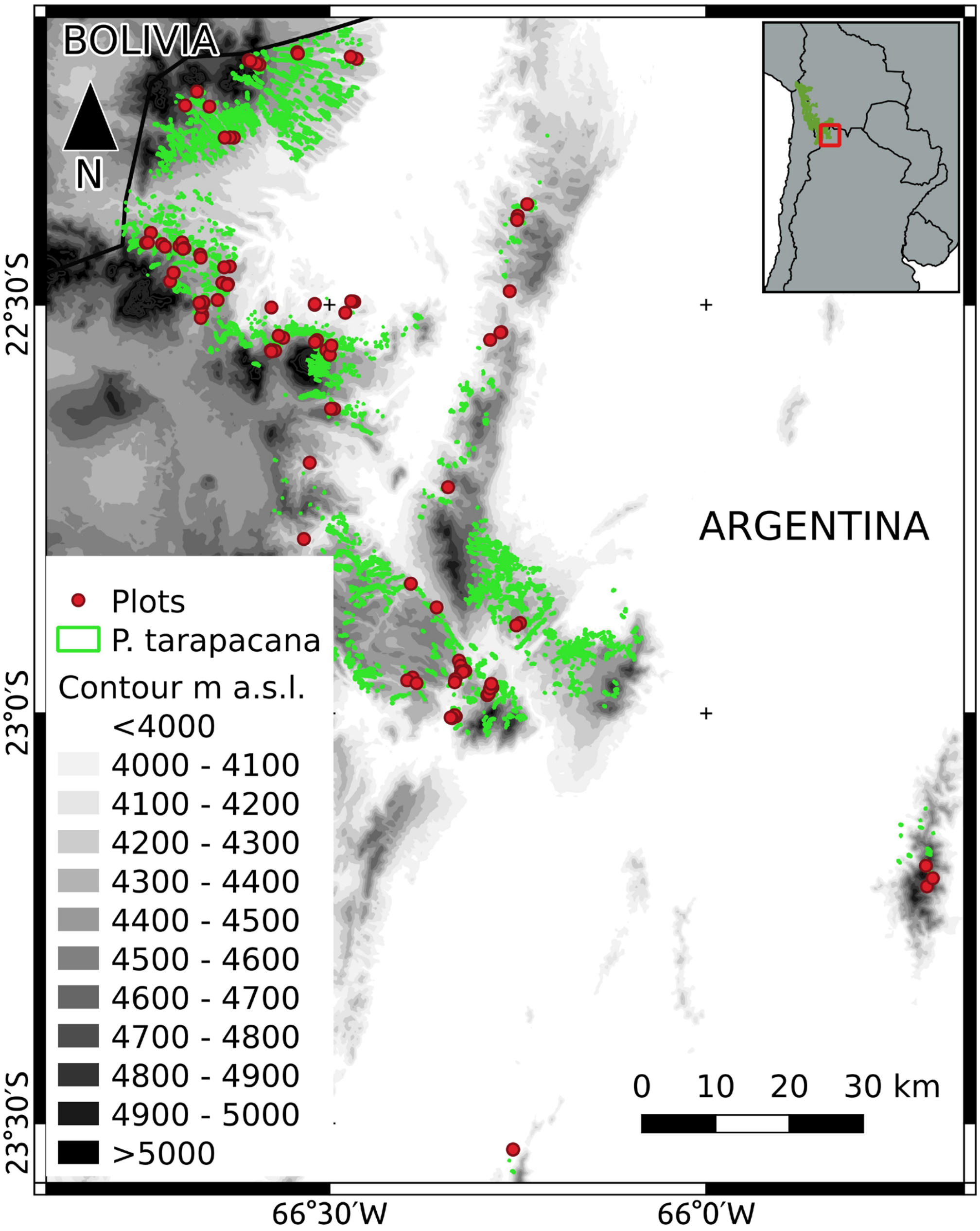

FIGURE 1: Plots (red circles) in the Argentine portion of Altiplano, distribution of *Polylepis tarapacana* (queñoa) in the study area (green), grayscale elevation contours from >4000 to <5000 m a.s.l.

The life forms of each individual were classified according to López et al. (2023): arborescent (Ar), that presented a single base with branches that cover the entire trunk, protecting the shoots close to the bark from the wind; dwarf tree (Dt), that showed the crown at the end of the main axis of the trunk, which is not covered by branches and frequently showed signs of crown dieback; shrub (Sh), that has multiple trunks, where the shortest ones were located at the periphery and the tallest ones in the center, and brousse tigrée (Bt), that occurs in bands, where the smallest trunks were down-slope and the tallest up-slope (Figure 2).

Each plot was characterised by the average DAB (cm), dominant height (DH-cm) as the average of the three tallest individuals (Assmann 1970), density (DEN-n ha^{-1}) as number of individuals per hectare, and crown cover (CC-%) as the ratio of the sum of the crowns area related to the area of the plot (López et al. 2022) for the different life forms.

In addition, each plot was characterised by topographic variables. The elevation (m a.s.l.) was measured with a global geo-positioning device (GPS), while slope was measured using a clinometer (degrees) and aspect by a compass (degrees). For further analyses, aspect was converted using the sine and cosine functions into two variables: (i) north-south (N aspect); and (ii) east-west (E aspect). The sine values range from −1 (west) to 1 (east), while cosine values range from −1 (south) to 1 (north) (Jenness 2004).

At each plot, the substrate coverage was surveyed using 100 sub-plots of 1 m^2 arranged in a 2 × 50 matrix along the main axis of the forest and shrubland structure plots. The substrate types were defined as: (i) plants (P) including monocots (e.g. mainly *Poaceae*), and dicots (including *P. tarapacana* sapling and other dicots of the understorey); (ii) bare soil (Bs); (iii) solid rocks (R) (rock outcroppings that are fixed in the ground); (iv) gravel (G) (rocky debris, loose stones of various sizes deposited on the surface or semi-fixed to the ground >2 mm). This determination was based on the methodology proposed by López et al. (2021) obtaining as a result the percentage of coverage of each substrate type.

Data analyses

A principal component analysis (PCA) was conducted to reduce the number of variables and avoid multicollinearity among them (DAB, DH, DEN and CC). The first two principal components explained 89.5% of the total variance in the data. Component 1, which accounted for 48.8% of the variance, was positively associated with DH and DAB, with correlations of 0.88 and 0.87, respectively. Component 2 explained 40.8% of the variance and exhibited strong correlations with CC and DEN, with correlations of 0.82 and 0.78, respectively. DH and CC were selected as representative variables for Components 1 and 2 for subsequent analyses.

For the independent (topographic) variables, PCA revealed that the first two components accounted for 63.4% of the total variance. The first component, which explained 33.3% of the variance, was strongly associated with the E aspect (0.76), while elevation (-0.43) and slope (-0.52) showed negative relationships. The second component, accounting for 30.1% of the variance, demonstrated a strong correlation with elevation (0.43) and a negative correlation with the N aspect (-0.52). These variables were selected for further analysis due to their strong representation in each dimension.

The influence of topographic variables on the structure of *P. tarapacana* was assessed using a Generalized Linear Model (GLM). For the response variable crown cover (CC), a Gamma distribution was applied, while dominant height (DH) was modeled using a normal distribution with a logit link function. Topographic variables were included as explanatory variables. A total of eight models were developed (four for each response variable). The first model included all possible combinations of the recorded variables, while subsequent models excluded variables that did not show significant effects (Table 1).

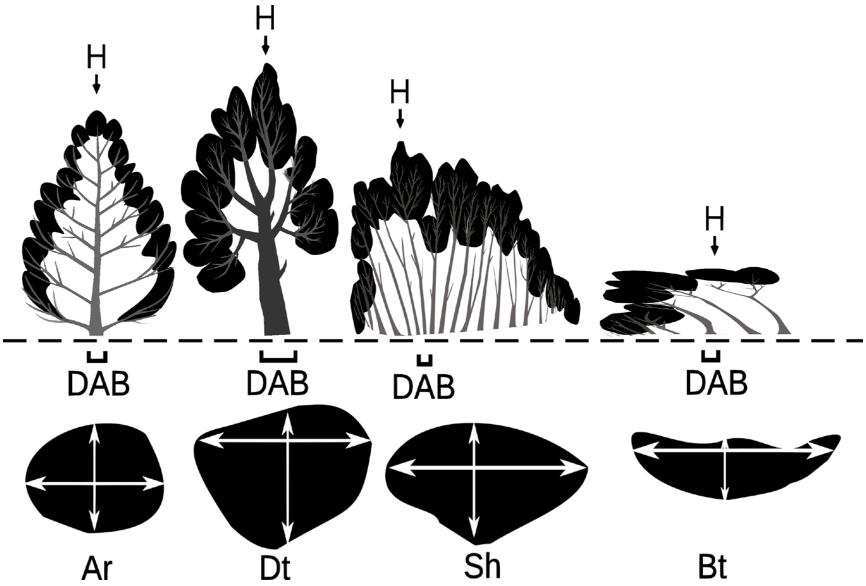

FIGURE 2: Determination of the height (H), diameter at the base (DAB) and crown cover (CC) for each life form in *Polylepis tarapacana* (queñoa). Ar: arborescent, Dt: dwarf tree, Sh: shrub, Bt: brousse tigrée.

TABLE 1: Model selection for assessing the influence of topographic variables on dominant height (DH) and Crown Cover (CC) using the Akaike Information Criterion (AIC).

Model	df[1]	AIC[2]	Feature
glm_log_normalDH	5	99.40	Elevation, slope and E aspect (scaled)
glm2_log_normalDH	**5**	**99.40**	**Elevation, slope and E aspect**
glm1_log_normalDH	6	99.73	Full model
glm0_log_normalDH	6	99.73	Full model with scaled variables

Model	df[1]	AIC[2]	Feature
glm2_CC	**4**	**-223.59**	**Elevation and slope**
glm3_CC	3	-222.99	Only slope
glm1_CC	5	-221.78	Without N aspect
glm0_CC	6	-219.93	Full model
glm_CC	6	-219.93	Full model with scaled variables

[1] Degrees of freedom (df) represent the number of estimated parameters in each model.

[2] Lower values of AIC indicate a better model fit.

Before conducting the analysis, each variable was centered and standardised to allow direct comparisons between the estimates. Additionally, collinearity and multicollinearity among the recorded variables were assessed using Pearson's correlation, where variables were considered correlated if the correlation coefficient (r) was ≥0.7 (Battin & Lawler 2006). No significant correlations were observed ($|r|<0.27$) among the variables recorded in the study. Subsequently, the most parsimonious models were selected based on the corrected Akaike Information Criterion (AICc), considering models with AICc ≤2 (Burnham & Anderson 2004; Delignette-Muller & Dutang 2015). Analyses were performed in R 4.2.2 (R Core Team, 2022). Values are presented as mean ± SE.

In addition to the previous analysis, the changes in structural variables in the life forms with topography were analyzed. ANOVAs were performed using topographic variables and life forms (Ar, Dt, Sh, Bt) as main factors to analyse DH and CC using Tukey post-hoc tests to separate the means ($p < 0.05$). Topographic variables were classified arbitrarily, following the same ranges used in other studies to facilitate comparisons. Normality was checked using Kolmogorov-Smirnov test, while the homogeneity (homoscedasticity) was analyzed using Levene test. In case of breach of assumptions, a non-parametric method (Kruskal-Wallis) was applied, and differences of means were determined by Conover-Iman test ($p < 0.05$).

Moreover, a structure index (SI) was calculated using the aforementioned variables, following Martínez Pastur et al. (2021). For this purpose, the structure values—DAB and DH—were standardised between 0 and 1 using the minimum and maximum values observed across all plots, as higher values of these variables correspond to more developed forests. Conversely, the DEN and CC variables were standardised using 1 as the minimum value, as these characteristics also indicate more developed forests (López et al. 2022). Then, the average of these values was the SI of each plot. An index for north-south orientation (IA) was also created, standardising the values between -1 and 1. To evaluate the occurrence of each substrate type (P = plants, R = rocks, G = gravel, BS = bare soil) of each plot in relation to topographic indices, each plot was categorised into single or double categories of substrate types. Single categories were considered when the cover was >50% (e.g. 54% type R substrate, 32% G, 8% P, 6% BS = Category R), and double categories when the sum of two categories were necessary to achieve >50% (e.g., 34% R, 28% G, 20% P, 18% BS = R-G Category). When one categories was observed in <5% of the plots, they were grouped together creating a new category (X) taking into account the one with the greatest coverage: e.g.: (i) P-X category included P-G = 3 plots, P-BS = 2 plots, P-R = 3 plots; (ii) G-X category included G-R = 4 plots, G-BS = 4 plots, G-P = 2 plots and BS-X category included BS-P = 2 plots, BS-G = 1 plots, BS-R = 1 plots. Average and standard deviation were calculated for each topographic and structure variable for each substrate type, to compare the indexes by graphical comparisons.

Results

A wide structural variation was observed in *P. tarapacana* communities across the studied gradient, particularly in the DAB and DH values of the different patches. The individuals presented small dimensions and a wide range of densities (DEN) and crown cover (CC), which indicates a low occupancy in the distribution area. The sampling plots presented an average DAB of 7.0 ± 3.3 cm (mean ± SD) and an average DH of 138.2 ± 59.6 cm, with the minimum and highest of 47.6 and 271.6 cm, respectively. DEN showed a high clustering of the individuals inside the plots (1772.9 ± 1657.2 n ha^{-1}), but CC indicated a low occupation of the plot area (11.9 ± 10.5%). CC showed great variability among patches, from relatively high (64.2%) to low covers (1.1%).

The plots covered a large area, the total surface area of the plots studied was 62,714 m^2: 170 km from N to S and 144 km from E to W, elevations between 4160 and 4952 m a.s.l., with an average of 4545 m a.s.l. The studied patches occurred at different slopes, from flat sectors (0°) to steep slopes of 43°, but more common on gently slopes (21° in average). Most of the plots (95%) were located at north and north-east aspects, with a marked gradient at the eastern and western aspects. For DH, the most parsimonious models according to the Akaike Information Criterion (AIC) were "glm_log_normalDH" and "glm2_log_normalDH", both with the lowest AIC values (99.407). These models included elevation, slope, and E aspect as predictors (Table 1). For CC, the most parsimonious model was "glm2_CC", which included elevation and slope as predictors, with the lowest AIC value (-223.59), indicating a better balance between fit and complexity compared to the alternative models evaluated (Table 1). Residual analysis and diagnostic plots supported the validity of the selected model, showing good fit and adherence to the model assumptions.

Topographic factors greatly influenced structural variables (Table 2). The parameter estimates from the selected model (*glm2_log_normalDH*) indicate that elevation has a significant positive effect on DH (β = 0.105, p = 0.011), while slope (β = -0.144, p = 0.001) and E aspect (β = -0.083, p = 0.040) have significant negative effects (a decrease in size with increased slope and eastward exposure) (Table 2). No significant differences were observed in N aspect, as the majority of the plots are oriented towards the north. This uniform orientation prevents differentiation along the north-south gradient; however, differences can be identified along the east-west gradient. The results indicate that those plots orientated east are mostly shrublands. Additionally, slope was the only significant explanatory variable with a positive effect on CC (β = 0.27, p = 0.001), indicating higher coverage on steep slopes (Table 2).

The crown cover presented differences given by the elevation from H between 50 to 100 cm (Figure 3A), with greater cover at lower elevations. It was observed that CC is greater at higher elevations in individuals with a H greater than 150 cm. In the slope gradient studied (Figure 3B), the height class <100 cm showed marked CC differences, with the highest values on higher slopes. Height classes greater than 150 cm presented lower cover on intermediate slopes.

The different life forms in *P. tarapacana* can be associated with different heights (H) and can be grouped into different DAB classes (Figure 4). For those individuals with DAB less than 5 cm, low heights and robust individuals were observed for the single-stem forms (Ar and Dt), while for Sh and Bt life forms were slimmer. This pattern was repeated in the diameter class ≥5<10, but the slimmest life form was Sh. For the class ≥10<15 the most common forms were Dt and Sh. In the diameter classes ≥15 cm no significant differences were observed in life forms.

The height (H) of individuals varied with elevation across the different life forms (Figure 5). Ar, Dt, and Sh forms showed an increase in height at higher elevations, while Bt remained unaffected. Regarding slope, the height of Dt and Sh decreased with steeper slopes, but Ar and Bt forms were not influenced. The aspect of the terrain did not show significant differences in height, although the W aspect showed the greatest heights for Ar and Sh, and the N aspect showed the greatest heights for Bt.

Greater SI values, associated to mature woody structures with higher DAB and DH values, were found in areas with a mixed substrates predominantly covered by understorey plants and bare soil (Figure 6). Other

TABLE 2: Parameter estimates and significance tests for selected GLMs assessing the influence of topographic variables on dominant height (DH) and crown cover (CC) of *Polylepis tarapacana.*

	variable	**estimate**	**SE**	***t* value**	***p* value**
DH					
	Intercept	4.83	0.04	122.81	<0.001
	elevation	0.10	0.04	2.58	**0.011***
	slope	-0.14	0.04	-3.55	**0.001*****
	E aspect	-0.08	0.04	-2.08	**0.040***
	variable	**estimate**	**SE**	***t* value**	***p* value**
CC					
	Intercept	-2.08	0.08	25.11	<0.001
	elevation	-0.11	0.08	-136.00	0.170
	slope	0.27	0.08	3.25	**0.001**

Parameter estimates, standard errors, and significance tests (t-values and p-values) from the selected generalized linear models "glm_log_normalDH" and "glm2_CC" assessing the effect of elevation (m a.s.l.), slope (degrees) and E aspect as sine values ranging from -1 (west) to +1 (east), on DH (dominant height-cm) (log-transformed) and evaluating the influence of elevation and slope gradient on CC (crown cover - %) of *P. tarapacana*. Significant predictors (p <0.05) are highlighted in bold text.

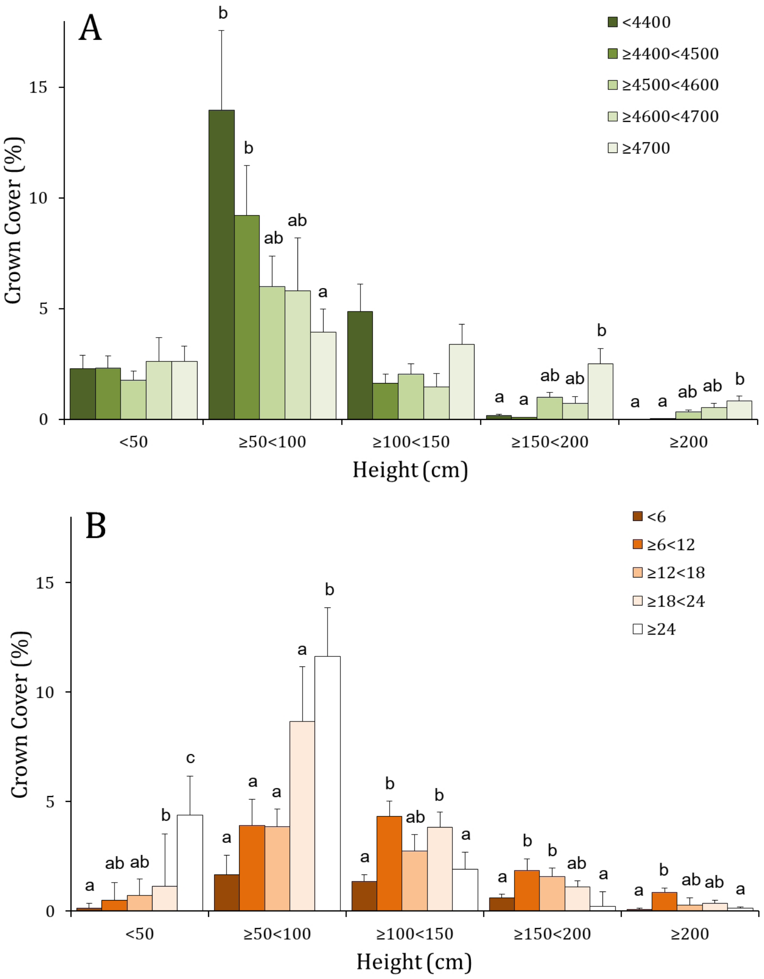

FIGURE 3: Variation in coverage of *Polylepis tarapacana* based on different categories A: elevation (m a.s.l.) and B: slope (%). CC: crown cover in %; Kruskal-Wallis was applied, and differences were determined by comparisons of the means with the Conover–Iman test at p <0.05.

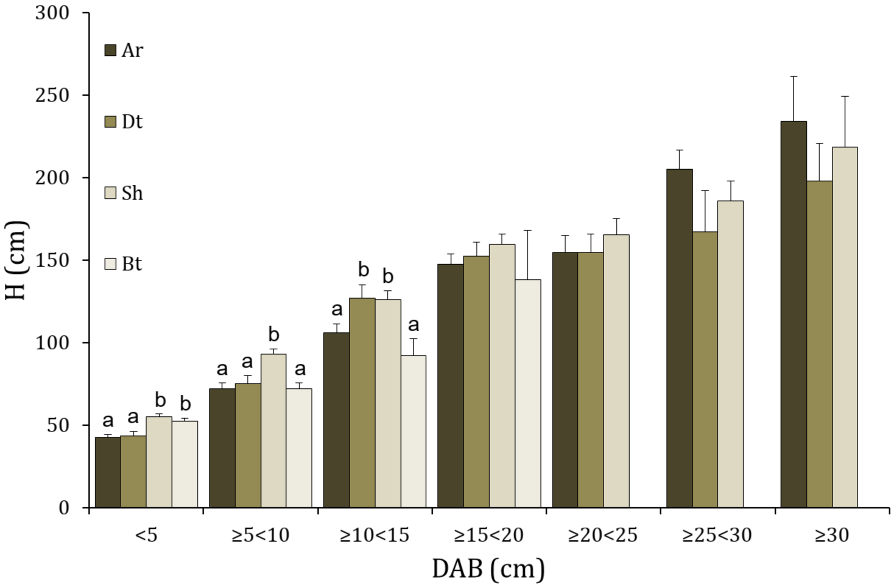

FIGURE 4: Relationship between diameter at the base (DAB) and height (H) of *Polylepis tarapacana* (queñoa) according the different life forms. Ar = Arborescent, Dt = Dwarf trees, Sh = Shrubs, Bt = Brousse tigrée. Kruskal-Wallis and Conover-Iman tests at p <0.05 were applied to compare H for the different DAB classes among the different life forms.

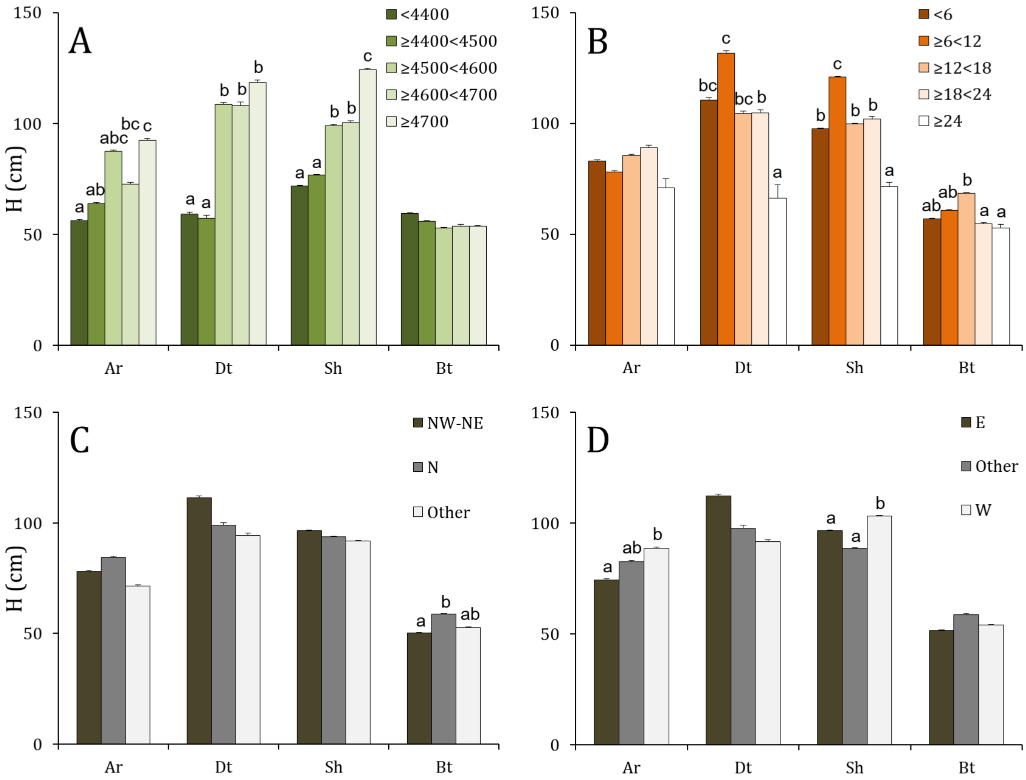

FIGURE 5: Variation in height (cm) of *Polylepis tarapacana* (queñoa) in different life forms, based on A: elevation, B: slope, C: North aspect, and D: East aspect. Ar = Arborescent, Dt = Dwarf trees, Sh = Shrubs, Bt = Brousse tigrée. Kruskal-Wallis and Conover-Iman tests at $p < 0.05$ were applied.

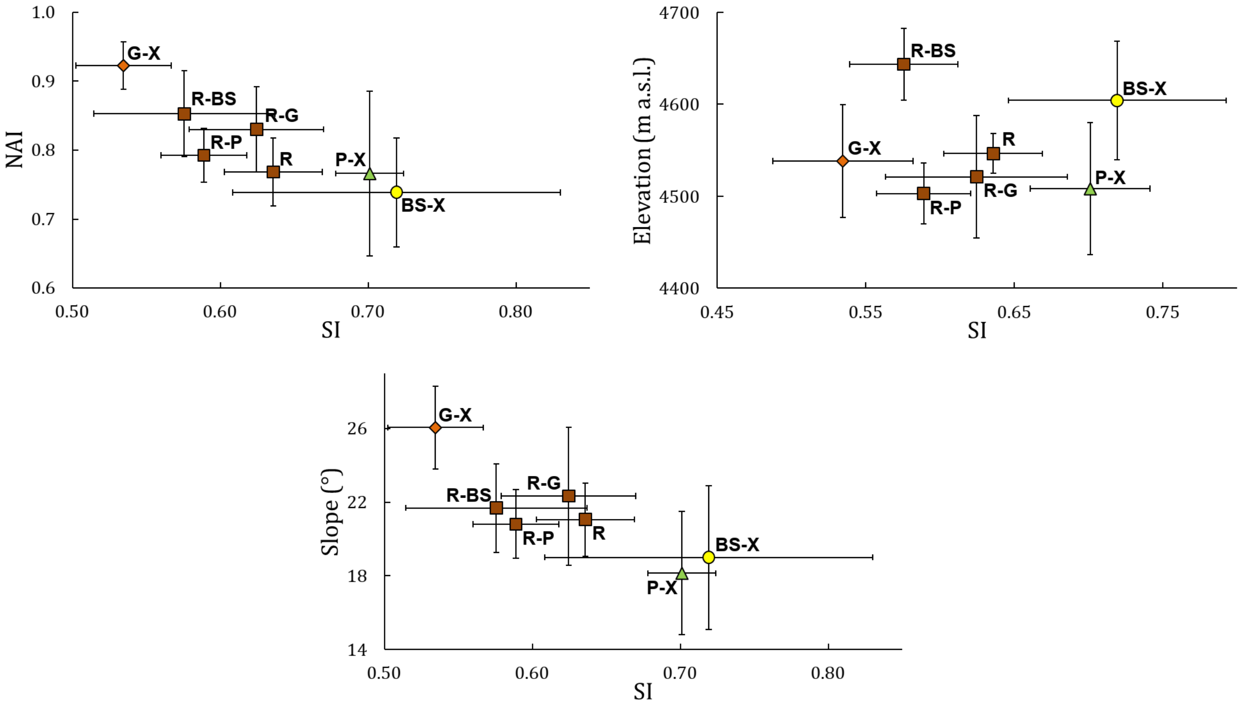

FIGURE 6: Relations of structure index (SI), topographic variables (elevation and slope and N aspect) and north-south aspects index (NAI), standardising the values between 0 and 1 respectively, comparing different substrate types (P = plants, R = rocks, G = gravel, BS = bare soil, single categories were considered when the cover was >50%, and double categories when the sum of two categories is necessary to achieve >50%, when one categories was observed in <5% of the plots, they were grouped together creating a new category (X) taking into account the one with the greatest coverage BS-X, P-X and G-X) in *P. tarapacana* woody communities. Bars showed standard error for both axes.

substrates types (R, R-G, R-P and R-BS) presented intermediate values of SI, while the substrate dominated by G presented dense shrublands and forests with greater CC, but with small individuals. Observations revealed that along the elevation gradient, the highest elevations were dominated by R-BS and BS-X substrates, whereas the lowest elevations were primarily characterised by R, G, and P substrates (Figure 6). At the lower slopes, plants and bare soil promoted developed woody areas, while steeper areas were dominated by G and the dense *P. tarapacana* communities. The north aspect index (NAI) presented values higher than 0.7, which indicates that forests and shrublands mostly occurred in northern aspects.

Discussion

Forest structure is shaped by factors such as topography, aspect, slope inclination and substrate type. These factors influence vegetation structure and composition, with elevation driving changes in population structure. For instance, shrubs are commonly found within forest patches but increase in frequency near the treeline, where shrublands may serve as a successful adaptation for the persistence of *P. tarapacana* populations (Macek et al. 2009; Renison et al. 2006; López et al. 2022). Elevation, as a complex proxy for climatic variables, is a key environmental factor affecting community structure and organisation (Stevens 1992; Heitz & Heitz-Seifert 1995). *Polylepis tarapacana* forests and shrublands exhibited a wide range of structural diversity, with the most developed woody communities occurring at higher elevations, where the substrates were predominantly composed of a mixture of bare soil and dicot understorey. These communities cover a wide range of topographic conditions, showing the adaptability of this species to these extreme environmental conditions (López et al. 2022). Several authors agree that *P. tarapacana* is strictly adapted to unfavourable climatic conditions, since it inhabits the western highland volcanic mountains at altitudes of 3900-5200 m a.s.l., accompanied by dwarf shrubs and cushion plants, with *P. tarapacana* generating the highest-elevation forests and shrublands in the world (Kessler 2006; Boza & Kessler 2022; López et al. 2022).

Our results show that *P. tarapacana* grows between 4160 and 4952 m a.s.l. in Argentina, consistent with previous reports: 4302-4942 m a.s.l. (Peng et al. 2015) and 4000-5000 m a.s.l. (Renison et al. 2013). In Chile, its elevation ranges from 4200 to 4700 m a.s.l. (Ríos 1998), while in Bolivia it occurs from 4250 to 5100 m a.s.l. (Braun 1997). These findings confirm that *P. tarapacana* is among the world's highest-altitude woody communities (Kessler & Schmidt-Lebuhn 2006). Our findings align with previous studies conducted in Peru, which report that *P. tarapacana* exhibits notable height variability, ranging from 120 cm to 380 cm (Morales-Aranibar et al. 2019). In Parinacota, Chile, Saavedra (2013) reported an average height of 147 cm, with maximum values exceeding 460 cm. Similarly, Kessler (2006) described heights ranging from 100 to 400 cm in southwestern Bolivia. In contrast, in Argentina, *P. tarapacana* forests and shrublands exhibit the lowest heights within its northern distribution, predominantly appearing as shrublands mixed with small trees and occasionally forming small forest patches.

In this study, taller individuals were found at higher elevations (>4700 m a.s.l.), while smaller individuals were associated with lower elevations (<4400 m a.s.l.) (Table 2). However, contrasting patterns have been reported. For instance, Hoch and Körner (2005) observed a significant decrease in average tree height with increasing elevation in the Sajama region, Bolivia, consistent with the general trend described by Young (1993) and others (Kessler et al. 2007; Domic & Capriles 2009). In contrast, Kessler et al. (2014) reported a unimodal height distribution for *Polylepis* forests in Peru, with tree height peaking at intermediate elevations (18.5 m at 4300 m a.s.l.) and decreasing at both higher and lower elevations. Taller trees at higher elevations have been linked to drought adaptations, as seen in Patagonian steppe ecotones (Hertel & Wesche 2008) and cloudy mountain valleys (Holtmeier 2009). Discrepancies between these results and those of the present study may be due to greater accessibility and utilisation of low-elevation forests by local communities, leading to the selective removal of larger individuals for construction and fuel (Ríos 1998; Kessler et al. 2014). As Ruthsatz (1983) mentions, the coincidence between the distribution of *P. tarapacana* and the elevation may be due to a greater precipitation at higher elevation, as in the Sajama volcano in Bolivia, where an average annual precipitation of 412 mm was observed at 4980 m a.s.l. (Ruthsatz 1983). Water stress would be decisive in the altitudinal distribution of the species (Macek et al. 2009).

The average canopy cover of these forests was 12%, with very marked extremes. Similar values were observed Chile, with an average of 13%, complying with the percentage of coverage necessary to constitute an arid forest in Chile according to Law 19561 (1998) (Saavedra 2013). Slope is a key topographic factor influencing the structure of *P. tarapacana*. In Tarapacá, Chile (Ríos 1998) and in the central Andes of Bolivia (Argollo et al. 2004) its distribution is reported to be wide, covering both flat areas and steep slopes (>25°). Our study confirmed this adaptability, showing in turn, an inverse relationship between size and slope: the largest individuals are found on gentle slopes, while the smallest individuals dominate the steeper slopes, a pattern also reported by Ríos (1998) and Saavedra (2013). Likewise, the steep slopes present a greater cover, reaching its maximum between 20° and 30°, a result attributed to the high rockiness of these areas, which favors the establishment of *P. tarapacana*. The presence or absence of the species is closely linked to the presence of rocks, as neighbouring areas with similar slopes but without rocks do not support the species (Ríos 1998; Toivonen 2018). This adaptation is reflected in the dominance of low shrubs (Sh) and Brousse tigrée (Bt) on the steepest slopes, where rocky conditions favor the establishment, growth and survival of seedlings (López et al. 2021).

The life forms greatly influenced the individual sizes in *P. tarapacana*, which presented a great variability within the sampled plots. In general, they are small in diameter and short in height, coinciding with the physiognomy of the species as described by Boza and Kessler (2022). López et al. (2023) described the species across the different life forms, presenting simple (Ar and Dt) or multiple stems (Sh and Bt), with a marked difference in their specific biometric characteristics. Also, indicate that these changes are due to the influence of topographic, climatic and human uses derived factors.

Polylepis tarapacana develops on northern aspects, with an east - west gradient (López et al. 2022). However, these aspects influenced the growth architecture of the species, with different life forms, such as Ar and Sh, occurring across the aspect gradients. Ríos (1998) and Saavedra (2013) informed that *P. tarapacana* in Chile preferred N aspects, as were informed by Hoch & Körner (2005), Braun (1997) and López et al. (2022). This preference for N aspects is attributed to the higher solar radiation (and consequently higher temperature) combined with rainfall, which increased at higher elevations and N-facing slopes (Braun 1997; Ríos 1998). These observations support our findings, where 95% of the plots were located at N and NE aspects. Although no significant differences were found in the structure variables with aspect (N aspect and E aspect), except when the indices were compares (IA and SI), where the distribution trend on N-facing aspects is notorious. This is also consistent with Braun (1997), who evaluated *P. tarapacana* distribution in Sajama (Bolivia), and concluded that N-facing slopes showed the highest individual densities, which gradually decreased towards southern slopes. This favourable condition promotes the coexistence of plants with broader temperature range requirements (Oberbauer et al. 2013). The plants must develop new growth strategies to face the landscape limitations of temperature, lack of rainfall or excessive wind exposure.

It can be observed that cushion plants, small shrubs and sub-shrubs are functional groups that exhibit greater resilience to extreme climates (Squeo et al. 1996; Sierra-Almeida et al. 2009), e.g. in our study Bt life form was predominantly found in northern aspects.

The substrate supporting *P. tarapacana* forests and shrublands in Argentina remains underexplored (López et al. 2021), with existing descriptions limited to the High Andean Ecoregion and studies on *Polylepis* forests in Chile (Braun 1997; Ríos 1998; Choque 2010). Analyzing the relationship between substrate and topographic variables provides valuable insights into the optimal conditions for the development of *P. tarapacana* communities. Our findings reveal a clear distinction between gravel soils (G) and substrates dominated by bare soil (BS), rocks (R), or vegetation (P).

Polylepis tarapacana thrives in gullies or rocky areas, allowing establishment at elevations within treeline areas with minimal precipitation (<250 mm year^{-1}) (Miehe et al. 2003; López et al. 2021). This is possible because shrubs and trees benefit from runoff and reduced soil evaporation in the vicinity of rocky or stony substrates (López et al. 2021). These forests predominantly occur on rocky soils, a trend observed in previous studies (Kowoll 1993; Ríos 1998; Choque 2010) and corroborated here, where rocky substrates exhibit a moderately high structure index (SI). Furthermore, regardless of the topographic factor, substrates with vegetation (P) and bare soil (BS) show the highest forest index value (SI). Conversely, gravel soils (G) consistently show low SI values, particularly on those areas with a combination of steep slopes and a predominance of G. This is consistent with the findings of López et al. (2019), who mention that microsites associated with R (Rock edge and soil protected by rocks) would be the most conducive sites for seedling development.

Interestingly, areas with vegetation-dominated substrates show the highest SI values, prompting questions about plant interactions. Do *P. tarapacana* individuals establish in areas avoided by other plants due to reduced competition for resources, or do neighboring species facilitate their growth through positive interactions? This dynamic warrants further investigation to better understand the ecological relationships within these high-Andean communities.

Conclusions

This study showed the significant influence of topographic variables (elevation, slope, aspect) and substrate type on the structure of *P. tarapacana* in the landscape. The largest plants were found predominantly at higher elevations, while slope negatively influenced plant size. Besides, CC of *P. tarapacana* tends to increase with the slope to a maximum at 43° but decrease at larger values. These steeper slopes tend to support smaller individuals, promoting some life forms, such as Ar and Sh. The dominant substrates in these patches were BS intermingled with understorey plants, which presented the highest SI. In these areas, the dominant life forms were Sh and Bt, which are the best adapted to these substrate types.

It is crucial to identify changes in the composition and structure of forests, taking into account both the substrate where they develop and the various life forms they adopt. Each life form occupies a specific ecological niche, and conserving these forests without recognising these differences risks losing important aspects of their ecological roles. *Polylepis* forests and shrublands are among the most threatened habitats in the high Andes, playing a vital role in providing essential ecosystem and environmental services. In this context, it is essential to deepen our understanding of the dynamics and tree structure of *Polylepis tarapacana* in relation to environmental factors. These findings can contribute to develop more suitable management and conservation planning for the local communities that live here for centuries in the High Andes.

Competing interests

The author(s) declare that they have no competing interests.

Authors' contributions

VLL and JMC were completed the statistical analyses and writing the manuscript draft. GMP contributed to the idea, review and editing the manuscript. All authors read and approved the final manuscript.

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