

Climatic, morphometric, and structural characteristics of *Polylepis rugulosa* Bitter forests on the arid slopes of the southwestern Andes in the Moquegua region - Peru

*Características climáticas, morfométricas y estructurales de *Polylepis rugulosa* Bosques amargos en las laderas áridas del suroeste de los Andes en la región de Moquegua - Perú*

Elizabeth Marina Ramos Saira ¹, Jorge Luis Tomas Florez Salas ¹, Víctor Yapuchura Platero ², Fabrizio Del Carpio Delgado ¹, Mariela Fresia Caihuaray Silva ², Suheily Corina Lanchipa Quiroga ³, Kevin Mario Laura De La Cruz ²

¹ Universidad Nacional de Moquegua, Peru

² Universidad Nacional Jorge Basadre Grohmann, Peru

³ Universidad Privada de Tacna, Peru

Corresponding author: Kevin De La Cruz | klaurac@unjbg.edu.pe

ORCID: <https://orcid.org/0000-0002-7083-1825>

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ABSTRACT

The purpose of the study is to characterize the species' preference patterns for physical factors to assist local and regional managers in identifying areas suitable for conservation, management, and restoration. The design of the study is founded on three primary questions: (i) How influential are factors such as slope, valley enclosure, proximity to groundwater resources, and radiation exposure on forest structure variables such as density, distribution patterns, and tree size? (ii) Is it possible to identify regeneration or recruitment patterns that are influenced by altitude, topography, morphometry, or climate? Lastly, (iii) could this disaggregated pattern be a natural characteristic of *Polylepis* forests in the Moquegua Region? After defining the general characteristics of climate and morphometry, Ripley K analysis was used to identify patterns of structure ordination in 36 plots (50 x 50 m) distributed at six distinct sites throughout the forest distribution. These concentrated patterns were associated with density differences between adult and juvenile plants based on altitude: while total tree abundance decreases with altitude, the abundance of juvenile trees increases. This pattern of turnover at higher altitudes may be influenced by climate change, but additional research is required to confirm or refute this hypothesis.

Keywords: Altitude, specimen distribution, protection index, humidity index, slope.

RESUMEN

El propósito del estudio es caracterizar los patrones de preferencia de las especies por factores físicos para ayudar a los gestores locales y regionales a identificar áreas adecuadas para la conservación, gestión y restauración. El diseño del estudio se basa en tres preguntas principales: (i) ¿Qué tan influyentes son factores como la pendiente, el cercamiento del valle, la proximidad a los recursos de agua subterránea y la exposición a la radiación en variables estructurales forestales como la densidad, los patrones de distribución y el tamaño de los árboles? (ii) ¿Es posible identificar patrones de regeneración o reclutamiento que estén influenciados por la altitud, topografía, morfometría o clima? Por último, (iii) ¿podría este patrón desagregado ser una característica natural de los bosques de *Polylepis* en la región de Moquegua? Tras definir las características generales del clima y la morfometría, se utilizó el análisis Ripley K para identificar patrones de ordenación estructural en 36 parcelas (50 x 50 m) distribuidas en seis sitios distintos a lo largo de la distribución forestal. Estos patrones concentrados se asociaron con diferencias de densidad entre plantas adultas y juveniles según la altitud: mientras que la abundancia total de árboles disminuye con la altitud, la abundancia de árboles juveniles aumenta. Este patrón de cambio de actividad a mayor altitud puede estar

influenciado por el cambio climático, pero se requieren investigaciones adicionales para confirmar o refutar esta hipótesis.

Palabras clave: Altitud, distribución de la muestra, índice de protección, índice de humedad, pendiente.

INTRODUCTION

Forests in arid and semi-arid regions are important elements of the landscape, providing a range of environmental services such as increasing habitat complexity, harboring herbaceous and shrub species, acting as reservoirs of genetic resources with potential economic uses, and preventing soil erosion (Andivia et al., 2018; Filazzola and Lortie, 2014; Zeng et al., 2020). The Central Andean Puna (Olson et al., 2001) is a continuous ecosystem of alpine grasslands and shrubs that dominates the high Andes mountain range (between 3500 and 6000 meters above sea level, masl) between central Peru, Bolivia, northern Argentina, and Chile. The aridity in this ecoregion increases following a gradient from northeast to southwest, with the wetter sectors (humid Puna) located on the eastern slopes facing the Amazon and Paraguay-Paraná basins. Meanwhile, the driest sectors are found on the western border of the Altiplano and the Pacific slopes, upstream of the Atacama Desert (Catorci et al., 2011; Madrigal-Martínez and Miralles, 2019). The western drainage in southern Peru constitutes the driest region of the entire national territory, with very low precipitation and high-water demand. Based on the rainfall regionalization on the Pacific slopes developed by Rau et al. (2017), the Puna ecosystems in these areas of the country belong to regions 8 and 9 with average annual precipitation below 300 mm and a generalized deficit in the water budget of around 120 to 480 mm/year (Rau et al., 2018). In these arid and semi-arid areas, the high-altitude forests are dominated by species of the genus *Polylepis* (Rosaceae), accompanied in the lower parts of the distribution range by other tree or shrub species belonging to the families Escalloniaceae (*Escallonia myrtilloides*), Buddlejaceae (*Buddleja coriacea*), Rhamnaceae (*Colletia spinosissima*), and Solanaceae (*Dunalia spinosa*). The genus *Polylepis* is widely distributed and diversified throughout the tropical and subtropical Andes (Herzog et al., 2002; Kessler, 2002), with 27 described species. Bolivia and Peru have the highest reported species richness and (probably) the central Andean Puna constitutes their center of origin and diversification (Schmidt-Lebuhn et al., 2010; Zutta et al., 2012). *Polylepis* species forests represent the highest tree line in the world (Cuyckens et al., 2016; Purcell et al., 2004; Zutta and Rundel, 2017), having been reported above 5000 meters above sea level (masl) in central Bolivia (Sajama National Park) and southern Peru (Vilacota-Maure Regional Conservation Area). However, the extent and current distribution patterns of *Polylepis* forests are controversial. Some authors (Hensen et al., 2012; Renison et al., 2018; Zutta et al., 2012) suggest that the current fragmented distribution of 8 *Polylepis* species is mainly due to anthropogenic factors, while others indicate that this "irregular" or "discontinuous" development pattern is a natural characteristic of the genus (Gareca et al., 2013). In the southern Andes of Peru (regions of Moquegua, Tacna, and partially Puno), only three species of *Polylepis* have been reported (Mendoza and Cano, 2011): *Polylepis tarapacana* Philippi, distributed mainly on the eastern slopes of the Western Cordillera facing the Altiplano (Franco et al., 2021); while *P. rugulosa* Bitter and *P. subtusalbida* (Bitter) are mainly distributed on the western slopes of the Andes facing the coastal desert. The three species recorded in this region exhibit the typical "irregular" distribution reported for the genus (Pacheco et al., 2019). However, this distribution could be influenced by anthropogenic and environmental factors, such as climate, soils, or topographic and morphometric characteristics (Toivonen et al., 2017).

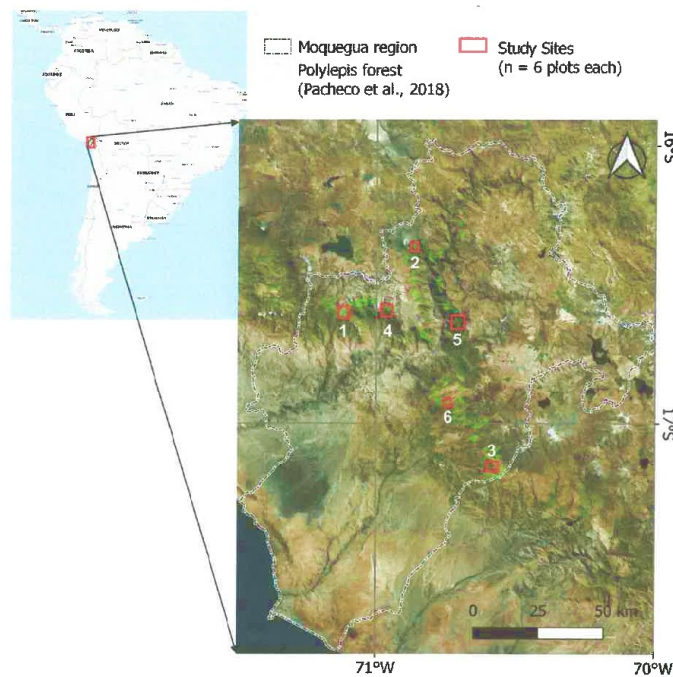
Based on the structure, density, and relationship between adults and seedlings, it is possible to partially infer whether a forest is in a condition of active regeneration or not and how environmental or altitudinal factors can influence these processes (Blundo et al., 2021; Schneider, 2001). Topographic and morphometric factors could substantially affect the development, reproduction, and recruitment of forests, especially in arid environments where the detrimental effects of wind or water scarcity can be mitigated by protective factors or access to groundwater (Swetnam et al., 2017). These relationships were recently documented for *Polylepis* forests in southeastern Peru (Toivonen et al., 2017), central Peru (Camel et al., 2019), and southern Peru (Franco et al., 2021). However, although some information related to the adaptations and preferences of *Polylepis* species has been developed and is available, national reforestation programs in the Peruvian Andes continue to propose approaches based on non-native species such as *Eucalyptus* and *Pinus* (Jonard et al., 2014; Renison et al., 2018; Rundel et al., 2014). Under current climate change conditions, *Polylepis* forests (like other ecosystems in the central Andes) are among the most threatened in the world, a situation that poses a serious threat to all natural and human communities that benefit from their ecosystem services (Bonnesoeur et al., 2019; Jameson and Ramsay, 2007). If local, regional, and national governments of South American countries aim to invest in the conservation, management, and eventual restoration of these valuable forests, it is essential to have reliable information on the adaptations, preferences, and characteristics of the most suitable areas for their development (Chazdon et al., 2020; Crouzeilles et al., 2017). This study evaluated the structure and allometry of *Polylepis rugulosa* forests in the Moquegua Region (southwestern Peru) and related them to climate, altitude, and morphometric characteristics. The objective of the study is to characterize the species' preference patterns for physical factors to help local and regional managers identify suitable areas for conservation, management, and restoration. The study design is based on three main questions: (i) How influential is slope, valley confinement, proximity to groundwater resources, or radiation exposure on forest structure factors such as density, distribution patterns, and tree size? (ii) Is it possible to identify some regeneration or recruitment patterns related to altitude, topography, morphometry, or climate? Finally, (iii) could it be a natural characteristic of the disaggregated patterns observed in the *Polylepis* forests in the Moquegua Region?

METHOD

STUDY AREA

This research was conducted in the headwaters of two hydrographic basins in the southern Pacific region of Peru: Tambo and Moquegua-Osmore. This area is part of the Central Dry Andean Puna (Olson et al., 2001), a biome of alpine grasslands and scrub that extends from central Peru to northern Argentina. Specifically, the *Polylepis* forests that constitute the subject of study for this research extend over an elongated territory from north to south between 16° 05' to 17° 30'S and 70° 45' to 71° 00'W in the Moquegua Region, the least populated administrative unit and one of the driest in Peru (Figure 1). Therefore, we used the *Polylepis* forest polygons generated for the Moquegua Region by Pacheco et al. (2019) as our initial source to select the study sites (forest structure plots) and conduct climatic and geomorphological analyzes.

Figure 1 - Region of Moquegua in Peruvian territory, showing the extent of *Polylepis rugulosa* forests (~320 km²) and the locations of 6 study sites (36 plots of 50 x 50 m)



CHARACTERIZATION AND REGIONALIZATION OF THE CLIMATE

To characterize the rainfall and temperature regimes of the study area, the national grid climate database PISCO Ver. 2.1 (Interpolated Peruvian Data of Climatological and Hydrological Observations from SENAMHI, Aybar et al., 2020). Previously, the PISCO database was validated using recorded values of rainfall and temperature from 4 climatic stations belonging to the national meteorological service (SENAMHI) and located within or near the forest polygons. The validation process consisted of applying a series of Goodness of Fit (GoF) indices that compare the values from each SENAMHI station (observed data) versus the PISCO data (simulated data). The results of these analyzes showed a high fit between the simulated PISCO data and the measured data from the stations (Table 1), which allowed us to advance in the characterization of changes in rainfall and temperature with altitude and location throughout the distribution area of *Polylepis* in Moquegua. Additionally, we used the precipitation values from PISCO to apply the Regional Vector Method (RVM, Brunet-Moret, 1979; Rau et al., 2017) to identify sectors with different climatic patterns throughout the distribution area of *Polylepis* in the Moquegua Region.

Table 1 - Goodness-of-fit indicators obtained for the comparison of PISCO data with four SENAMHI climate stations located within or near the areas of *Polylepis* forests in the Moquegua region

	Ichuña		Ubinas		Calacoa		Quinistaquillas	
	16.13°S, 70.53°W 3792 m a.s.l.		16.38°S, 70.85°W 3403 m a.s.l.		16.74°S, 70.66°W 3457 m a.s.l.		16.75°S, 70.87°W 1789 m a.s.l.	
	Pp	temp	pp	temp	pp	pp	temp	
Analysis period	1965 - 2018	2001 - 2018	1964 - 2020	1969 - 2020	1964 - 2013	1964 - 2020	2001 - 2020	
Validation period	1981 - 2016	2001 - 2016	1981 - 2016	1981 - 2016	1981 - 2013	1981 - 2016	2001 - 2016	
RMSE	1.12	0.38	0.85	1.08	0.95	1.17	0.84	

PBIAS	4.4	6.3	5.01	8.42	5.36	6.26	7.42
R²	0.85	0.78	0.92	0.69	0.79	0.83	0.75
Nash-Sutcliffe	0.91	0.84	0.90	0.77	0.84	0.91	0.80

MORPHOMETRIC AND TOPOGRAPHIC ANALYSIS

To characterize and describe the morphometric and topographic preferences of *Polylepis rugulosa* forests in the Moquegua region, different terrain attributes with the potential to influence forest density, tree size, water availability, and other limiting factors were analyzed (Olaya, 2009; Toivonen et al., 2017). Five topographic and morphometric characteristics were selected based on their potential influence on the distribution and structure of the forest. Those morphometric or topographic factors were: slope, terrain curvature, morphometric protection index (MPI), topographic wetness index (TWI), and orientation. All topographic and morphometric indices were calculated based on the Global Digital Elevation Model Aster downloaded from USGS Earth Explorer (horizontal resolution of 30 x 30 m) and using algorithms available in Q GIS 3.16.4 Hannover (Q GIS Development Team, 2020).

FOREST STRUCTURE

To record the allometric measurements of trees in different stands, altitudes, and sectors of the Moquegua region, we established 36 plots of 50 x 50 m distributed across six different stands throughout the distribution area. The location of each plot was selected using a stratified random procedure. Therefore, we have at least two alternative locations to relocate the plots if they fall in areas of difficult access. In each plot, we measured the diameter at ground level (DGL), total height (TH), and crown projection (CP) of all individuals with a DGL ≥ 1 cm. Additionally, we obtained the total density of individuals, the ranges of DGL and TH for each plot, which were analyzed and compared based on altitude. Finally, to evaluate whether the distribution of trees in each plot is random or has some aggregation, we conducted a Ripley's K analysis to compare the spatial pattern of tree distribution with a theoretical random pattern based on the Poisson distribution (Camel et al., 2019; Fibich et al., 2016).

DATA ANALYSIS

We conducted a mixed linear model to analyze whether some climatic or morphometric indices influence tree abundance. After identifying the most influential factors, a simple linear model was considered that included the most suitable forest allometry indicators, such as density, basal diameter, and height. All numerical and statistical procedures, such as the extraction of PISCO data for the area of interest, the estimation of the GoF, the application of the RVM, the estimation of forest patterns, and the estimation of linear mixed models, were carried out in the statistical software R 4.0.5 (R Core Team, 2021).

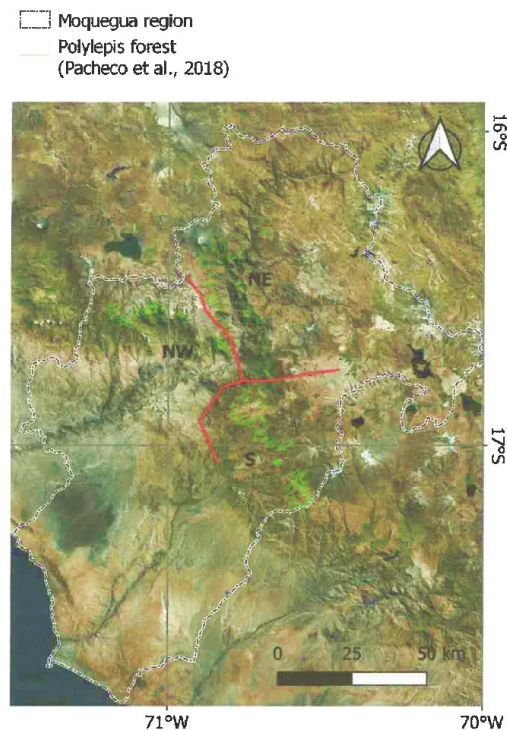
RESULTS

PRECIPITATION AND TEMPERATURE

The regionalization of the study area, based on the RVM method using precipitation data, identified three homogeneous zones (Figure 2). The southern sector presented the driest conditions, with an average annual precipitation of 101.9 mm and the highest variability in average daily temperature ranges of 21.4 °C between the maximum of 21.8 °C and the minimum daily temperature of 0.4 °C. The northwestern sector of the forest showed intermediate values of precipitation and daily temperature, with an average annual precipitation of 176.8 mm and a daily temperature variability of 19.2 °C (from 2.9 to 22.1 °C). Finally, the northeastern sector of the *Polylepis* forest distribution had the wettest and warmest conditions, with an average annual precipitation of 232.8 mm and the smallest

range of variability for daytime temperature, fluctuating on average by 18.6 °C (Tmin = 4.6 °C, Tmax = 23.2 °C).

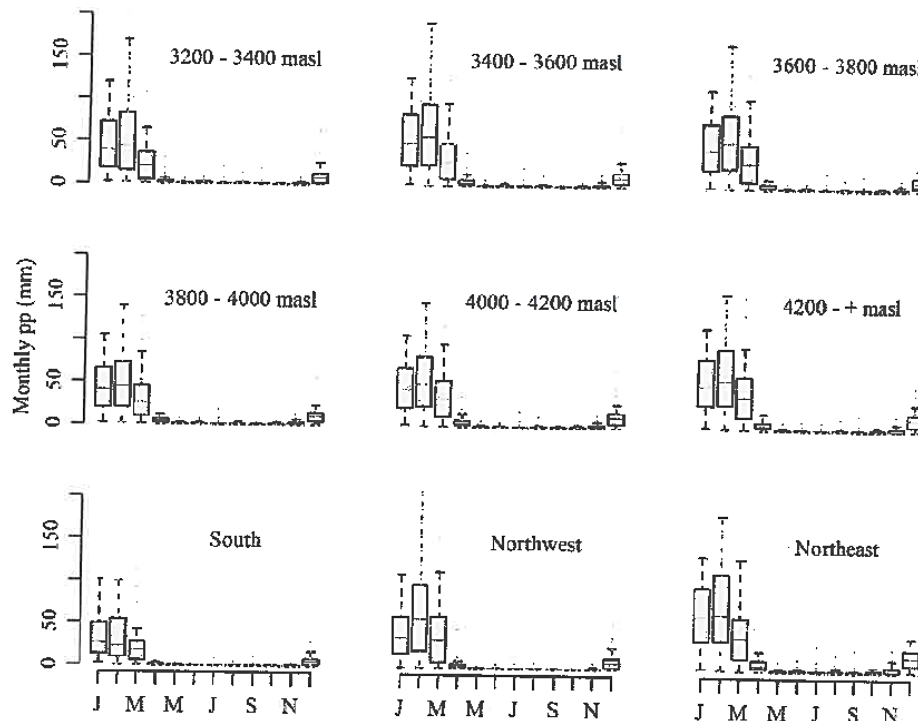
Figure 2 - The red lines are the boundaries between three homogeneous precipitation sectors identified by applying the RVM across the entire distribution area of *Polylepis* forests in the Moquegua region. The three sectors were: the driest in the south (S), the northwest (NW), and the wettest in the northeast (NE)



Despite the homogeneous sectors or altitudinal bands, the precipitation data showed a typical seasonality throughout the distribution range of the forest in the Moquegua region (Figure 3). The rainy season extended from December to March, with a peak in February. Meanwhile, precipitation during the long dry season (April to November) is very scarce, with numerous periods without rain. The analyzed 200-meter elevation bands presented a relatively simple pattern of increase following the altitude rise, with the minimum average interannual precipitation of 149.1 mm. y-1 recorded in the lower band (3200-3400 m.a.s.l.), and the maximum of 199.3 mm. y-1 obtained for the upper range (4200 - + m.a.s.l.). However, a specific variability of the general pattern was observed at the different altitudes analyzed. For example, the altitude band of 3400-3600 meters above sea level, located immediately above the lower levels, recorded a significant increase in precipitation, reaching an average of 185.2 mm per year. However, in the next two bands, the average precipitation decreased to 172.4 mm per year in the range of 3600 to 3800 meters above sea level and 152.5 mm per year in the range between 3800 and 4000 meters above sea level. Above those areas, precipitation increases again in the band from 4000 to 4200 meters above sea level, reaching an interannual average of 173.5 mm. Unlike the altitudinal behavior of precipitation, the temperature decreases steadily as altitude increases. The highest interannual daytime temperatures were observed in the 3200-3400 m.a.s.l. band, with a minimum of 5.7 °C and a maximum of 24.3 °C. On the other hand, in the highest band (4200 - + m.a.s.l.), the average minimum daily temperature was 0.7 °C and the maximum was 21.2 °C. The daily variability

of temperatures among the six altitudinal bands slightly increased with altitude, ranging from 18.7 °C at 3200-3400 m.a.s.l. to 20.5 °C at 4200 - + m.a.s.l..

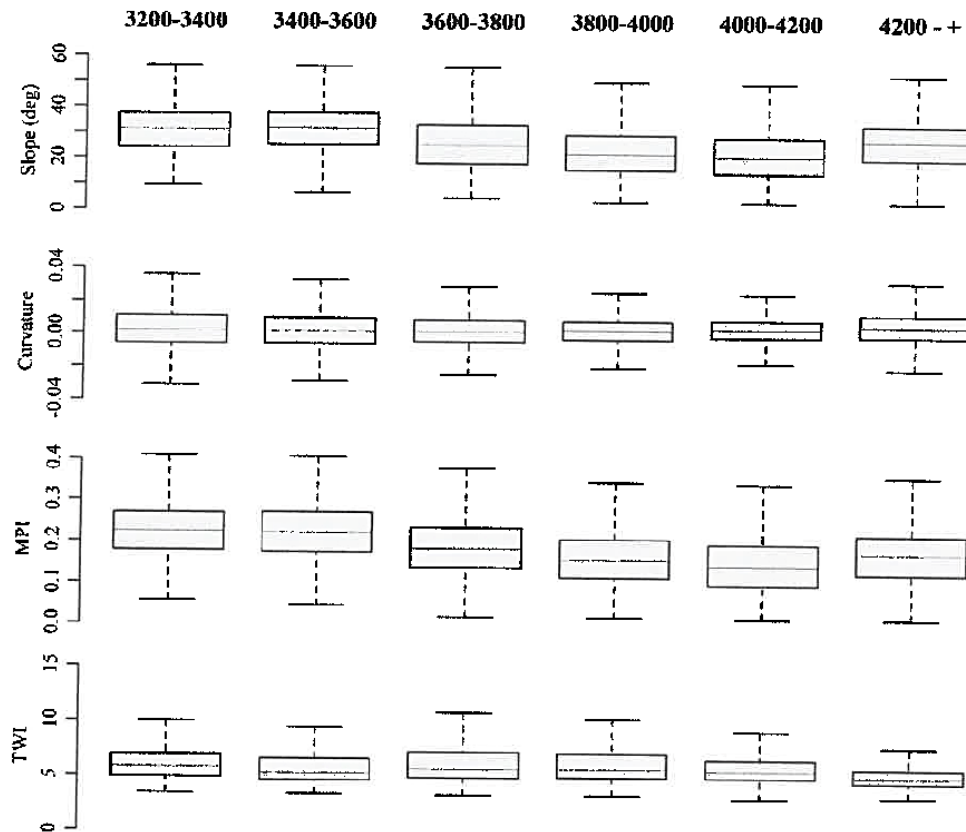
Figure 3 – Monthly and interannual average precipitation, and interannual average of daily maximum and minimum temperatures. The values are expressed in mm and °C for different altitudinal ranges and sectors of the Polylepis forests in the Moquegua region, in the southwest of Peru. In the lower graphs, the black line with squares represents the total annual precipitation, the red line represents the average daily maximum temperature, and the blue line represents the average daily minimum temperature



MORPHOMETRIC CHARACTERISTICS

Mild but common changes occurred in their nature, intensity, and direction in the morphometric variables with altitude (Figure 4), apparently related to climatic variables and geographical configuration. The two lowest altitudinal bands, from 3200 to 3400 and from 3400 to 3600 meters above sea level, exhibit forest formations developed on terrains with slopes ranging from 10 to 60 degrees and an average of 28.8 degrees. For the next three altitudinal levels, the average slope where the forests developed decreased. In the band from 3600 to 3800, the average slope is 24 degrees, and the specific values range from 5 to 55 degrees. The band from 3800 to 4000 meters above sea level had a slope that varied from 3 to 56 degrees with an average of 21 degrees, and in the band from 4000 to 4200 meters above sea level, the average slope where forests develop is 20 degrees with a total range of 4 to 56. In the upper band (from 4200 meters above sea level and above), there was an increase in the slopes where the forests developed, with an average of 25 degrees, although the total range of 5 to 54 degrees was like that observed for the previous three bands.

Figure 4 – Boxplots of morphometric variables and orientation radar charts explaining the distribution of *Polylepis rugulosa* forests in the Moquegua Region. MPI: morphometric protection index, TWI: topographic wetness index



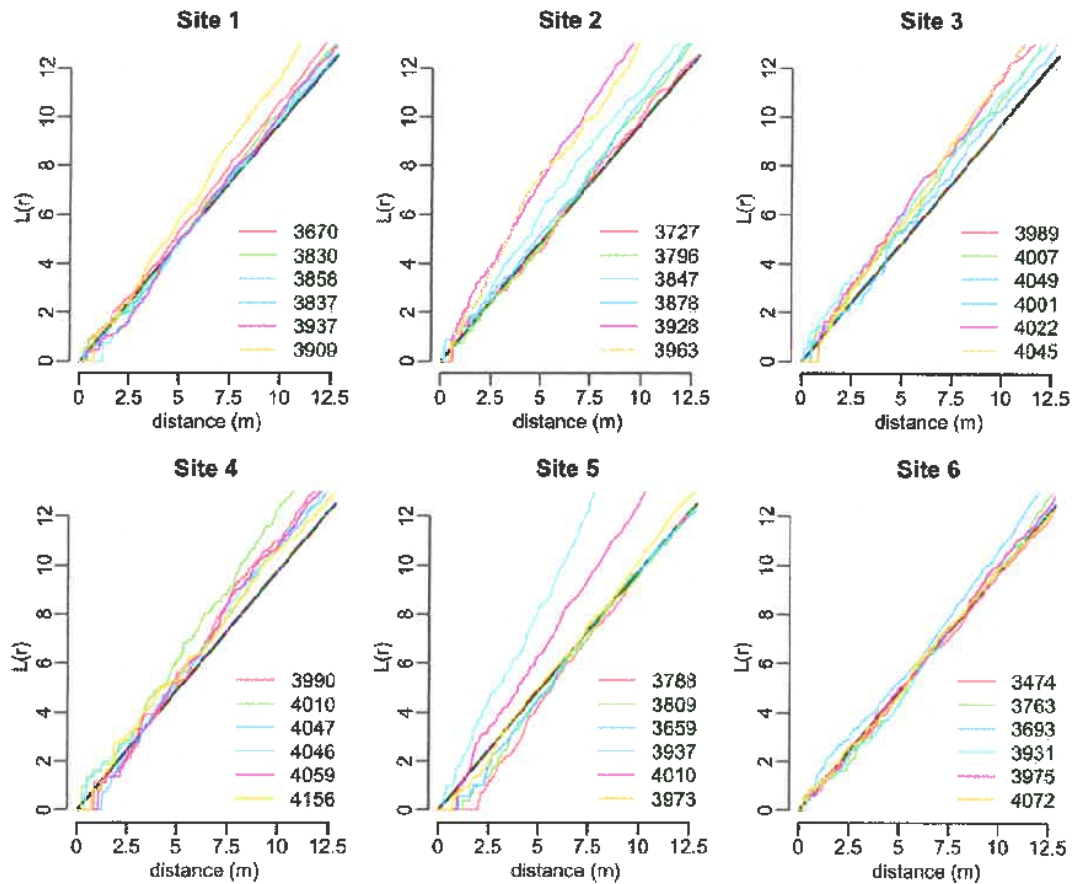
The curvature of the terrain in the areas where these forests were established is remarkably homogeneous, with a small variability of ± 0.04 units around the value of 0 in all bands, with a decrease in the total range observed for the bands from 3600 to 3800, 3800 to 4000, and 4000 to 4200 meters above sea level. In general terms, these forests developed on relatively straight slopes, without significant convexities or concavities. The morphometric protection index (MPI) and the topographic wetness index (TWI) have similar but oppositely directed variability patterns. The two lowest altitude bands (3200 to 3400 and 3400 to 3600 meters above sea level) have relative average values for MPI (0.21 and 0.20 units respectively) and TWI (5.69 and 5.44 units, respectively). In the next three 200-meter elevation bands, ranging from 3600 to 4200 meters above sea level, the average MPI decreased to 0.17, 0.15, and 0.13 units in the segments from 3600 to 3800, 3800 to 4000, and 4000 to 4200 meters above sea level, respectively. Meanwhile, the average TWI slightly increased from 3600 to 3800 (5.77 units) and from 3800 to 4000 (5.75 units) but decreased to 5.44 units in the 4000 to 4200 m.a.s.l. band. Finally, in the highest altitude band (4200 meters above sea level and above), the MPI increased, reaching an average of 0.16 units, and the TWI recorded its minimum value (4.80 units). The opposite change in MPI and TWI would be related to the climatic characteristics and water needs of the studied plant species, but it is quite direct and notable how these two morphometric variables were related to the observed slope changes.

The predominant orientation (aspect) also had changes related to altitude, the most common distribution of the studied plots was on slopes facing the O - OS - S directions, but some deviations could be observed according to elevation. The lowest altitudinal band (3200-3400) has most of the plots on slopes facing south and southwest, but a critical proportion facing northeast also developed. In the three immediately higher bands (3400 to 4000 meters above sea level), the development of forest plots facing north (or any orientation related to the north) was significantly reduced. Here, the predominant directions were typical for the southern hemisphere: W - SW - S. Some significant plots were observed on northwest-facing terrains in the 4000 to 4200 band, but the W - SW and S directions remained the most populated. Finally, in the highest altitude band (4200 meters above sea level and above), the pattern changes, with the western and northwestern orientations becoming the most important for forest development, and a marginal contribution from south-facing slopes.

PATTERNS OF TREE DISTRIBUTION

The distribution of *Polylepis rugulosa* trees showed a random to slightly clustered pattern (Figure 5), with a generalized increase in aggregation related to elevation. Sites one and four were in the northwest sector with medium humidity. At site 1, only one of the higher plots (3909 m.a.s.l.) showed a particular aggregation pattern. Meanwhile, at site four, all forest plots show a slight aggregation starting from a radial distance of 5 meters. The altitude-related clustering pattern is undeniable at sites two and five, both in the humid northeastern region. At site two, the two highest plots (3928 and 3963 meters above sea level) were significantly clustered, and at site five, the plots located at 3937 and 4010 meters above sea level also have a significantly aggregated distribution. Significant aggregation patterns begin from very short radial distances (less than 2.5 meters) in both cases. In the case of the two study sites located in the drier southern sector, only the measured plots showed a slightly clustered pattern at site three. Meanwhile, the results for site six could all be considered as trees distributed completely at random.

Figure 5 - The L estimator in the Ripley function for each plot (represented by altitude) at each study site in the distribution area of *Polylepis* forests in the Moquegua region



FACTORS INFLUENCING TREE ABUNDANCE

The mixed linear model developed to analyze the influence of environmental factors on three abundance values per plot (Table 2) indicated that the combined effect of five factors (Altitude, MPI, TWI, Slope, and precipitation) was statistically significant (p-value = 0.003).

Table 2 - The Linear Mixed Model analyzes the effects of morphometric factors on the abundance of trees per plot

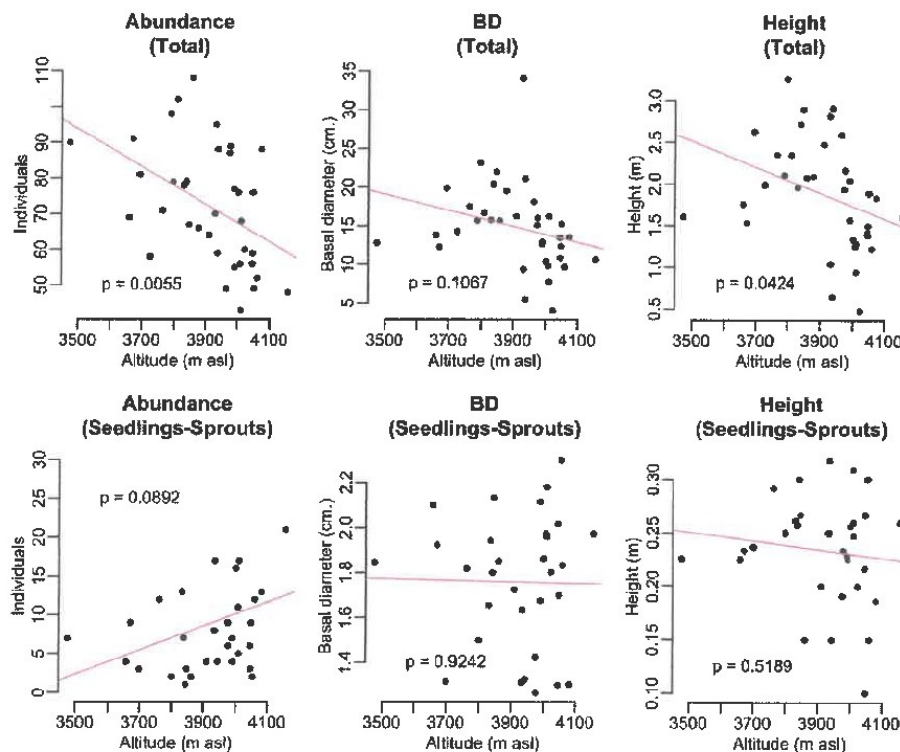
	Estimate	Std. Error	T value	Pr(> t)
(Intercept)	731.648	637.816	2.15	0.026
Log(Altitud)	-81.468	76.941	1.59	0.098
MPI	94.800	75.820	1.25	0.121
Precipitación	35.476	41.752	0.84	0.226
TWI	-0.719	1.895	-0.38	0.707
Slope	0.171	0.653	0.262	0.795

Residual standard error: 13.93 on 31 degrees of freedom
 Multiple R-squared: 0.3919, Adjusted R-squared: 0.3135
 F-statistic: 4.995 on 4 and 31 degrees of freedom, p-value: 0.003169

However, the individual effects of each component could be smaller than the combined effect for all the environmental variables considered (p-value > 0.05 for each factor). Despite this, although the individual effects were not significant, the lowest p-values were obtained for altitude and the Morphometric Protection Index (MPI), so direct linear correlation

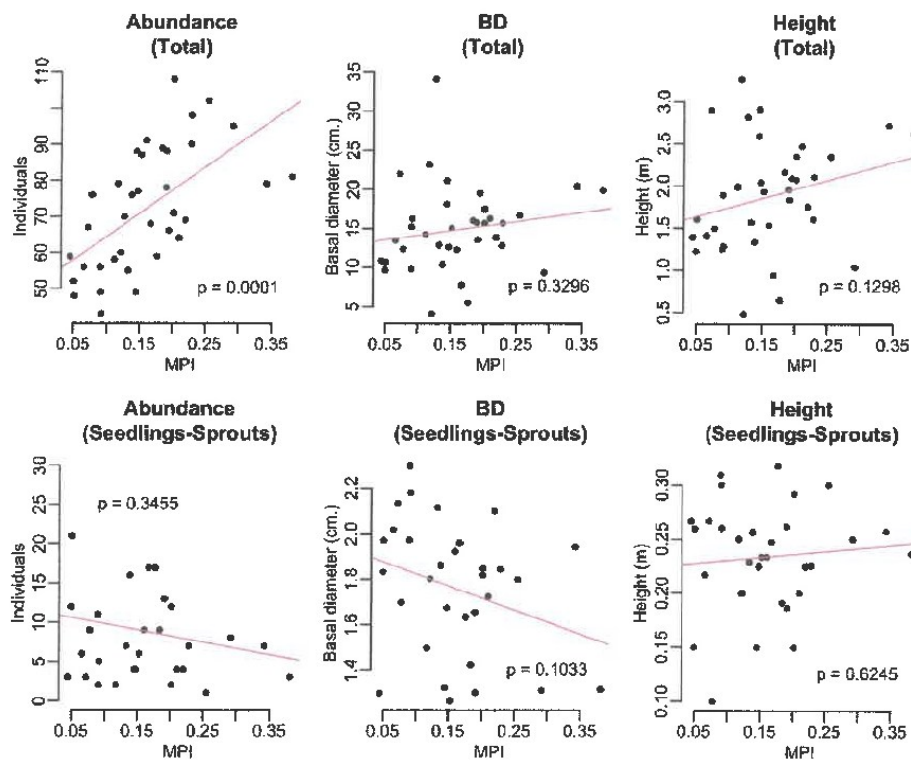
analyses were conducted between these environmental variables and some forest patterns generalized by plot. The linear correlations between altitude and the average values per plot for abundance, basal diameter, and plant heights showed an interesting difference between the total number of individuals recorded and the juvenile specimens (Figure 6).

Figure 6 – The abundance, basal diameter, and height of *Polylepis* specimens (total individuals and juvenile stages) in relation to altitude



The correlations between altitude and total records were all inverse (increases in altitude mean decreases in plot metrics) and were only significant with tree abundance (p-value = 0.0055) and average height per plot (p-value = 0.0424). The linear correlations between altitude and the recorded values for seedlings and sprouts were, in all cases, not significant (p-values greater than 0.05 in all cases). However, the only case close to being significant is the correlation between altitude and the abundance of specimens, and in this case, the correlation was direct, indicating an increase in juvenile individuals with altitude. In the morphometric protection index (Figure 7), the only significant correlation obtained was with the total abundance of individuals. In this case, the relationship was direct, indicating that the characteristics of the terrain with greater protection were related to the higher density of plants.

Figure 7 – The number of individuals, basal diameter, and height of *Polylepis* specimens (total individuals and juvenile stages) in relation to the morphometric protection index (MPI)



DISCUSSION

The current distribution of *Polylepis* forests along the Andes is remarkably fragmented, and this pattern was commonly attributed to modern human impacts (Ellenberg 1979; Mendoza and Cano, 2011; Zutta et al., 2012). However, genetic, paleoecological (Gareca et al., 2013; Valencia et al., 2018), and morphometric analyzes (Franco et al., 2021; Toivonen et al., 2017) have shown that these "punctuated" patterns could be partially related to the natural history of the genus and some specific adaptations to live in high-altitude environments. Our study and previous work conducted in the same region (Pacheco et al., 2019) found that the forests of *Polylepis rugulosa* have an irregular distribution, with some differences in density and structural characteristics among the different stands that can be attributed to physical variables. The climate of the area studied is slightly heterogeneous, but the forest exhibits a relatively homogeneous distribution pattern among the different climatic and altitudinal zones, except in the lower (3200-3400 m.a.s.l.) and higher (4200 m.a.s.l. and above) altitudinal zones. Since altitude is related to a series of environmental constraints (Toivonen et al., 2017), we expected some changes in niche preferences with altitude. Meanwhile, only notable variations were recorded at the extremes. The differences observed in the lower altitude range would be related to the presence of human activities (livestock farming and agriculture) and the fact that, at these altitudes, the forests are mixed, composed of a series of species that accompany *P. rugulosa* (De Souza and Batista, 2004; Dieler et al., 2017; Ellenberg, 1979; Kessler, 2002). In contrast, above 3600 meters above sea level, all forest stands were composed solely of *P. rugulosa*, and the adaptations of this species determine the observed patterns of distribution, orientation, and morphometry. Like the results obtained by Toivonen et al. (2017) in Cusco (southeast Peru), the higher parts of the distribution range show some changes in morphometric preferences, especially in aspect

(orientation). Northward orientation may be preferred at higher altitudes due to the higher temperature requirements to ensure forest development, despite the effects of increased radiation on water retention, wind effects, and water stress (Kašpar et al., 2017; Körner, 1998; Noroozi and Körner, 2018).

Understanding these preferences in physiographic, topographic, and morphometric characteristics, along with other factors such as water and soil, could also help managers and stakeholders focus conservation efforts in more suitable areas (Fuhlendorf et al., 2018; Laterra et al., 2016). Commonly, investment in ecosystem restoration (generally only reforestation) in many South American countries has been developed solely based on expert opinion and not necessarily on systematic approaches developed considering the specific requirements of the ecosystem (Zhang et al., 2018). The opinion of experts is a valuable tool for defining initial objectives in restoration and management approaches, but the specificities of each organism and the particularities of each area are two critical elements that require specialized studies (Gann et al., 2019; Stevenson et al., 2018). In *Polylepis* forests, it is important to focus some research efforts to understand the different effects of human interventions and species adaptations to the observed patchy distribution. If the most influential factor in defining the location, extent, and structure of individual forests is the specific adaptation to morphometric, climatic, or soil characteristics, this is a critical factor that must be included in the future approach to conservation and restoration efforts. This is particularly critical for a group of species distributed along the Andes but with the highest occurrence in the central Puna (Valencia et al., 2018; Zutta and Rundel, 2017), one of the most threatened regions in the world due to climate change (IPCC, 2021, 2014). Just like in other forest regions of the world (Boulanger et al., 2018; Bussotti and Pollastrini, 2017; Kaplan et al., 2003; MacDonald et al., 2008), the distribution ranges of *Polylepis* forests are also expected to change under the influence of climate change (Cuyckens et al., 2016; Zutta and Rundel, 2017). However, changes in distribution ranges are not the only ones to be expected because of global warming processes; changes in forest structure, density, species composition, wildfire frequency, and many other factors are also anticipated (Mitchard, 2018; Seidl et al., 2017; Stevens-Rumann et al., 2018). We found some divergences in structural patterns (Figure 5) and total versus juvenile abundance by altitude (Figure 6) that could indicate an increased forest renewal rate at high altitudes for *P. rugulosa*. These patterns are also related to the areas with the most climatically suitable distribution, such as the northeastern sector of the study area, where water availability is higher. However, these patterns may also be related to some other environmental variables, such as the occurrence of warm and humid years or the low density of adult specimens and, therefore, reduced intraspecific competition (Fibich et al., 2016). At this level, we do not have enough information to confirm whether these divergences in forest structure and density occurred due to altitudinal expansion or some local phenomenon. However, reporting on this type of finding is essential to propose new lines of research that could help improve our knowledge and increase the likelihood of conserving these unique forests and their critical ecosystem services.

CONCLUSIONS

Our study showed that the forests of *Polylepis rugulosa* are distributed throughout the study area in Moquegua in a fragmented pattern due to a series of adaptations that generate preferences for specific morphometric and topographic characteristics. These findings do not imply that human intervention has not contributed to this irregular distribution, but they compel us to reevaluate concepts about potential distribution and even the official name of "Polylepis relict forests" used by the Peruvian Ministry of the Environment (MINAM, 2018).

We also found evidence of a more clustered structure and a predominance of juvenile specimens at higher elevations; both potentially related to changes in forest size and growth due to climate change. This last statement is not absolute because the observed changes may also be related to other temporal or spatial characteristics, but their existence is essential for future, more specific research.

In general, except in the higher and wetter areas included in our study, the forest showed a very homogeneous and probably stable structure, indicating that only some higher parts of the distribution range are experiencing renewal. Combined with the more northerly orientation in the higher areas, these forests may cope with climate change by migrating to new, more suitable areas. However, the slow rate of renewal and colonization raises concerns about their future. Based on this work, we identify more specific research on germination and sprouting rates, displacement, and climate trends as necessary to understand whether mitigation or adaptation approaches are needed to preserve these forests or face future changes.

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AUTHORS' CONTRIBUTIONS (CREDIT)

Conceptualization, JLTF, VYP, FDC; methodology, EMRS, MFCS, SCLQ, KMLDC; formal analysis, EMRS, JLTF, FDC, MFCS, SCLQ, KMLDC; investigation, JLTF, FDC, KMLDC; data curation, EMRS, JLTF, VYP, FDC, MFCS, SCLQ, KMLDC; writing—original draft preparation, EMRS, VYP, MFCS, SCLQ, KMLDC; writing—review and editing, JLTF, VYP, FDC, MFCS, SCLQ; project administration, EMRS, JLTF, FDC, SCLQ, KMLDC; supervision, VYP.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data supporting the findings of this study are available upon reasonable request.

ETHICS STATEMENT

This study did not involve human participants or animals and therefore did not require ethical approval.

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