Contents lists available at ScienceDirect

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Optimal environmental drivers of high-mountains forest: *Polylepis tarapacana* cover evaluation in their southernmost distribution range of the Andes

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ARTICLE INFO

Keywords:
High mountain ecosystems
Forest area
Climate change
Environmental variables

ABSTRACT

The Andes Mountains are considered a global biodiversity hotspot, where *Polylepis* forests are one of the most threatened forests in the area. We evaluate the *P. tarapacana* forest's distribution and cover and relate this pattern with topographic, climatic and geographic environmental factors at the landscape level. Along 93 plots, forest structure data was conducted according to their homogeneity, accessibility, and size (patches up to > 1 ha each). Hexagon binning processes were used to estimate the forest cover, as the proportion of hexagon area covered by forests, and one-way ANOVAs were conducted to evaluate its variation according to the environmental factors. Our results show that *P. tarapacana* forests are widely distributed, occupying a forest area of 8519.8 ha among 2462 forest patches and an average of 6.7% of forest cover (1296 hexagons - 129600 ha). According to the findings, the entire forest distribution encompasses a wide range of environmental conditions. We identify that the slopes and elevations were the main environmental drivers that shaped *P. tarapacana* distribution and cover. Variations in forest area and cover indicate a strong preference for north and east-facing slopes (18 and 24°) and intermediate elevations (4400 - 4500 m a.s.l), with a life zone of Tropical subalpine dry scrub accounting for 62.1%. Our research shows that remote sensing mapping and geographic information systems are effective methods for identifying habitat variables linked to threatened forest cover and evidence of forest vulnerability in the face of continuous global change.

1. Introduction

Mountain forests share multiple characteristics across different continents and climate zones. They are particularly suitable ecosystems for the development of transdisciplinary research approaches that support anticipatory and proactive policy responses for conservation (Körner, 1999). Mountains are characterized by steep environmental gradients (e.g. snow cover, thermal amplitude, solar radiation), which influence organisms developing spatial adaptations to survive and thrive (Rahbek et al., 2019; Marcora et al., 2021), as well as, in their spatial distribution (e.g. spatial discontinuities of plant communities) (Renison et al., 2013). In the face of rapid climate change, it becomes increasingly important to identify the set of environmental conditions associated with large forest areas and covers, to define key areas for conservation under predicted future conditions.

The Andes Mountains, a mountain formation extending from western Venezuela to Argentina, is considered a global biodiversity hotspot (Myers et al., 2000). In Andean high-altitude regions, climate changes are expected to be faster, increasing temperatures and sharply decreasing precipitation, creating uncertain conditions for the future of its ecosystems (Cuyckens et al., 2016). These changes can generate greater impacts on the distribution of species that are approaching their physiological tolerance (Díaz and Bradley, 1997; Cuyckens et al., 2016). This is the case of *Polylepis* (*Rosaceae*), an endemic arboreal genus that makes up the highest altitude forests in the world (Kessler and Schmidt-Lebuhn, 2006), but at the same time, is one of the most

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https://doi.org/10.1016/j.tfp.2022.100321
Received 24 May 2022; Received in revised form 16 August 2022; Accepted 17 August 2022

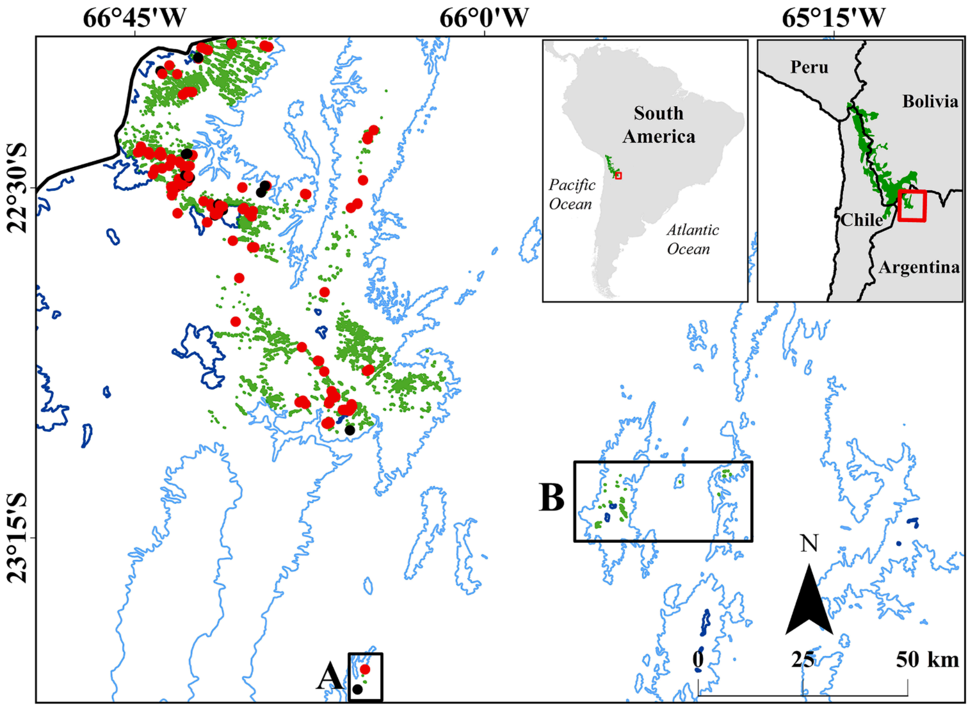


Fig. 1. Distribution of *Polylepis tarapacana* forests in the study area. Relic forests of the Susques sector (A) and the Mina Aguilar sector (B). The digitized contour of forests (green), line elevation at 4000 m a.s.l. (light blue) and at 5000 m a.s.l. (blue), false-positive control points (black points), positive control points (red points).

threatened in the Anthropocene (Kessler and Schmidt-Lebuhn, 2006). *Polylepis tarapacana* Phil., is a tree species that grows in the central Andes at an elevation between 4000 and 5200 m a.s.l. in the western section of the so-called Altiplano (16° - 23° S) (Braun, 1997; Navarro et al., 2010; Renison et al., 2013). This species is considered Near Threatened (IUCN 2020), due to human impact that mainly resulted in habitat degradation, caused especially by the extraction of wood for fuel and construction in the area (Renison et al., 2013). Remote sensing technology offers a practical and cost-effective way to study changes in land cover, especially over large areas (Langley et al., 2001; Nordberg and Evertson, 2003). Due to the potential ability to make systematic observations at different scales, remote sensing technology extends possible data repositories from the present to several decades ago. For this benefit, researchers have made enormous efforts to delineate land cover from a local scale to a global scale by applying remote sensing images (Xie et al., 2008).

In this context, species distribution and remote-sensing data are essential for monitoring dynamic processes (Eklundh and Jönsson, 2016) to create a precise distribution map to increase the available information on forest status, where a geographical information system allows map and prioritize sites for conservation (Huertas Herrera et al., 2020; Martinuzzi et al., 2021). The aim of this study is to evaluate the *P. tarapacana* forest status (distribution, cover and structure) and relate this pattern with topographic, climatic, geographic and vegetation factors at the landscape level. Specifically, we want to answer the following questions: (i) Which is the *P. tarapacana* forest cover across the Argentinean altiplano?; (ii) What are the optimal environmental conditions for the development of these forests?; and (iii) based on the previous answers, how environmental factors can explain the forest cover? This study might contribute to understanding the ecological drivers of high-altitude forest regions for biodiversity conservation and land planning.

2. Methods

2.1. Study area

The study was carried out in habitats associated with *P. tarapacana* forests, covering an area of 129600 ha, in the Andean mountains of northern Argentina (22°04′-23°40′ SL to 66°46′-65°49′ WL, Fig. 1). Low grasses and shrubs constitute the diverse landscapes of this area (Matteucci, 2012). Its vegetation combines species with traits linked to extremely low temperatures, wind, and xerophytism (Morello et al., 2012). In addition, to the occasional monospecific forest of *P. tarapacana*, dwarf shrubs and cushion plants that grow on plates adhering to the ground are common (Oyarzabal et al., 2018).

The climate is cold and dry with powerful winds, characterized by a reduced temperature seasonality, but a marked precipitation seasonality (Garreaud et al., 2003; Matteucci, 2012). Summer precipitation (December-February) represents more than 80% of the total annual precipitation of 100 to 500 mm (Garreaud et al., 2003; Vuille and Keimig, 2004). The mean temperature of the warmest month (January) is 13°C and the mean temperature of the coldest month is 3°C (Wawrzyk and Vilá, 2013; Cuyckens et al., 2016). The highest peaks have permanent snow, where 80-90% of the surface is bare, and the limit of vegetation is above 5000-5600 m a.s.l. (Matteucci, 2012).

2.2. Remote-sensing forest data

A supervised or semi-automatic classification was performed to determine the contour of the *P. tarapacana* forests, generating results with high error rates because of the low forest cover of these forests (10 to 20%), the small size of these trees (1 to 2 m), and the distance between individuals (average 5 m). The bare soil's spectral signature and accompanying vegetation are more significant than the forest itself. Because of this, high-resolution imagery was used as the base layer for manually digitizing the *P. tarapacana* woods.

Satellite images were used for digitizing *P. tarapacana* forests area, through visual interpretation of Bing Aerial Maps (Microsoft, USA) and Google Earth (Google, USA) high-resolution aerial imagery for the entire study area as a base layer. Using QGIS Software and interpreting satellite images, we obtained the polygons of the forest, where trees of *P. tarapacana* were distinguishable using a scale of 1:2500. In addition, the Kyoto Protocol's CDM defines a "forest" as an area with a minimum "tree" crown cover (CC) of 10 to 30 %, with a "tree" being a plant that can

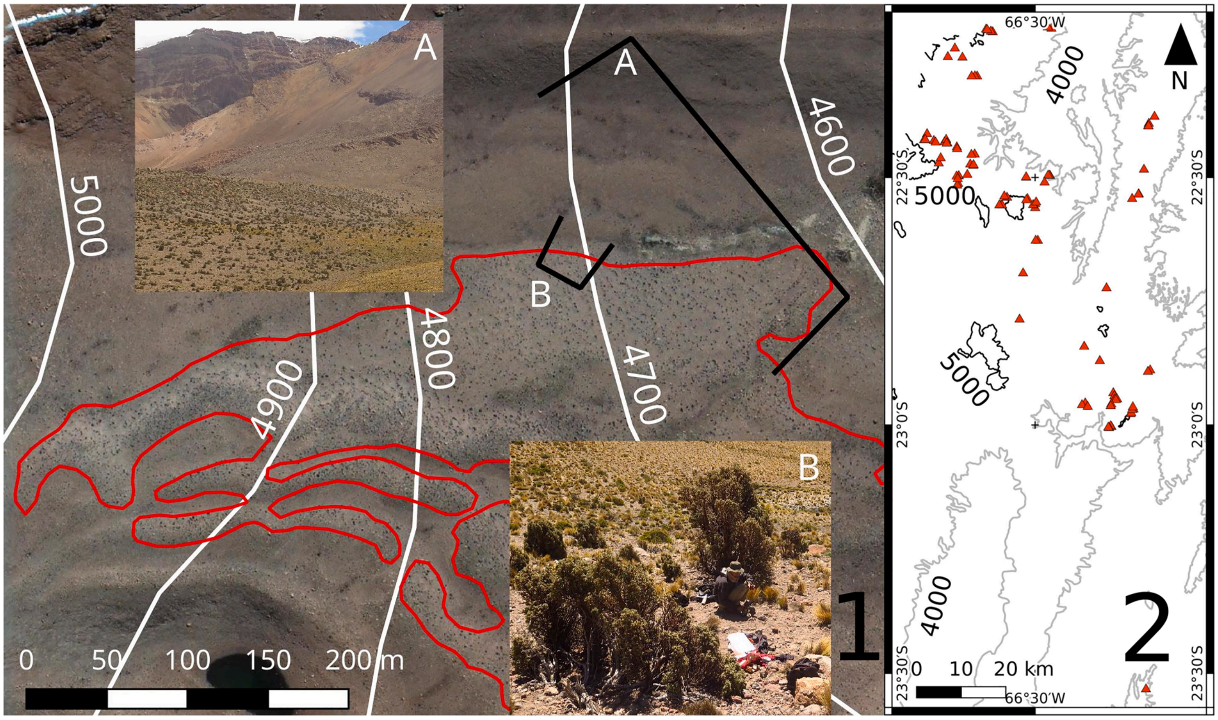


Fig. 2. (1) Example of digitization of the contour of *P. tarapacana* forests (red line) based on Bing Aerial Maps (Microsoft, USA) images at 1:2500 scale. White lines represent local elevation in m a.s.l., A = Photo taken from bracket «A», B = installation of forest structure plot (photos by J.M. Cellini). (2) Distribution of recently installed verification plots (red triangles) distribution in the Argentine portion of Altiplano.

reach a height of more than 2 to 5 meters (UNFCCC 2002). Because of this, a forest must have a CC of 10% and have trees closer together than 10 meters. We manually mapped these formations using this information. The total area of the polygons for the forest was used to determine the forest area (FA).

2.3. Geoprocessing and analyses of the environmental factors

The environmental factors (n = 8) consisted of topographic (elevation, slope, and two aspects), climatic (temperature, precipitation) and geographical and vegetation (Normalized Difference Vegetation Index-NDVI and life zones) datasets. The digital elevation model (DEM) produced by the Shuttle Radar Topography Mission (SRTM) was used to calculate the slope, the elevation and other topographic parameters that were analyzed (Farr and Kobrick, 2000). This data was collected from the Google Earth Engine website (https://earthengine.google.com/) (Google, USA). The slope was determined with Qgis 3.4′s DEM (Terrain Models) tool's Slope mode. The gradient's slope measured the elevation change rate expressed in degrees. The aspects were calculated as sine and cosine functions of the north magnetic direction, where sine values range from -1 (west) to 1 (east), while cosine values range from -1 (south) to 1 (north) (Jenness, 2004). The climatic factors included the annual mean temperature (AMT) (°C) and annual precipitation (AP) (mm.year^{-1}) for the period 1970-2000, which were taken from WorldClim (Fick and Hijmans, 2017). The geographic factor (Holdridge life zones, following Derguy et al. (2019)), was categorized as Tropical alpine moist tundra (TAMT), Tropical alpine wet tundra (TAWT), Tropical subalpine dry scrub (TSDS), and Tropical subalpine moist forest (TSMF). Finally, vegetation factor (NDVI data) was obtained from Application for Extracting and Exploring Analysis Ready Samples (AρρEEARS) (https://lpdaacsvc.cr.usgs.gov/appeears/). We used the intersection function in Qgis software to combine each digitized *P. tarapacana* forest with environmental factors.

The Hexagonal binning process aggregates individual data (in this study, pixel values) into hexagonal regions (Battersby et al., 2016). Then, these processes were used to estimate forest cover (as the proportion of hexagon area covered by forests) and to evaluate its variation (mean ± standard error) according to the environmental factors. For this, we created a grid of 1296 hexagons (each hexagon = 100 ha) that covered the entire study area. Five categories were defined for each environmental factor considering a minimum threshold of 25 hexagons to define a suitable sampling size for the statistical analyses.

2.4. Forest field data

A total of 93 *P. tarapacana* polygons of forest selected from a total of 2462 were selected throughout the distribution range according to (i) a homogeneous forest cover where the distance between individuals was constant; (ii) their accessibility and forest patch size (> 1 ha each). In the center of each patch, one measure plot (20 × 50 m) was established to describe the forest structure and to check the polygons of forest contour as field verification plots. In forest structure plots of all live trees >0.2 m height was characterized by measuring: (i) diameter at the base corresponding to the trunk or the tallest trunk of multi-stem trees (DBT - cm); (ii) dominant height (DH - cm) by averaging the height the three tallest trees per plot; (iii) Tree crown area using the diameter of the maximum axis and the axis at 90 degrees. These data allowed us to determine tree density (DEN) as the number of trees per hectare and crown cover (CC %) as the sum of the tree crowns area related to the area of the plot (for more information see López et al., 2021).

Moreover, we used this field data to construct a confusion matrix to calculate the error in mapping the forests based upon the differences between the marked visual survey, and the field verified forest locations (including false negatives and false positives) (Fig. 2).

2.5. Data analyses

Firstly, one-way ANOVA analyses using Statgraphics software (Statistical Graphics Corp., USA) were conducted to associate forest cover with the different environmental factors and were expressed as mean ± standard error. Secondly, we calculated forest cover deviations from the mean (x cover mean - x total cover mean) to visualize the variations of

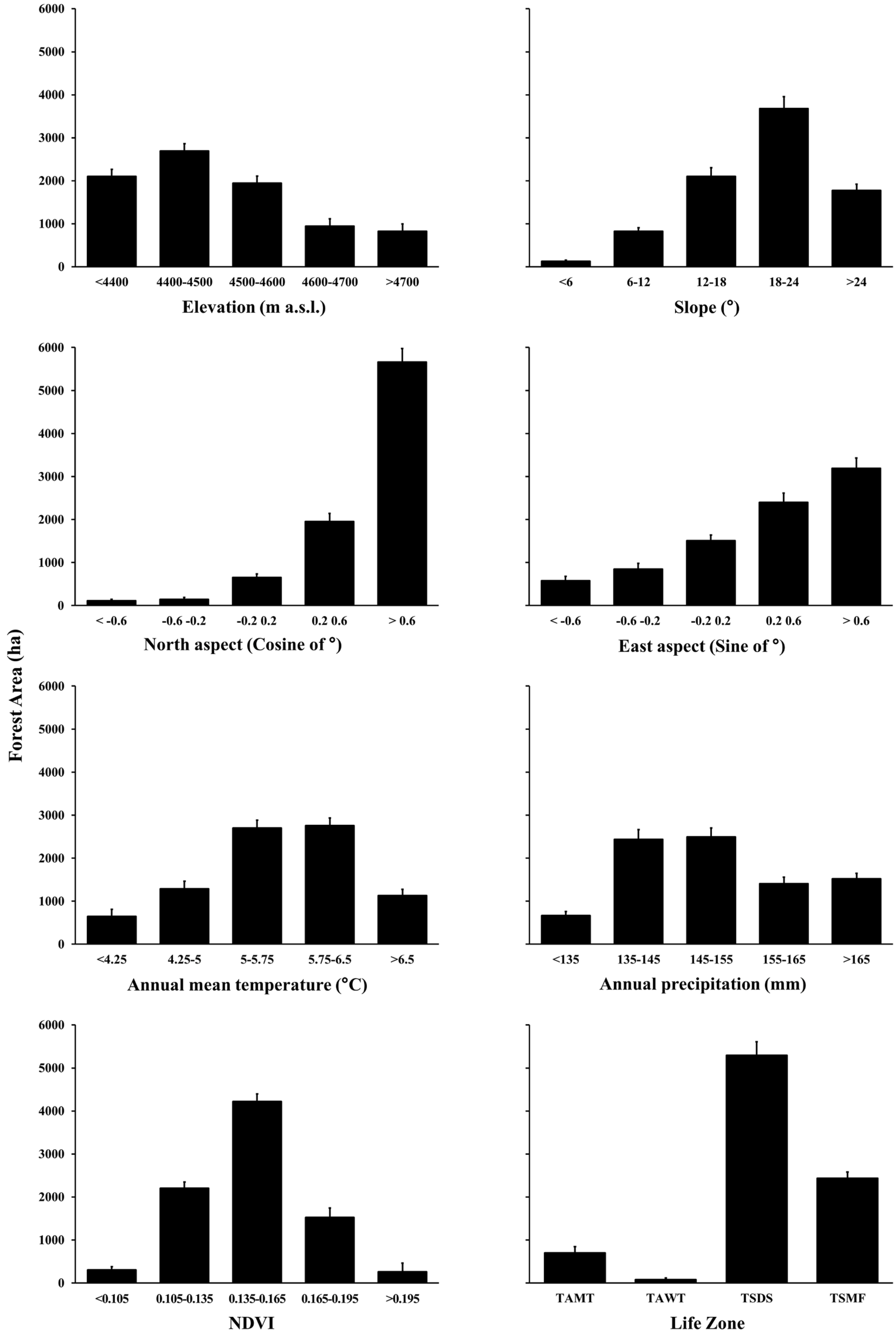


Fig. 3. Mean forest area (+ standard deviation) at different levels of each analyzed topographic, climatic, geographic and vegetation factors. The aspects were calculated as sine and cosine functions where sine values range from -1 (west) to 1 (east), while cosine values range from -1 (south) to 1 (north). Tropical alpine moist tundra (TAMT), Tropical alpine wet tundra (TAWT), Tropical subalpine dry scrub (TSDS), and Tropical subalpine moist forest (TSMF).

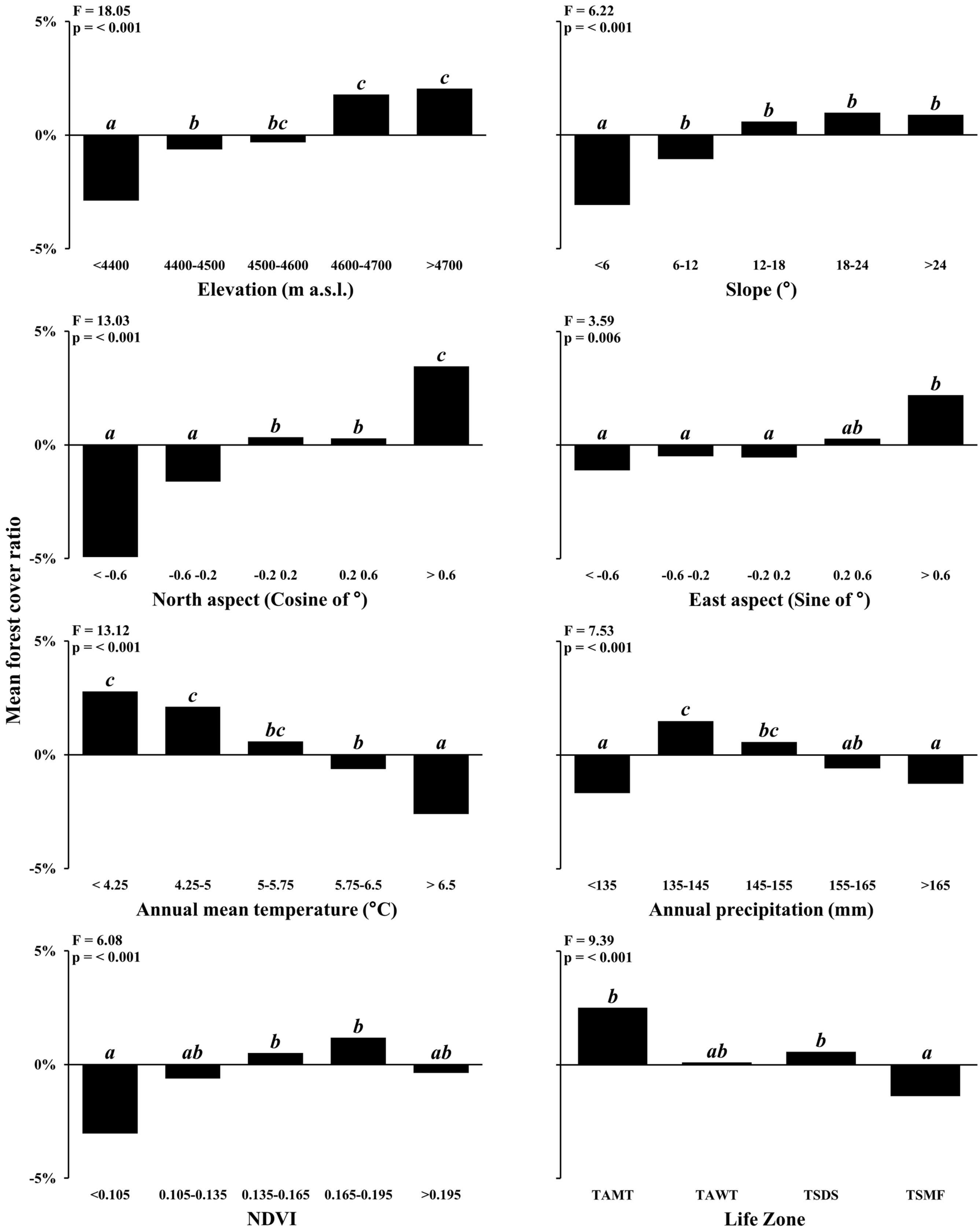


Fig. 4. ANOVAs for forest cover mean ratio (as the proportion of hexagon area covered by forests) comparing the analyzed topographic, climatic, geographic and vegetation factors. Different letters showed significant differences between levels (Tukey test at p <0.05). The aspects were calculated as sine and cosine functions, where sine values range from -1 (west) to 1 (east), while cosine values range from -1 (south) to 1 (north). Tropical alpine moist tundra (TAMT), Tropical alpine wet tundra (TAWT), Tropical subalpine dry scrub (TSDS), and Tropical subalpine moist forest (TSMF).

Table 1
One-way ANOVA for forest structure variables comparing the analyzed topographic, climatic, geographic and vegetation factors.

Source of variation		DBT	DH	DEN	CC
Elevation	<4400	5.9 a	107.2 a	1537	18.7
	>4400<4500	6.1 a	114.6 a	1115	9.1
	>4500<4600	7.8 ab	150.6 ab	1975	11.0
	>4600<4700	8.0 ab	142.3 ab	1501	10.3
	>4700	10.2 b	192.0 b	1953	13.5
F		5.04	6.72	1.57	1.88
p		0.001	<0.001	0.189	0.125
Slope	<6	9.6 ab	165.1 ab	873	6.0
	>6<12	8.8 b	161.6 ab	1132	10.3
	>12<18	9.1 b	161.2 b	1485	10.8
	>18<24	6.9 ab	137.1 ab	1791	14.6
	>24	6.0 a	115.7 a	1912	14.2
F		4.10	3.06	1.99	0.60
p		0.004	0.021	0.103	0.662
AMT	<4.25	10.8 c	208.6 b	1373	10.1 a
	>4.25<5	9.4 bc	165.7 ab	1921	15.7 ab
	>5<5.75	6.4 a	129.5 a	1609	9.4 a
	>5.75<6.5	6.6 ab	120.6 a	1636	10.9 a
	>6.5	6.9 ab	116.2 a	1586	24.1 b
F		5.56	6.84	0.29	4.04
p		<0.001	<0.001	0.885	0.006
AP	<135	7.5	142.2	1054	7.9
	>135<145	7.4	133.3	1989	15.6
	>145<155	7.3	136.4	1632	13.8
	>155<165	7.0	135.3	1705	10.8
	>165	8.6	164.2	1599	9.6
F		0.35	0.58	1.12	1.50
p		0.641	0.681	0.351	0.221
N aspect	<-0.6	-	-	-	-
	>-0.6<-0.2	5.3	99.7	1448	19.3
	>-0.2<0.2	6.2	145.5	1169	6.6
	>0.2<0.6	8.1	154.6	1449	11.5
	>0.6	7.5	136.2	1735	13.2
F		0.90	0.92	0.54	0.96
p		0.445	0.434	0.657	0.416
E aspect	<-0.6	7.8	142.1	1512	12.9 ab
	>-0.6<-0.2	7.2	135.2	2185	20.5 b
	>-0.2<0.2	6.6	122.5	1786	11.7 ab
	>0.2<0.6	7.7	143.8	1599	13.5 ab
	>0.6	7.9	151.2	1234	7.7 a
F		0.53	0.72	1.37	2.60
p		0.714	0.582	0.249	0.044
NDVI	<0.105	6.8	127.7	728	4.5
	>0.105<0.135	9.3	169.3	1466	10.6
	>0.135<0.165	6.9	130.5	1864	14.7
	>0.165<0.195	7.4	140.2	1426	12.9
	>0.195	6.9	136.9	1371	8.0
F		1.55	1.69	1.41	1.72
p		0.195	0.158	0.238	0.156
Life Zone	TAMT	11.0 b	201 b	1621	11.5
	TAWT	10.8 ab	217 ab	1367	10.0
	TSDS	6.7 a	127 a	1576	12.2
	TSMF	7.9 ab	139 a	1874	14.9
F		6.29	6.90	0.50	0.47
p		0.001	<0.001	0.685	0.701

DBT = diameter at the base of the tree in cm, DH = dominant height in cm, DEN = tree density in trees.hectare^{-1}, CC = crown cover in %, Elevation in m a.s.l., Slope in grades, AMT = Annual mean temperature, AP = Annual precipitation, aspect were calculated as sine and cosine functions, NDVI = Normalized Difference Vegetation Index and Life Zone: Tropical alpine moist tundra (TAMT), Tropical alpine wet tundra (TAWT), Tropical subalpine dry scrub (TSDS) and Tropical subalpine moist forest (TSMF). F = Fisher distribution value; p = significance. Different letters represent significant differences by Tukey test ($p < 0.05$).

each environmental factor at the landscape level, where negative values indicate that the value of forest cover (FC) in the analyzed range is lower than the average FC of the entire study area. For example, the average value of FC for the 1296 hexagons is 6.72%. If the value of an interval of a variable is 3.72% of FC, it results in a variation of -3.00%, and when the value is greater than the general average, it is a positive variation. In addition, one-way ANOVAs were conducted to test the differences in the following forest structure variables: (i) average diameter at the base of the tree (DBT); (ii) dominant height (DH); (iii) tree density (DEN) and crown cover (CC) considering the environmental factors and levels. In this way, two analysis scales are used in the present study, one at the landscape level using the hexagon binning processing (FC), and another where the forest structure is analyzed with the data from the plots. For all one-way ANOVA analysis data, normality and homoscedasticity were verified with the Shapiro-Wilk and Levene test, respectively, and we used the post-hoc Tukey test ($p < 0.05$) for further mean comparisons.

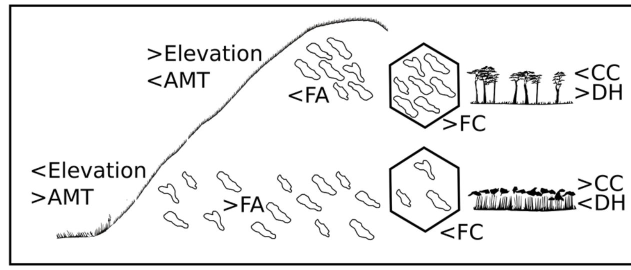


Fig. 5. Diagram of the forest area, forest cover and crown cover of *P. tarapacana* in an elevation and temperature gradient in the Argentine highlands. AMT = annual mean temperature, FA = forest area, FC = forest cover, CC = crown cover, DH = dominant height.

3. Results

A total of 8519.8 ha of the study area (1296 hexagons - 129600 ha) were occupied by *P. tarapaca* forest, where the highest presence was in the north and northwest of the Andes mountain range of Argentina, where two remnant sectors were observed (Fig. 1A, and 1B). A total of 2462 *P. tarapacana* forest polygons were manually identified, with a maximum area of 126.5 ha and an average of 3.4 ha. According to the hexagonal binning processes, the average percentage of FC in the study area was 6.7% (see forest cover map in Appendix A). As a result of the confusion matrix, we observed that the remote survey underestimated the detected forests by 8.7% (Fig. 2, Appendix B), where the main errors occurred at <4300 m a.s.l. (12.5%) mainly because of shrubs of *Baccharis* spp. and *Parastrephia* spp. present similarities in color, shape, and size with the *P. tarapacana* forests.

Manually identified polygons of *P. tarapacana* forests occupy a wide range of environmental conditions, with marked environmental preferences (Fig. 3 and Appendix C). Of a total of 8519.8 ha of forest area, it was found that 2694.3 ha (31.6%) are located at elevation values between 4400 and 4500 m a.s.l. Forest area decreased with elevation to 827.7 ha above 4700 m a.s.l. The largest areas of these forests (5657.1 ha - 66.4%) were found on the slopes facing north (315 and 45° azimuth) and on the eastern slopes (3194.9 ha - 37.5%). The forest area increased with the slope, where the highest area (3683.8 ha - 43.2%) was related to values between 18 and 24°, nevertheless, the forest area decreased in extreme slope values (1773.8 ha - >24°). The highest occupancy range was with annual mean temperature between 5 and 6.5°C (5459.2 ha - 64.1%), annual precipitation between 135 and 155 mm (4928.6 ha - 57.8%) and NDVI between 0.135 and 0.165 (4221.9 ha - 49.6%). The Tropical subalpine dry scrub (TSDS) (5294.1 ha - 62.1%) and Tropical subalpine moist forest (TSMF) (2439.0 ha - 28.6%) life zones were the most occupied, while Tropical alpine moist tundra (TAMT) (704.6 ha - 8.3%) and Tropical alpine wet tundra (TAWT) (82.1 ha - 1.0%) those with the least forest area.

FC showed notable changes across environmental conditions when topographical (Elevation, $F = 18.05$, $p < 0.001$; Slope, $F = 6.22$, $p < 0.001$; N aspect, $F = 6.08$, $p < 0.001$; E aspect, $F = 3.59$, $p < 0.001$),

climatic (AMT, F = 13.10, $p < 0.001$; AP, F = 7.53, $p < 0.001$), geographic (NDVI, F = 6.08, $p < 0.001$), and vegetation (Life Zone, F = 9.39, $p < 0.001$) factors were considered (Fig. 4). Considering elevation, areas below 4600 m a.s.l. presented lower FC (from -0.6 to -2.9%) than areas above >4600 m a.s.l. (+1.8 to +2.0%). Lower FC was observed on slopes <12° (-3.1%) than in areas with slopes greater than 12°, where the FC increased to a maximum of +0.9%. The north and east aspects showed higher FC at the highest level of this factor, with +3.5% and +2.2%, respectively. AMT showed greater FC at lower temperatures (<5.75°C, +2.8 to +0.6%) and less FC at higher temperatures (>5.75°C, -0.6 to -2.6%). Precipitation showed the lowest FC (-1.7%) both in arid zones with <135 $mm.year^{-1}$ and in zones with >155 $mm.year^{-1}$ (-0.5 to -1.2%). The highest FC was found for rainfall between 135 and 155 mm. $year^{-1}$, with a value of +1.5%. Lower FC (-0.4 to -3.0%) was found in the lowest (0.135) and highest (>0.195) NDVI values and higher FC (+0.5 to +1.2%) was found in intermediate NDVI values. For life zones, higher FC was found in Tropical alpine moist tundra (TAMT) (+2.5%) and Tropical subalpine dry scrub (TSDS) (+0.6%) and lower FC in the Tropical subalpine moist forest (TSMF) (-1.4%) and Tropical alpine wet tundra (TAWT).

The forest structure variables showed DBT of 7.4 ± 3.4 cm and DH of 139.1 ± 58.7 cm (mean ± SD), as well as a wide range in DEN and CC that point to the low occupation (1631.5 ± 1321.8 $trees.ha^{-1}$ and 11.9 ± 10.5%, respectively). Table 1 shows that topographic, climatic, geographic and vegetation factors affect forest structure variables, with significant changes in DBT, DH, DEN, and CC with elevation, slope, AMT, and Life Zone.

Higher elevations, on the other hand, had trees that doubled in size. Similarly, there is an inverse relationship between size and slope (DBT: F = 4.10 $p = 0.004$; DH: F = 3.06 $p = 0.021$). For temperature, DBT and dominant height are inversely associated, with small trees growing in environments with higher AMT. As a result, the size has exhibited significant differences among Life Zones, with larger trees in the alpine Life Zone (TAMT and TAWT) and smaller trees in the subalpine (TSMF and TSDS). The alpine life zones, being found at a higher elevation than the subalpine zones, corroborate the change in forest structure observed in the elevation variable. The rest of the environmental variables did not show significant differences in the size of the individuals.

There were no significant differences in tree density (DEN - $ind.ha^{-1}$) among the analyzed factors. The evidence suggests that the different topographic, climatic and geographic factors show significant local variability in the studied levels and treatments. However, crown cover showed significant differences in some temperature (AMT) and topographic (E aspect) variables across the different studied treatments (Table 1). In regions with greater AMT (>6.5°C), we discover that the crown cover is higher. Moreover, crown covers are opposite related to East aspects, being the crown cover more closed in West aspects.

4. Discussion

In the high Andes, *Polylepis tarapacana* forests have spread over large areas. According to previous research, these forests occur as isolated patches at high elevations in environments that are generally dominated by shrubs or grasslands (Kessler, 2002; Toivonen et al., 2018). Topographic variables, as well as water availability and the edaphic substrate, all contribute to a varied mosaic of habitats and microenvironments (Matteucci, 2012). Previous research has found that different *Polylepis* species respond differently to the elevation gradient, with noticeable differences in their upper altitudinal limits (Macek et al., 2009). The disjunct distribution of *P. tarapacana* forests, on the other hand, has long been thought to be a natural occurrence caused by micro suitable areas implanted in the landscape, which are distinguished primarily by temperature and precipitation regimes, soil texture, and hydrological conditions (Kessler, 2002; Pinos, 2020). However we showed that *P. tarapacana* has a low FC and a "random" distribution for some environmental factors.

P. tarapacana occupies a wide variety of environmental conditions but has clear preferences. For example, we discovered that *P. tarapacana* FC was highest on slopes facing north and east (315 and 45° azimuth), as has also been seen in northern Chile (Choque, 2010; Saavedra, 2013) and the Sajama volcano in Bolivia (Hoch and Körner, 2005). Because they receive long periods of sunlight, these are the warmest exposures (Garreaud et al., 2003). Low temperatures at high-elevation treelines establish important constraints to tree growth, according to worldwide measurements (Hoch and Körner, 2005; Toivonen et al., 2018). Moreover, these data support that *P. tarapacana* forests are restricted to rocky slopes and rock edges, which can be attributed in part to human influence and in part to the rare formation of suitable microhabitats (Simpson, 1986; López et al., 2021). Toivonen et al. (2018) showed that the distribution of *Polylepis* forests appeared to be the result of numerous environmental and anthropogenic restrictions at low elevations, with the role of the environment increasing stronger towards high elevations.

We discovered that the largest forest area is found at low to intermediate elevations (4400-4500 m a.s.l.) when temperatures are high to moderate (5 to 6.5°C) and rainfall is moderate (135-155 mm). In turn, under these circumstances, we find a negative FC, below the average FC of all the hexagons under study. These findings demonstrate that forests of *P. tarapacana* are widely dispersed in the landscape at low altitudes and are concentrated in regions with steep slopes and north or east exposures (Fig. 5). Compared to forests at higher elevations, the forest structure generally features smaller trees and a higher crown cover. This response could be the result of the combined effect of the decrease in temperature and the increase in precipitation as elevation increases (Luebert and Gajardo, 2005). The intermediate zones of the altitudinal gradient exhibit the greatest structural development of the vegetation due to their moderate thermal and umbric conditions (Luebert and Gajardo, 2005), whereas the vegetation of the higher zones are constrained by temperature decreases (Hoch and Körner, 2005; Macek et al., 2009).

The slopes where this species develops are considered moderate to steep (Saavedra, 2013), because such landscapes provide safe sites suitable for regeneration (e.g. rocky slopes and rock edges). These considerations are consistent with those of López et al. (2021), who found that the highest moisture concentration is found in the soil in sites under the influence of rocks, which improves germination, growth and seed survival, especially in environments where surface desiccation can be a significant factor (Jumpponen et al., 1999). We observe that the highest occupation and highest DEN were found in the TSDS and TAMT zones, which can be explained because these zones include low temperatures and intermediate precipitation values, optimal factors for the development of this species. The intermediate NDVI values found in this study are optimal for *P. tarapacana* development; one probable explanation is that high levels suggest intensive competition with the understory or surrounding wetlands, while low values indicate drier conditions. Another possibility is that distinct amounts of water stress exist, particularly near the treeline (Macek et al., 2009).

The elevation gradient for *P. tarapacana* forests for Argentina was studied by Peng et al. (2015) where the observed range was from 4302 to 4942 m a.s.l., and Renison et al. (2013) modeled the potential distribution of these forests, resulting in a range of 4000 to 5000 m a.s.l. The results of our study partially coincide with the previous authors, showing a distribution of *P. tarapacana* forests from 4152 to 5010 m a.s.l., and a range of 4160 to 4952 m a.s.l. for field verification plots. The tree heights varied greatly, as in prior studies of *P. tarapacana* forest structure (Rios, 1998; Saavedra, 2013). The results of this study contrast with those observed by Hoch and Körner (2005), where the height of adult trees (>1 m high) decreased significantly from the lowest to the uppermost site, while there was no significant change in average stem diameter with elevation. Low temperatures impact the size of trees, where they experience a reduction in height with elevation (Körner, 1999; Paulsen et al., 2000). *P. tarapacana* forests experience this reduction in height (Hoch and Körner, 2005; Domic and Capriles, 2009), where a drastic reduction in size is observed at higher altitudes. Altitude

also produces changes in population structure, with shrubs commonly found within forest patches but increasing in frequency at tree line limits. In these settings, shrublands may become a successful adaptation allowing populations to persist (Renison et al., 2006). This difference with the results of this study could be related to the use and access of these forests since forests at lower altitudes would be the most accessible for the communities, cutting larger trees (Rios, 1998). Likewise, the slope had an inverse effect on forest structure variables, particularly tree height and base, as observed by Ríos (1998), Saavedra (2013), and López et al. (2021). The increase in temperature had a clear link with the FC, indicating the presence of individuals with a larger surface area and more often as the temperature increases.

Water availability and temperature have opposing effects on *P. tarapacana* growth in the southern, drier regions of the Altiplano (Argollo et al., 2004; Morales et al., 2004; Christie et al., 2009; Rodriguez-Caton et al., 2021), demonstrating the complexity of the climate-controlling tree growth in these forests. The availability of water in the area may also impact tree growth, according to Rodriguez-Caton et al. (2021). According to an ecophysiological study conducted in the Chilean Altiplano, this tree species' photosynthetic processes and carbon assimilation are well adapted to withstand cold temperatures (García-Plazaola et al., 2015), enabling them to flourish at elevations higher than 4700 m a.s.l.

Increased water stress and a reduction in summer rainfall (Minvielle and Garreaud, 2011; Neukom et al., 2015), together with increased temperature (Urban, 2015), is expected in the Altiplano for the next decades (Cox et al., 2000; Macek et al., 2009), which could result in a decrease in available habitats (Macek et al., 2009; Cuyckens et al., 2016). According to Toivonen et al. (2018), trees grow at low air and soil temperatures near the treeline, indicating that temperatures play a role in limiting forest growth at high elevations. In this context, projected climatic changes may lower forest areas and cover in the short term, resulting in a reduction in the optimum elevation. In addition, according to Peng et al. (2015), this austral cluster of *P. tarapacana* forests is a reservoir of genetic diversity, essential for providing critical ecological functions in a vulnerable environment, as well as a variety of environmental goods and services, including hydrological regulation, soil protection, biodiversity conservation (Segovia-Salcedo et al., 2021), and carbon capture (Cranford and Mourato, 2011; Pinos, 2020), as well as, harbor for endemic biota (Fjeldså and Kessler, 2004).

5. Conclusions

Our results reveal that *P. tarapacana* forests are linked to specific environmental conditions, where forest cover increases drastically with intermediate elevations (4400 - 4500 m a.s.l) and slopes (18 and 24°), but decreases as temperature and precipitation rise, especially in their southernmost distribution. The analyses of species distribution and optimal environmental drivers of specific forest species, such as *P. tarapacana*, allowed us to identify probable losses or setbacks caused by climate change's impact on high-mountain environments. Further, remote sensing mapping is a useful technique for studies on forest vulnerability. This tool, therefore, remains critical to identify the threatened native forests, which is important to counteract the adverse effects of climate change through conservation. In future studies (e.g. management and/or control strategies), distribution data (map of forest area or forest cover) and defined habitat requirements for *P. tarapacana* (e.g. optimal conditions) can be used to develop mitigation strategies to conserve the species.

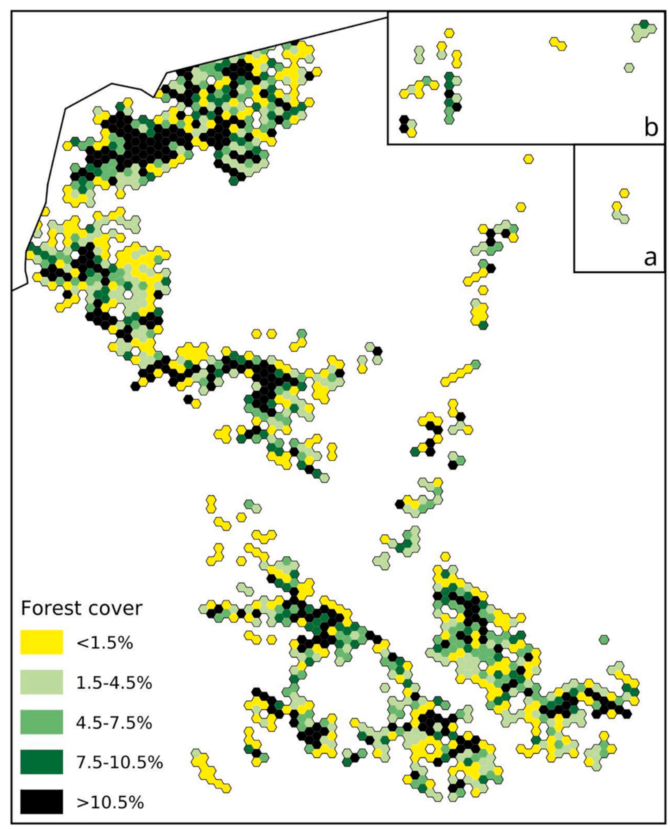
Declaration of Competing Interest

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.

Acknowledgements

We thank the residents of Altiplano for their availability to share their knowledge about the *P. tarapacana* forest and for permission to research within their lands. The authors gratefully thank all those graduates of the National University of La Plata, of the Biology and Forest Engineering majors, who from 2018 to the present participated in the field trips where we shared mutual learning and discussion in different places in the provinces of Jujuy and Salta. We are grateful to Karin Schrieber for assisting with the English editing and for helpful comments on the manuscript. We also want to thank Guillermo Martinez Pastur, for his contributions and advice for the realization of this research. This research is part of the doctoral thesis of Victoria Lien López "Regeneration dynamics, vertical and horizontal structure in *Polylepis tarapacana* Philippi forests in different environmental gradients" (Facultad de Ciencias Agrarias y Forestales, Universidad Nacional de La Plata).

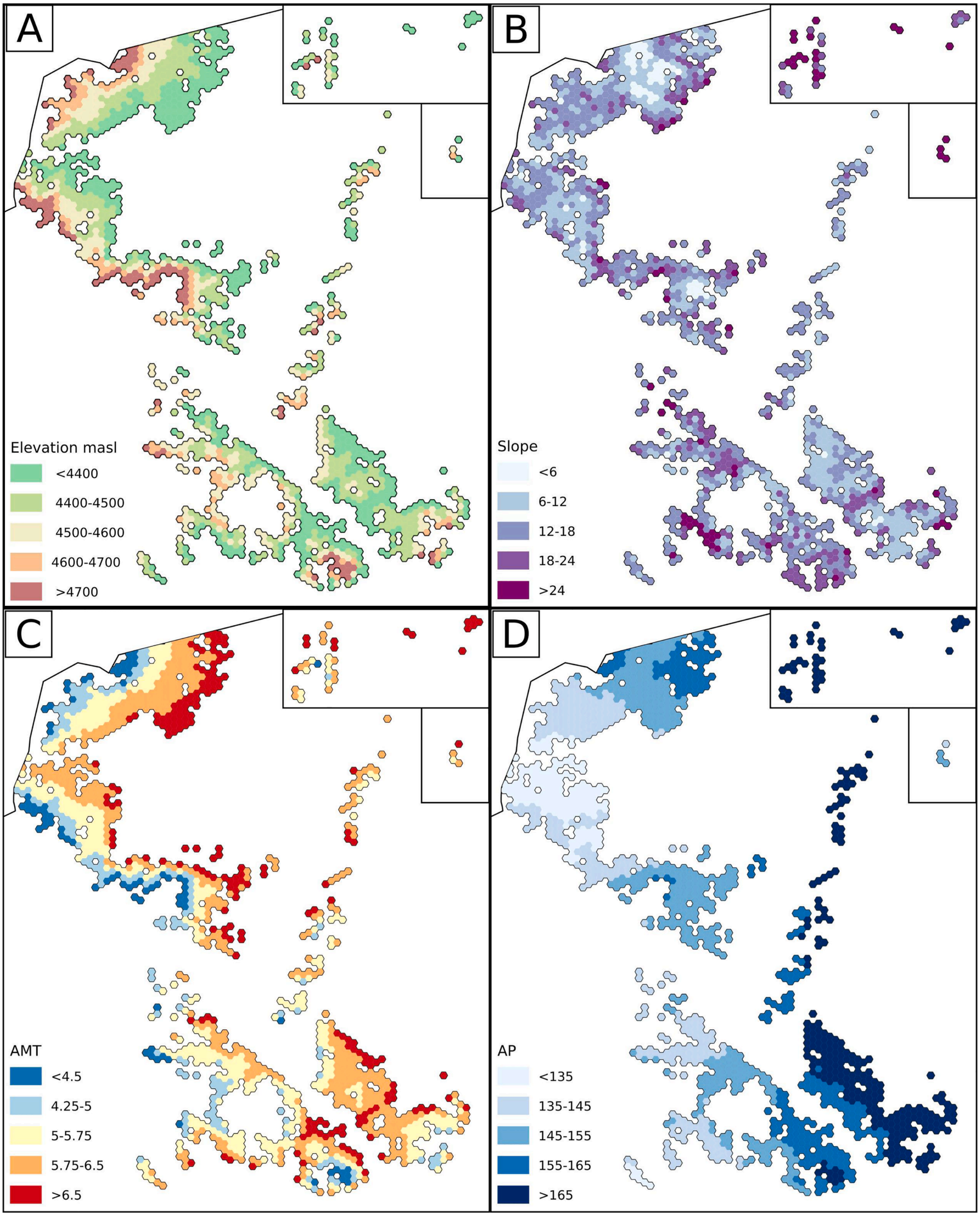
Appendix



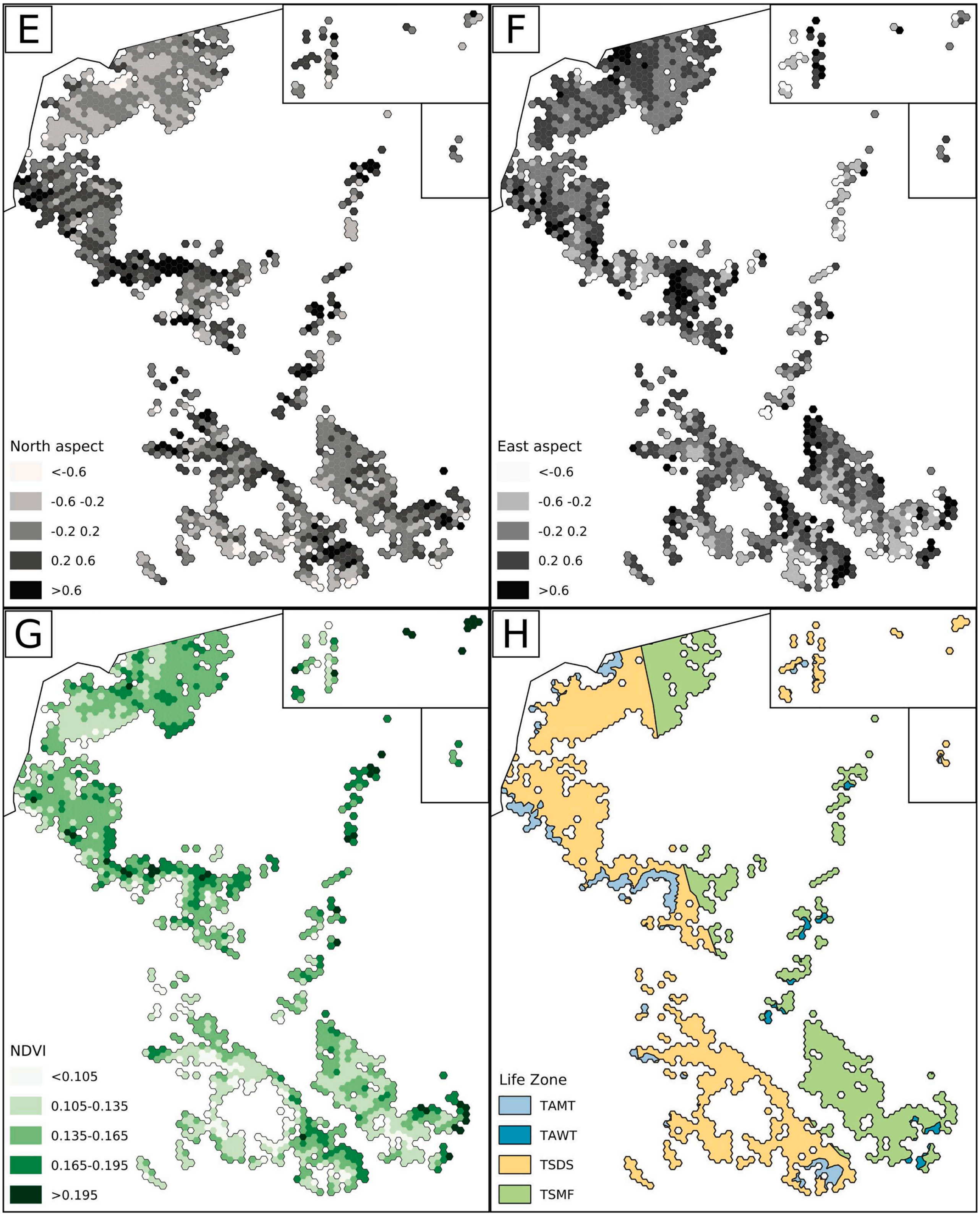
Appendix A. *Polylepis tarapacana* forest cover (as the proportion of hexagon area covered by forests). Each hexagon has 1 km^2 of area. a: Susques area forest sector, b: Mina Aguilar forest sector.

Appendix B
Confusion matrix for the calculated error in forest area based upon the differences between the marked visual survey and the field verified *Polylepis tarapacana* forest location. Where: FVP: Field verification plots Installed for this study, error: plots inside a visual survey of forest area / total points.

Elevation (m a.s.l.)	FVP	error FVP
<4300	3	12.5%
>4300<4500	35	12.0%
>4500<4700	38	6.2%
>4700	17	7.1%
Total	93	8.7%



Appendix C. Distribution of the analyzed topographic (A, B, E, F), climatic (C, D), geographic (H) and vegetation (G) factors on the *Polylepis tarapacana* forest distribution. (A) Elevation in m a.s.l. and (B) Slope in grades were obtained from https://earthengine.google.com/. (C) Annual mean temperature (AMT) and (D) Annual precipitation (AP) were taken from WorldClim (Fick and Hijmans, 2017). (E) North aspect and (F) East aspect were obtained from https://earthengine.google.com/, and were calculated as sine and cosine functions following Jenness (2004). (G) NDVI data were obtained from https://lpdaacsvc.cr.usgs.gov/appeears/. (H) Holdridge life zones were obtained from Derguy et al. (2019), which were categorized as Tropical alpine moist tundra (TAMT), Tropical alpine wet tundra (TAWT), Tropical subalpine dry scrub (TSDS), and Tropical subalpine moist forest (TSMF).



Appendix C. (*continued*).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2022.100321.

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