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A Height Threshold Redefines Functional Communities: Structural Transition Between Shrublands and Alpine Forests of *Polylepis tarapacana* in the Argentine Altiplano

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Abstract. The high-Andean forests of *Polylepis tarapacana* at the global treeline form a structural continuum between shrublands and forests, complicating their functional classification. This study evaluates whether a discrete height threshold – Mean Dominant Height ≥ 2 m – defines a genuine ecological transition between these formations in the Argentine Altiplano, aiming to validate this threshold, identify its predictors, and assess its consequences for the ground-layer vegetation. Ninety-six forest inventory plots were analyzed and classified as “Forest” (mean dominant height ≥ 2 m) or “Shrubland” (mean dominant height < 2 m). Structural variables (basal area, density, diameter distribution), proportions of life forms (arborescent, dwarf tree, shrub, *brousse tigrée*), allometric parameters, and ground cover composition were compared. Analyses included Principal Component

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Analysis, non-parametric tests, logistic regression models, and indicator species analysis. The 2 m threshold discriminated two clearly distinct communities. “Forests” (19.4 % of plots) exhibited greater basal area (2.8 times higher), diameter diversity, structural complexity, and a higher proportion of arborescent life forms. They showed a more efficient height-diameter relationship and a distinctive ground cover with greater cover of cushion plants and specialist indicator species (e.g., *Senecio nutans*). “Shrublands” were dominated by juvenile individuals, shrubby forms, and heliophytic perennial shrubs. The probability of achieving a forest state was positively predicted by the presence of arborescent forms and a favorable substrate (Favorable Substrate Index). The mean dominant height ≥ 2 m threshold constitutes a quantifiable ecological tipping point separating distinct successional and functional states in *Polylepis tarapacana*. This structural criterion synthesizes profound changes in community architecture, microclimate, and associated biotic assemblages. The findings provide a robust framework for the operational classification, monitoring, and priority conservation of these vulnerable alpine ecosystems, moving beyond purely morphological definitions towards a characterization based on ecological functionality.

Keywords: *Polylepis tarapacana*, treeline, structural threshold, mean dominant height, high-Andean forests, functional classification, alpine ecosystems, Argentine Altiplano

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Научная статья

Порог высоты как структурный переход между кустарниковыми зарослями и альпийскими лесами *Polylepis tarapacana* на плато Альтиплано в Аргентине

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Аннотация. Высокогорные леса *Polylepis tarapacana* в Андах образуют структурный переход по верхней границе своего распространения от кустарниковых формаций до сомкнутых древостоев, что затрудняет их однозначную функциональную классификацию. Цель работы заключалась в оценке дискретного порога по средней доминантной высоте (≥2 м) как критерия, определяющего экологический переход между кустарниковыми и лесными сообществами *P. tarapacana* на плато Альтиплано в Аргентине, для его валидации, выявления предикторов и оценки влияния на состав подлеска. На основе данных сплошной таксации 96 пробных площадей (от 25 до 4000 м²) насаждения распределены по следующим типам: лес (средняя доминантная высота ≥ 2 м) и кустарниковые заросли (средняя доминантная высота < 2 м). Проведен анализ и сравнение структурных показателей (средний диаметр у шейки корня, площадь сечения, густота, распределение по ступеням толщины), состава жизненных форм (древовидная, стланиковая, кустарниковая, тигровый буш *brousse tigrée*), аллометрических показателей (высоты и диаметра) и состава живого напочвенного покрова. Использованы метод главных компонент (PCA), непараметрические критерии (Манна–Уитни, Уилкоксона), логистическая регрессия и анализ индикаторных видов (IndVal). Установленный порог средней доминантной высоты 2 м позволяет четко разграничить 2 типа сообществ с различной структурой, таксационными показателями и флористическим составом. Для леса характерны большая площадь сечения (в 2,8 раза выше), разнообразие диаметров и структурная сложность, а также большая доля древовидных жизненных форм. Аллометрическая модель показывает более эффективное соотношение высоты и диаметра. Напочвенный покров лесов имеет в составе значительную долю подушкообразных растений, и встречаются виды-индикаторы, строго связанные с этим типом (например, *Senecio nutans*). В кустарниковых зарослях доминируют ювенильные особи и кустарниковые жизненные формы, а в подлеске – многолетние светолюбивые кустарники. Вероятность отнесения участка к лесу прямо связана с наличием древовидных форм и благоприятными условиями субстрата (высокий индекс его пригодности). Пороговая средняя доминантная высота является количественно определяемым и экологически значимым показателем, разделяющим различные сукцессионные стадии и функциональные состояния в сообществах *P. tarapacana*. Этот структурный показатель интегрирует кардинальные изменения в пространственной структуре древостоя, микроклимате и ассоциированных биоценозах. Полученные результаты формируют научную основу для классификации, мониторинга и приоритетной охраны этих уязвимых высокогорных экосистем, предлагая переход от морфологических описаний к критериям, отражающим экологическую функциональность.

Ключевые слова: *Polylepis tarapacana*, верхняя граница леса, структурный переход, средняя доминантная высота, высокогорные леса Анд, функциональная классификация, альпийские экосистемы, плато Альтиплано в Аргентине

Благодарности: Благодарим исследователей, которые на протяжении многих лет ставили под сомнение правомерность использования термина «лес» для обозначения сообществ *Polylepis tarapacana*, отдавая предпочтение таким терминам, как «лесные заросли» или «кустарниковые заросли». Их стойкий скептицизм подтолкнул нас к написанию данной работы, а их критическое отношение к вопросу способствовало улучшению ее качества. Также выражаем признательность системе государственных, бесплатных и совместно управляемых университетов Аргентины. Мы смогли опубликовать эту работу за счет слаженной и плодотворной работы нашего коллектива, несмотря на сокращение финансирования и непростые времена. Публикация данного исследования доказывает, что ученые из государственных университетов не бросают дело на полпути.

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Introduction

Alpine and treeline ecosystems are among the most sensitive to climate change, serving as key indicators of environmental shifts [30] – a concept also widely studied in the boreal and mountain ecosystems of Eurasia [21]. In the Andes, trees and shrubs of the genus *Polylepis* reach some of the highest elevations on Earth. Notably, *Polylepis tarapacana* Phil. forms woodlands up to 5200 m above sea level [3]. These ecosystems are subjected not only to extreme conditions of temperature, radiation, and water availability [11, 23] but also exhibit high phenotypic plasticity. This plasticity is expressed as a continuum of life forms, ranging from multi-stemmed shrubs to single-stemmed trees [26]. Such structural variability complicates the ecological distinction between what constitutes a “Shrubland” and a “Forest” – a critical distinction for understanding ecosystem service provision, carbon storage, and the conservation of associated biodiversity in these vulnerable environments.

The definition of “forest” is not universal; it varies across institutional and scientific frameworks. In Argentina, for example, Native Forest Law 26331/07 defines native forests in terms of natural forest ecosystems predominantly composed of mature native tree species but does not establish explicit minimum height thresholds [32]. At the international level, instruments such as the Kyoto Protocol and the UNFCCC [45] define a forest as an area with a minimum canopy cover of 10–30 % and trees capable of reaching heights of more than 2–5 m, thereby recognizing the importance of quantifiable structural thresholds for classification and monitoring. This definitional flexibility highlights the need for contextualized criteria that capture the true ecological functionality of woody formations, especially in extreme environments like the Altiplano. The literature on native forests in Argentina has emphasized the ambiguity of current definitions and their implications for management and monitoring [32]. It has been noted that definitions based solely on structural aspects, such as cover and height, may overlook functional and landscape components, which is particularly relevant in high-mountain ecosystems where connectivity and microclimate are critical determinants.

Previous studies in the region have laid the groundwork for understanding the determinants of *P. tarapacana* structure. On one hand, López et al. [26] characterized the diversity of life forms (arborescent, dwarf tree, shrub, and *brousse tigrée*) and demonstrated that their distribution responds to topographic and climatic gradients. On the other hand, López et al. [30] evaluated the influence of topography and substrate on structural variables such as dominant height, canopy cover, and density, revealing that the more developed communities are associated with higher elevations and mixed substrates of bare soil and vegetation. However, structure has not been addressed as a continuum, nor has it been explored whether discrete thresholds exist that separate communities with differentiated ecological functioning.

Defining when an assemblage of *P. tarapacana* individuals constitutes a functional forest, beyond its morphological designation, has profound ecological and management implications. A height threshold, such as a Mean Dominant Height (MDH) ≥ 2 m, could act as a tipping point from which changes in canopy architecture substantially modify the microclimate, soil properties, and associated biotic assemblages [16, 20]. This approach aligns with proposals highlighting the need to include patch size, connectivity, and landscape composition thresholds in forest definitions to capture their integral ecological functionality [32]. The marked preference of *P. tarapacana* for specific elevations [29] and its association with moisture-retaining rocky microsites [28] suggest that local abiotic conditions are fundamental for achieving a forest structure. Key questions thus arise: (*i*) Does this threshold discriminate between communities with significant differences in life-form composition, population structure, and ground cover assemblage attributes? (*ii*) Which abiotic and biotic factors predict the likelihood of a site reaching this “forest” state? (*iii*) Is there a specialized ground-layer assemblage associated with this structural threshold?

The objective of this study is to assess whether the MDH (≥ 2 m) threshold defines a transition in the structure, diversity, and environment of *P. tarapacana* communities. This assessment aims to discriminate between shrub and forest formations with distinct environmental, structural, and compositional properties at the treeline elevation of the Argentine Altiplano, with the purpose of: 1) validating the structural threshold, 2) identifying its predictors, and 3) evaluating its ecological consequences for the associated plant assemblage.

This study had three specific objectives. First, to validate whether classification based on the MDH > 2 m threshold captures differences in structure and life forms beyond previously described topographic gradients (H1: Forest plots (MDH ≥ 2 m) will exhibit a higher proportion of arborescent (Ar) life forms, greater basal area, different diameter distribution, and greater vertical complexity than shrubland plots (MDH < 2 m), independently of elevation and slope). Second, to identify the abiotic (topography, substrate) and biotic (life form composition) factors predicting the likelihood of a site reaching the forest state (H2: This probability will be positively determined by a higher proportion of Ar and dwarf tree (Dt) life forms and a favorable substrate (high Favorable Substrate Index – FSI), with a secondary negative effect of slope). Third, to evaluate the ecological consequences of the structural threshold on the ground-layer vegetation (H3: Forest sites will host a ground layer with greater species richness, a distinctive floristic composition (higher proportion of perennial herbs and cushion plants), and lower grass cover compared to shrublands, where heliophytic perennial shrubs will dominate).

Research Objects and Methods

Study Area and Data. The study was conducted in the Argentine Altiplano (22°04′–23°40′ S; 66°46′–65°49′ W), the southern distribution limit of *P. tarapacana*.

We worked with an integrated dataset of 96 complete forest inventory plots (25–4000 m^2) from previous studies [30]. In each plot, we measured the diameter at the base (DAB, cm), defined as the stem diameter measured at 10 cm above ground level, following standard protocols for shrub and multi-stemmed tree measurements in high-Andean ecosystems [30], total height (H, m), and classified each individual into a life form following the typology of López et al. [26]: Ar, Dt, shrub (Sh), or *brousse tigrée* (Bt). Topographic and substrate variables were also recorded: elevation (m a.s.l.) and slope (degrees). Substrate cover was quantified in 100 subplots of 1 m^2, categorizing: 1) Monocotyledons (MONO) – species of the Poaceae family; 2) Dicotyledons (DICO) – dicotyledons ground-layer vegetation; 3) Litter (L) – surface plant residues; 4) Bare Soil (BS) – open soil, organic or mineral, earthy or sandy surfaces not covered by vegetation; 5) Rock (R) – bedrock outcrops fixed to the soil; 6) Scree (S) – loose stones of various sizes deposited on the surface or semi-fixed; grain size always larger than the sand fraction; 7) Rock Edge (RE) – influence zone between rocks and the surrounding soil or scree; and 8) Soil under Rock Protection (SRP) – area shaded by overlying rocks. This resulted in two categories of microsites characterized by plant types and six by substrate types [28].

Ground-layer vegetation data (including herbaceous plants, cushion plants, and low shrubs) were obtained from species and functional group cover, using the Ramsay & Oxley [34] classification adapted for GLORIA-Andes [5]: perennial shrubs, cushion plants, perennial herbs, annual herbs, and perennial subshrubs. Within each plot, a 50 m transect was established, and vegetation cover was recorded using the point-intercept method at 1 m intervals (50 points per transect) [27]. This procedure was repeated across all 96 plots to ensure consistent sampling of ground-layer vegetation.

Classification and Derived Variables. The main response variable was created using a discrete structural threshold, classifying plots as “Forest” (MDH $\geq$ 2 m) and “Shrubland” (MDH < 2 m). The following variables were calculated: 1) DAB: Mean DAB (cm) of individuals per plot; 2) GiniDAB: Gini index for inequality [15] in diameter distribution (0 = all trees have the same DAB; 1 = maximum inequality); 3) ShannonDAB: Shannon index of diametric diversity [37], based on 5 cm classes (0 = all trees in a single class; high values = greater size/age diversity); 4) Density (DEN, stems/ha); 5) Basal area (BA, m^2/ha), measured from the DAB of all live individuals $\geq$0.05 m tall [30]; 6) GiniBA: Gini index for inequality in BA distribution (0-1), expressing BA inequality among individuals; high values indicate dominance by few large trees; 7) HT: Mean height (m) of individuals; 8) MDH (m) as the average H of the three tallest individuals; 9) DAB/HT index: Diameter-to-height relationship, calculated using Spearman’s correlation coefficient [42]; values close to 1 indicate a strong positive relationship (greater diameter with greater height); 10) Canopy cover (CC, %); 11) ShCoverI (%): Proportion of individuals with H < 1.3 m relative to the total; 12) SCI: Structural Complexity Index calculated as the ShannonDAB combined with total BA [43]; 13) FSI: Index calculated as the sum of RE and SRP; 14) Life Form Diversity Index: Simpson’s index [39] calculated from the proportions of Ar, Dt, Sh, and Bt.

Statistical Analyses. To validate the 2 m MDH threshold separating forests and shrublands, we used non-parametric t-tests (Wilcoxon-Mann-Whitney) [31] and ANOVAs to compare structural variables (BA, DEN, cover) and life form proportions between the two types.

A Principal Component Analysis (PCA) with variable scaling was performed using seven variables previously identified to differentiate *Polylepis* communities [30]: ShCoverI, BA, CC, FSI, elevation, slope, and DEN. MDH was excluded from the PCA as it was the classification criterion. The significance of group separation in multivariate space was tested using Wilks' MANOVA [47], complemented with independent t-tests for the first two principal components (PC1 and PC2).

The population structure of *P. tarapacana* across 96 plots (77 shrublands, 19 forests) was analyzed using the diameter-height allometric relationship (DAB-H) modeled with a power function (H = a × DAB^b). Separate models were fitted for each community and compared using parametric bootstrap (500 iterations) [8], likelihood ratio tests (F-test), and 95 % delta-method confidence intervals [33]. Goodness-of-fit was assessed with R^2, mean squared error (MSE), and mean absolute error (MAE). The Vertical Stratification Index (height_stratification) was calculated as the standard deviation of normalized heights within each plot, expressing the vertical heterogeneity of the community. Community types were compared using a non-parametric median difference test. Diameter class distribution was analyzed by grouping DAB into 5 cm intervals (0–5, 5–10, 10–15, 15–20, 20–25, >25 cm). This class width was selected because it is standard in high-Andean forest inventories [30], allows for detection of fine-scale structural differences between shrublands and forests, and minimizes the occurrence of empty classes in these low-density populations. Proportions per class were compared using chi-square tests with Yates' correction [48]. Diametric diversity was quantified with the ShannonDAB index, which measures heterogeneity considering both richness and evenness of classes. Diametric inequality was assessed with the Gini index, ranging from 0 (perfect equality) to 1 (maximum inequality). Both metrics were analyzed multivariately using MANOVA.

Simpson's Index as a Measure of Life Form Diversity. To assess Life Form Diversity Index within each plot, Simpson's index (1-D) was calculated – a diversity measure considering both richness (number of forms present) and evenness (proportional distribution of individuals among forms). The index was calculated for each plot, with values ranging from 0 (maximum dominance, a single form present) to ~0.75 (maximum evenness among the four forms). The average diversity per community type (forest vs. shrubland) was compared using the Wilcoxon test, given the non-normality of the data.

Analysis of the Ground-Layer Vegetation Community. Cover by ground-layer functional growth forms – perennial shrubs (P Sh), cushion plants (C P), perennial herbs (P H), annual herbs (A H), and perennial subshrubs (P Ss) – was compared between community types using Wilcoxon rank-sum tests [46], as data did not meet assumptions of normality (Shapiro-Wilk) [38] or homogeneity of variances [25]. Differences were considered significant at $p < 0.05$. For functional groups showing significant differences, an Indicator Species Analysis was performed using the Indicator Value (IndVal) index [7]. The statistical significance of the IndVal for each species was evaluated with 14,999 permutations (significance level $\alpha = 0.05$). To focus on the most ecologically relevant associations, only species with an IndVal > 0.35 were considered indicators. This threshold corresponds to a 'moderate' association level according to the classic interpretation of the index [7] and was adopted to identify the most robust indicators.

Software: All analyses were performed in R v4.3+, using the vegan, FactoMineR, indicspecies, ggplot2, lme4, boot, and MuMIn packages.

Results and Discussion

The application of the MDH (≥ 2 m) threshold classified 19 plots (19.4 %) as “Forest” and 79 plots (80.6 %) as “Shrubland”, evidencing the low relative frequency of developed woodland formations in the Altiplano.

Forests and Shrublands Along an Environmental-Structural Gradient. PCA explained 61.1 % of the total variability (PC1: 31.8 %, PC2: 29.3 %). Figure 1 shows a separation between the two community types along PC2. Forests clustered at positive PC2 values, strongly associated with greater BA (loading: 0.741), elevation (0.719), and a higher FSI (0.330). Shrublands concentrated at negative PC2 values, characterized by a high proportion of juveniles (ShCoverI: loading -0.840). MANOVA confirmed significant differences between communities ($F = 50.16$, $p < 0.001$), with differences along PC2 being the most marked ($t = -9.574$, $p < 0.001$), while no significant differences were found along PC1 (associated with DEN and cover) ($t = 0.771$, $p = 0.446$). This indicates that although both types can present similar densities, they are fundamentally separated by attributes related to structural maturity and environmental conditions. The PCA clearly separated forest and shrubland communities along PC2, which is associated with variables related to structural development (BA, elevation, FSI) and juvenile abundance (ShCoverI). Forests are positioned in the positive PC2 space, indicating higher BA, elevation, and favorable substrate, while shrublands cluster in the negative PC2 space, characterized by a higher proportion of juvenile individuals.

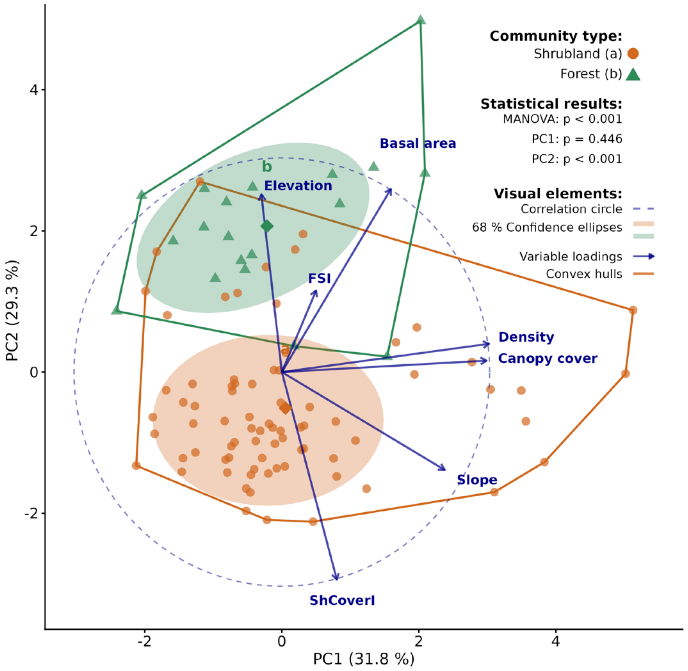


Fig. 1. PCA ordination of forest (MDH ≥ 2 m) and shrubland (MDH < 2 m) communities based on seven structural and environmental variables. Arrows represent variable loadings on PC1 (31.8 % of variance) and PC2 (29.3 % of variance): basal area (m^2/ha); Elevation (m a.s.l.); FSI – Favorable Substrate Index; ShCoverI – shrub cover index; Canopy cover (%); Slope (°); Density (ind/ha). Points represent individual plots, ellipses show 95 % confidence intervals around group centroids. The separation along PC2 reflects differences in structural maturity and substrate quality

Univariate validation confirmed the PCA patterns. The application of the MDH ≥ 2 m threshold clearly differentiated two community types. Shrublands showed higher DEN (1349.1 ± 988.0 stems/ha vs. lower values in forests; $p < 0.05$), dominated by small-sized individuals (ShCoverI significantly greater in shrublands, $p < 0.001$), representing on average more than 50 % of individuals, while in forests this proportion was reduced to less than 30 %. Forests presented significantly higher values in all structure and development variables (Table 1), except for GiniBA, which showed $p = 0.072$. Specifically, forests had a total BA 2.8 times greater, higher mean diameters (DAB) and heights, and greater diametric diversity (ShannonDAB). GiniDAB was higher in Forests, reflecting a more heterogeneous size distribution. The SCI, which combines diametric diversity with BA, was 2.35 times greater in Forests, confirming a more complex and developed structure. The left-skewed distribution of key structural variables (e.g., BA, DAB) reflects high heterogeneity within the population, likely resulting from environmental gradients and historical disturbances. Thus, while mean values are informative, they should be interpreted alongside measures of dispersion.

Table 1

Comparison of structural and diametric diversity variables between shrublands (Sh) and forests (F) of *P. tarapacana*

Variable	Sh (n = 77)	F (n = 19)	Test statistic	p-value
DAB (cm)	4.70 ± 2.09	8.43 ± 1.79	Wilcoxon, W = 126	<0.001
GiniDAB	0.39 ± 0.11	0.51 ± 0.08	t-test, t = –4.81	<0.001
ShannonDAB	1.32 ± 0.39	1.99 ± 0.20	t-test, t = –7.142	<0.001
BA (m^2/ha)	5.10 ± 4.78	14.37 ± 9.10	Wilcoxon, W = 185	<0.001
GiniBA	0.59 ± 0.11	0.64 ± 0.08	t-test, t = –1.822	0.072
H (m)	0.58 ± 0.19	0.87 ± 0.16	Wilcoxon, W = 163	<0.001
SCI	2.22 ± 1.42	5.22 ± 1.25	Wilcoxon, W = 98	<0.001
DAB/H Index	0.77 ± 0.17	0.94 ± 0.03	Wilcoxon, W = 134	<0.001

Note: DAB – mean diameter at the base; GiniDAB – Gini index for diameter inequality; ShannonDAB – Shannon diametric diversity index; BA – Basal area; GiniBA – Gini index for basal area inequality; H – Mean height; SCI – Structural Complexity Index; DAB/H Index – Diameter-to-height relationship index.

Structural and Functional Consequences of the Threshold: Life Form Composition and Diversity. Life form distribution differed between community types (Fig. 2). Forests were dominated by tree-like forms: the proportion of Ar individuals was significantly greater (34.0 vs. 21.8 % in shrublands; $p = 0.0028$), as was that of Dt (18.9 vs. 7.3 %; $p < 0.0001$). In contrast, shrublands – characterized by multi-stemmed forms – presented a higher proportion of shrubs (Sh) (52.4 vs. 40.8 %; $p = 0.0212$) and Bt (18.4 vs. 6.3 %; $p = 0.0034$).

Life Form Diversity Index was greater in forests (0.644 ± 0.069) than in shrublands (0.553 ± 0.090) (Wilcoxon, W = 172, $p = 0.028$) (Table 2). The mean difference was 0.091 index units, equivalent to 16.5 % greater functional diversity in forests. Internal variability was greater in shrublands (SD = 0.090) than in forests (SD = 0.069), reflecting greater heterogeneity in life form composition among shrubland plots.

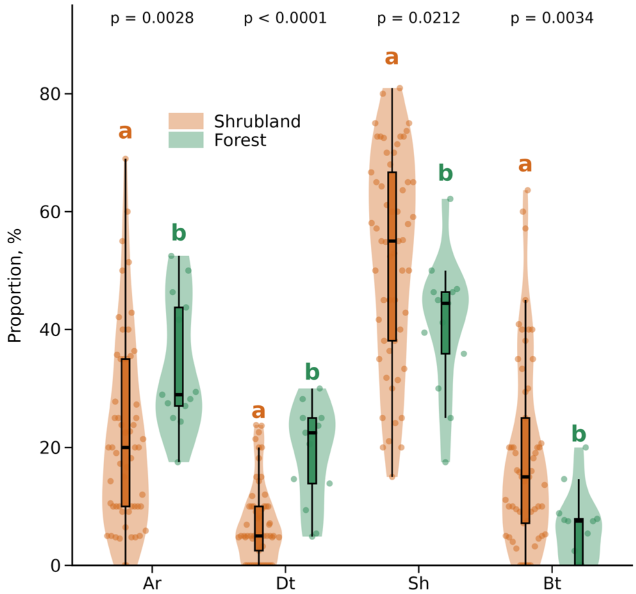


Fig. 2. Proportion of *P. tarapacana* life forms in forests (green) and shrublands (brown). Different letters (a, b) indicate significant differences between community types (Wilcoxon, $p < 0.05$). Points represent individual plots, violins show the distribution density, and boxplots show the quartiles

Table 2

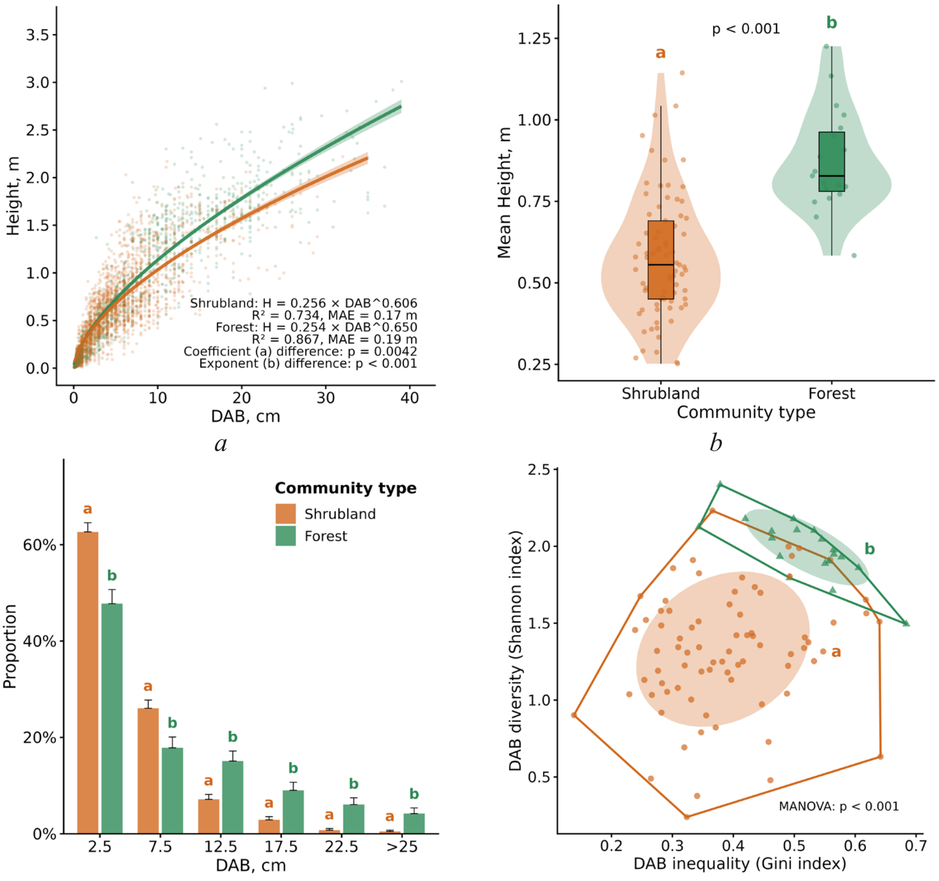
Life Form Diversity Index in forests and shrublands of *P. tarapacana*

Community Type	LFDI (± SD)	Range	p-value (Wilcoxon)
Forest	0.644 ± 0.069	0.534–0.743	0.028
Shrubland	0.553 ± 0.090	0.331–0.727	

Note: LFDI – Life Form Diversity Index, SD – Standard Deviation, Wilcoxon test $p < 0.05$ indicates significant difference between groups.

Population Structure, Allometry, and Diversity. Forests exhibited a more efficient height-diameter allometry (exponent 7.2 % greater than shrublands; $p < 0.001$; Fig. 3*a*) and significantly greater mean heights ($p < 0.001$; Fig. 3*b*). Diameter distribution contrasted between types: shrublands were dominated by small individuals (49.3 % in 0–5 cm class vs. 30.0 % in forests), while forests showed a more balanced structure with larger trees present (>25 cm: 7.3 vs. 0.9 %; Fig. 3*c*). Forests also displayed higher diametric diversity (ShannonDAB index ~1.8 vs. ~1.4) with lower size inequality (GiniDAB ~0.45 vs. ~0.55), reflecting multi-cohort, and equitable stands (Fig. 3*d*). MANOVA confirmed significant multivariate differences ($p < 0.001$).

Ground-Layer Functional Group Cover. Comparison of ground-layer functional group cover between shrublands and forests revealed significant differences for two of the five analyzed groups (Fig. 4). The forest ground layer showed a composition with greater cover of C P (4.05 vs. 2.68 % – $p = 0.0225$, Wilcoxon), while shrublands were dominated by P Sh (9.59 vs. 4.85 % – $p = 0.0021$, Wilcoxon). PERMANOVA was significant, and indicator species analysis revealed a set of 5–10 specialist forest species (e.g., SENU, OXHY) and shrubland species (e.g., SEVI). DB-RDA ordinated the plots primarily based on Ar proportion and FSI, showing a clear transition in ground-layer assemblage composition as the structural threshold is crossed.



a *b*

c *d*

Fig. 3. Structural contrasts between shrublands and forests: *a* – Height-DAB relationship; *b* – HT in Forests and shrublands; *c* – Diameter distribution; *d* – Diametric diversity and inequality. Different letters indicate significant differences

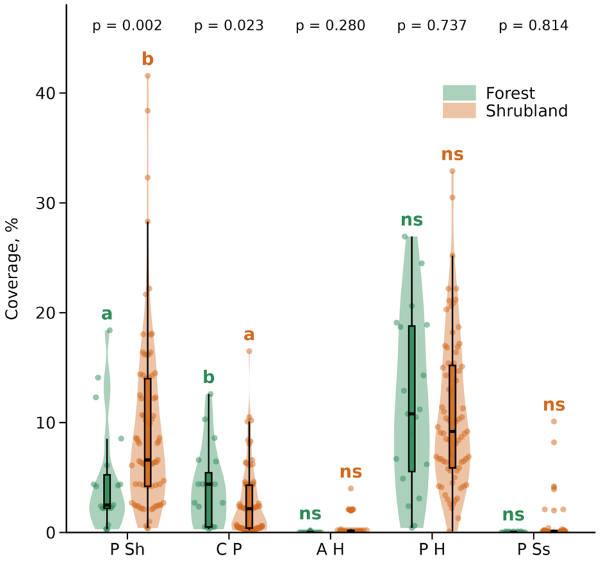


Fig. 4. Ground-layer functional group cover in shrublands (brown) and forests (green) of *P. tarapacana*. Different letters (a, b) indicate significant differences between community types (Wilcoxon, $p < 0.05$)

Indicator Species in Forests and Shrublands. Indicator species analysis revealed a predominance of forest-associated species: 4 of the 5 significant indicator species (80 %) corresponded to this community type (Table 3). The species *Senecio nutans* Sch. Bip. presented an indicator value (IndVal) of 0.938, reflecting an almost perfect association with forests and 100 % specificity (present in 19 plots, all classified as forest). The most represented functional group was P Sh (*S. nutans, Senecio viridis* Phil. var. *Viridis, Senecio punae* Cabrera and *Chiliotrichiopsis keidelii* Cabrera), followed by a single cushion plant (*Oxalis hypsophila* Phil.). In contrast, *S. viridis* was the only indicator species for shrublands (IndVal = 0.724), present mainly in this community type (83 % specificity). Globally, indicator species were found in 94.7 % of forests versus only 44.2 % of shrublands.

IndVal ranges from 0 (no association) to 1 (perfect association). Values > 0.35 indicate moderate to strong association with the given community type [7].

Table 3

Significant indicator species ($p < 0.05$) by functional group and community type

Species	Functional Group	Community	IndVal	p-value	Interpretation
SENU	P Sh	Forests	0.938	<0.0001	Strong indicator
SEVI	P Sh	Shrublands	0.724	0.0067	Moderate indicator
SEPU	P Sh	Forests	0.585	0.0045	
OXHY	C P		0.498	0.0193	
CHKE	P Sh		0.358	0.0227	Weak Indicator

Note: Asteraceae: SENU (*Senecio nutans* Sch. Bip.), SEVI (*Senecio viridis* Phil. var. *Viridis*), SEPU (*Senecio punae* Cabrera) and CHKE (*Chiliotrichiopsis keidelii* Cabrera); Oxalidaceae: OXHY (*Oxalis hypsophila* Phil.).

Forests and Shrublands Along an Environmental-Structural Gradient. Our findings demonstrate that the MDH ≥ 2 m threshold is an ecological tipping point, beyond which microclimatic conditions enabling the development of a functional forest are established. This threshold marks a transition in the architecture, diversity, and structural complexity of *P. tarapacana*. The greater BA, diametric diversity, and vertical stratification in forests reflect an advanced successional state with greater occupancy and a complex structure that diversifies microenvironmental niches. This pattern aligns with observations in other high-Andean *P. tarapacana* woodlands, where shrublands show a marked reduction in H and diameter but high juvenile DEN, suggesting active regeneration with limited H growth [18]. The greater diametric inequality in forests could indicate heterogeneous recruitment and mortality dynamics, typical of mature communities, possibly mediated by thermal limitations that restrict meristematic activity more than carbon acquisition, as documented globally at treelines [17, 22].

The consistency of these patterns reinforces the utility of the threshold as a tool for classifying, monitoring, and conserving these vulnerable ecosystems. Although they operate under thermal conditions similar to other tropical treelines [24], *Polylepis* forests show unique adaptations in carbon allocation and root morphology to cope with the multiple stresses of the world's highest elevations [20, 44]. For example, high-elevation *Polylepis* species have smaller leaves and a greater abundance of root apices-genetically determined traits that facilitate colonization of cold, dry environments [44]. Identifying this functional threshold, linked to measurable structural attributes and specific microsite conditions, provides a quantitative framework for prioritizing conservation areas and designing effective restoration strategies in the Altiplano. Furthermore, protecting these forests is important for conserving associated biodiversity, including ground layer medicinal plants that constitute a vital resource for local communities and whose richness is influenced by forest structure and topographic variables [27].

P. tarapacana communities primarily develop along an environmental structural gradient, where forests – with greater BA and elevation – represent advanced successional stages or sites with more favorable environmental conditions [26]. Shrublands, characterized by a higher proportion of juveniles, could correspond to early developmental stages or environments with more severe constraints, such as poorly developed soils that promote high regeneration but restrict recruitment into larger size classes [16]. Indeed, previous studies have shown that human accessibility (distance to roads and market centers) is a strong predictor of structural degradation, with less accessible forests being better conserved [44].

The absence of significant differences on PC1 (associated with DEN and cover) suggests these attributes are common to both forests and shrublands, reflecting shared adaptive strategies to high-mountain stress [23]. Ecologically, PC1 represents a structural development gradient linked to DEN and slope, suggesting that denser sites are located on steeper slopes, possibly related to colonization processes in specific microsites [28]. PC2, in contrast, reflects an environmental structural gradient, with positive values associated with greater BA, Elev, and substrate quality. Forests at higher elevations show greater BA and better substrate, a pattern linked to greater insolation on north-facing slopes, which provides a thermal window for growth [18, 29]. In the Altiplano, solar radiation is exceptionally high and the daily thermal oscillation is the greatest in the world, creating an extreme environment where north exposure favors higher air temperatures [36]. In contrast, shrublands present a higher proportion of juveniles (<1.3 m), consistent with studies reporting high seedling abundance at the upper forest limit, where regeneration is not limiting, but post-emergence survival and growth beyond the protected microclimate near the ground are limiting [18, 28]. This differential distribution of growth forms has also been documented in Ecuadorian páramos, where P Sh and cushion plant cover varies with altitude and exposure [34].

For conservation, the strong separation on PC2 suggests that: (1) shrublands may be early successional stages or sites with strict environmental constraints, where carbon investment is preferentially directed to the root system as an adaptation to cold and low nutrient availability [16]; (2) forests correspond to mature stages under more favorable conditions, acting as unique carbon and biodiversity reservoirs [29]; and (3) juvenile cover (ShCoverI) is a sensitive indicator of developmental state and environmental pressures, useful for monitoring. Effective conservation of these forests requires considering these structural differences and their relationship with topographic and climatic factors [9, 29].

The ecology of *P. tarapacana* shows complex responses to environmental gradients, highlighting elevation as a structuring factor, associated mainly with soil temperature during the growing season, which globally averages 6–7 °C at the treeline [24]. However, *Polylepis* can grow at notably lower soil temperatures (~4.5–5.5 °C), suggesting specific physiological adaptations or that air temperature could be the more critical limiting factor [20, 36]. The pyramidal population structure (high proportion of juveniles) is common even at the upper limit, indicating continuous recruitment [18], while environmental heterogeneity (exposure, substrate) modulates local growth potential [26]. Future research should incorporate variables such as extraction of large individuals for firewood (e.g., distance to settlements), microclimatic data to validate canopy thermal buffering, detailed edaphic characteristics – given the marked root investment under limiting conditions [16] – and long-term regeneration data to discern whether shrublands represent a stable successional stage or a persistent alternative state.

Population Structure and Dynamics. The results reveal profound structural contrasts between shrublands and forests of *P. tarapacana*, reflecting different successional stages and environmental conditions. The divergent H growth results suggest differentiated growth strategies: shrublands show a strategy with limited investment in H growth relative to diameter, possibly due to water, nutrient, or competitive stress [30]. This response is consistent with the restrictive conditions of the treeline, where low soil and air temperatures primarily limit meristematic activity and growth, more than photosynthesis [18, 21]. Indeed, studies of functional traits in *Polylepis* have shown that high-elevation species have reduced photosynthetic rates, suggesting source carbon limitation at the treeline, but also morphological adaptations like smaller leaves that may be linked to conservative growth [10, 44]. In contrast, forests, with greater H growth rates, optimize light capture in dense, stratified communities, indicating they surpass a critical threshold of environmental conditions that allows greater investment in vertical canopy expansion [20, 30]. The pronounced heterogeneity in structural parameters, evidenced by left-skewed distributions (Fig. 3), suggests that *P. tarapacana* communities are shaped by a mosaic of microsite conditions and possibly past anthropogenic impacts, a pattern also documented in other high-elevation woodlands [16].

The observed structural differentiation aligns with the concept of site quality, where the MDH is an indicator of a stand's productive capacity [1, 32]. Shrublands, presenting limited H growth relative to diameter [30], suggest establishment on lower-quality sites. These less favorable conditions, particularly at lower elevations and with a lower proportion of optimal microsites, impose thermal constraints that limit meristematic activity and growth more than carbon acquisition through photosynthesis [18, 21]. The lower investment in vertical expansion in shrublands is also interpreted as an adaptive strategy against water or nutrient stress [30], forcing a greater allocation of biomass to the root system to compensate for low nutrient availability and cold soil conditions [16]. Conversely, forests, which exhibit greater H growth rates and a more complex structure [30], occupy higher-quality sites where they have managed to mitigate or overcome these critical thresholds of environmental limitation [20, 30]. The lower HT in shrublands agrees with their simplified architecture, where most individuals occupy low strata (< 2 m), while forests develop multiple strata that increase structural complexity and niche diversity. This contrast may be related to microclimatic changes: under the forest canopy, the attenuation of extreme thermal amplitudes and reduced wind stress facilitate the survival of individuals in different strata [16]. The diameter distribution skewed towards small classes in shrublands (< 5 cm: ~50 %) suggests high regeneration but low recruitment into larger sizes, possibly due to differential mortality or growth limitations [6]. This demographic pattern, dominated by young, small individuals, has been interpreted as evidence that the critical phase is not germination, but the transition from seedling to sapling, when apical meristems emerge from the warmer air layer near the ground [18, 28].

The greater evenness (higher ShannonDAB) alongside lower inequality (lower GiniDAB and GiniBA) in forests indicates more mature communities with multiple coexisting cohorts, reflecting stable population dynamics and sustained recruitment [30]. These patterns align with the successional development model of high-Andean forests, where shrublands represent early stages or marginal sites subject to "sink limitations" for growth [17], and forests correspond to more advanced stages with better conditions for the full structural development of *P. tarapacana*, possibly associated with greater resource acquisition efficiency due to modifications in root morphology and better substrate quality [16, 26].

Structural and Functional Consequences of the Threshold: Life Form Composition and Diversity. Life forms in *P. tarapacana* respond to community type, reflecting differences in structural maturity, environmental conditions, and successional processes, consistent with the phenotypic plasticity of the genus documented along elevation gradients [26, 44]. This plasticity can include genetically determined functional traits, such as reduced leaf size and multiplied apices in high-elevation species, representing climatic adaptations to cold, dry conditions [10, 44]. The Bt form, associated with steep slopes, highlights the topographic influence on the configuration of these communities [26]. Furthermore, the distribution of *Polylepis* is often associated with terrain features that offer microclimatic refuge or protection from fire and grazing, especially at mid and low elevations [44]. In the Maure basin, Peru, *P. tarapacana* forests develop in sectors of low topographic protection, with low probability of aquifer interception, conditions that shape their architecture [9, 29].

Life forms can be used as rapid indicators of successional state [26]. The transition from shrubland to forest implies not only DEN changes but a compositional replacement towards more complex forms. For restoration, promoting seedlings with Ar potential could accelerate structural recovery, although the main limitation is not initial recruitment – often high even at the treeline [28] – but the conditions allowing subsequent survival and vertical growth [16, 18]. Factors such as the accessibility of forests and shrublands (distance to roads and settlements) also strongly predict structural degradation, so restoration must consider anthropogenic pressure [29, 44].

The greater Life Form Diversity Index suggests greater structural and functional complexity. This is interpreted from: (1) greater evenness in the distribution of forms, with coexistence of contrasting strategies facilitated by a canopy that moderates extreme microclimate [16]; (2) successional implications, where lower diversity in shrublands reflects dominance by few strategies in response to severe and homogeneous environmental limitations [23]; and (3) greater ecosystem resilience, as diversity of forms allows complementary responses to disturbances and favors functional stability. The greater form diversity in forests reinforces their character as an advanced successional stage with greater functional complexity, which has implications for the conservation and restoration of these high-Andean ecosystems.

Ground-layer Functional Group Cover. The results show a clear differentiation of ground-layer functional groups between shrublands and forests of *P. tarapacana*, reflecting microenvironmental and resource availability changes, consistent with patterns observed along Andean elevation gradients [27, 34]. The greater CC of P Sh in shrublands suggests pioneering strategies in exposed environments with greater thermal amplitude and water stress [18], extreme conditions that characterize the Altiplano, where daily thermal oscillation is the greatest in the world and solar radiation is very intense [36]. In contrast, the greater abundance of C P in forests indicates more stable microclimatic conditions, with a canopy that buffers extreme thermal amplitudes [16] and more developed soils, reflecting conservative strategies typical of mature communities [27]. This closed canopy not only moderates temperature but may also reduce moisture loss and create protected microsites that favor regeneration [28, 44], a phenomenon also observed in high-Andean ground-layer assemblage studies where plant cover varies with elevation [5, 34].

A taller, more closed canopy modifies the underlying microclimate, buffering the extreme thermal amplitudes of the Altiplano and creating more stable conditions for the establishment of specialized ground layer species [16]. Studies in the Peruvian Andes highlight that *P. tarapacana* forests on dry, sunny slopes reach greater heights than on humid slopes, due to higher maximum air temperatures and greater solar radiation [20]. Likewise, ground-layer assemblage composition changes according to canopy structure: in Ecuadorian páramos, C P and P Sh cover varies significantly with elevation [34], a pattern consistent with the functional differentiation observed between our shrublands and forests. The marked preference of *P. tarapacana* for north exposures [9, 29] and its association with moisture-retaining rocky microsites [28] underscore the importance of local abiotic conditions for reaching this structural threshold. In the Argentine Altiplano, the cover and richness of ground layer medicinal plants also vary significantly with elevation [27].

The transition from shrubland to forest implies a functional replacement towards more specialized forms, signaling ecosystem maturation. The coexistence of both groups in forests suggests greater functional diversity and resilience, supported by the ability of *P. tarapacana* to maintain positive photosynthesis under limiting conditions [10]. Physiological studies on *Polylepis* have shown that, despite low temperatures, high-mountain species maintain photochemical efficiency and photoprotection mechanisms that enable survival in extreme environments [10, 36]. On the other hand, the absence of differences in P H, A H, and P Ss indicates these are generalist components regulated at the landscape scale, whose conservation requires broad habitat strategies [29]. Notably, many of these generalist species include widely distributed medicinal plants whose presence in the ground-layer assemblage does not vary significantly between structural types but constitutes a valuable ethnobotanical resource [27].

Future research should evaluate the causal mechanisms behind these differences, such as the role of canopy thermal buffering versus soil property changes mediated by root architecture [16], as well as the influence of historical and current anthropogenic factors in shaping these assemblages [44]. Integrating these dimensions is important for designing effective conservation and management strategies that ensure the persistence of these high-Andean forests [9, 29], considering both their ecological value and their importance as reservoirs of functional biodiversity and medicinal resources for local communities [27].

Beyond statistical indicators, the ecological roles of dominant life forms and indicator species underscore functional shifts across the threshold. Arborescent forms in forests likely act as nurse plants, moderating microclimate and facilitating the establishment of shade-tolerant herbs and C P. In contrast, shrublands are dominated by heliophytic shrubs that tolerate high radiation and temperature fluctuations, reflecting a pioneer strategy. This functional replacement highlights how the MDH $\geq$ 2 m threshold captures not only structural but also ecosystem-level transitions.

Indicator Species in Forests and Shrublands. The indicator species analysis reveals that the shrubland-to-forest transition in *P. tarapacana* involves a complete replacement of the specialized ground-layer assemblage. *S. nutans* acts as a flagship species for mature forests, suggesting strict microenvironmental requirements dependent on conditions created by the closed *Polylepis* canopy [16]. These conditions result from a canopy that attenuates the extreme thermal amplitudes of the Altiplano, favoring organic matter accumulation and moisture retention [44], and generating microsites that buffer thermal stress for accompanying vegetation [2, 12]. It is noteworthy that *S. nutans* is recognized as a medicinal plant widely used in Andean pharmacopoeia [13, 27], adding ethnobotanical value to its role as an ecological indicator.

In contrast, *S. viridis* is associated with shrublands, reflecting tolerance to more extreme conditions – greater thermal amplitudes and wind exposure – typical of open-canopy sites [18], and could act as a pioneer species in active restoration. The marked preference of indicator species for specific canopy and microclimate conditions reinforces the idea that the MDH ≥ 2 m structural threshold acts as an environmental filter that completely reorganizes ground-layer assemblages, selecting species based on their capacity to tolerate or benefit from the generated microclimatic conditions [14, 40, 41]. The marked asymmetry in indication (4 forest species vs. 1 shrubland) suggests greater niche specialization under forest conditions, where the stable canopy generates a diversity of exploitable microhabitats for specialists [14], while stronger environmental filters in shrublands, such as greater wind exposure and thermal amplitude [18], limit successful strategies to tolerant generalists [26]. The overrepresentation of P Sh among indicator species (4 of 5) confirms this group contains habitat specialists with strong microenvironmental preferences.

For monitoring and conservation, the presence of *S. nutans*, *S. punae*, and *O. hypsophila* signals mature forest with stable microclimatic conditions; the presence of *S. viridis* indicates early stages or degradation. Human accessibility (distance to roads and settlements) has been shown to be a strong predictor of structural degradation in *Polylepis* forests [44], so monitoring of indicator species should be complemented with measures of anthropogenic pressure [29]. Protecting these forests conserves not only forest structure but also the resource of associated medicinal plants, whose sustainable use should be integrated into management strategies [27], especially considering these ecosystems face constant threats from habitat loss and fragmentation [19, 35].

Among the limitations, the analysis does not consider interspecific interactions (facilitation, competition) that could modulate the patterns [4, 40, 41], nor abiotic factors such as human impact, soil depth, water availability, or soil temperature, which could better explain the relationship between *P. tarapacana* structure and its environment [16].

Conclusion

This study demonstrates that the transition between shrublands and functional forests of *Polylepis tarapacana* at the altitudinal treeline is defined by a discrete MDHthreshold (MDH ≥ 2 m) that synthesizes profound changes in community architecture, microenvironmental conditions, and associated biotic assemblages. The transition is mediated by the abundance of Ar life forms and the presence of favorable substrates, which together create a habitat supporting a distinctive and specialized ground-layer assemblage. These substrates provide the necessary thermal window to overcome the growth limitations imposed by the low temperatures characteristic of the Altiplano.

Adopting a MDH threshold to define forests in these ecosystems aligns with the need for operational definitions that integrate structure, function, and landscape context, as proposed for native forests in Argentina. This approach makes it possible to move beyond merely morphological classifications and advance toward an ecological characterization that reflects the provision of ecosystem services, biodiversity conservation, and resilience to disturbance. The functional composition of the ground layer differs significantly between shrublands and forests: P Sh characterize early stages under exposed and variable conditions, while C P are associated with mature communities with stable microclimates. Complementarily, the indicator species analysis identified five species with strong associations to specific community types, providing valuable tools for monitoring, restoration assessment, and conservation.

Together, these findings provide a quantitative and ecologically robust framework for classifying, monitoring, and prioritizing conservation efforts in these extreme alpine ecosystems, which are particularly vulnerable to global climate change.

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