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Influence of Microclimate, Ground Cover, and Canopy Openness on the Regeneration of *Polylepis* in the Peruvian Andes

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Abstract *Polylepis* forests, considered relict ecosystems of great ecological importance in the Andes, face significant threats from degradation and climate change. This study evaluated the influence of microclimate, ground cover, and canopy openness on the natural regeneration of three *Polylepis* species (*P. rodolfo-vasquezii*, *P. canoi*, and *P. flavipila*) in high Andean Forest relics in the Junín and Lima regions of Peru. To achieve this, permanent plots were established in three representative forest patches: María Moya, Curimarca, and Laraos. At each site, 20 m × 20 m plots were delineated and subdivided into 5 m × 5 m quadrants. Within each plot, a central quadrant was selected where microclimatic variables (temperature and relative humidity), structural characteristics (vegetation and plant cover) and reproduction modes (sexual or asexual) in seedlings and/or saplings were recorded. Preliminary findings suggest that *Polylepis* regeneration may be shaped by canopy cover, which appears to influence the microclimatic conditions of the understory. Soil temperature also seems to play a meaningful role, varying according to the reproductive strategy of each species studied. Interestingly, the presence of lichens and bryophytes showed a potential inverse relationship with sexual regeneration, while more open canopies tended to support greater height in regenerating individuals. Taken together, these patterns point to a possible interplay between microclimate, ground cover, and canopy structure as key factors driving the natural regeneration dynamics of *Polylepis* ecosystems. These findings underscore the importance of understanding these dynamics to develop conservation strategies that maintain a balance between tree cover and understory functionality in high-Andean ecosystems.

Keywords Natural Regeneration, Seedlings, High-Andean Forests, *Polylepis*, Microclimatic Variables

1. Introduction

Forests of the genus *Polylepis*, endemic to the high-Andean mountain ranges of South America [1], represent one of the highest tree lines in the world, occurring between 1,800 and 5,200 meters above sea level [2]. These forests, which form small patches on mountain slopes and rocky ravines, are considered relicts of once more extensive vegetation [3]. Their ecological importance lies in the ecosystem services they provide, such as water capture and distribution, reduction of soil erosion, and the sheltering of unique biodiversity [4]. However, these ecosystems are highly sensitive to climate change, which significantly affects their composition, structure, and dynamics [5].

The natural regeneration of *Polylepis* forests is influenced by a range of biotic and abiotic factors, among which microclimatic variables, ground cover, and canopy openness are particularly important [6]. Microclimatic conditions, such as temperature and humidity, vary along altitudinal gradients and have a direct impact on seedling germination, establishment, and growth [7]. Additionally, ground cover composed of grasses, lichens, bryophytes, and bare soil can either facilitate or inhibit seedling establishment, depending on resource competition and the presence of allelopathic substances [8]. Meanwhile, canopy openness, which regulates the amount of solar radiation reaching the forest floor, influences regeneration patterns by favoring seedling growth in areas with lower canopy cover and sapling development in more exposed areas [9].

Natural regeneration is a complex process that depends on the interaction of multiple factors, including the availability of propagules, proximity to mature forests, and levels of soil disturbance [10]. However, regeneration can be negatively affected by anthropogenic activities such as grazing, agriculture, and fire, which alter soil conditions and reduce its water retention capacity, thereby hindering seedling germination and establishment [11]. Furthermore, climate change with rising temperatures and increased drought frequency poses an additional threat to these ecosystems, as it may disrupt regeneration patterns and reduce population viability [12].

At the international level, several studies have explored the relationship between microclimatic variables [13], vegetation cover [14,15], and canopy openness in the regeneration of *Polylepis*. For example, it has been shown that fire and grazing negatively affect sexual regeneration, while species functional traits, such as leaf size and photosynthetic rate, are closely linked to their adaptation to specific climatic conditions [16]. However, in Peru, research on sexual or asexual regeneration of *Polylepis* remains limited, hindering the implementation of effective conservation and management strategies [17]. Nevertheless, recent studies have provided valuable insights into regeneration patterns in relation to vegetation cover and environmental conditions, highlighting the importance of factors such as soil moisture, terrain slope, temperature, and light availability [18,19].

In this context, understanding how these variables influence the natural regeneration of *Polylepis* both in terms of plant height and reproductive mode (sexual or asexual) is essential [20]. Previous research has shown that sexual regeneration tends to be more frequent in areas with lower canopy openness and higher humidity, where microclimatic conditions are less extreme [21,22]. In contrast, asexual regeneration is more prevalent in areas with greater solar radiation and harsher conditions, such as forest edges. Nonetheless, knowledge gaps remain unchanged regarding how these variables interact across different *Polylepis* species and ecological contexts, particularly in high-Andean ecosystems with unique characteristics.

Therefore, the objective of this study is to determine the influence of microclimatic variables (air temperature, air humidity, and soil temperature), vegetation cover (grasses, bare soil, rocks, lichens, and bryophytes), and canopy openness on the natural regeneration of three *Polylepis* species (*P. rodolfo-vasquezii*, *P. canoi*, and *P. flavipila*) in remnant forests in the Junín and Lima regions of the Peruvian Andes. This research aims to provide valuable information for the conservation, management, and restoration of these unique and highly vulnerable ecosystems, contributing to the sustainable development goals outlined in the 2030 Agenda [23].

2. Materials and Methods

2.1. Study Area

The study was conducted in three relic *Polylepis* forests located in the Junín and Lima regions of Peru (Figure 1), within high-Andean ecosystems that offer specific environmental conditions for natural regeneration.

The *Polylepis rodolfo-vasquezii* forest is located in the Ricriscancha sector of the María Moya community, Comas District, Concepción Province, Junín Region, at the geographic coordinates (Datum WGS 84, Zone 18S): 484135 E, 8704058 N. The elevation ranges from 4,185 to 4,407 meters above sea level, and the site is characterized by a very humid climate, with an average temperature of 11.5 ℃ and an annual precipitation of 715 mm. This forest forms part of the Palis River basin.

The *Polylepis canoi* forest is situated in the Jucha sector of the Curimarca community, Molinos District, Jauja Province, Junín Region (466584 E, 8723206 N). Elevation ranges from 3,743 to 3,914 meters above sea level, with an average temperature of 8.7 ℃ and an annual precipitation of 776 mm. Additionally, it lies near the Huasicocha Lagoon and the Pui Pui Protected Forest.

Finally, the *Polylepis flavipila* forest is located in the Shuctocayón sector of the Laraos community, Laraos District, Yauyos Province, Lima Region (416642 E, 8635513 N), at elevations ranging from 3,900 to 4,159 meters above sea level. The site features a humid climate, with an average temperature of 9.6 °C and an annual precipitation of 638 mm. This forest is part of the Nor Yauyos Cochas Landscape Reserve and the Cañete River basin.

2.2. Biological and Ecological Description and Ontogenetic Strategies

The *P. canoi* defies extreme cold and reproduces mainly asexually, an ability that allows it to expand into deteriorated soils where few plants manage to thrive [24]. In contrast, *P. flavipila* has adapted exceptionally well to arid environments; its deep roots almost seem as if searching for hidden underground water and its compact leaves minimize moisture loss, which is key to enduring prolonged droughts [25].

On the other hand, *P. rodolfo-vasquezii* prefers humid and shady areas, under the protection of closed-canopy forests. This species grows quickly and depends mostly on sexual reproduction, a strategy well suited to environments where humidity and filtered light create ideal conditions for its development [26].

2.3. Tree Clustering Principle in Renewal

The principle of tree clustering in *Polylepis* forest regeneration reveals a tendency to establish non-random spatial patterns, often clustered around adult trees or within specific microhabitats [27]. Moreover, the expression of this pattern varies depending on the species and local ecological conditions. *P. rodolfo-vasquezii* exhibits an aggregated distribution pattern, whereas *P. canoi and P. flavipila* display random spatial patterns [28,29].

In general, taxa of the genus *Polylepis* show a distribution where asexual regeneration occurs closer to the trunks of adult trees, while sexual regeneration is more frequently found near the canopy edges. Thus, the spatial distribution of regeneration is influenced by the presence of adult trees and the surrounding microclimatic conditions [27].

2.4. Methodological Framework

Figure 2 shows the comprehensive methodological framework used, and the study is divided into several stages: the first consisted of fieldwork, where the evaluation of natural regeneration in relic forests was carried out, considering parameters such as vegetation cover, microclimatic conditions, and canopy openness.

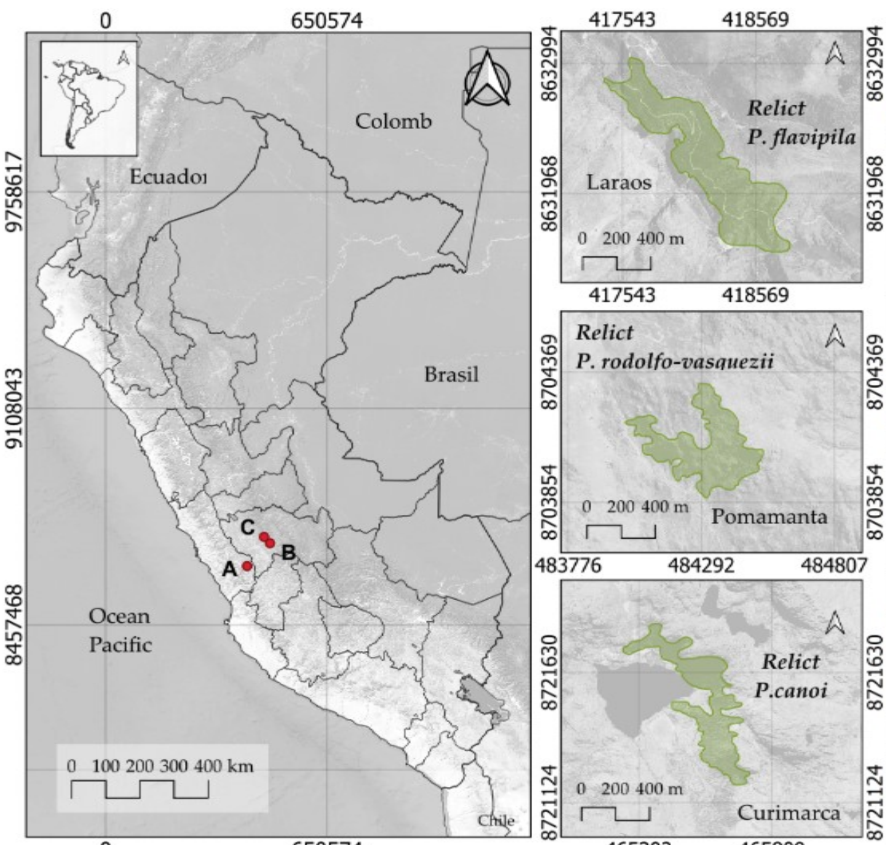

Figure 1. Location of study plots in *Polylepis* forests. A: (*P. flavipila*), Laraos, Lima; B: (*P. rodolfo-vasquezii*), María Moya, Junín; C: (*P. canoi*), Curimarca, Junín

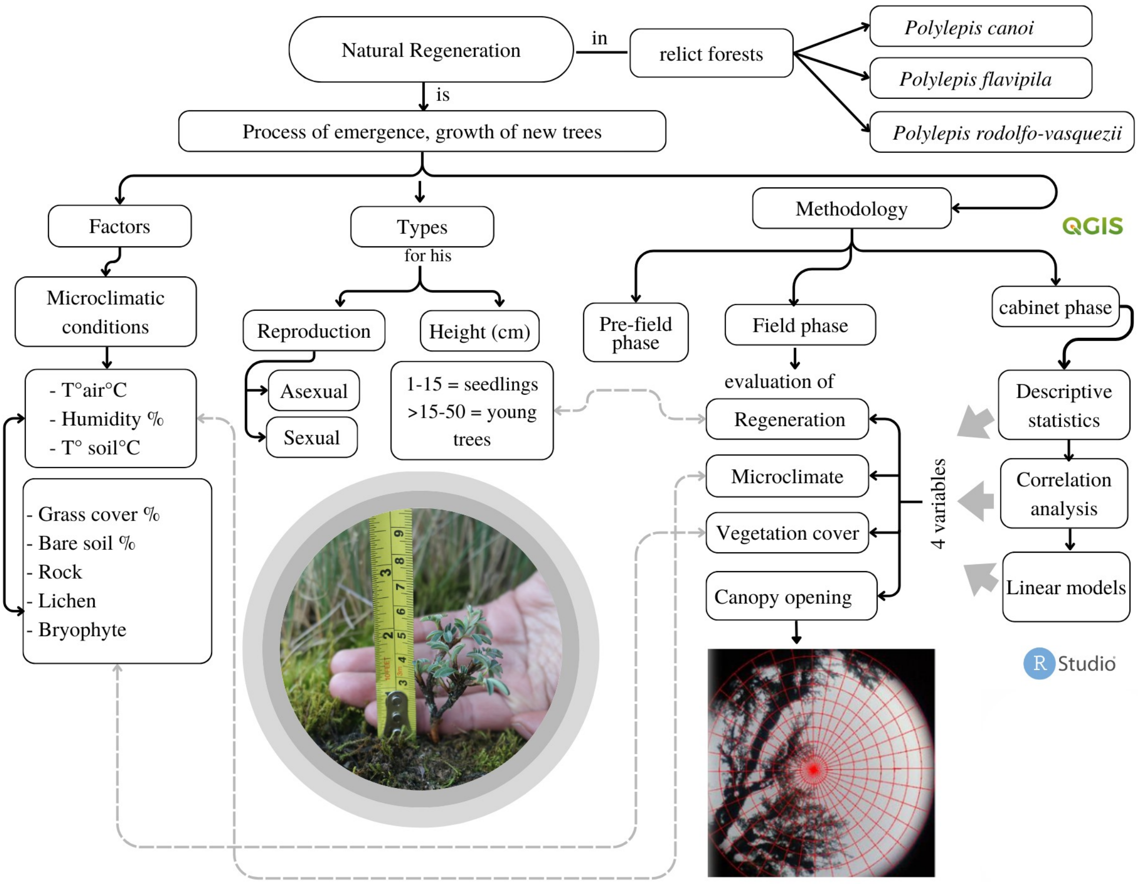

Figure 2. Overview of the methodological framework applied in this research

These measurements allowed for the collection of direct data reflecting the ecological dynamics and factors influencing the growth of *Polylepis* species.

The second phase was conducted in the laboratory, where the collected data were processed and analyzed. Descriptive statistical analyses were used to characterize the variables, correlation analyses to identify relationships between them, and linear models to evaluate regeneration patterns.

2.5. Design and Type of Research

The research design was experimental. A total of 28 plots, each measuring 15 m × 15 m, were established across three *Polylepis forests: P. rodolfo-vasquezii* in Mar á Moya (7 plots), *P. canoi* in Curimarca (7 plots), and *P. flavipila* in Laraos (7 plots), following the methodology proposed by Morales et al. [30]. The plots were systematically distributed to encompass the environmental variability of each site. Within each plot, five 5 m × 5 m subplots were delineated one in each corner and one in the center to assess natural regeneration, vegetation cover, and microclimatic variables.

In total, 105 subplots were analyzed (35 per forest). The study was classified as applied research, at experimental, relational, explanatory, and mixed levels. Field data collection began in March 2022 and is expected to continue through 2023.

2.5.1. Evaluation of Natural Regeneration

In each subplot, the height of regenerated individuals was recorded [31], and they were classified into two categories: seedlings (height ≤ 15 cm) and saplings (height > 15 cm and ≤ 50 cm). The mode of reproduction (sexual or asexual) was also determined, as *Polylepis* species regenerate both via seeds (sexual) and vegetative (asexual) [32]. This was assessed by excavating the roots to identify whether individuals originated from seeds or resprouts. Regeneration density was calculated as the number of individuals per square meter.

2.5.2. Measurement of Microclimatic Variables

Temperature and air humidity were measured using DHT22 sensors, while soil temperature was measured using VW-1 HFT sensors. Sensors were installed in each plot, positioned 1.5 m above ground for air measurements and 20 cm below ground for soil measurements. Data were recorded every 2 seconds over a 24-hour period under representative climatic conditions. The variables assessed included air temperature (℃), air humidity (%), and soil temperature (℃).

2.5.3. Evaluation of Vegetation Cover

Vegetation cover was evaluated using the line interception method. Five quadrants of 2 m × 2 m were installed within the 5 m × 5 m subplots, located at the corners and center of each plot. In each quadrant, a 10-meter line was used to quantify the extent of soil cover. Coverage of grasses, bryophytes, lichens, as well as bare soil and rocks in the forest understory, was recorded [33,34].

2.5.4. Measurement of Canopy Openness

Canopy openness was assessed using hemispherical photographs taken with a digital camera equipped with a 180 ° fisheye lens. The camera was placed in the center of each 5 m × 5 m subplot, 25–30 cm above the ground, and oriented toward the canopy, according to Del Castillo [35] methodology. Photographs were taken in diffuse light, both at dawn and dusk, or on overcast days to avoid underestimating canopy cover. The images were analyzed using the Gap Light Analyzer software, which calculated the percentage of canopy openness based on the amount of solar radiation reaching the forest floor.

2.5.5. Data Analysis

The data were analyzed using R statistical software, version 3.6.0. Generalized Linear Mixed Models (GLMMs) were applied to evaluate the relationship between the independent variables microclimate (including the covariates air temperature, air humidity, and soil temperature), vegetation cover (including grasses, bare soil, rocks, lichens, and bryophytes), and canopy openness and the dependent variables (regeneration height and type of reproduction: sexual or asexual).

Significance tests ($p < 0.05$) were conducted to determine the influence of each variable on natural regeneration. In addition, correlation analyses were performed to identify specific patterns in each forest, followed by the analysis and interpretation of representative results

3. Results

3.1. Influence of Microclimate, Vegetation Cover, and Canopy Openness on Regeneration Based on Height in *Polylepis*

The microclimatic variables (air temperature, air humidity, and soil temperature), vegetation cover variables (grasses, soil, rocks, bryophytes, and lichens), and canopy openness showed both significant and non-significant effects on regeneration by plant height, as presented in Table 1.

Regarding the relationship between vegetation cover and height-based regeneration, the results indicated that grass and lichen cover had variable effects but were not statistically significant ($p > 0.05$); therefore, they were excluded from the analysis. However, bare soil cover showed a significant effect on height-based regeneration in *P. canoi* in the Curimarca (CM) forest, with a p-value of 0.025. In contrast, variables related to rock, lichen, and bryophyte cover did not show statistically significant effects ($p > 0.05$).

Figure 3 illustrates the relationship between the height of regenerating individuals and three environmental variables: air humidity, bare soil cover, and canopy openness. In Figure 3a, a negative correlation ($r = -0.23$) is observed between air humidity and sample height, and lower humidity levels are associated with taller individuals, whereas higher humidity corresponds to shorter ones. In Figure 3b, P. *rodolfo-vasquezii* in the Mar á Moya (MM) forest exhibits a weak negative correlation with bare soil cover ($r = -0.11$), suggesting that reduced soil exposure may promote greater regeneration height. Finally, Figure 3c shows a positive correlation between canopy openness and plant height in *P. flavipila* from the Laraos (L) forest ($r = 0.39$), indicating that more open canopies favor the development of taller individuals, while reduced openness is associated with shorter regeneration.

Table 1. Height-based regeneration of *P. rodolfo-vasquezii, P. canoi, and P. flavipila* as a function of air temperature, air humidity, soil temperature, vegetation cover, and canopy openness in the María Moya (MM), Curimarca (CM), and Laraos (L) forests, according to the Generalized Linear Mixed Model (GLMM)

Polylepis Forest	Location	Variable	Estimate	Est Error	t value	Pr(>|t|)	
		Intercept	2.432826	0.117525	20.7	<2e-16	***
P. rodolfo-vasquezii	MM	Air Temperature (℃)	0.021468	0.036831	0.583	0.561	
P. canoi	CM	Air Temperature (℃)	-0.03788	0.02125	-1.783	0.078	
P. flavipila	L	Air Temperature (℃)	-0.00472	0.013514	-0.349	0.728	
		Intercept	2.599625	0.208828	12.449	<2e-16	***
P. rodolfo-vasquezii	MM	Air Humidity (%)	0.000379	0.00272	0.139	0.8895	
P. canoi	CM	Air Humidity (%)	-0.00601	0.0027	-2.226	0.0285	*
P. flavipila	L	Air Humidity (%)	-0.0119	0.009871	-1.205	0.2311	
		Intercept	2.375008	0.104484	22.731	<2e-16	***
P. rodolfo-vasquezii	MM	Soil Temperature (℃)	0.02743	0.044958	0.61	0.543	

Table 1 continued

P. canoi	CM	Soil Temperature (℃)	-0.02346	0.019775	-1.187	0.239	
P. flavipila	L	Soil Temperature (℃)	0.001583	0.019758	0.08	0.936	
		Intercept	2.336066	0.096228	24.276	<2e-16	***
P. rodolfo-vasquezii	MM	Grass Cover (%)	0.007304	0.003745	1.95	0.054	
P. canoi	CM	Grass Cover (%)	-0.00735	0.00459	-1.602	0.113	
P. flavipila	L	Grass Cover (%)	-0.0015	0.00441	-0.34	0.735	
		Intercept	2.406779	0.079578	30.244	<2e-16	***
P. rodolfo-vasquezii	MM	Bare Soil Cover (%)	0.007321	0.007731	0.947	0.346	
P. canoi	CM	Bare Soil Cover (%)	-0.02392	0.010512	-2.276	0.025	*
P. flavipila	L	Bare Soil Cover (%)	-0.00205	0.002679	-0.763	0.447	
		Intercept	2.32825	0.07169	32.477	<2e-16	***
P. rodolfo-vasquezii	MM	Rock Cover (%)	0.004616	0.002698	1.711	0.0904	
P. canoi	CM	Rock Cover (%)	-0.0451	0.041649	-1.083	0.2813	
P. flavipila	L	Rock Cover (%)	0.017567	0.031554	0.557	0.5791	
		Intercept	2.304665	0.112474	20.491	<2e-16	***
P. rodolfo-vasquezii	MM	Bryophyte Cover (%)	0.005792	0.003035	1.908	0.0595	
P. canoi	CM	Bryophyte Cover (%)	-0.00208	0.001778	-1.167	0.2462	
P. flavipila	L	Bryophyte Cover (%)	0.006058	0.004334	1.398	0.1654	
		Intercept	2.31421	0.06913	33.475	<2e-16	***
P. rodolfo-vasquezii	MM	Lichen Cover (%)	0.03049	0.02892	1.055	0.294	
P. canoi	CM	Lichen Cover (%)	0.00797	0.03317	0.24	0.811	
P. flavipila	L	Lichen Cover (%)	0.08006	0.04994	1.603	0.112	
		Intercept	2.016313	0.15627	12.903	< 2e-16	***
P. rodolfo-vasquezii	MM	Canopy Openness (%)	0.008349	0.002581	3.235	0.00167	**
P. canoi	CM	Canopy Openness (%)	0.003812	0.004899	0.778	0.43844	
P. flavipila	L	Canopy Openness (%)	0.007339	0.003298	2.225	0.02847	*

Significance Code: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

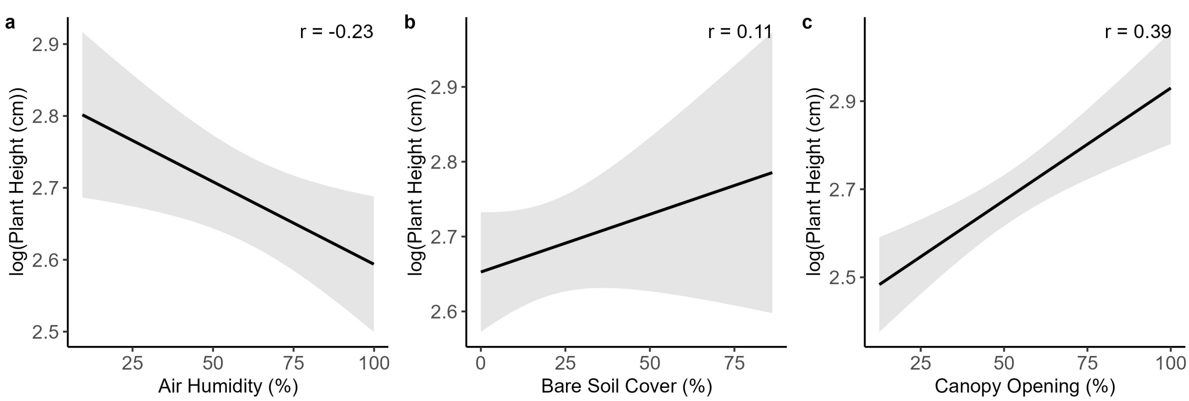

Figure 3. Linear correlation of the variables (a) air humidity; (b) Bare Soil Cover; (c) Canopy Opening with the height of natural regeneration

Table 2. Regeneration by reproductive type (sexual vs. asexual) of *P. rodolfo-vasquezii, P. canoi, and P. flavipila* as a function of air temperature, air humidity, soil temperature, vegetation cover, and canopy openness according to the Generalized Linear Mixed Model (GLMM)

Polylepis Forest	Location	Variable	Estimate	Est Error	t value	Pr(>|t|)	
		Intercept	1.55905	0.42236	3.691	0.000223	***
P. rodolfo-vasquezii	MM	Air Temperature (℃)	0.06874	0.12681	0.542	0.58775	
P. canoi	CM	Air Temperature (℃)	0.36527	0.09805	3.725	0.000195	***
P. flavipila	L	Air Temperature (℃)	-0.05863	0.04609	-1.272	0.203331	
		Intercept	2.022622	0.825882	2.449	0.0143	*
P. rodolfo-vasquezii	MM	Air Humidity (%)	-0.0068	0.010573	-0.643	0.52	
P. canoi	CM	Air Humidity (%)	0.019623	0.010689	1.836	0.0664	
P. flavipila	L	Air Humidity (%)	-0.03422	0.038559	-0.887	0.3748	
		Intercept	2.69797	0.39596	6.814	9.51×10^{-12}	***
P. rodolfo-vasquezii	MM	Soil Temperature (℃)	-0.31393	0.15959	-1.967	0.049169	*
P. canoi	CM	Soil Temperature (℃)	0.16471	0.08051	2.046	0.040785	*
P. flavipila	L	Soil Temperature (℃)	-0.23246	0.07009	-3.317	0.000911	***
		Intercept	2.30521	0.40063	5.754	8.72×10^{-9}	***
P. rodolfo-vasquezii	MM	Grass Cover (%)	-0.01259	0.015	-0.839	0.4013	
P. canoi	CM	Grass Cover (%)	0.03855	0.01948	1.979	0.0479	*
P. flavipila	L	Grass Cover (%)	-0.02995	0.01789	-1.674	0.0941	
		Intercept	2.22458	0.3364	6.613	3.77×10^{-11}	***
P. rodolfo-vasquezii	MM	Bare Soil Cover (%)	-0.02678	0.02938	-0.912	0.362	
P. canoi	CM	Bare Soil Cover (%)	0.25751	0.11325	2.274	0.023	*
P. flavipila	L	Bare Soil Cover (%)	-0.01781	0.01051	-1.694	0.0902	
		Intercept	2.32154	0.31546	7.359	1.85×10^{-13}	***
P. rodolfo-vasquezii	MM	Rock Cover (%)	-0.01376	0.01056	-1.303	0.193	
P. canoi	CM	Rock Cover (%)	0.30178	0.24567	1.228	0.219	
P. flavipila	L	Rock Cover (%)	-0.19234	0.12125	-1.586	0.113	
		Intercept	2.078788	0.41916	4.959	7.07×10^{-7}	***
P. rodolfo-vasquezii	MM	Bryophyte Cover (%)	-0.00921	0.010648	-0.865	0.38695	
P. canoi	CM	Bryophyte Cover (%)	0.019623	0.00679	2.89	0.00385	**
P. flavipila	L	Bryophyte Cover (%)	-0.04311	0.015032	-2.868	0.00414	**
		Intercept	2.31421	0.06913	6.9659	$<2 \times 10^{-16}$	***
P. rodolfo-vasquezii	MM	Lichen Cover (%)	-0.23455	0.11022	-2.128	0.03333	*
P. canoi	CM	Lichen Cover (%)	-0.01563	0.12404	-0.126	0.89972	
P. flavipila	L	Lichen Cover (%)	-0.54862	0.18223	-3.011	0.00261	**
		Intercept	3.09496	0.60981	5.075	7	***
P. rodolfo-vasquezii	MM	Canopy Openness (%)	-0.02114	0.00983	-2.15	0.03153	*
P. canoi	CM	Canopy Openness (%)	0.01171	0.01886	0.621	0.5346	
P. flavipila	L	Canopy Openness (%)	-0.03984	0.01223	-3.257	0.00112	**

Significance Code: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 forests of towns Mar á Moya (MM), Curimarca (CM), and Laraos (L)

Table 2 shows the regeneration by type reproductive (sexual vs. asexual) of *P. rodolfo-vasquezii*, *P. canoi*, and *P. flavipila* as a function of air temperature, air humidity, soil temperature, vegetation cover, and canopy openness in the Mar ía Moya (MM), Curimarca (CM), and Laraos (L) forests, according to the Generalized Linear Mixed Model (GLMM).

3.2. Influence of Microclimate, Vegetation Cover, and Canopy Openness on Regeneration according to the Reproductive Type in *Polylepis*

Likewise, Table 2 shows microclimatic variables (air temperature, air humidity, soil temperature), vegetation cover variables (grass, soil, rock, bryophyte, lichen), and canopy openness, highlighting significant ($p < 0.05$) and non-significant effects on regeneration according to the reproductive type of *P. rodolfo-vasquezii*, *P. canoi*, and *P. flavipila*. Non-significant variables ($p > 0.05$) were excluded. Lichen cover is significant for *P. rodolfo-vasquezii* ($p = 0.03333$) in Mar ía Moya (MM) and *P. flavipila* ($p = 0.00261$) in Laraos (L), while bryophyte cover is significant for *P. canoi* ($p = 0.00385$) in Curimarca (CM) and *P. flavipila* ($p = 0.00414$) in Laraos (L). Finally, canopy openness is significant for *P. rodolfo-vasquezii* ($p = 0.03153$) in Mar ía Moya (MM) and *P. flavipila* ($p = 0.00112$) in Laraos (L).

Figure 4 displays the correlations between environmental variables and plant height, used as an indirect indicator of the reproductive mode (asexual vs. sexual) in regenerating individuals of *P. canoi and P. flavipila*.

In Figure 4a, *P. canoi* in the Curimarca (CM) forest shows a weak positive relationship between air temperature and plant height, suggesting that higher temperatures may be linked to increased sexual reproduction. Figure 4b presents a negative relationship between soil temperature and height, indicating that lower soil temperatures may favor the growth of taller individuals, potentially associated with asexual reproduction.

Figures 4c and 4d show weak positive correlations between plant height and both grass cover and bare soil cover, suggesting that greater cover may be related to increased plant height, possibly indicating sexual reproduction.

In Figure 4e, *P. flavipila* in Laraos (L) shows a positive correlation between lichen cover and plant height, implying that a higher presence of lichens may promote sexual reproduction. In contrast, Figure 4f reveals a negative relationship between bryophyte cover and plant height *in P. canoi*, suggesting that areas with dense bryophyte cover may be more favorable to asexual reproduction. Lastly, Figure 4g shows the strongest correlation ($r = 0.39$), with a positive association between canopy openness and plant height, supporting the idea that more open environments promote the growth of individuals likely derived from sexual reproduction.

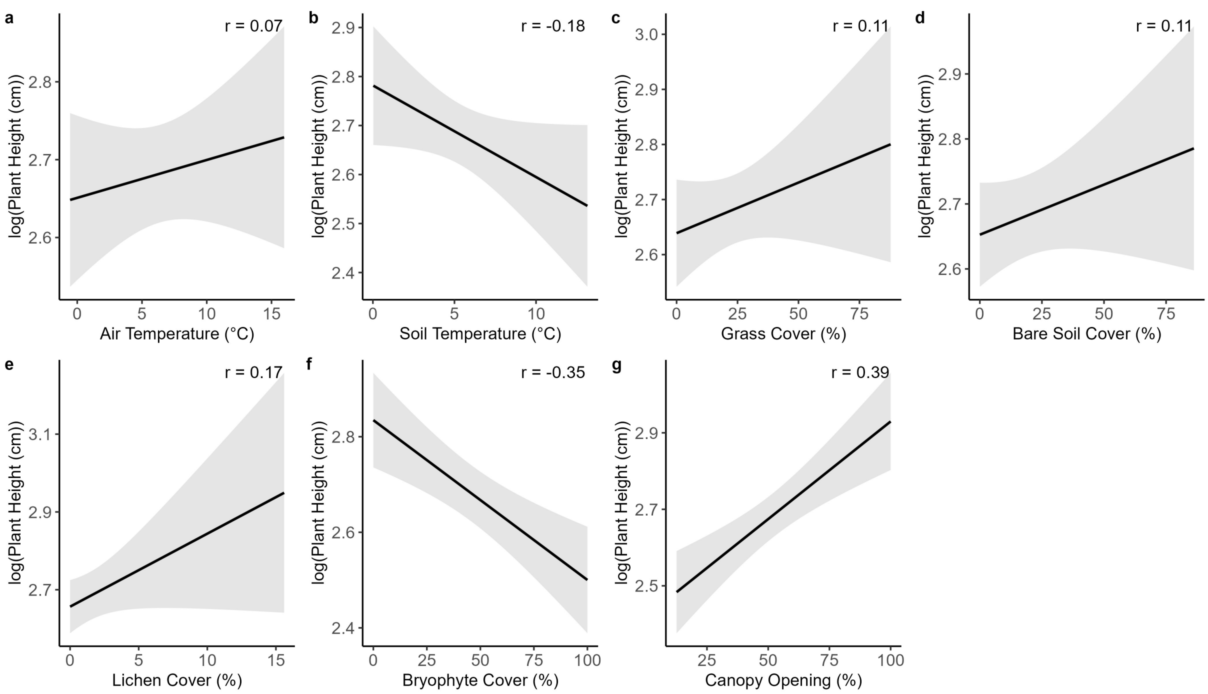

Figure 4. Linear correlation of the variables: (a) air temperature; (b) soil temperature; (c) grass cover; (d) bare soil cover; (e) lichen cover; (f) bryophyte cover; (g) Canopy opening with the reproduction type of regenerating individuals

4. Discussions

The patterns observed in the regeneration of *Polylepis canoi* in the Curimarca (CM) forest suggest a possible direct correlation with air temperature (℃). At lower temperatures, asexual regeneration appears to be more prevalent, whereas higher temperatures may be associated with a greater proportion of sexually regenerated individuals. These indications align with findings reported by Hertel et al. [16], who observed increased asexual regeneration in colder environments and a predominance of sexual reproduction under warmer conditions.

Similarly, humidity records within the forest suggest a trend toward a higher abundance of seedlings in the forest interior, which would be consistent with the observations of Cierjacks et al. [9], who proposed that internal forest microclimatic conditions tend to be more favorable than those at the edges. In the case of *P. canoi*, air humidity appeared to influence the height of regenerating individuals, whereas this effect was not clearly observed in *P. rodolfo-vasquezii* or *P. flavipila*, although vegetative development in *Polylepis* typically occurs during the wet and relatively warm season rather than year-round.

This may indicate that humidity does not act as a limiting factor for growth in the latter two species, in agreement with Hoch et al. [36], who concluded that humidity does not restrict the development of *Polylepis* trees. However, in warmer and more humid environments such as Curimarca, the slow growth observed may be related to competition for resources with faster-growing species such as *Gynoxis*, bryophytes, and grasses, as suggested by J. Hamrick et al. [39]. In fact, a possible inverse relationship was identified between air humidity and regeneration height in *P. canoi* within this forest.

Lower humidity levels appeared to be associated with taller individuals, while higher humidity seemed to favor the regeneration of shorter seedlings. This pattern could suggest that, during the early stages of development, *Polylepis* seeds may require higher moisture levels for successful establishment, as also noted by Seltmann et al. [37].

Air temperature appeared to influence the reproductive strategy in *P. canoi*, but not in *P. rodolfo-vasquezii* or *P. flavipila*. This difference may be due to variations in altitude and climatic conditions across the study sites, which would support the suggestion made by Alinari et al. [38]. In warmer and more humid forests such as Curimarca, *P. canoi* may experience slower growth, possibly as a result of competition with more vigorous species like *Gynoxis* and grasses, rather than due to microclimatic factors alone. These observations support the hypothesis that microclimatic conditions influence regeneration dynamics differently depending on forest type [39].

As reported by Chen et al. [40], soil temperature in this study was lower than air temperature. Soil temperature appeared to significantly affect regeneration in *P. rodolfo-vasquezii*, *P. flavipila*, and *P. canoi*, while air temperature showed a significant effect only in *P. canoi*. These results are consistent with the observations of Körner [41], who indicated that soil temperature tends to reflect the average air temperature beneath tree canopies, unlike in open areas. Although Rada et al. [31] emphasized the importance of soil temperature for seedling growth, no significant effect on seedling height was found in this study. However, a possible correlation was observed between soil temperature and reproductive strategy in *P. canoi*: lower temperatures were associated with asexual reproduction, while higher temperatures appeared to favor sexual reproduction. In contrast, the opposite trend was found in *P. flavipila* and *P. rodolfo-vasquezii*, differing from the findings of Renison et al. [42], who reported that low nighttime temperatures do not significantly influence reproductive mode.

Grass cover appeared to influence regeneration in *P. canoi* according to reproductive type but did not show significant effects in *P. rodolfo-vasquezii* or *P. flavipila*. This may be due to the patchy distribution of grasses in the *P. canoi* forest, particularly near forest edges and in areas close to the Huasicocha lagoon. In this forest, a possible relationship between grass cover and reproductive strategy was identified: asexual reproduction was more common in areas with low grass cover, whereas higher grass cover seemed to favor sexual reproduction. These patterns contrast with those observed by Alinari et al. [38], who found that in warm and humid forests, grasses compete more intensely with sexually regenerated individuals, while asexually regenerated ones are less affected. In the case of *P. canoi*, the opposite pattern emerged: grasses appeared to compete more strongly with asexually regenerated individuals.

Rock cover did not show significant effects on regeneration in *P. canoi*, *P. rodolfo-vasquezii*, or *P. flavipila*. However, positive effects of rocky substrates have been reported in the literature. For instance, Fjeldså [43] found higher survival and growth rates in *P. australis* seedlings growing in areas with abundant rock. Many *Polylepis* forests are located on steep slopes, among rocky outcrops, or along narrow stream corridors. Several hypotheses have been proposed to explain this distribution, including the idea that these forests are remnants of a once more extensive habitat, or that they persist in compact, nutrient-poor soils typical of high-altitude plateaus and puna ecosystems [44].

Canopy openness appeared to influence regeneration in *P. rodolfo-vasquezii* and *P. flavipila*. In areas with lower canopy openness, a higher proportion of shorter seedlings was observed, whereas more open sites were generally associated with taller individuals. A potential negative correlation was also identified between solar radiation and seedling density, possibly due to increased stress and mortality under conditions of excessive exposure [45].

At forest edges where canopy openness is typically greater sexually regenerated individuals (from seeds) appeared more frequently, while in the forest interior, where light availability was more limited, asexual regeneration seemed to be more common. Although some studies suggest that regeneration should be analyzed separately according to reproductive origin (sexual vs. vegetative), this study adopted an integrated approach. In natural settings, both reproductive modes likely coexist and respond simultaneously to environmental drivers, jointly shaping the structure and dynamics of high-Andean ecosystems [46]. Analyzing them separately could reduce the ecological representativeness of the results, especially considering that in early ontogenetic stages, it is often difficult to distinguish reproductive origin due to the lack of clearly differentiated morphological traits [47]. For this reason, the methodological decision was made to better reflect the regeneration patterns observed in the field.

While the findings of this study provide valuable insights into the potential effects of microclimate on *Polylepis* regeneration, further research is needed to understand how interactions with competing species—such as grasses and shrubs may be affecting regeneration dynamics, particularly under changing climatic scenarios. A promising line of investigation would be to assess how projected climate changes, such as rising temperatures and shifts in humidity regimes, might significantly alter regeneration patterns and species distributions along altitudinal gradients. Moreover, incorporating advanced tools such as remote sensing and predictive ecological modeling could improve both the precision and scope of environmental impact assessments related to regeneration processes in these vulnerable ecosystems.

It is important to recognize that the evaluations in this study were conducted during a specific period and therefore reflect the climatic conditions present at that time. However, these conditions are not stable throughout the year and may vary considerably. In this regard, it is recommended that future assessments be extended over longer timeframes to capture a more robust and representative picture of climatic behavior in the study area. This would contribute to a more comprehensive and accurate understanding of natural regeneration processes in response to a dynamic environmental context.

Another relevant aspect to consider is the use that local populations make of the ecosystem's natural resources. Based on direct field observations, it was identified that many activities involving the collection of wood, firewood, and other forest products are carried out without prior assessment of the impact on native species, particularly on juvenile *Polylepis*. The latter, being in early stages of development, are highly susceptible to physical damage during these extractive practices. Furthermore, the frequent entry of larger animals (livestock) was recorded, which increases pressure on seedlings and the understory, thus limiting natural regeneration processes.

Furthermore, the extraction of *Bryophytes* motivated by their demand in urban nurseries represents an additional problem that, although less visible, could have significant ecological consequences by altering moisture retention and habitat microstructure. These situations highlight the need for a more in-depth and systemic analysis of the dynamics of local resource use and its effects on the ecological integrity of the ecosystem, in order to guide sustainable management and restoration strategies that involve communities as key players throughout the process.

5. Conclusions

This study observed that the natural regeneration of *Polylepis rodolfo-vasquezii*, *P. canoi*, and *P. flavipila* may be influenced by a combination of interacting factors, including microclimatic conditions, ground cover, and canopy openness. The patterns identified suggest that air and soil temperatures, along with relative humidity, could be linked to the predominant mode of reproduction: colder environments appeared to favor sexual reproduction, while drier conditions seemed to promote asexual reproduction.

It was also noted that areas with lower coverage of lichens, bryophytes, and grasses tended to show higher levels of sexual regeneration, indicating that understory vegetation might play a role in seedling establishment. Canopy openness, in turn, showed a possible relationship with the height of regenerating individuals, as reduced light levels appeared to support early seedling growth.

While these findings are not conclusive, they provide valuable insights into how different environmental factors may be shaping the natural regeneration processes in these ecosystems. Further research will be necessary to confirm and expand upon these observations.

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REFERENCES

[1] R. C. Torres, D. Renison, I. Hensen, R. Suarez, and L. Enrico, "*Polylepis australis* regeneration niche in relation to seed dispersal, site characteristics and livestock density," *For Ecol Manage*, vol. 254, no. 2, pp. 255–260, 2008, doi: 10.1016/j.foreco.2007.08.007.

[2] W. Mendoza, "Diversity of the genus Polylepis (*Rosaceae*

Sanguisorbeae) in the Peruvian Andes,", Peruvian Journal of Biology, vol. 18, no. 2, pp. 197–200, 2011.

[3] D. H. Urrego, B. A. Niccum, C. F. La Drew, M. R. Silman, and M. B. Bush, "Fire and drought as drivers of early Holocene tree line changes in the Peruvian Andes," *J Quat Sci*, vol. 26, no. 1, pp. 28–36, 2011, doi: 10.1002/jqs.1422.

[4] C. Körner and J. Paulsen, "A world-wide study of high altitude treeline temperatures," *J Biogeogr*, vol. 31, no. 5, pp. 713–732, May 2004, doi: 10.1111/J.1365- 2699.2003.0 1043.X.

[5] M. Kessler, J. M. Toivonen, S. P. Sylvester, J. Kluge, and D. Hertel, "Elevational patterns of Polylepis tree height (*Rosaceae*) in the high Andes of Peru: Role of human impact and climatic conditions," *Front Plant Sci*, vol. 5, p. 81290, May 2014, doi: 10.3389/FPLS.2014.00194/BIBTE X.

[6] J. Muñoz, "Natural Regeneration: A review of ecological aspects in the tropical montane forest of southern Ecuador," *Zero Latitude Forests*, vol. 7, no. 2, pp. 130-143, 2017, Available: https://dialnet.unirioja.es/servlet/articulo?codig o=9349944&info=resumen&idioma=SPA

[7] L. Enrico, G. Funes, and M. Cabido, "Regeneration of *Polylepis australis* Bitt. in the mountains of central Argentina," *For Ecol Manage*, vol. 190, no. 2–3, pp. 301–309, Mar. 2004, doi: 10.1016/J.FORECO.2003.10.020.

[8] D. Renison, A. M. Cingolani, and R. Suarez, "Effects of fire on a grove of Polylepis autralis (*Rosaceae*) in the mountain of Córdova, Argentina," *Chilean journal of natural history*, vol. 75, no. 4, pp. 719–727, Dec. 2002, doi: 10.4067/S0716-078X2002000400007.

[9] M. Muñoz, K. Klanderud and D. Sheil, "Canopy openness modifies tree seedling distributions along a tropical forest elevation gradient," *Nordic Society Oikos*, vol. 2022, no. 11, Oct. 2022, doi: 10.1111/oik.09205.

[10] N. Thiffault, L. Coll, and D. F. Jacobs, "Natural regeneration after harvesting," Routledge Handbook of Forest Ecology, pp. 371–384, Oct. 2015, doi: 10.4324/9781003324072-31.

[11] R. Arasa-Gisbert, V. Arroyo-Rodríguez and J. A. Meave, "The impact of human disturbances on the regeneration layer of tropical rainforests," *Environmental Research Letters*, vol. 19, no. 12, pp. 123004, Nov. 2024, doi: 10.1088/1748-9326/AD95A0.

[12] M. F. Bertacchi, N. T. Amazonas, P. H. Brancalion, G. E. Brondani, A. C. Oliveira, M. A. Pascoa and R. R. Rodriguez "Establishment of tree seedlings in the understory of restoration plantations: natural regeneration and enrichment plantings," *Restor Ecol*, vol. 24, no. 1, pp. 100–108, Jan. 2016, doi: 10.1111/REC.12290.

[13] J. M. Toivonen, V. Horna, M. Kessler, K. Ruokolainen, and D. Hertel, "Interspecific variation in functional traits in relation to species climatic niche optima in Andean Polylepis (*Rosaceae*) tree species: Evidence for climatic adaptations," *Functional Plant Biology*, vol. 41, no. 3, pp. 301–312, Oct. 2013, doi: 10.1071/FP13210.

[14] A. Cierjacks, K. Wesche, and I. Hensen, "Potential lateral expansion of *Polylepis* forest fragments in central Ecuador," *For Ecol Manage*, vol. 242, no. 2–3, pp. 477–486, Apr. 2007, doi: 10.1016/J.FORECO.2007.01.082.

[15] W. R. Rouse, K. A. Kershaw, and K. A. Kershawi, "Vegetation Structure and Temperature Regimes of Tropical Alpine Treelines," *Arctic and Alpine Research*, vol. 3, no. 4, pp. 291–304, 1971, doi: 10.1657/1523-0430(06-055).

[16] D. Hertel and K. Wesche, "Tropical moist *Polylepis* stands at the treeline in East Bolivia: The effect of elevation on stand microclimate, above and below-ground structure, and regeneration," *Trees - Structure and Function*, vol. 22, no. 3, pp. 303–315, Jun. 2008, doi: 10.1007/S00468-007-0185-4.

[17] Y. Z. Cáceres, B. C. Torres, G. C. Archi, R. Z. Mallqui, L. E. Pinedo, D. C. Trucios, and K. A, Ortega "Analysis of Soil Quality through Aerial Biomass Contribution of Three Forest Species in Relict High Andean Forests of Peru," *Malaysian Journal of Soil Science*, vol. 28, pp. 38–52, 2024.

[18] H. Shaheen, S. Nasar, S. Aziz, N. Mumtaz and S. Aziz, "Regeneration Pattern in Subtropical and Moist Temperate Forest Stands of Kashmir Himalayas," *Environment and Ecology Research*, vol. 5, no. 5, pp. 340-346, 2017, doi: 10.13189/eer.2017.050503.

[19] G. E. Cuyckens, I. Hensen, V. L. López, J. M. Cellini, and D. Renison, "Germination of high Andean treeline species of contrasting environments and along elevational gradients in northwest Argentina," *Neotrop Biodivers*, vol. 7, no. 1, pp. 111–120, Jan. 2021, doi: 10.1080/23766808.2021.1906 137.

[20] C. K. Vega, C. Gabriela Villegas, P. A. Rocabado, J. A. N. Quezada, M. Y. López, and A. W. Quevedo, " Reproductive biology of three Polylepis species (*P. neglectus*, *P. incarum and P. pacensis*), with emphasis on their germination behavior," *Southern Ecology*, vol. 28, no. 1, pp. 310–324, Jun. 2018, doi: 10.25260/EA.18.28.1.1.703.

[21] Z. Wang, K. Qin, W. Fang, and H. Wang, "Neighborhood Competition and Understory-Associated Vegetation Are Important Factors Influencing the Natural Regeneration of Subtropical Mountain Forests," *Forests*, vol. 15, no. 6, p. 1017, Jun. 2024, doi: 10.3390/F15061017/S1.

[22] V. L. López, "Regeneration dynamics, vertical and horizontal structure in *Polylepis tarapacana* Philippi forests across different environmental gradients in Argentina," *Faculty of Agricultural and Forestry Sciences*, Jul. 2024, doi: 10.35537/10915/168178.

[23] F. M. Kerton, "UN Sustainable Development Goals 14 and 15 – Life below water, Life on land," *Royal Society of Chemistry*, vol. 1, pp. 401-403, Apr 2023, doi: 10.1039/D3SU90010J.

[24] R. Yaranga, M. Arizapana, E. Orellana, V. Pariona, and I. Castañeda, "Water Status of Polylepis Forests Related to Altitudinal Gradient, Microclimate Variables and Slope," *Journal of Ecological Engineering*, vol. 22, no. 3, pp. 151–160, Mar. 2021, doi: 10.12911/22998993/132425.

[25] M. Kessler and A. N. Schmidt-Lebuhn, "Erratum to 'Taxonomical and distributional notes on Polylepis (*Rosaceae*)," *Org Divers Evol*, vol. 6, no. 2, p. 163, May 2006, doi: 10.1016/J.ODE.2006.02.002.

[26] L. Valenzuela and I. Villalba, "A new species of *polylepis* (*rosaceae*) from Peru," *Arnaldoa*, vol. 22, no. 2, Dec. 2015.

[27] F. Rada, C. García-Núñez, and S. Rangel, "Microclimate

and regeneration patterns of Polylepis sericea in a treeline forest of the Venezuelan Andes," *Ecotropics*, vol. 24, no. 1, pp. 113–122, 2011, [Online]. Available: http://ecotropicos.saber.ula.ve

[28] V. L. López, A. Huertas Herrera, Y. M. Rosas, and J. M. Cellini, "Optimal environmental drivers of high-mountains forest: *Polylepis tarapacana* cover evaluation in their southernmost distribution range of the Andes," *Trees, Forests and People*, vol. 9, p. 100321, Sep. 2022, doi: 10.1016/J.TFP.2022.100321.

[29] Y. Chen, T. Shen and R. Condit, "Disentangling multi-species aggregate versus overlapping distributions," *Journal of Vegetation Science*, vol. 32, no. 1, pp. e12973, Nov. 2020, doi: 10.1111/jvs.12973.

[30] L. V. Morales, C. S. Sevillano-Rios, S. Fick, and T. P. Young, "Differential seedling regeneration patterns across forest–grassland ecotones in two tropical treeline species (*Polylepis* spp.)," *Southern Ecology*, vol. 43, no. 5, pp. 514–526, Aug. 2018, doi: 10.1111/AEC.12588.

[31] F. Rada, C. Nuñez and S. Rangel, "Low temperature resistance in saplings and ramets of Polylepis sericea in the Venezuelan Andes", *Acta Oecologica*, vol. 35, pp. 610–613, Oct 2004, doi: 10.1016/j.actao.2009.05.009.

[32] D. Renison and A. M. Cingolani, "Experiences in germination and vegetative reproduction applied to reforestation with *Polylepis australis* (Rosaceae) in the Sierras Grandes of Córdoba, Argentina," *AgriScientia*, vol. 15, pp. 47–53, 1998, [Online]. Available: https://dialnet.unirioja.es/servlet/articulo?codigo=9827624

[33] C. Gaillard and M. Pece, "Sampling and assessment techniques for vegetation and fauna," Argentina: National University of Santiago del Estero – UNSE, Dec 2014, ISBN 978-987-1676-44-6.

[34] P. Franco, C. Cáceres, M. Navarro, C. Jove, J. Ignacio, and E. Oyague, "*Polylepis tarapacana* forests in the Maure Basin, in the far south of Peru. Opportunities for their conservation," *Estud Geogr*, vol. 82, no. 290, pp. e059–e059, Jun. 2021, doi: 10.3989/ESTGEOGR.202071.071.

[35] Y. Zacarías and R. F. Del Castillo, "Plant communities of the Sierra Juarez, Oaxaca: altitudinal zones and their potential implications for climate change," *Bol. Soc. Bot. Méx*, no. 87, Dic. 2010.

[36] G. Hoch and C. Kessler, "Growth, demography and carbon relations of Polylepis trees at the world's highest treeline," *Funct Ecol*, vol. 19, no. 6, pp. 941–951, Dec. 2005, doi: 10.1111/J.1365-2435.2005.01040.X.

[37] P. Seltmann, I. Leyer, D. Renison and I. Hensen, "Variation of seed mass and its effects on germination in Polylepis australis: implications for seed collection," *New Forests*, vol. 33, pp. 171–181, Nov. 2006, doi: 10.1007/s11056-006-9021-8.

[38] J. Alinari, A. von Müller, and D. Renison, "The contribution of fire damage to the restriction of high-altitude Polylepis australis forests to gullies: From an unreplicated comparison," *Ecología Austral*, vol. 25, no. 1, pp. 11–18, Apr. 2015, doi: 10.25260/EA.15.25.1.0.53.

[39] J. L. Hamrick and J. M. Lee, N. K. Rühr, K. Wesche, and I. Hensen, "Effect of soil surface topography and litter cover on the germination, survival, and growth of musk thistle (*Carduus nutans*)," *American Journal of Botany*, vol. 74, no. 3, pp. 451–457, Mar. 1987, doi: 10.1002/j.1537-2197.1987.tb08627.x.

[40] J. Chen, S. Saunders, T. Crow, R. Naiman, K. Brosofske, G. Mroz, B. Brookshire and J. Franklin, "Microclimate in Forest Ecosystem and Landscape Ecology: Variations in local climate can be used to monitor and compare the effects of different management regimes," *BioScience*, vol. 49, no. 4, pp. 288–297, Apr. 1999, doi: 10.2307/1313612

[41] C. Körner, "Alpine plant life: Functional plant ecology of high mountain ecosystems," Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems, *Nature Link*, pp. 1–500, May 2021, doi: 10.1007/978-3-030-59538-8/COVER.

[42] D. Renison, A. Cingolani, R. Suarez, E. Menoyo, C. Coutsiers, A. Sobral, I. Hensen "The Restoration of Degraded Mountain Woodlands: Effects of Seed Provenance and Microsite Characteristics on Polylepis australis Seedling Survival and Growth in Central Argentina," *Restor Ecol*, vol. 13, no. 1, pp. 129–137, Mar. 2005, doi: 10.1111/J.1526-100X.2005.00015.X.

[43] J. Fjeldså, "The avifauna of the Polylepis woodlands of the Andean highlands: the efficiency of basing conservation priorities on patterns of endemism," *Bird Conserv* Int, vol. 3, no. 1, pp. 37–55, 1993, doi: 10.1017/S0959270900000770.

[44] H. Shemesh, "A systematic review of nurse objects as safe sites for seedling establishment and implications for restoration," *New Phytologist*, vol. 245, no. 6, pp. 2428–2438, Mar. 2025, doi: 10.1111/NPH.20247.

[45] K. Wesche, A. Cierjacks, Y. Assefa, S. Wagner, M. Fetene, and I. Hensen, "Recruitment of trees at tropical alpine treelines: Erica in Africa versus Polylepis in South America," *Plant Ecol Divers*, vol. 1, no. 1, pp. 35–46, 2008, doi: 10.1080/17550870802262166.

[46] M. Kessler, "The 'Polylepis problem': Where do we stand?," *Ecotropica*, vol. 8, pp. 97-110, 2014.

[47] M. R. Spater, R. Montufar, C. Luzuriaga, N. Bolta, M. Trapote, R. Smedley, R. Marchant, and E. Montoya, "Vegetation response to Holocene hydroclimatic variability in the aseasonal forests of the north-western Amazon," *Palaeogeogr, Palaeoclimatol Palaeoecol*, vol. 649, Sep. 2024, doi: 10.1016/j.palaeo.2024.112303.