

Article

Mountaintop-Extinction Risk for *Polylepis tarapacana*: An Elevational-Ceiling and No-Escape Framework in the South-Central Andes

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Abstract

Sustained warming is displacing montane species upslope, yet trees already at the upper limit of their mountains face a finite vertical refuge. This study assessed whether the world's highest-elevation tree, *Polylepis tarapacana*, can remain within climatically suitable terrain as the climate warms across its South-Central Andean range (Peru, Bolivia, Chile, and Argentina), with field validation in Tacna, southern Peru. The aim was to quantify, under CMIP6 scenarios extending to 2100, how much suitable habitat the species retains and what fraction of any loss leaves no reachable higher-elevation refuge. A MaxEnt model, benchmarked against Random Forest, was calibrated on the full known range from GBIF occurrences and field plots using collinearity-filtered bioclimatic predictors and a sampling-bias-corrected background, projected as a multi-GCM ensemble under CMIP6 twenty-first-century scenarios, and validated externally against 148 field-mapped stand polygons (12,874 ha). A novel elevational-ceiling and “no-escape” framework quantified, for each scenario, the suitable area lost without any reachable higher-elevation refuge. The models discriminated suitable habitat well (external AUC = 0.85, Boyce = 0.98). Under the highest-emission pathway, suitable habitat in Tacna contracts from −13% (2030s) to −100% (2090s) and the highly suitable class collapses by 99.4%; across the partial-loss scenarios, the suitability centroid shifts upslope by up to +195 m. By 2081–2100 the no-escape fraction reaches 100% at every tested dispersal buffer—to date the first quantitative evidence of mountaintop-extinction risk for the world's highest-elevation tree. These results argue for anticipatory ex situ conservation and Peru–Bolivia cross-



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border protection of the highest-elevation Altiplano refugia, before the vertical escape route closes.

Keywords: climate change; treeline; MaxEnt; species distribution model; assisted migration; SSP scenarios

1. Introduction

One of the most consistent biological signatures of a warming climate is the movement of species toward cooler ground—poleward in latitude and upslope in elevation [1–5]. Beyond the horizontal and vertical displacement of ranges, warming stress at the upper limit is also expressed in situ as reduced growth, declining biomass, and recurrent shoot dieback, and any upslope movement is bounded by the elevational vegetation belts, so that a population pushed above the alpine treeline ecotone enters a tier that cannot support forest [6,7]. For organisms already restricted to the upper elevational limit of their host mountain range, this upward tracking is constrained by a finite amount of land above: as isotherms rise, the area of climatically suitable terrain contracts toward the summits until, for the highest-dwelling taxa, it can disappear altogether [8,9]. This “escalator to extinction” has made high-mountain species emblematic sentinels of climate change [2], yet the severity of the threat hinges on a balance that is rarely quantified explicitly: the upward shift a species must make to stay within suitable climate versus the upward shift its topography can physically supply. Woody species at the upper tree limit meet this squeeze on every continent, from *Pinus* and *Juniperus* in the Northern Hemisphere to *Nothofagus* in the southern temperate zone and *Polylepis* in the tropical Andes, making the elevational ceiling a globally recurrent constraint on treeline trees rather than a regional peculiarity.

Few woody systems embody this predicament as sharply as the high-Andean *Polylepis* (Rosaceae) woodlands. The genus forms the highest-elevation forests on Earth, fringing the upper Andean treeline between roughly 3000 and 5000 m and sustaining hydrological regulation, soil retention, carbon storage, and a distinctive endemic biota across the tropical and subtropical Andes [6,7,10,11]. Within the genus, *Polylepis tarapacana* is exceptional: it reaches approximately 5200 m in the Altiplano of Peru and Bolivia, making it the highest-elevation angiosperm tree species known [12,13]. Its confinement to a narrow altitudinal band on isolated, finite cordilleras makes it a paradigmatic case of a species with little vertical room to escape a warming climate, while ongoing fragmentation and land-use pressure already erode its populations [13], even as high-elevation *Polylepis* forests prove acutely sensitive to climate [14,15].

Correlative species distribution models (SDMs) have become the standard tool for anticipating how climate change will redistribute suitable habitat [16–18], and maximum-entropy models (MaxEnt) and Random Forest (RF) classifiers are among the most widely applied algorithms for this purpose and perform competitively in benchmark comparisons [19–21]. For Andean trees, such models have been used to map current distributions, identify climatic refugia and prioritize restoration, including recent range-wide and national applications in Peru and treeline modeling in the southern Andes [22–24].

For *Polylepis tarapacana*, however, distribution models remain scarce and are typically calibrated on national subsets of the range [12]; as in studies of congeneric treeline species such as *P. quadrijuga*, they are validated almost exclusively against presence/absence records [25]. Calibrating over a truncated extent biases the estimated niche and the projections derived from it [26,27], and binary validation cannot reveal whether a population displaced upslope will actually find suitable ground above it—nor whether the species

could reach it. Present warming is proceeding far faster than the climatic shifts of the geological past, while long-lived trees migrate slowly, so isotherms rise roughly an order of magnitude faster than a treeline can advance; this mismatch propagates into losses first at the individual, then the population, and ultimately the species level [28]. The complementary concept of mountaintop extinction—the loss of high-elevation species as their climate space rises off the top of the available terrain—has been articulated mainly for tropical mountain birds and other animals [8,29–33]; it is seldom operationalized for trees and almost never confronted with independent field data. Consequently, the central question for the world’s highest tree—whether the upslope shift it requires can be topographically supplied—remains unanswered.

This study addresses three questions. (1) How much climatically suitable habitat is *Polylepis tarapacana* projected to lose across twenty-first century emission scenarios? (2) What fraction of that habitat lies in locations with no higher-elevation refuge within reach—a quantitative “no-escape” fraction? (3) Is this climate-driven compression corroborated by an independent, field-observable signature of stress at the upper niche edge? In treeline trees, the stunted, multi-stemmed krummholz architecture is a recognized phenotypic response to sustained cold and wind stress [7], so its prevalence in a population is itself a field-readable marker of life at the climatic edge. Three falsifiable hypotheses follow: (i) suitable area contracts as the species is pushed upslope, with the topographic ceiling driving a substantial net loss—rather than a mere redistribution—of suitable area under the highest-emission pathway by the end of the century; (ii) the no-escape fraction rises steeply with emission severity; and (iii) the species is predominantly multi-stemmed and krummholz in growth form—the morphology expected of a tree population persisting under chronic climatic stress at its upper limit [34].

Because suitability maps increasingly guide where high-mountain woodlands are protected and restored, yet cannot by themselves show whether escape upslope is possible, this study models the current and future habitat suitability of *Polylepis tarapacana* across its full South-Central Andean range and, from those range-wide projections, quantifies its climate-driven mountaintop-extinction risk within its Peruvian stronghold, the Tacna region of southern Peru, where the elevational squeeze is most acute and independent field data exist. Framed by an elevational-ceiling and “no-escape” framework that makes the mountaintop-extinction concept measurable for a tree, hitherto operationalized almost exclusively for animals, and validated against field ground truth, it converts habitat-loss maps into spatially explicit statements of extinction risk. As the world’s highest-elevation tree, confined to a narrow altitudinal band on finite cordilleras, *Polylepis tarapacana* thereby serves as a model species whose elevational-ceiling analysis transfers to elevation-limited trees at the upper tree limit worldwide.

2. Methods

A reproducible, single-configuration workflow couples range-wide species distribution modeling of *Polylepis tarapacana* with the novel elevational-ceiling analysis (Figure 1). Occurrence and environmental data feed predictor reduction, spatially cross-validated MaxEnt and Random Forest models, and multi-scenario Coupled Model Intercomparison Project Phase 6 (CMIP6) projection; the resulting range change is combined with a Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) to quantify climate-driven elevational compression and no-escape (mountaintop-extinction) risk (Section 2.6).

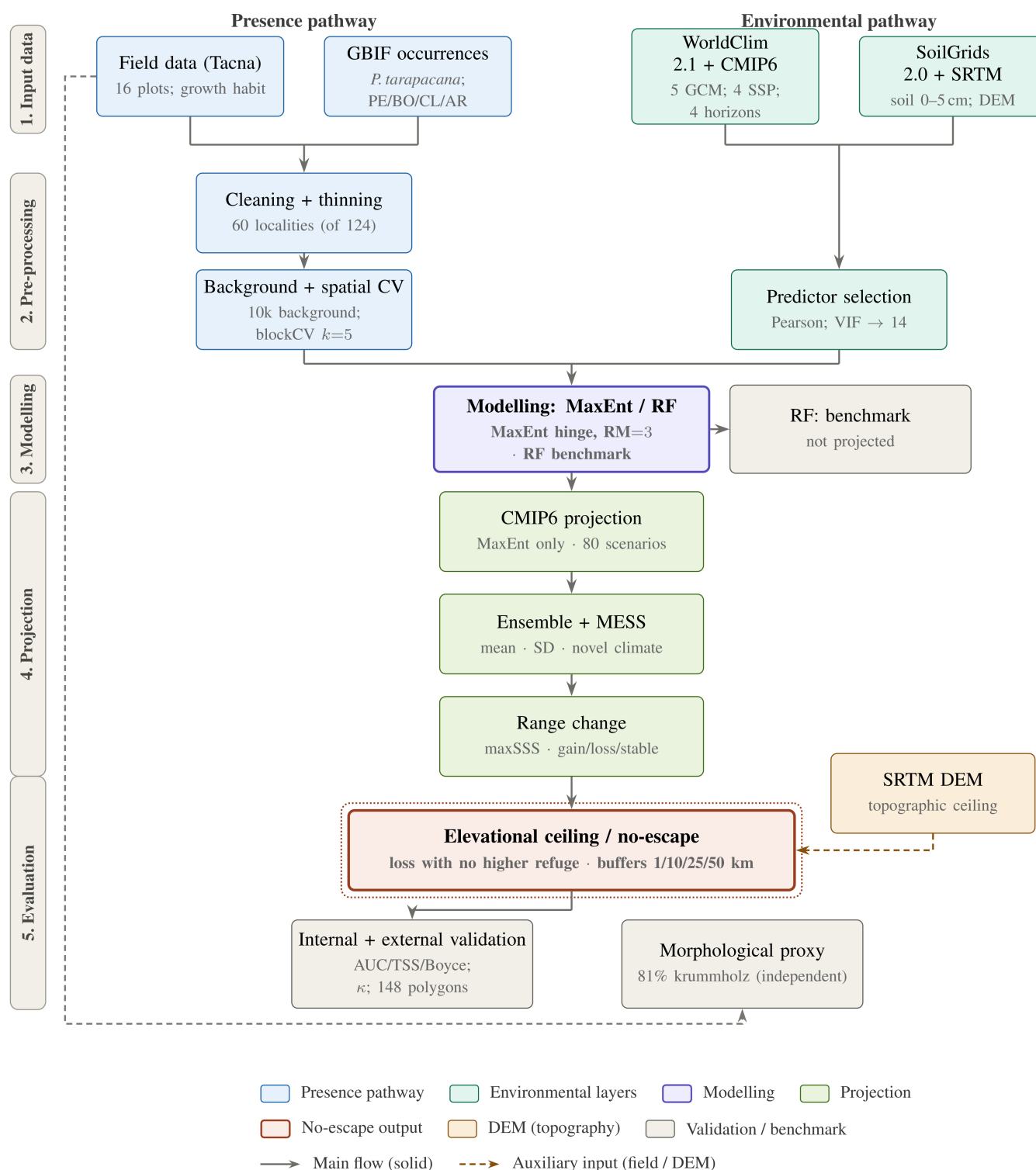


Figure 1. Analytical workflow for the *Polylepis tarapacana* distribution model and mountaintop-extinction (no-escape) analysis.

2.1. Study Species and Area

Polylepis tarapacana (Rosaceae) is a small evergreen tree restricted to the high-elevation grasslands and shrublands of the South-Central Andes (~15–26° S, 3500–5200 m), spanning Peru, Bolivia, Chile, and Argentina. In Tacna, southern Peru (Figure 2), it occurs in the eastern cordillera near the Bolivian border, typically above 4000 m. Field measurements from this study (Section 2.7) document a predominantly krummholz growth habit (81%

multi-stemmed individuals), consistent with persistent cold/wind stress at the upper niche edge (field photographs in Figure S6).

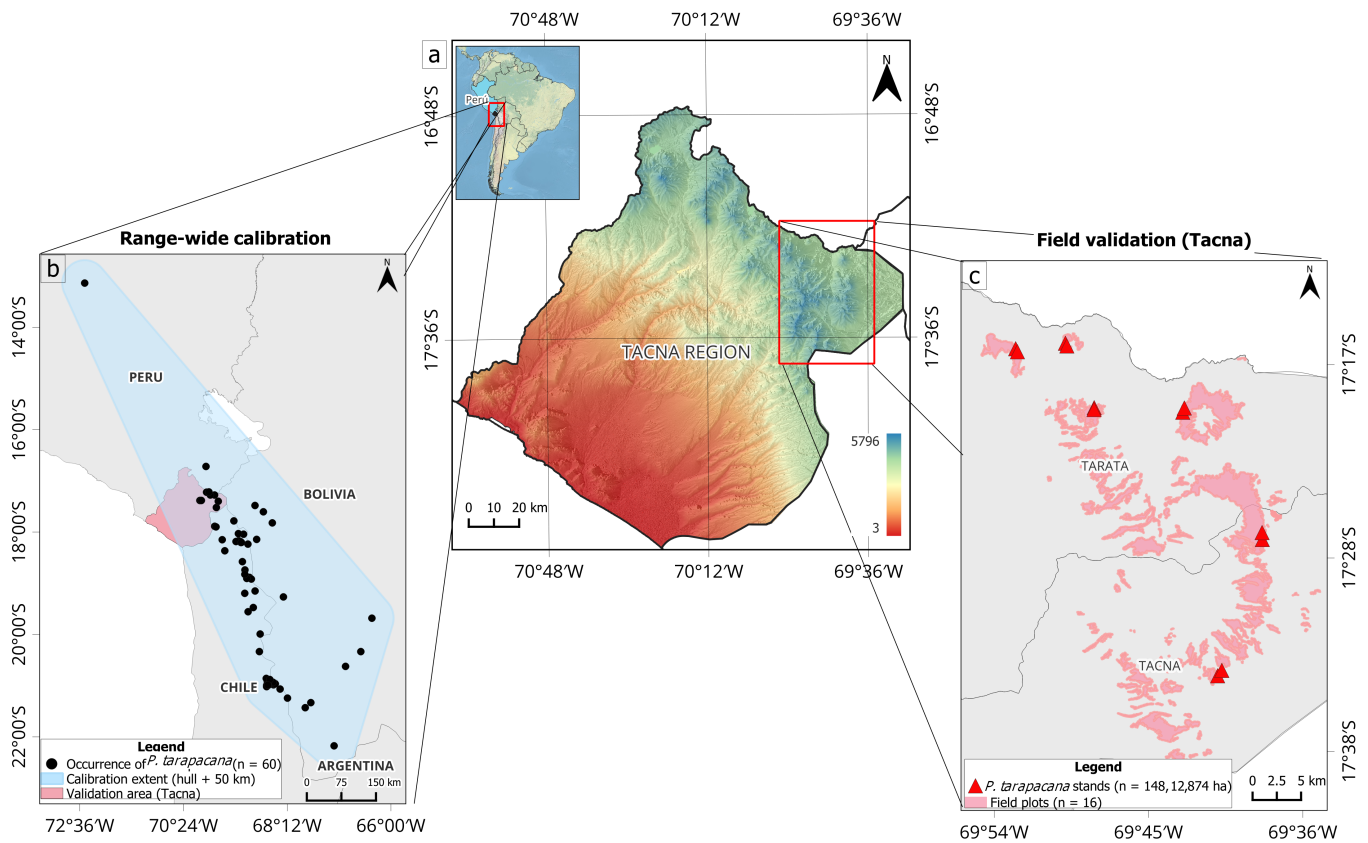


Figure 2. Study design for *Polylepis tarapacana*: (a) Tacna study area and South American locator; (b) range-wide calibration domain (60 occurrences; convex hull + 50 km); (c) field validation in Tacna (148 stand polygons, 16 inventory plots).

2.2. Occurrences and Calibration Extent

All *Polylepis tarapacana* occurrences were retrieved from the Global Biodiversity Information Facility (GBIF), whose taxonomic backbone follows the Catalogue of Life [35], for the four-country range, records were filtered with CoordinateCleaner [36] (coordinate uncertainty < 5 km, post-1980, no centroid/herbarium flags) and a species-specific elevation filter (3500–5300 m—a margin slightly above the documented upper limit, retaining genuine high-elevation records while removing low-elevation database errors), and 16 field plots inventoried in the Tacna region for the present study were added. Records were spatially thinned to a 1 km minimum distance (spThin; [37]), yielding 60 spatially independent presence localities (from 124 raw records) for calibration (Table 1). These localities occupy the high-Andean cordillera, predominantly between about 4000 and 5000 m, on the cool upper slopes above the intensively used valley floors, consistent with a cold-adapted, high-elevation niche; human-disturbance and NDVI layers were not used as predictors, which keeps the future projection climate- and terrain-based. A target-group background of 10,000 points was drawn with sampling effort proportional to the density of all Rosaceae GBIF records within the calibration extent, correcting for survey bias [38]. Calibration used the convex hull of the cleaned occurrences with a 50 km buffer, encompassing the entire South-Central Andean range to avoid niche truncation [26,39]. Calibration was the only range-wide step: all subsequent products—the projected range change, the elevational-compression and no-escape metrics, and the external field validation—were computed

on the prediction clipped to the Tacna region of southern Peru, the species's Peruvian stronghold and the only part of its range with field data.

Table 1. Data sources and sample sizes for the *Polylepis tarapacana* distribution model and its external validation.

Data Source	n/Extent	Notes
Cleaned presence localities (calibration)	60	GBIF plus field plots, after <code>CoordinateCleaner</code> , the 3500–5300 m elevation filter and 1 km spatial thinning
Field inventory plots (Tacna, this study)	16	457 individual trees measured (diameter at breast height, DBH; height; basal area; crown; growth habit)
Target-group background points	10,000	sampled in proportion to Rosaceae record density (sampling-bias correction)
Stand polygons—external presence	148 (12,874 ha)	field-mapped <i>Polylepis tarapacana</i> stands
Genus-prospected absence mask	26,587 ha	<i>Polylepis</i> -prospected area; source of external absences
External validation grid cells	166/171	presence/absence cells at the maxSSS threshold

2.3. Environmental Predictors

Candidate predictors comprised the 19 WorldClim 2.1 bioclimatic variables at 30 arc-seconds [40], five SoilGrids 2.0 0–5 cm edaphic layers (pH; soil organic carbon, SOC; clay; sand; nitrogen, N; [41]), and SRTM-derived elevation, slope, topographic position index (TPI) and aspect [42], with aspect decomposed into northness and eastness—29 candidate layers in total. Collinearity was reduced with a Pearson filter ($|r| < 0.8$) followed by variance inflation factor (VIF) stepwise selection (<5 ; `usdm::vifstep` [43]), the same protocol recently adopted for Peruvian dryland and Andean tree SDMs [22,23]. Fourteen predictors were retained—five bioclimatic (bio2, mean diurnal range; bio3, isothermality; bio8, mean temperature of the wettest quarter; bio15, precipitation seasonality; bio19, precipitation of the coldest quarter), four topographic (slope, TPI, northness, eastness), and five edaphic (pH, SOC, clay, sand, nitrogen)—while elevation was dropped as collinear with temperature; all 19 WorldClim bioclimatic variables were screened as candidates, and the complete candidate list with variance inflation factors is given in Table S1. Because the model requires all predictors to be non-missing, grid cells lacking any layer—notably the Pacific lowlands of western Tacna, outside SoilGrids coverage and below the species' elevational range—fall outside the modeled domain. The SRTM elevation surface is nonetheless retained as the geometric reference for the elevational-ceiling analysis (Section 2.6), where it enters as topography rather than as a niche predictor. Future climate was drawn from the WorldClim CMIP6 archive [44] at 2.5 arc-minutes, for five global climate models (GCMs: ACCESS-CM2, EC-Earth3-Veg, GFDL-ESM4, MPI-ESM1-2-HR, MRI-ESM2-0), four Shared Socioeconomic Pathways (SSPs: 126, 245, 370, 585; [45,46]), and four horizons (2021–2040/2041–2060/2061–2080/2081–2100; the four-period convention of [22,23]), totaling 80 future scenarios. The five global climate models are identified by their official CMIP6 names (ACCESS-CM2, EC-Earth3-Veg, GFDL-ESM4, MPI-ESM1-2-HR, and MRI-ESM2-0), which are standard model identifiers rather than further-expandable acronyms; the four horizons span the twenty-first century, so the projections extend to its end (2081–2100,

referred to as 2100 throughout). Only the bioclimatic predictors vary across these scenarios; the edaphic and topographic layers are held constant at their present-day values, and because SoilGrids 2.0 is a global machine-learning product with lower accuracy in steep, sparsely surveyed high-mountain terrain than in intensively sampled lowlands, its layers were used only as static, coarse background predictors, so that no projected change is attributed to soil.

Spatial Resolution and Grid Contract

Present-day predictors are at 30 arc-sec (~ 1 km); CMIP6 futures are kept at their native 2.5 arc-min (~ 5 km) and are *never* upsampled to 1 km, which would inject fake sub-grid detail. All elevational-compression metrics are computed on the future 5 km grid, with the DEM and the present-day suitability raster aggregated down to it once. Within that 5 km grid, the 1 km no-escape buffer corresponds to the source cell plus its immediate ring (a strict in-place persistence proxy); 10 km is approximately 2 cells radius (the biologically realistic primary), 25 km ≈ 5 cells, 50 km ≈ 10 cells. The standalone 1 km present-day map is shown for context only.

2.4. Modelling

Two complementary algorithms were fitted. MaxEnt is a maximum-entropy method that contrasts the environment at presence localities against a background sample to estimate relative habitat suitability, whereas Random Forest is an ensemble of classification trees grown on bootstrap resamples; because the two make different bias–variance trade-offs, their agreement provides an algorithm-independent check on the projected range change. MaxEnt [47] was fitted with maxnet [20] via ENMeval [48] using a per-species tuning grid over feature classes (FC; L, linear; Q, quadratic; H, hinge) and the regularization multiplier (RM): FC $\in \{LQ, LQH, H\}$, RM $\in \{1, 2, 3\}$; the broader pure-linear and RM = $\{0.5, 4\}$ extremes were excluded a priori to avoid flat-response or over-shrunken models [49]. Following Cotrina-Sanchez et al. [22], the optimal model was selected by the *highest* regularization multiplier, with the fewest feature classes as primary tie breaker and the validation area under the receiver operating characteristic curve (AUC) as secondary tie breaker; the legacy lowest-10%-omission-rate rule was also computed for audit. Both rules converged on the same optimal configuration—hinge features at a regularization multiplier of 3, which also gave the lowest 10% omission rate in the candidate set (Table S2). As an algorithmic benchmark, a Random Forest [21,50] of 1000 trees with majority-class down-sampling was fitted on the same data. Spatial block five-fold cross-validation (blockCV, block size ~ 140 km, estimated from the residual autocorrelation range [51]; Figure S5) yielded AUC, the true skill statistic (TSS; at the maximum sum of sensitivity and specificity, maxSSS; [52]) and the Continuous Boyce Index (CBI; [53,54]). Suitability was predicted on the cloglog scale, and the Random Forest permutation importance is reported in the Supplementary Materials (Table S4).

2.5. Future Projection and Uncertainty

For each of the 80 future scenarios, the optimal MaxEnt model was projected and ensemble means and standard deviations (SDs) were built across the five GCMs by SSP $\times$ horizon [55], the among-GCM SD mapping inter-model uncertainty (Figure S3). Novel climate conditions were identified with multivariate environmental similarity surfaces (MESS; [19]) and predictions were clamped to the calibration range to mitigate extrapolation. Binary suitable/unsuitable rasters were thresholded with maxSSS derived from the full-extent (range-wide) present-day prediction [56]. For visualization, continuous rasters were also classified into four habitat-quality classes using the extinction-risk-oriented scheme of Barboza et al. [23]: *unsuitable* (<0.1), *little suitable* (0.1–0.3), *moderately suitable* (0.3–0.5),

and *highly suitable* (≥ 0.5). This scheme resolves the low-suitability range more finely, which is appropriate for detecting the marginal, extinction-prone habitat that is the focus here.

2.6. Mountaintop-Extinction Metric (No-Escape Area)

The novel post-processing module quantified the climate-driven elevational compression for each future scenario as follows. Let $\text{cur}(x)$ and $\text{fut}(x)$ denote the binary suitability at grid cell x at present and under a given future scenario, and let $\text{elev}(x)$ denote the SRTM elevation resampled to the suitability grid. For each cell x that is currently suitable ($\text{cur}(x) = 1$), the maximum elevation of future-suitable cells was computed within a square moving window of half-width B km centered on x (its cell equivalents on the 5 km grid are given in Section 2.3), $M_B(x) = \max\{\text{elev}(y) : \|y - x\|_\infty \leq B, \text{fut}(y) = 1\}$. Cell x was classified as *no-escape* when $\text{fut}(x) = 0$ and $M_B(x) < \text{elev}(x)$, i.e., no future-suitable cell at higher (or equal) elevation exists within the species's plausible upslope dispersal range. Because the realistic upslope colonization capacity of a long-lived, slow-colonizing treeline tree over the ~ 80 -year horizon is poorly constrained and is generally about an order of magnitude slower than the rate at which isotherms rise [3,6,28], the no-escape fraction was evaluated across a graded set of dispersal buffers rather than a single assumed value: $B = 1$ km approximates virtual non-dispersal (in-place persistence, $\approx 12 \text{ m yr}^{-1}$) and is adopted as the precautionary reference; $B = 10$ km ($\approx 125 \text{ m yr}^{-1}$) is an optimistic upper bound; and $B = 25$ and 50 km represent progressively more extreme dispersal optimism. All four buffers are reported for every SSP $\times$ horizon combination. The no-escape fraction is the ratio of no-escape area to the present-day suitable area. Because all elevational-compression products are computed on the prediction clipped to the Tacna region, the upslope-refuge search is confined to that area; the metric therefore quantifies the loss of an *in-region* refuge and does not credit potential refugia immediately across the regional border (Section 4). The upward shift of the elevation-weighted centroid of suitable area per scenario, and the suitable area per 100 m elevational band, are also reported.

2.7. Field Validation

Two external validation layers were applied for the Tacna projection:

1. **Stand polygons.** A total of 148 field-mapped *Polylepis tarapacana* stand polygons (12,874 ha) provided presence, and the *Polylepis*-prospectored absence mask (26,587 ha, outside the polygons) provided absence; both were rasterized to the ~ 1 km prediction grid, yielding 166 presence and 171 absence cells from which sensitivity, specificity, TSS, and κ were computed at the maxSSS threshold, together with the threshold-independent AUC and CBI.
2. **Morphological proxy of stress.** On 16 inventory plots, growth habit (single- vs. multi-stemmed) was recorded per stem. A high multi-stemmed (krummholz) proportion at the upper-elevation edge is independent morphological evidence of persistent climatic stress (see Section 4).

The 148 validation polygons were not themselves used in model calibration; because the 16 inventory plots falling within them did contribute to the calibration presences; however, the polygon-based validation tests transfer to the field-mapped stand extent rather than to fully held-out localities. Most calibration localities nonetheless lie outside the Tacna region across the range, and the maxSSS threshold is derived from the full-extent present-day prediction.

3. Results

3.1. Field-Validated Current Distribution

Under spatial block cross-validation the MaxEnt model discriminated suitable from unsuitable conditions well, with $AUC = 0.863 \pm 0.071$, $TSS = 0.717 \pm 0.140$, and $CBI = 0.490 \pm 0.385$ across the five spatial folds (per-fold values in Table S3); Random Forest performed similarly ($AUC = 0.893 \pm 0.094$, $TSS = 0.731 \pm 0.157$, $CBI = 0.574 \pm 0.277$). Validated externally against the field-mapped stand polygons (166 presence and 171 absence cells at the maxSSS threshold of 0.519), MaxEnt was highly sensitive (0.940) with moderate specificity (0.386; $TSS = 0.326$, $\kappa = 0.323$, $AUC = 0.848$), and the Boyce index against the same independent polygons was very high (0.981; Table 2). Although the internal cross-validated Boyce index was low and variable across the spatial folds ($CBI = 0.490 \pm 0.385$; per-fold values in Table S3)—a consequence of the small presence sample partitioned among blocks—the strong AUC together with the very high *external* Boyce confirms that the model ranks habitat quality reliably; the moderate threshold-dependent specificity reflects the inherent difficulty of separating occupied from prospected-but-unoccupied stands on climate alone at the regional scale.

Table 2. External validation against the field-mapped stand polygons (presence cells) and the genus-prospected absence mask, at the maxSSS threshold derived from the full-extent prediction.

Model	n_+	n_-	Thr.	Sens	Spec	TSS	κ	AUC	CBI
MaxEnt	166	171	0.519	0.940	0.386	0.326	0.323	0.848	0.981
Random Forest	166	171	0.708	0.747	0.620	0.367	0.366	0.781	0.952

n_+/n_- , presence/absence cells; Thr., maxSSS threshold; Sens, sensitivity; Spec, specificity; TSS, true skill statistic; κ , Cohen's kappa; AUC, area under the receiver operating characteristic (ROC) curve; CBI, Continuous Boyce Index.

The present-day suitability surface, both range-wide and clipped to Tacna, is mapped in Figure 3; the gray western third of Tacna is the Pacific coastal lowland below the species' Andean elevational range, out-of-domain rather than missing data.

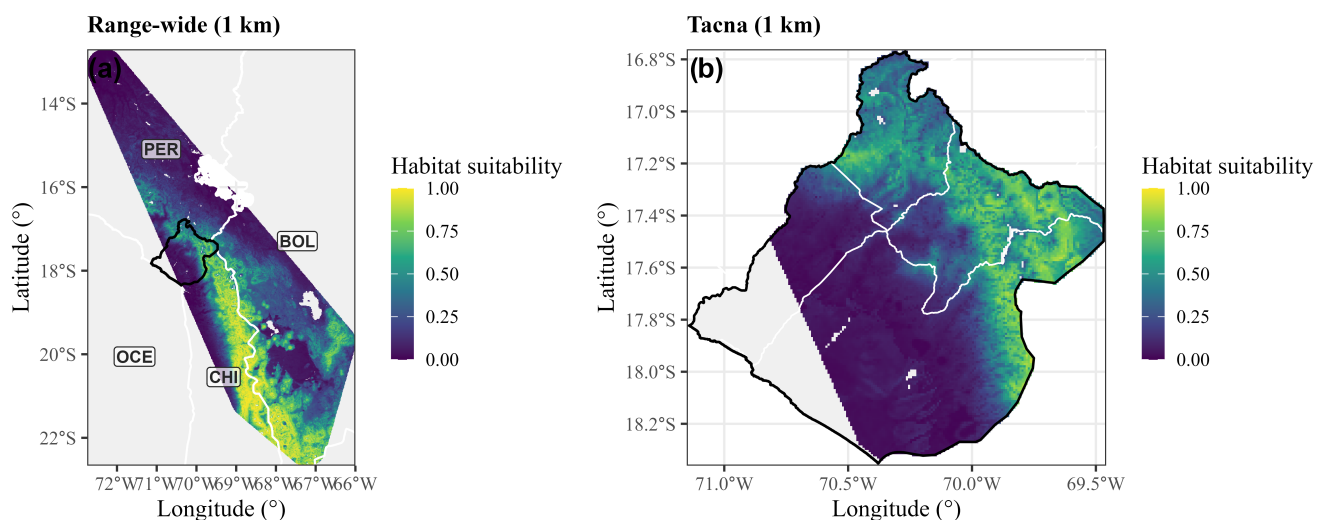


Figure 3. Present-day habitat suitability for *Polylepis tarapacana* at 1 km: (a) range-wide; (b) Tacna region.

The 16 inventory plots in Tacna documented 457 measured individuals of *Polylepis tarapacana* (mean diameter at breast height 24.6 cm, mean height 2.2 m), of which 81% were multi-stemmed. This krummholz-dominated morphology is typical of trees at the upper elevational edge of their physiological tolerance and provides independent, qualitative corroboration of climatic stress at the upper limit, consistent with Hypothesis (iii), complementing rather than formally testing the projected elevational compression.

3.2. Projected Habitat Shifts

Climatically suitable habitat for *Polylepis tarapacana* in Tacna contracts as emission severity rises across the four CMIP6 horizons (2030s/2050s/2070s/2090s; Table 3; ensemble-mean maps for the full scenario set in Figure S1); the loss is ordered *monotonically* by scenario from mid-century onward, with only the near-term 2030s departing from that ordering because of ensemble spread. Relative to the current suitable area of 3306 km² (suitability centroid at 4385 m), the trajectory is mild and stable under SSP126 (−6.2 to −20.4% across the four periods), intermediate and worsening under SSP245 (−11.1% in the 2030s, −48.8% by 2081–2100), severe under SSP370 (−4.3% in the 2030s steepening to −56.2% by the 2070s and −93.2% by 2081–2100), and catastrophic under SSP585: the species loses 13% of its area in the 2030s, 43% by mid-century, then *collapses* to −88.3% during the 2061–2080 decade and to −100% by 2081–2100—the last leaving no suitable habitat above the maxSSS threshold within Tacna, the most extreme outcome the binary metric can take. The decline is accompanied by a consistent *upslope* displacement of the suitability centroid for the partial-loss scenarios—+115 m (SSP126), +195 m (SSP245), +167 m (SSP370) by 2081–2100, and +188 m already by the 2070s under SSP585—so that the surviving habitat is progressively compressed onto the highest ground; under the end-of-century SSP585 horizon, the elevational squeeze is complete and the centroid is no longer defined; the per-cell pattern of gain, loss, and stable habitat across scenarios is mapped in Figure S2. Class-area accounting under Scheme B (Table 4) sharpens the headline: the *highly suitable* class (≥ 0.5) collapses from 3551 to 20 km² (−99.4%, on the common 5 km grid) by 2081–2100 under SSP585, an even sharper decline than the binary maxSSS metric records. Together, the area loss and the upslope centroid shift confirm Hypothesis (i): under the highest-emission pathway the topographic ceiling drives a net loss of suitable area rather than a mere redistribution.

Table 3. Projected change in climatically suitable habitat for *Polylepis tarapacana* in Tacna across four CMIP6 horizons (MaxEnt ensemble, native ~5 km grid).

Scenario	Area (km ²)	ΔArea (%)	Centroid (m)	ΔCen. (m)	No-Esc. (km ²)	No-Esc. (%)
Current	3306	—	4385	—	—	—
SSP126 2021–2040	3102	−6.2	4461	+75	184	5.6
SSP126 2041–2060	2755	−16.7	4499	+114	204	6.2
SSP126 2061–2080	2632	−20.4	4508	+122	204	6.2
SSP126 2081–2100	2693	−18.5	4500	+115	204	6.2
SSP245 2021–2040	2938	−11.1	4476	+91	204	6.2
SSP245 2041–2060	2469	−25.3	4517	+131	307	9.3
SSP245 2061–2080	1856	−43.9	4559	+174	593	17.9
SSP245 2081–2100	1693	−48.8	4580	+195	838	25.3
SSP370 2021–2040	3163	−4.3	4463	+78	123	3.7
SSP370 2041–2060	2244	−32.1	4534	+149	388	11.8
SSP370 2061–2080	1448	−56.2	4620	+235	1042	31.5
SSP370 2081–2100	224	−93.2	4552	+167	2694	81.5
SSP585 2021–2040	2877	−13.0	4482	+97	204	6.2
SSP585 2041–2060	1877	−43.2	4560	+175	572	17.3
SSP585 2061–2080	387	−88.3	4573	+188	2348	71.0
SSP585 2081–2100	0	−100	—	—	3306	100

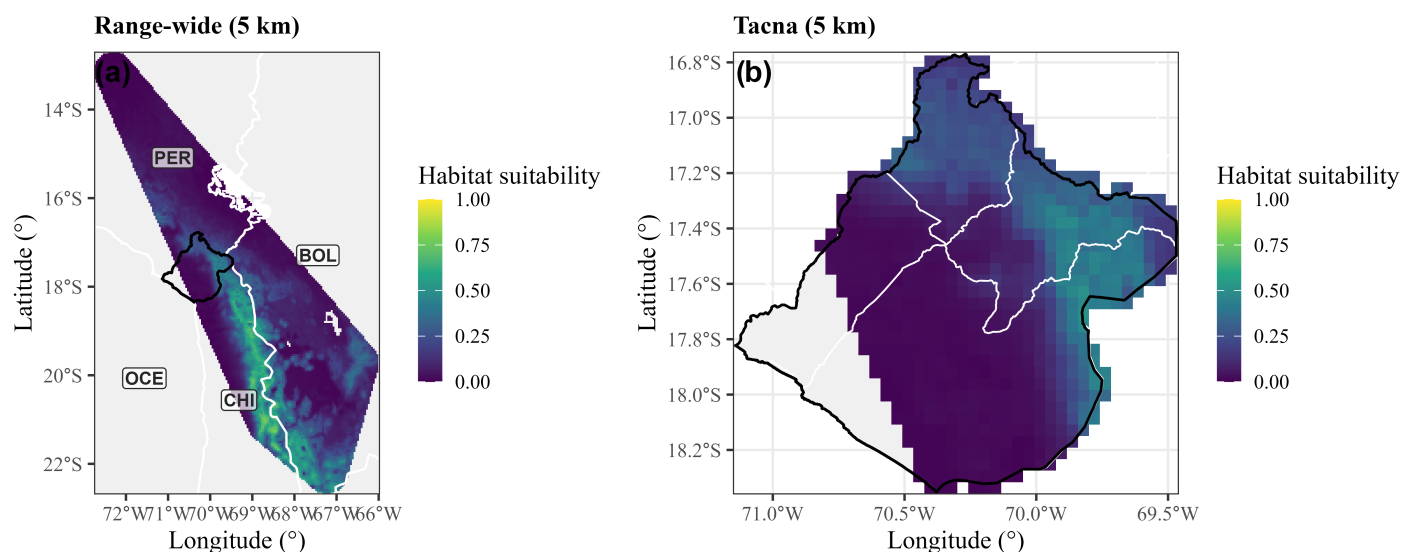
Horizons 2030s/2050s/2070s/2090s = 2021–2040/2041–2060/2061–2080/2081–2100, following Cotrina-Sanchez et al. [22] and Barboza et al. [23]. Centroid, area-weighted mean elevation of suitable cells; no-escape, suitable cells projected to lose suitability with no future-suitable cell at $\geq$ elevation within the precautionary 1 km dispersal buffer (virtual non-dispersal), as % of the current suitable area; the optimistic 10 km value and the full 1/10/25/50 km sensitivity are in Table 5.

Table 4. Suitable-area accounting in Tacna by habitat-quality class (Scheme B), present versus SSP585 2081–2100 (MaxEnt ensemble).

Class	Now @ 1 km (km ²)	Now @ 5 km (km ²)	SSP585 2100 (km ²)	Δ% (5 km → 5 km)
Unsuitable (<0.1)	5648	6089	8027	+31.8
Little suitable (0.1–0.3)	2488	2448	4515	+84.4
Moderately suitable (0.3–0.5)	2516	3105	2489	−19.8
Highly suitable (≥0.5)	3280	3551	20	−99.4

Scheme B cut-offs 0.1/0.3/0.5 after Barboza et al. [23] and Cotrina-Sanchez et al. [22]. Now @ 1 km, present classification at native WorldClim/SoilGrids resolution; now @ 5 km, the same present aggregated to the CMIP6 grid (the comparison grid for the change column); Δ% computed on the common 5 km grid (5 km → 5 km). This table contrasts the present with the end-of-century SSP585 endpoint; the full, non-monotonic time course across all four horizons is in Table 3.

The spatial contraction of suitable habitat to a high-elevation core under this scenario is mapped in Figure 4.

**Figure 4.** Ensemble-mean projected suitability for *Polylepis tarapacana* under SSP5-8.5 by 2081–2100 (~5 km): (a) range-wide; (b) Tacna region.

3.3. Mountaintop-Extinction: No-Escape Fraction

Of the currently suitable area, the entirety (100%) corresponds to *no-escape* cells under SSP585 by 2081–2100 across all four sensitivity buffers (1, 10, 25, 50 km)—a direct arithmetic consequence of the complete loss of suitable habitat in Tacna under that scenario: with no future-suitable cells anywhere in the region, no upslope refuge can exist (Tables 3 and 5). The no-escape signal is also already substantial during the previous decade (SSP585 2061–2080: 71.0% at the precautionary 1 km buffer, 50.7% at the optimistic 10 km buffer, 14.8% at 25 km, 6.2% at 50 km), marking the 2061–2080/2081–2100 transition as the catastrophic step. Under intermediate (SSP245) end-of-century warming, the fraction stays moderate (25.3% at 1 km, 15.5% at 10 km, 11.8% at 25 km, 2.5% at 50 km); under SSP370, it is high by end of century (81.5% at the precautionary 1 km buffer, 62.4% at the optimistic 10-km buffer, 27.8% at 25 km, 15.4% at 50 km), intermediate between SSP245 and SSP585; and under SSP126 it is essentially negligible across all buffers and periods ($\leq 6.2\%$). Mountaintop-extinction risk for *Polylepis tarapacana* is therefore total and buffer-invariant by the end of the century under high-end warming, decade-driven during the 2070s under that scenario, and modest under low-to-intermediate forcing—confirming Hypothesis (ii) that the no-escape fraction rises steeply with emission severity. Figure 5 shows the elevational profile of suitable area shifting upward while total area collapses, and Figure 6

summarizes the no-escape fraction per scenario, while Figure 7 maps where the no-escape cells fall: under intermediate (SSP2-4.5) end-of-century warming a high-elevation core persists with a reachable upslope refuge, whereas under SSP5-8.5 every currently suitable cell becomes no-escape.

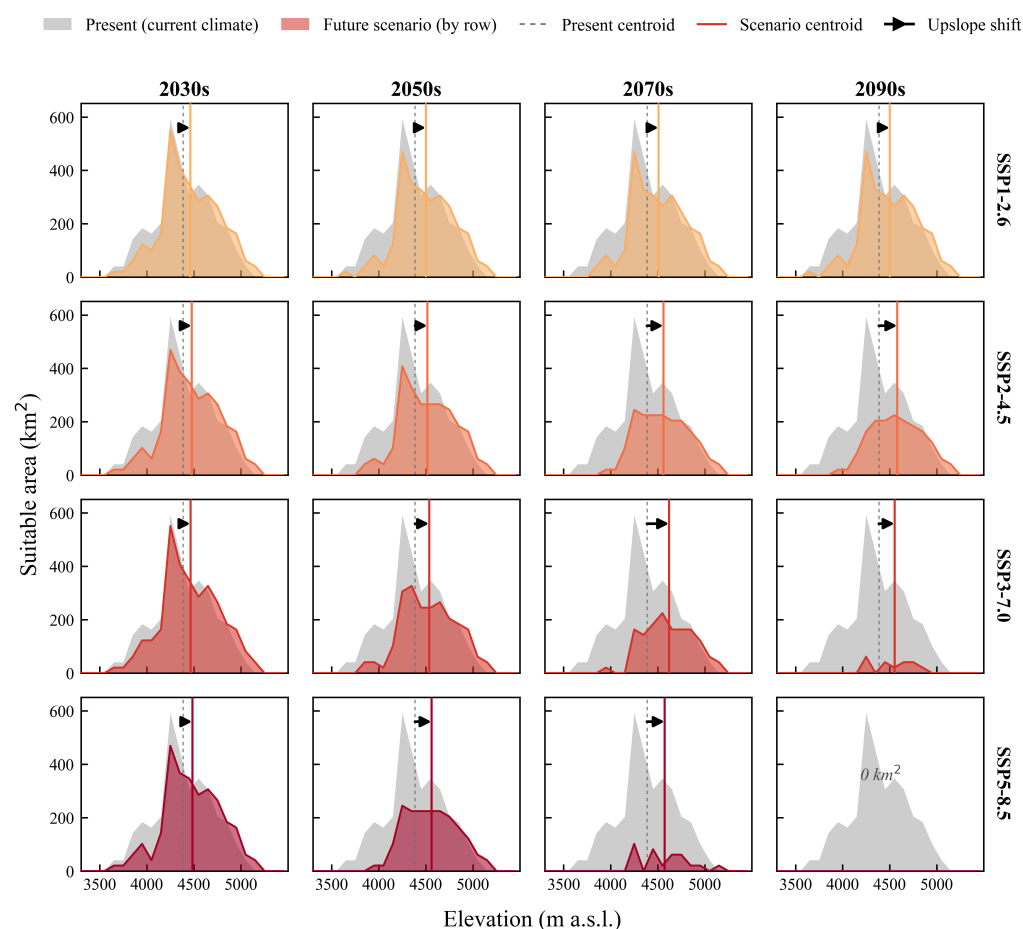


Figure 5. Elevational profile of suitable habitat for *Polylepis tarapacana* in Tacna, by scenario (rows, SSP; columns, horizon).

Table 5. Sensitivity of the no-escape fraction (% of the current suitable area) to the assumed centennial dispersal buffer for *Polylepis tarapacana*, across all SSP $\times$ horizon combinations.

Scenario	1 km	10 km	25 km	50 km
SSP126 2021–2040	5.6	0.6	0	0
SSP126 2041–2060	6.2	4.3	0	0
SSP126 2061–2080	6.2	4.3	0	0
SSP126 2081–2100	6.2	4.3	0	0
SSP245 2021–2040	6.2	1.9	0	0
SSP245 2041–2060	9.3	4.3	0	0
SSP245 2061–2080	17.9	10.5	2.5	0
SSP245 2081–2100	25.3	15.5	11.8	2.5
SSP370 2021–2040	3.7	0.6	0	0
SSP370 2041–2060	11.8	6.8	1.2	0
SSP370 2061–2080	31.5	18.6	11.8	2.5
SSP370 2081–2100	81.5	62.4	27.8	15.4
SSP585 2021–2040	6.2	3.1	0	0
SSP585 2041–2060	17.3	10.5	2.5	0
SSP585 2061–2080	71.0	50.7	14.8	6.2
SSP585 2081–2100	100	100	100	100

1 km, virtual non-dispersal (in-place persistence; the precautionary reference); 10 km ($\sim 125 \text{ m yr}^{-1}$), an optimistic upper bound for this slow-migrating treeline tree; 25 and 50 km, progressively more extreme dispersal optimism.

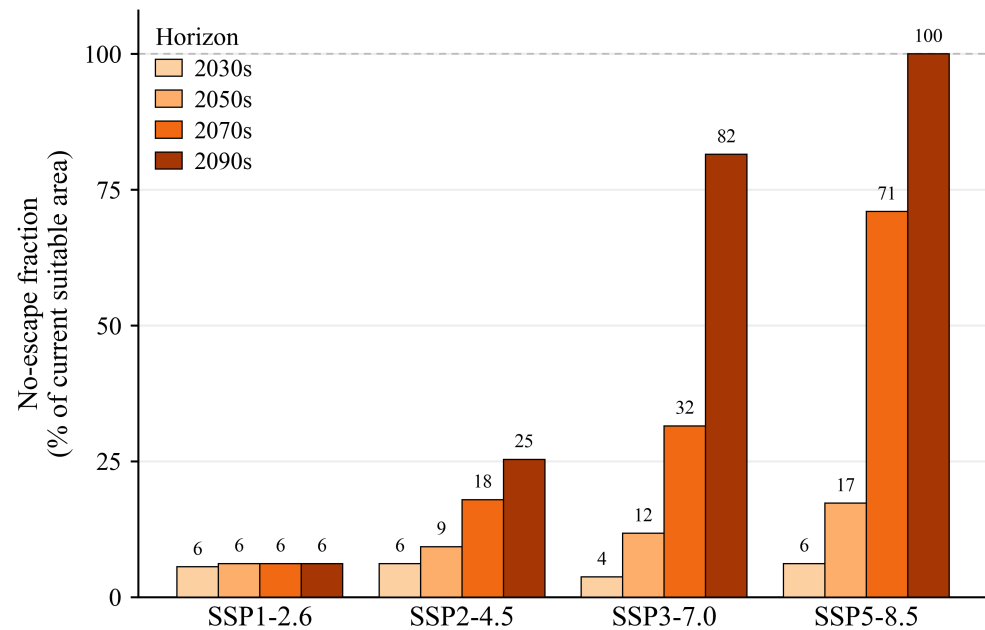


Figure 6. No-escape fraction per scenario for *Polylepis tarapacana* in Tacna, at the precautionary 1 km dispersal buffer (virtual non-dispersal; the full 1/10/25/50 km sensitivity is in Table 5).

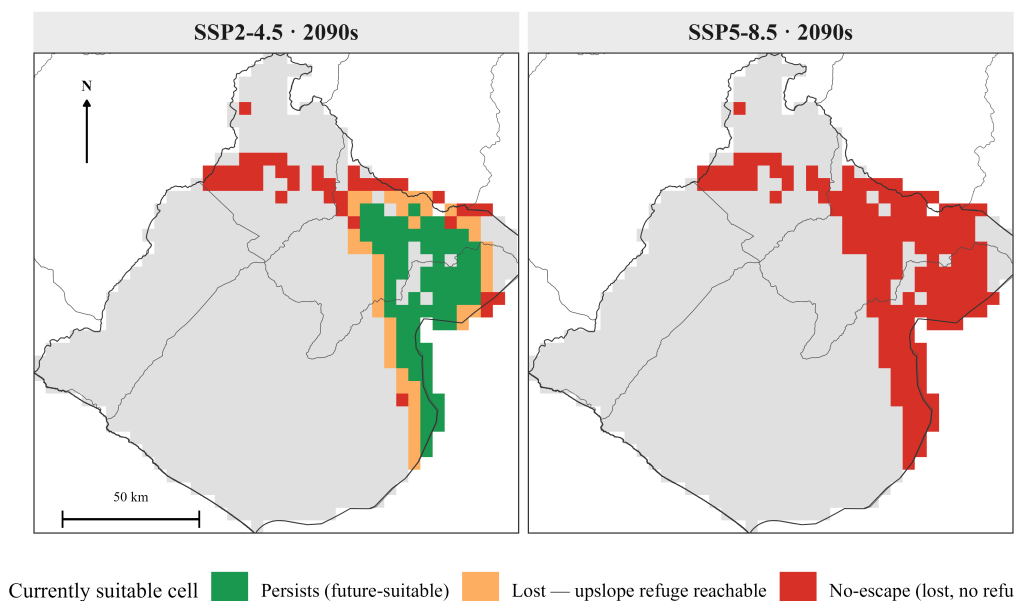


Figure 7. Spatial no-escape classification for *Polylepis tarapacana* in Tacna (1 km buffer) under two end-of-century scenarios (SSP2-4.5 and SSP5-8.5).

4. Discussion

4.1. Mountaintop-Extinction Quantified for the World's Highest-Elevation Tree

The three questions posed at the outset are answered directly here. The projected habitat loss (Question 1) is severe and ordered monotonically by emission severity from mid-century onward, reaching the complete loss of the Tacna suitable area under the highest-emission pathway. The no-escape fraction (Question 2) rises from negligible under SSP1-2.6 to the entire present range under SSP5-8.5, and becomes buffer-invariant once no in-region refuge remains. The field-observable signature (Question 3), a krummholz-dominated growth form in 81% of inventoried trees, corroborates a population already at its climatic edge. Each is taken in turn below.

The “escalator to extinction” has been documented chiefly for mobile mountain taxa—tropical birds and other animals tracking isotherms toward the summits [8,29,30]—and, at the community level, for plant functional types across tropical mountains [31], but it has rarely been quantified for an individual tree species and almost never confronted with field data. The no-escape fraction introduced here is, to date, the first operational metric of mountaintop-extinction risk for a tree species that is explicitly defined as the loss of suitability without a future-suitable refuge *at higher elevation* within a plausible centennial dispersal range, and validated against field-mapped stand polygons (148 stands, 12,874 ha). It makes the elevational-ceiling concept of Körner [7] quantitative at the cell level and tractable for regional conservation planning.

For *Polylepis tarapacana* in Tacna it reveals that under the intermediate SSP245 scenario a moderate fraction of present habitat already lacks an upslope refuge by 2081–2100 (25.3% at the precautionary 1 km buffer, 15.5% at 10 km), rising to the entire suitable area under SSP585, when the species disappears from Tacna and no in-region upslope refuge remains. The accompanying upslope displacement of the suitability centroid mirrors the range contractions and summit colonizations documented across temperate and tropical mountains [1,2]; and because treelines advance roughly an order of magnitude more slowly than isotherms rise [3,6,57], even the higher ground that remains climatically suitable is unlikely to be reached within the century, which supports the precautionary, near-zero-dispersal buffer as the more realistic reference. These findings extend to the world’s highest tree the acute climate sensitivity already reported for high-elevation *Polylepis* [14] and for the congeneric treeline species *P. quadrijuga* [25]. The South-Central Andes do not therefore provide, within this region, the vertical refuge needed to compensate for the projected climatic displacement of *Polylepis tarapacana*; suitable conditions persist mainly in the higher Bolivian Altiplano, the species’ core range [12], outside the study area—more extensively under lower-emission pathways—underscoring the value of cross-border coordination.

The magnitude of the projected contraction is consistent with the wider distribution-modeling literature rather than anomalous. End-of-century suitability losses of comparable or greater magnitude under high-emission scenarios have been reported for temperate and Mediterranean trees growing under far milder conditions than *Polylepis tarapacana*, including Anatolian chestnut (*Castanea sativa*) in Türkiye [58] and English yew (*Taxus baccata*) [59]; and warming-driven range shifts of the same direction have been documented for high-mountain shrubs on the Tibetan Plateau [4] and for expanding tropical species [5]. That a near-total high-emission loss emerges here therefore reflects the species’ extreme elevational confinement rather than an unusually pessimistic model.

4.2. Morphological Evidence of Stress at the Upper Edge

The dominance of multi-stemmed (krummholz) growth (81% of inventoried individuals in Tacna) provides independent, qualitative morphological support for the hypothesis that *Polylepis tarapacana* operates at the upper limit of its physiological tolerance in the northern part of its range [7,34,60]. At the treeline, a stunted, basally branched architecture is a recognized response to chronic cold, wind, and frost and to the recurrent shoot dieback they impose [6], so its prevalence marks a population living at its climatic edge. This field signal converges with the model: the distribution model places the species near the ceiling of the available elevational gradient, while the growth form independently indicates an edge-of-tolerance population—two lines of evidence pointing to the same conclusion that further warming will compress, rather than merely shift, the distribution.

This inference is corroborative rather than conclusive. Multi-stemming is not uniquely diagnostic of climate: basal resprouting can also follow disturbance such as browsing, fire, or cutting, pressures that already affect high-Andean *Polylepis* woodlands [13], and the growth-habit data were not designed to separate these drivers. The morphology therefore complements rather than formally tests the projected elevational compression; nevertheless, its consistent association with the upper-elevation edge, together with the convergent model result, makes a climatic interpretation the most parsimonious.

4.3. Methodological Choices and Uncertainty

The dispersal buffer is the main methodological choice. The 10 km buffer ($\sim 125 \text{ m yr}^{-1}$) is an optimistic upper bound: global treelines advance close to an order of magnitude more slowly than isotherms rise, and many do not advance at all [3,6], so the slow-recruiting *Polylepis tarapacana* [13] is unlikely to reach higher ground that remains suitable. The precautionary 1 km (near-zero-dispersal) buffer is therefore the more appropriate reference, with the 10 km values as a lower bound. The choice matters only at intermediate forcing—under SSP245 by 2081–2100 the no-escape fraction decays from 25.3% (1 km) to 2.5% (50 km; Table 5)—whereas under SSP585 it is 100% at every buffer, the species having disappeared from Tacna with no in-region target for upslope dispersal.

Other choices were robustness-tested. Present-day predictors ($\sim 1 \text{ km}$) and CMIP6 futures ($\sim 5 \text{ km}$) are compared on a common 5-km grid (the future is never upsampled), and the present-day elevational profile is near-identical at 1 km and 5 km (Figure S4), confirming no loss of signal. That grid nonetheless smooths the rugged Andean topography and may underestimate local microclimatic refugia [1,61]; and because observed elevational shifts can fall within the random expectations of geometric constraints [62], the no-escape fractions are best read as a measure of climatic exposure rather than a demographic extinction forecast. The projected trajectory is also non-monotonic (for instance the slight recovery under SSP1-2.6 after the 2061–2080 minimum), but a slow-recruiting treeline tree cannot recolonize ground it has already lost within the time scale of such fluctuations, so habitat lost during a low should be treated as effectively irreversible under natural conditions rather than as recoverable when the class area later rebounds [6,28]. Residual uncertainty stems from holding soil and topography constant and from inter-GCM variability (Figure S3), whereas model selection is unambiguous—the Cotrina-Sanchez [22] and lowest-OR10 rules converged on the same model (hinge, RM = 3; Table S2). Extrapolation beyond the calibration envelope (MESS) was small and was clamped. Two data limitations nonetheless temper the results. The range-wide model rests on a modest presence sample (60 spatially thinned localities) that, although bias-corrected, constrains how finely the four-country niche can be resolved; this also explains why the internal cross-validated Boyce is low and variable ($\text{CBI} = 0.49 \pm 0.39$, with one negative fold), as a small presence set partitioned among $\sim 140 \text{ km}$ spatial blocks leaves few records per fold. The much higher external Boyce (0.98) confirms reliable ranking of habitat quality, but is evaluated over the Tacna subdomain where the independent field polygons lie, so the internal and external indices bound rather than contradict the model's performance.

4.4. Conservation Implications

As the highest-elevation tree of the South-Central Andes and a keystone of high-Andean woodland biodiversity [10,11], *Polylepis tarapacana* warrants conservation measures matched to the projected trajectory. Under the high-emission pathway, no in-region refugium remains by 2081–2100—the entire Tacna suitable area is lost above maxSSS and the no-escape fraction is 100% at every buffer (Tables 3 and 5)—so priority shifts away from in situ climatic refugia toward ex situ conservation (seed banking and common-garden

trials of provenances spanning the range) and cross-border coordination with Bolivia, whose higher Altiplano holds the species' core range [12] and retains suitable conditions for longer. Under the intermediate SSP245 trajectory, by contrast, the highest-elevation portion of the range persists (centroid rising to 4580 m) as a genuine in situ refugium: here protection and assisted-migration trials toward the highest available ground in Tacna (e.g., the northern flanks of Volcán Yucamane and the >4500 m crests near the Bolivian border) are warranted for early action, alongside relief of the ongoing land-use pressure on the remaining stands [13]. *Polylepis tarapacana* thus emerges as a flagship species for South-Central Andean conservation and for international (Peru–Bolivia–Chile–Argentina) coordination on high-Andean treeline ecosystems.

5. Conclusions

Mountaintop extinction has mostly been studied in animals mobile enough to follow the climate uphill. The present work shows that the same threat can be measured, and grounded in field data, for a tree. Habitat suitability for *Polylepis tarapacana*, the highest-elevation tree on Earth, was modeled across its full range in the South-Central Andes, and those range-wide projections were then used to estimate its risk of climate-driven mountaintop extinction in the Tacna region of southern Peru, the species' Peruvian stronghold. While climate-driven range projections exist for many tree species, we are not aware of a comparable cell-level, field-validated no-escape assessment for *Polylepis tarapacana* specifically. The study contributes three elements:

1. a *no-escape* metric that distinguishes future habitat loss where suitable ground still lies within reach upslope from loss where none remains, so that the elevational ceiling can be measured cell by cell;
2. MaxEnt and Random Forest models fitted over the species' entire distribution and tested against stands mapped independently in the field at Tacna; and
3. evidence from growth form, since most inventoried trees grow as low, multi-stemmed krummholz, the habit of populations near the upper edge of their tolerance.

The three guiding questions point the same way. Across every scenario, suitable habitat is projected to shrink and move upslope; under the most extreme emissions it all but disappears from Tacna before the century is out, and that loss is real rather than a shift to higher ground, because no higher ground is left to occupy. The share of habitat with no reachable refuge above it grows quickly as emissions rise, until under the strongest warming it covers the whole of the present range and no longer depends on how far the species could disperse; under the mildest pathway, it stays small. The krummholz growth form adds an independent sign that the population already sits at its climatic limit.

Two cautions follow. The constraint identified here is geometric, set by the terrain and by where the climate is heading rather than by any single model run, which makes it difficult to dismiss. Even so, it measures exposure to climate, not extinction itself; whether that exposure becomes decline will turn on dispersal, recruitment, and survival, which the present study does not resolve. With those limits in mind, *Polylepis tarapacana* serves as a sentinel for other range-restricted mountain species. When a summit-bound plant's climate space lifts off the top of the land it grows on, no dispersal can follow it. Mapping where escape is still possible, and where it is not, points to the refuges worth protecting in the South-Central Andes and gives a method that can be applied to other elevation-limited species, treeline trees among them. In practice, this points to a two-track strategy: under lower-emission pathways, protect the persisting high-elevation core and trial assisted migration toward the highest available ground; under high-emission pathways, where no in-region refuge remains, prioritize ex situ seed banking

across provenances and Peru–Bolivia coordination to safeguard the Altiplano populations that retain suitable climate longest.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d18070423/s1>, Figure S1: Ensemble-mean future habitat suitability for *P. tarapacana* across the full set of SSP scenarios and horizons; Figure S2: Per-cell range change (gain, loss, stable) at the maxSSS threshold for each SSP $\times$ horizon, with per-panel net change; Figure S3: Among-GCM standard deviation of the ensemble projections, mapping inter-model uncertainty across the five-GCM ensemble; Figure S4: Resolution-robustness check: present-day elevational profile of suitable habitat at 1 km native versus 5 km aggregated resolution; Figure S5: Spatial-block cross-validation design; Figure S6: Field photographs of *Polylepis tarapacana* in the Tacna study area (moved here from the study-design map); Table S1: Complete list of the 29 candidate environmental predictors screened for the *Polylepis tarapacana* distribution model; Table S2: MaxEnt candidate-model tuning grid (ENMeval); Table S3: Per-fold predictive performance under five-fold spatial block cross-validation for both algorithms; Table S4: Random Forest permutation importance per predictor for *P. tarapacana*; Table S5: Projected change in climatically suitable habitat for *Polylepis tarapacana* in Tacna, split by scenario (the per-SSP view of Table 4 in the main text; MaxEnt ensemble, native ~5 km grid).

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Abbreviations

The following abbreviations are used in this manuscript:

AUC	area under the receiver operating characteristic curve
CBI	Continuous Boyce Index
CMIP6	Coupled Model Intercomparison Project Phase 6
DBH	diameter at breast height
DEM	digital elevation model
FC	feature class (MaxEnt)

GBIF	Global Biodiversity Information Facility
GCM	global climate model
MaxEnt	maximum-entropy model
maxSSS	maximum sum of sensitivity and specificity (threshold)
MESS	multivariate environmental similarity surface
ODMAP	Overview, Data, Model, Assessment, and Prediction (protocol)
RF	Random Forest
RM	regularization multiplier (MaxEnt)
SD	standard deviation
SDM	species distribution model
SOC	soil organic carbon
SRTM	Shuttle Radar Topography Mission
SSP	Shared Socioeconomic Pathway
TPI	topographic position index
TSS	true skill statistic
VIF	variance inflation factor

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