

Article

Climate-Informed Conservation and Restoration Priorities for High-Andean *Polylepis* Forests Under Climate Change

Sebastian Mantilla-Valdivia ¹, Karla Paliza del Carpio-Banda ¹, Andrea Chanove-Manrique ^{1,*},
Marcelino de la Cruz ² and Berly Cárdenas-Pillco ¹

- ¹ Escuela Profesional de Ingeniería Ambiental, Facultad de Arquitectura e Ingenierías Civil y del Ambiente, Universidad Católica de Santa María, Arequipa 04013, Peru; sebastian.mantilla@estudiante.ucsm.edu.pe (S.M.-V.); karla.palizadelcarpio@estudiante.ucsm.edu.pe (K.P.d.C.-B.); bcardenas@ucsm.edu.pe (B.C.-P.)
- ² Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnología (ESCET), Universidad Rey Juan Carlos, 28933 Móstoles, Spain; marcelino.delacruz@urjc.es
- * Correspondence: achanove@ucsm.edu.pe

Abstract

The high-Andean forests formed by *Polylepis rugulosa* in southern Peru are key ecosystems for biodiversity conservation and the provision of ecosystem services; however, they are facing fragmentation and degradation processes associated with human activities and climate change. In this context, the present study modeled the near-term and future potential distribution of *P. rugulosa* under the SSP1-2.6, SSP3-7.0, and SSP5-8.5 shared socioeconomic pathways, considering three analysis periods: 2011–2040, 2041–2070, and 2071–2100. To achieve this, occurrence records, bioclimatic variables, and topographic variables were integrated in BIOMOD2 and complemented with spatial analyses in QGIS. After controlling for multicollinearity using the Variance Inflation Factor (VIF), seven non-redundant environmental predictors were retained and incorporated into an ensemble model built from the four algorithms with the highest predictive performance: Random Forest (RF), Gradient Boosting Machine (GBM), Flexible Discriminant Analysis (FDA) and Artificial Neural Network (ANN). The final ensemble model achieved high predictive accuracy, with True Skill Statistic (TSS) values close to 0.94 and ROC/AUC values ranging from 0.997 to 0.998. Continuous habitat suitability projections were subsequently reclassified into four habitat suitability categories: most unsuitable, marginally unsuitable, marginally suitable, and most suitable. Under the SSP3-7.0 scenario, the most suitable areas decreased from 30,965 ha during 2011–2040 to 374 ha during 2071–2100, indicating a progressive contraction of favorable habitat. A spatiotemporal analysis was then conducted, in which areas of habitat loss, stability, and gain were further disaggregated into specific projected habitat categories: immediate loss, long-term loss, stable niche, expansion and establishment, and delayed expansion. The probability density curves of key environmental variables revealed that stable habitat was mainly associated with mean diurnal temperature ranges of 10.5–11.5 °C, precipitation during the driest quarter of 35–45 mm, slopes of 30–40°, and altitudes of 4000–4500 m a.s.l. Finally, based on the projected habitat trajectories of *P. rugulosa*, three strategic management typologies were defined: conservation in stable areas, restoration in areas experiencing habitat loss, and preventive conservation and monitoring in areas with future establishment potential.

Keywords: *Polylepis*; high-Andean forests; BIOMOD2; climate change; habitat suitability; spatiotemporal habitat dynamics; conservation; ecological restoration



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1. Introduction

In recent decades, climate change has become one of the main drivers of global ecological transformation, altering the dynamics and distribution of numerous species. One of its most evident effects is the geographic shift of organisms toward higher altitudes or latitudes in search of more favorable environmental conditions [1]. This phenomenon highlights the high sensitivity of ecosystems to climatic variations [2]. In addition, land-use change reduces and fragments habitats, intensifying negative impacts on biodiversity and compromising essential ecosystem services, such as water regulation, soil conservation, and carbon sequestration [3].

In the Peruvian Andes, particularly in the southern region, temperature increases and heterogeneous changes in precipitation have been recorded in recent decades [4]. These trends may intensify and affect fragile ecosystems such as high-Andean forests. Among them, *Polylepis* forests stand out for their ability to grow at extreme altitudes and for their importance in the provision of ecosystem services [5]. In particular, their populations are vulnerable due to their slow and limited regeneration, which increases their sensitivity to external disturbances [6].

The conservation and restoration of *Polylepis* forests require recognizing not only current habitat conditions, but also their possible future behavior. Areas that are currently suitable may lose suitability under future climate scenarios, while other areas may acquire favorable conditions over time, as reported in studies on the potential distribution of *Polylepis* under climate change [7,8]. In this regard, identifying areas of potential habitat persistence, loss or gain makes it possible to understand the spatiotemporal trajectories of habitat in high-Andean landscapes subjected to climate change [7,9].

In this context, the present study aimed to evaluate the near-term and future potential distribution of *Polylepis rugulosa* in southern Peru under different climate change scenarios, using species distribution models (SDM) [10] and spatial analysis. Previous *Polylepis* studies have generally focused on static habitat-suitability projections at broad geographic scales, or species and regions other than *P. rugulosa* in southern Peru. Consequently, an integrated regional assessment combining ensemble modeling, high-resolution micro-topographic variables, multiple climate scenarios and periods, and explicit multitemporal habitat trajectories remains lacking for this species in southern Peru.

To address this knowledge gap, the present study applies a robust ensemble modeling approach using BIOMOD2 [11] and spatial map algebra to quantify specific spatiotemporal trajectories including immediate loss, long-term loss, stable habitat, expansion and establishment, and delayed expansion. These trajectories are subsequently translated into operational strategic typologies for conservation, restoration, and preventive conservation and monitoring. Altogether, this approach provides a spatially explicit framework to support the ecological planning of high-Andean forests under climate change.

2. Materials and Methods

2.1. Study Area and Sampling Design

The study was developed in the high-Andean ecosystem of the southern region of Peru (Arequipa, Moquegua, and Tacna). The modeling domain was defined by the combined political boundaries of the Arequipa, Moquegua, and Tacna departments, encompassing a total fixed spatial extent of 9,497,758 ha. This area is characterized by its topographic heterogeneity and extreme climatic conditions that condition the spatial distribution of relict forests. For the collection of occurrence data of *Polylepis rugulosa*, a preferential, directed and stratified sampling design was carried out; this was based on expert judgment, where the confirmed presences of the species were recorded and allowed the contextual evaluation of the ecosystem, capturing the representativeness of the microhabitats without

increasing field effort [12]. Expert knowledge was used to prioritize field surveys in areas where *P. rugulosa* was considered likely to occur, an approach previously applied to guide surveys of species of conservation concern [13].

For correct data structuring and to mitigate the regional aggregation bias, spatial sampling by zones was carried out. The in situ evaluations were distributed across independent study areas, establishing a minimum separation distance of 1000 m between areas. Within each area, the information survey was limited to the georeferencing of the confirmed presences of the individuals at the scale of the bioclimatic variables (pixel). The occurrence dataset was compiled from mixed sources, including direct field surveys and project records, herbarium records, scientific articles, books, theses, and technical reports. The spatial network of *Polylepis rugulosa* occurrence records throughout the model domain is illustrated in Figure 1. In total, 324 georeferenced presence records were compiled; no population was manually excluded, and the complete dataset was incorporated into the modeling environment.

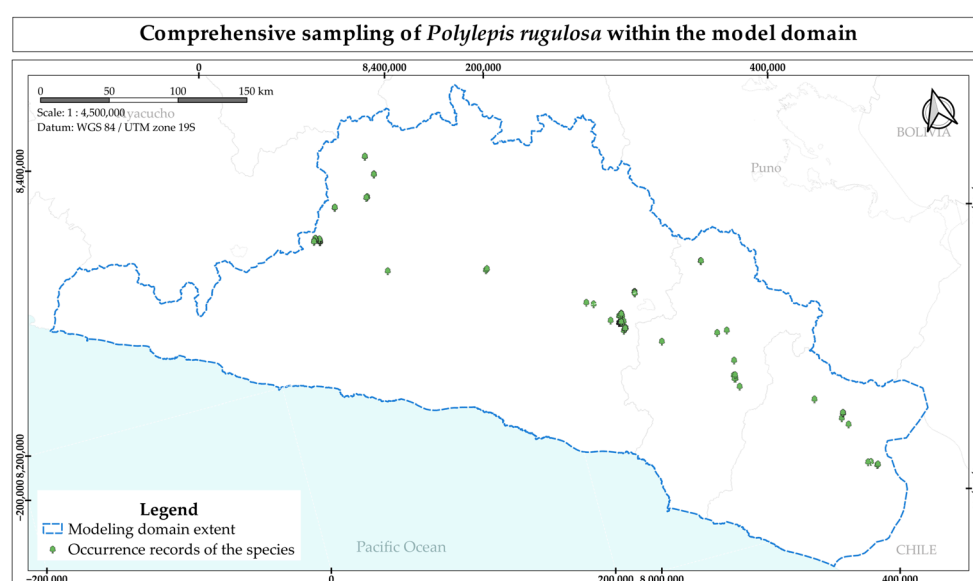


Figure 1. Spatial distribution of *Polylepis rugulosa* occurrence records across the modeling domain. Green points indicate the 324 spatially independent presence locations comprising the comprehensive dataset utilized for the modeling environment. The dashed blue line delineates the spatial extent of the study area.

Following the standardized methodological guidelines for SDM, the design required the generation of background data or pseudo-absences, which allow the habitat to be adequately discriminated [14,15]. The pseudo-absences were generated using the “disk” strategy implemented in BIOMOD2, which allows the definition of minimum and maximum distances with respect to the presence records for the generation of pseudo-absences [16]. Three independent datasets of 1000 pseudo-absences each were generated. The number of pseudo-absences corresponded approximately to three times the 324 presence records, consistent with the guidance provided in the official BIOMOD documentation, and provided adequate representation of the available environmental background. Multiple datasets were used because repeated pseudo-absence selections are recommended to evaluate the influence of alternative spatial samples on model performance; the use of three sets of 1000 pseudo-absences has also been applied in previous BIOMOD2-based plant modeling [14,16,17]. These three pseudo-absence datasets were subsequently combined with repeated training and testing partitions to evaluate the stability of model performance across alternative data configurations [18].

A minimum distance of 1000 m was established to avoid selecting pseudo-absences too close to confirmed presences where similar local environmental conditions and spatial pseudoreplication may occur. This distance also matched the minimum separation between sampling areas and corresponded to ten cells of the 100 m environmental grid. A maximum of 50 km was used to avoid selecting excessively distant background environments while retaining contrasting climatic and topographic conditions within the regional context. Because both overly restricted and overly broad background extents can influence model calibration, variable importance, and spatial projections, this value was treated as a study-specific geographic restriction rather than an ecological or dispersal threshold [19].

2.2. Environmental Variables and Collinearity Analysis

To characterize the ecological niche, bioclimatic and topographic variables were collected from high-resolution databases. A total of 19 bioclimatic variables were collected from the Climatologies at High Resolution for the Earth's Land Surface Areas version 2.1 (CHELSA v2.1) dataset and its projections derived from the Coupled Model Intercomparison Project Phase 6 (CMIP6) [20] because they provide high-resolution climatic information for ecological applications and species distribution models [21]. CMIP6 brings together standardized climatic simulations from different global models, useful for evaluating future climate change scenarios [22]. Three Shared Socioeconomic Pathways (SSPs) were used: SSP1-2.6, SSP3-7.0, and SSP5-8.5, which represent a gradient of low, medium, and high climate pressure, respectively. The projections were obtained from the Max Planck Institute Earth System Model version 1.2 high-resolution configuration (MPI-ESM1-2-HR), developed by the Max Planck Institute for Meteorology, whose data are available through the Earth System Grid Federation (ESGF) archive [23]. The periods analyzed were 2011–2040, 2041–2070, and 2071–2100, consistent with the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR6) for the exploration of possible climate futures [24].

In addition to the bioclimatic variables, topographic variables derived from the Digital Elevation Model (DEM) and from Advanced Land Observing Satellite (ALOS) Phased Array type L-band Synthetic Aperture Radar (PALSAR) [25] were used to capture the microclimatic variations that may modify the local suitability of the site [7] and improve the capacity of the model to understand the heterogeneity of mountainous regions [26]. The variables derived from the DEM were altitude, slope, the Topographic Wetness Index (TWI), the Topographic Position Index (TPI), and the Mid-Slope Position Index (MPI). The last three topographic variables were mathematically defined as follows:

- TWI: Estimates the potential accumulation of water in the soil, an important factor for plant development [27], especially when dealing with areas of high heterogeneity. This index was formulated as:

$$TWI = \ln\left(\frac{\alpha}{\tan\beta}\right), \quad (1)$$

where α represents the catchment area of a basin and β expresses the local slope in radians.

- TPI: Quantifies the difference in altitude between a central cell and the mean elevation of its adjacent cells; empirically, it identifies ridges, valleys, and flat areas [28]. It was formulated as:

$$TPI = Z_0 - \frac{1}{n} \sum_{i=1}^n Z_i, \quad (2)$$

where Z_0 expresses the altitude of the central cell and Z_i is the elevation of each cell adjacent to the central one.

- MPI: Identifies the relative spatial location of a point within an elevation profile, allowing discrimination between a valley bottom and the top of a mountain [29]. Mathematically, it is defined as follows:

$$\text{MPI} = \frac{Z_0 - Z_{\min}}{Z_{\max} - Z_{\min}}, \quad (3)$$

where Z_0 expresses the altitude of the cell, while $Z_{\max}$ and $Z_{\min}$ respectively represent the maximum and minimum altitude within the study area. Consequently, integrating the topographic variables, the initial set of predictors was made up of 24 variables.

To guarantee the spatial comparability between variables and allow their integration into the modeling, all layers were standardized to a common grid of 100×100 m [30]. The layers with different resolutions were adjusted through bilinear interpolation, with the purpose of obtaining a homogeneous grid for the analysis [31].

Prior to model calibration, the initial set of 24 environmental predictors was screened for multicollinearity using the *vifcor* function of the *usdm* package (version 2.1.7) in R (version 4.4.3; R Core Team, Vienna, Austria), with the threshold parameter set to $th = 0.8$.

Correlation thresholds used to control predictor collinearity in species distribution modeling vary among studies, including values of 0.7, 0.8, and 0.85 [32]. In this study, a threshold of 0.8 was selected to remove strongly redundant predictors while retaining moderately correlated variables representing complementary climatic and topographic processes within the environmentally heterogeneous high-Andean landscape.

This procedure iteratively identified the pair of variables with the highest correlation above the established threshold. After collinearity screening, seven non-redundant environmental predictors were retained, including four bioclimatic variables, Mean Diurnal Temperature Range (BIO 02), Temperature Seasonality (BIO 04), Precipitation Seasonality (BIO 15), and Precipitation of the Driest Quarter (BIO 17), and three topographic variables, slope, TWI, and TPI. The excluded predictors were BIO 01, BIO 03, BIO 05, BIO 06, BIO 07, BIO 08, BIO 09, BIO 10, BIO 11, BIO 12, BIO 13, BIO 14, BIO 16, BIO 18, BIO 19, altitude, and MPI. The definitions of the bioclimatic variables follow the standard CHELSA nomenclature [20,21]. All retained predictors showed VIF values below 3, indicating the absence of severe multicollinearity, as shown in Table 1. This selection reduced redundancy among predictors while retaining complementary climatic and topographic information.

Table 1. Environmental variables resulting from the collinearity analysis.

Variable	Type	VIF ¹
BIO 02	Temperature	2.186
BIO 04	Temperature	1.798
BIO 15	Precipitation	1.867
BIO 17	Precipitation	2.493
Slope	Topography	1.554
TWI	Topography/Moisture	1.733
TPI	Topography/Relief	1.235

¹ VIF: Variance Inflation Factor.

The complete Pearson correlation matrix of the 24 initial environmental predictors is provided in Table S1 in the Supplementary Materials. This subset was introduced into the BIOMOD2 environment for the generation of the projections.

2.3. Species Distribution Modeling

Spatial pre-processing was performed in QGIS (version 3.44.11; QGIS Association, Grüt, Switzerland). The ALOS PALSAR DEM (native resolution of 12.5 m) and the con-

tinuous bioclimatic variables were resampled to a 100 m resolution grid using bilinear interpolation. No categorical variables were included in the model. Within this framework, the high-resolution topographic layers carry the true fine-scale environmental signal, whereas the interpolated bioclimatic layers represent smoothed macroclimatic gradients. The ensemble modeling framework was implemented using the BIOMOD2 package (version 3.4.6) within the R environment (version 4.4.3; R Core Team, Vienna, Austria).

In SDM, calibration acts as a learning process. It consists of jointly analyzing the presence data and the variables introduced to identify the environmental preferences of the species, which allows empirical establishment of which characteristics define its habitat.

For model calibration, the CMIP6 projection for 2011–2040 under SSP3-7.0 was used as a near-term reference period rather than as a historical climatological baseline. This period corresponds to the first 30-year projection interval available in CHLSA-CMIP6 and allows consistent comparison with the subsequent 2041–2070 and 2071–2100 periods using the same climate model, spatial resolution, and downscaling procedure [20]. A recent plant species distribution study similarly used 2011–2040 as the reference period for comparison with mid- and long-term climate projections [33]. SSP3-7.0 was selected as an intermediate-to-high pathway without representing the most extreme scenario. Although the three SSPs show comparatively limited differences in temperature during 2011–2040, their trajectories diverge more clearly toward the middle and end of the century [24], as shown in Figure 2. Therefore, projected changes were interpreted relative to the 2011–2040 SSP3-7.0 near-term reference period.

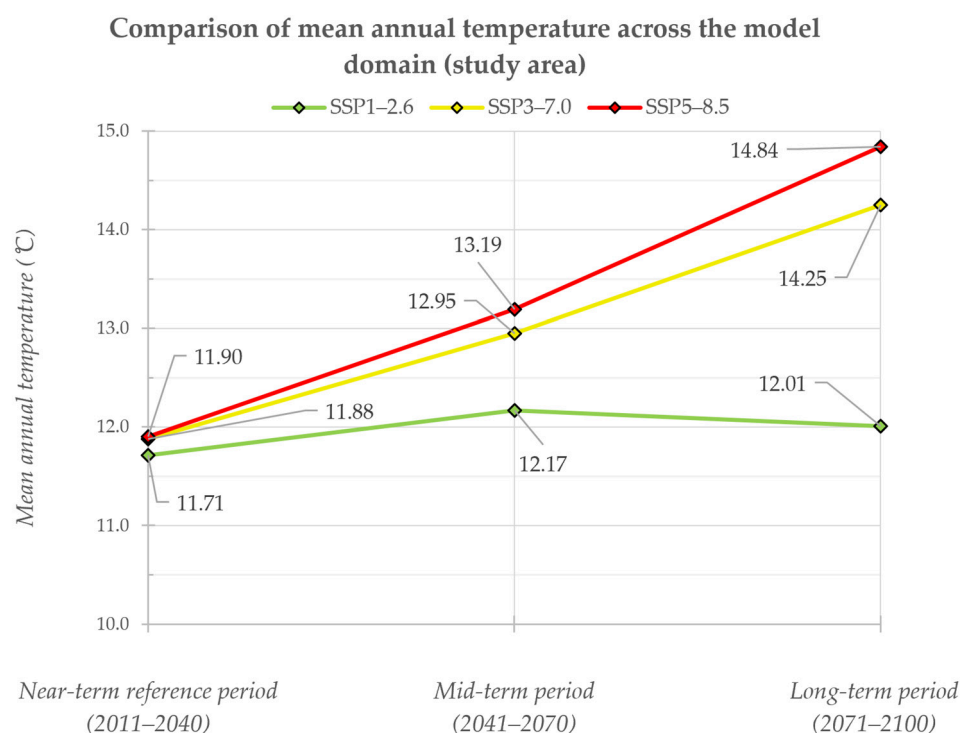


Figure 2. Mean annual temperature averaged across the model domain under SSP1-2.6, SSP3-7.0, and SSP5-8.5 for the 2011–2040, 2041–2070 and 2071–2100 periods.

The modeling strategy is based on an ensemble forecasting approach. This method allows the generation of individual projections from different algorithms/models; then, these projections are assembled into a TSS-weighted mean ensemble model (EMwmeanByTSS), which helps reduce inter-algorithmic uncertainty [11].

A cross-validation design was established through the random partitioning of the 324 presence data. A total of 80% of the records were assigned to the training set for the

calibration of the algorithms, reserving 20% of the data as a testing set for the independent evaluation. A comparable 80/20 training–testing partition has been previously applied in BIOMOD2-based habitat-suitability modeling using repeated cross-validation [34]. This random partition was repeated 3 times to reduce dependence on a single data split.

Under this data partitioning system, multiple predictive algorithms/models were calibrated, grouped into four analytical families:

- Regression-based models: Generalized Linear Models (GLM) [35] and Generalized Additive Models (GAM) [36];
- Classification models: Flexible Discriminant Analysis (FDA) [37] and Classification Tree Analysis (CTA) [38];
- Machine learning models: Artificial Neural Networks (ANN) [39], Random Forest (RF) [40], and Generalized Boosting Models (GBM) [41];
- Ecological profile models: Surface Range Envelope (SRE) [42].

To guarantee the stability of the modeling, each algorithm was subjected to an iterative calibration design [43]. The replicates were obtained by combining the three independent sets of pseudo-absences with the three iterations of partitioning for cross-validation. Consequently, each algorithm was adjusted through 9 independent mathematical executions, ensuring that the predictive performance does not depend on a single spatial or sample configuration.

After calibration, the predictive capacity of the individual models was evaluated using the 20% of data reserved during partitioning, repeating this process three times, from which the following performance metrics were obtained: True Skill Statistic (TSS) and Receiver Operating Characteristic/Area Under the Curve (ROC/AUC). This type of partitioning is frequently used in predictive models, since it allows evaluation of the performance of a model without using data that were included in its training [44].

The predictions of the different models were assembled through EMwmeanByTSS, which assigns greater statistical weight to those algorithms that showed better performance in the cross-validation [16], which allows consideration of the inter-algorithmic uncertainty associated with the variability between models [11] and, in this study, favored greater sensitivity of the ensemble.

The assembled model was evaluated using the same performance metrics on the 20% of the test data [45] used for the calibration of the individual models (TSS and ROC/AUC). However, with the purpose of maximizing the understanding of the model performance, the sensitivity rate was previously extracted, which refers to the capacity of the model to correctly predict presences, and the specificity rate, which refers to the capacity to correctly identify absences. Both rates are obtained automatically when applying a cutoff threshold, allowing the real precision to discriminate the suitable habitat to be quantified.

Raster-format outputs were generated corresponding to three modeling products: habitat suitability, relative probability of occurrence, and inter-algorithmic uncertainty. Habitat suitability was represented through binary values of 0 and 1, where 0 indicated unsuitable conditions and 1 indicated suitable conditions for the species [16]. The relative probability of occurrence was expressed through continuous values between 0 and 1, which indicate the relative degree of environmental favorability of each cell for the presence of the species. For its part, inter-algorithmic uncertainty was estimated through the coefficient of variation of the predictions between models [16], whose values start from 0 and increase as the disagreement between models increases. This approach allows representation of the methodological variability associated with species distribution modeling [11], both for the near-term reference period and for the climate pathways introduced.

For each modeled period–scenario combination, BIOMOD2 generated continuous habitat-suitability rasters with values ranging from 0 to 1, where higher values represented

greater relative environmental suitability for *P. rugulosa*, as well as binary suitability rasters with values of 0 and 1. These two outputs were processed separately. The continuous rasters were used for categorical habitat-suitability analysis, whereas the binary rasters were reserved for the subsequent multitemporal assessment of habitat loss, stability, and gain.

2.4. Multitemporal Evaluation and Dynamics Analysis

For the categorical interpretation of habitat suitability, the continuous rasters generated by BIOMOD2 were exported to SAGA GIS (version 9.12.4; SAGA User Group Association, Hamburg, Germany) and independently reclassified for each period–scenario combination using the Jenks Natural Breaks method. This data-driven procedure identifies breakpoints that minimize variability within classes while maximizing differences among classes. Following previous species distribution studies [15,46], the continuous values were grouped into four categories: most unsuitable, marginally unsuitable, marginally suitable, and most suitable.

Because each period and climate scenario produced a different distribution of continuous suitability values, the Jenks breakpoints were calculated separately for each projection and therefore varied among maps. This variation was an expected consequence of applying a data-driven classification to different projected conditions and has also been reported when Jenks was applied separately to current and future habitat-suitability projections [47]. The resulting categories were interpreted as relative suitability levels specific to each period–scenario combination rather than fixed absolute probability intervals shared by all projections.

The categorical rasters were subsequently imported into QGIS, where the same category names and cartographic scheme were maintained across projections. The number of raster cells assigned to each category was quantified and converted into hectares according to the raster-cell area. Accordingly, comparisons among periods and scenarios referred to changes in the spatial extent assigned to each relative suitability class. Consequently, the relative percentage for each suitability class was calculated using the total categorized area of its respective projection as the denominator, rather than a fixed regional extent.

To visualize the spatial changes in habitat suitability across the three analyzed periods, the binary habitat suitability maps corresponding to the near-term reference period, the medium-term future, and the long-term future were used. In these maps, each cell presents only two possible values: 1 when it was classified as suitable for the species and 0 when it was classified as unsuitable. Subsequently, the three binary maps were combined through map algebra by applying Equation (4)

$$(R_{BL} * 1) + (R_{MT} * 10) + (R_{LT} * 100), \quad (4)$$

where R_{BL} represents the binary raster layer of habitat suitability for the near-term reference period (2011–2040), R_{MT} represents the binary raster layer of the medium-term future period (2041–2070), and R_{LT} represents the binary raster layer of the long-term future period (2071–2100). The multipliers 1, 10, and 100 were used to assign a different temporal position to each period within the final code: units for the near-term reference period, tens for the medium term, and hundreds for the long term. In this way, the resulting value does not represent a weighted sum of suitability, but rather a temporal code that indicates in which periods a cell was classified as suitable.

From this operation, areas of habitat loss, gain, and stability were identified, categories used in studies of potential distribution of plant and tree species to summarize the projected

spatial changes in suitable habitat [7,9]. For example, a cell suitable in the three periods generates the code 111, calculated as:

$$(1 * 1) + (1 * 10) + (1 * 100) = 111, \quad (5)$$

which corresponds to stability; whereas a cell suitable only in the near-term reference period generates the code 1, calculated as:

$$(1 * 1) + (0 * 10) + (0 * 100) = 1, \quad (6)$$

which corresponds to loss. The codes that indicated suitability in the three periods were classified as stability. The codes that indicated suitability in the near-term reference period, but absence of suitability in one or both future periods, were classified as loss. In contrast, the codes that indicated absence of suitability during the near-term reference period, but presence of suitability in one or both future periods, were classified as gain. In addition, map algebra allowed the generation of more specific categories, subdividing loss into “immediate loss” and “long-term loss”, and gain into “expansion and establishment” and “delayed expansion”. Specifically, stable habitat corresponded to cells classified as suitable during all three periods; immediate loss represented cells suitable only during the near-term reference period; long-term loss represented cells that remained suitable through the medium-term period but became unsuitable in the long term; expansion and establishment represented cells initially unsuitable but suitable from the medium-term period onward; and delayed expansion represented cells classified as suitable only during the long-term period.

Each generated category was quantified in hectares, and a net balance was calculated to analyze the general behavior of the available habitat across the three periods in each of the analyzed scenarios.

2.5. Influence of Environmental Variables and Proposal of Strategic Typologies

Finally, the relative importance of the climatic and topographic variables in habitat suitability was analyzed. To estimate the influence of each predictor, a method was used that consisted of randomly permuting the data of each environmental variable (predictor), converting the information of this variable into erratic information. For each predictor, 10 random permutations were executed. The importance of each predictor was estimated by quantifying the decrease in the correlation between the original prediction and the prediction obtained after the permutation of each variable.

To diagnose the relationship between habitat dynamics and the associated environmental variables, value density curves were developed for the variables introduced. The curves were generated through kernel density estimation, which allowed identification of ranges of environmental conditions associated with habitat loss, stability, or gain.

Finally, a reclassification oriented toward the formulation of strategic typologies was carried out, so that the projected spatial dynamics of the habitat could be translated into useful operational categories for planning conservation and restoration actions, given that distribution models can be used as support tools for spatial decision-making and the definition of management priorities [48–50]. For the reclassification, the temporal behavior of the habitat was considered, and the dynamic categories were reorganized into three strategic typologies: stable habitat areas were assigned to conservation; immediate loss and long-term loss areas were grouped as restoration; and expansion and establishment areas, together with delayed expansion areas, were classified as preventive conservation and monitoring.

3. Results

The findings derived from both the predictive modeling and the environmental analysis for the *Polylepis* forests are presented below.

3.1. Predictive Performance and Inter-Algorithmic Uncertainty Evaluation of the Ensemble Model

The evaluation through cross-validation demonstrated that supervised machine learning algorithms such as RF, GBM, and ANN, as well as the classification algorithm FDA, outperformed the linear statistical models in predictive capacity, a performance that is reflected in the metrics shown in Table 2.

Table 2. Performance metrics of the algorithms (Testing data).

Algorithm	True Skill Statistic (TSS) (Mean $\pm$ SD) ¹	ROC/AUC ² (Mean $\pm$ SD) ¹
RF ³	0.933 $\pm$ 0.016	0.991 $\pm$ 0.006
GBM ⁴	0.925 $\pm$ 0.003	0.987 $\pm$ 0.006
FDA ⁵	0.915 $\pm$ 0.021	0.968 $\pm$ 0.001
ANN ⁶	0.894 $\pm$ 0.033	0.967 $\pm$ 0.024
CTA ⁷	0.892 $\pm$ 0.018	0.956 $\pm$ 0.008
GAM ⁸	0.888 $\pm$ 0.041	0.946 $\pm$ 0.022
GLM ⁹	0.820 $\pm$ 0.034	0.910 $\pm$ 0.017
SRE ¹⁰	0.643 $\pm$ 0.051	0.822 $\pm$ 0.025

¹ SD: Standard Deviation. ² ROC/AUC: Area Under the ROC Curve. ³ RF: Random Forest. ⁴ GBM: Gradient Boosting Machine. ⁵ FDA: Flexible Discriminant Analysis. ⁶ ANN: Artificial Neural Network. ⁷ CTA: Classification Tree Analysis. ⁸ GAM: Generalized Additive Model. ⁹ GLM: Generalized Linear Model. ¹⁰ SRE: Surface Range Envelope.

By applying EMwmeanByTSS to the 9 modeling replicates, a sensitivity rate of 98.45% and a specificity rate of 95.88% were obtained. From these parameters, it can be concluded that the model showed adequate discriminatory performance, recording a ROC/AUC value of 0.997 and a TSS of 0.943.

Additionally, the evaluation of spatial inter-algorithmic uncertainty evidenced high predictive consistency in the cores of the projected presence zones, supported by coefficient of variation (CV) values lower than 10%. In biometry and spatial modeling, this threshold is accepted as a statistical indicator of low variance and high reliability [51,52], demonstrating robust algorithmic consensus for these areas. In contrast, the methodological divergence of each model caused the highest peaks of inter-algorithmic uncertainty to remain confined to the ecotonal margins. This increase in variance toward the geographic limits is an expected analytical behavior in the ensemble approach, since in the zones of change the environmental conditions become suboptimal. In response to this change in habitat suitability, the different algorithmic families respond with greater sensitivity and define their mathematical tolerance thresholds in a divergent manner, which naturally increases predictive disagreement and, consequently, the coefficient of variation.

3.2. Habitat Suitability and Spatiotemporal Change

3.2.1. Near-Term and Future Habitat Suitability

The classification through Natural Breaks (Jenks) allowed the quantification of habitat suitability into four categories. For the near-term reference period (2011–2040), it was determined that the “Most suitable” category covers an extension of 30,965 ha, constituting 12.12% of the total categorized surface for that period, while for the period 2041–2070 (SSP3-7.0 pathway), it is shown that the “Most suitable” category decreases to 9990 ha, representing only 4.86% of the total categorized area for that period. Finally, toward the

long-term future period (2071–2100), it is observed that the “Most suitable” category covers a total surface of 374 ha, representing only 0.22% of the total categorized area for that period.

Figure 3 shows the habitat suitability projections for the near-term reference period (2011–2040).

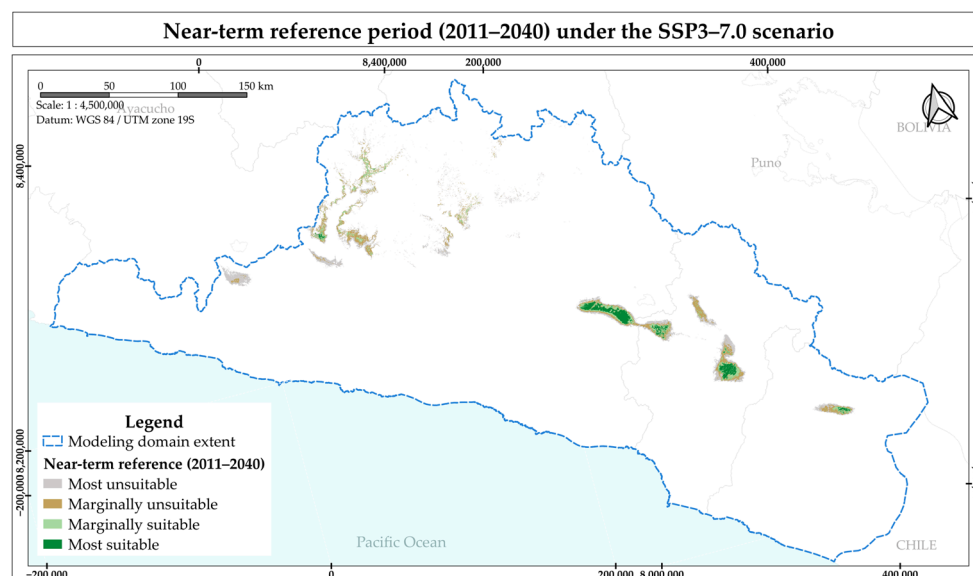


Figure 3. Spatial distribution of the four habitat-suitability categories projected for *Polylepis rugulosa* during the near-term reference period (2011–2040) under SSP3-7.0.

Similarly, Figure 4 shows the habitat suitability projections for the medium-term future period (2041–2070) for the SSP3-7.0 pathway.

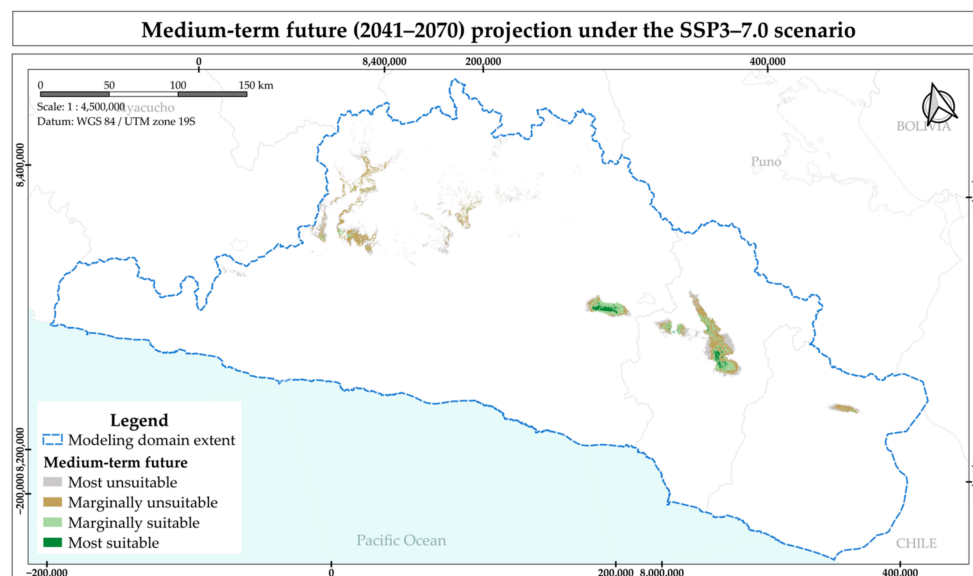


Figure 4. Spatial distribution of the four habitat-suitability categories projected for *Polylepis rugulosa* during the medium-term period (2041–2070) under SSP3-7.0.

Finally, Figure 5 shows the habitat suitability projections for the long-term future period (2071–2100) for the SSP3-7.0 socioeconomic pathway.

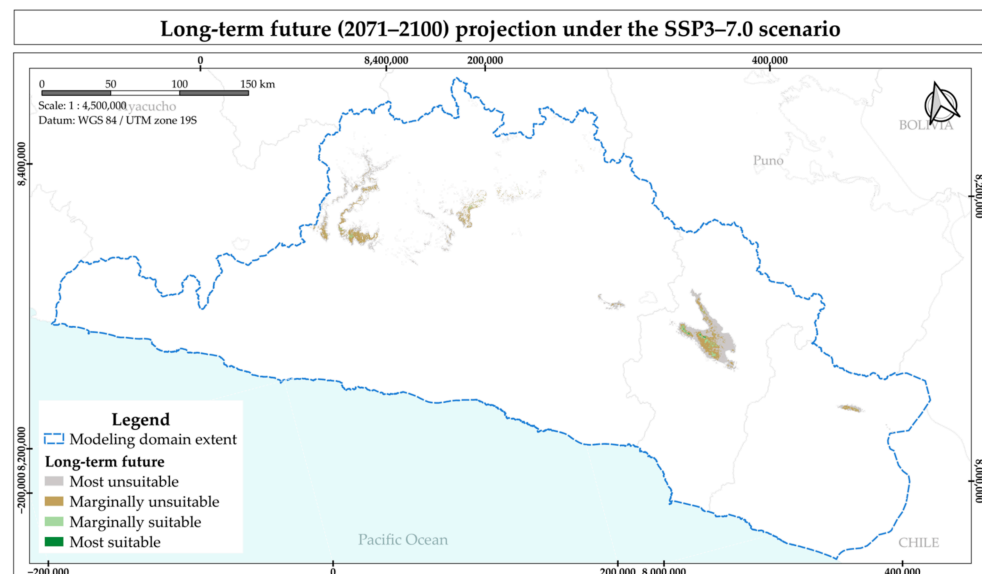


Figure 5. Spatial distribution of the four habitat-suitability categories projected for *Polylepis rugulosa* during the long-term period (2071–2100) under SSP3-7.0.

The quantification of habitat suitability has shown coincidence patterns for the three future pathways, showing greater criticality in the most extreme scenario, the long-term future period of the SSP5-8.5 pathway. Figure 6 synthesizes the quantification for the three pathways.

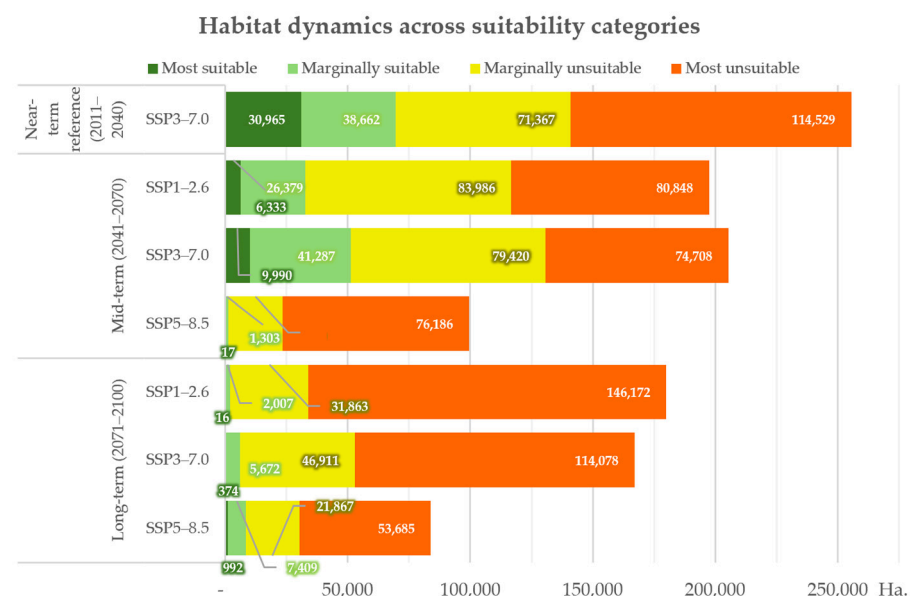


Figure 6. Projected area, expressed in hectares, of the four habitat-suitability categories for *Polylepis rugulosa* across the three SSPs and analysis periods.

3.2.2. Future Change Scenarios and Net Territorial Balance

The dynamics analysis through map algebra estimated a progressive deterioration until the end of the century (period 2071–2100). The net territorial balance evidences that, in the SSP3-7.0 socioeconomic pathway, there are approximately 100,663 ha of stable habitat. This stability contrasts sharply with the 154,086 ha that have been categorized as medium- and long-term loss. When evaluating the compensation offered, 67,915 ha was estimated as habitat gain, mostly by altitudinal expansion; the ecosystem registers a net deficit of −86,171 ha.

Figure 7 shows the spatial distribution of the five habitat-dynamics categories projected under SSP3-7.0: stable habitat, immediate loss, long-term loss, expansion and establishment, and delayed expansion.

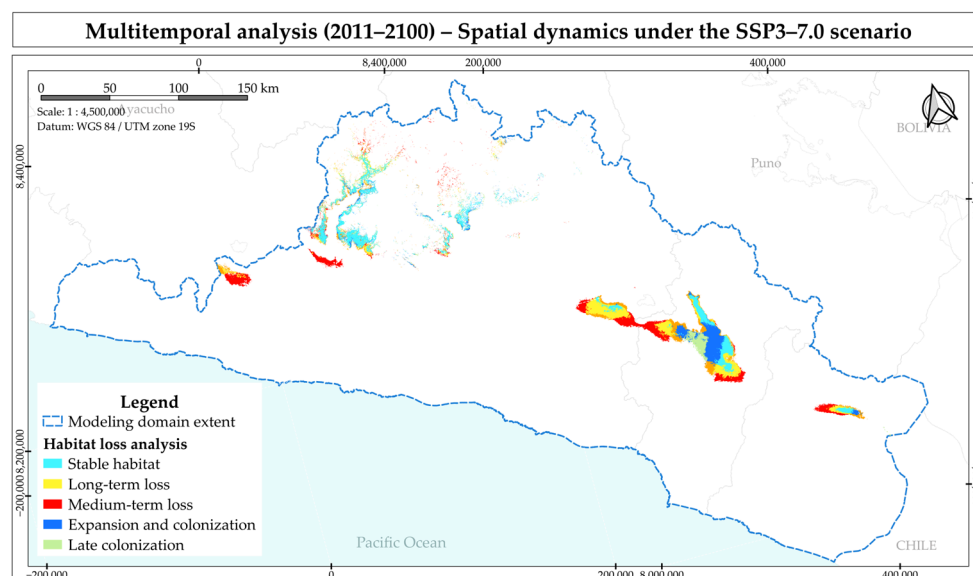


Figure 7. Spatiotemporal habitat dynamics of *Polylepis rugulosa* under SSP3-7.0, derived by overlaying binary suitability maps for 2011–2040, 2041–2070 and 2071–2100. The mapped trajectories comprise stable habitat, immediate loss, long-term loss, expansion and establishment, and delayed expansion.

Habitat vulnerability showed a greater dependence on the severity of the climate scenario. While in optimistic pathways such as SSP1-2.6 a negative net balance of $-68,516$ ha was recorded, in more critical pathways such as SSP5-8.5 this deficit reached its greatest magnitude, with a net loss of $-101,636$ ha.

As illustrated in Figure 8, the total net balance for the three analyzed pathways is shown, confirming the generalized trend toward ecosystem deterioration and habitat contraction, establishing SSP5-8.5 as the scenario of greatest criticality.

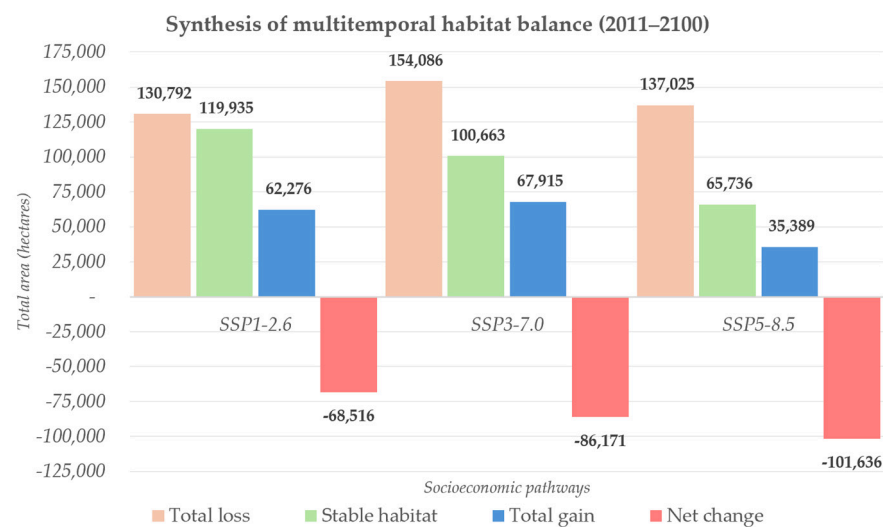


Figure 8. Total projected areas of habitat loss, stability, gain, and net change for *Polylepis rugulosa* under SSP1-2.6, SSP3-7.0, and SSP5-8.5 from 2011 to 2100. Areas are expressed in hectares.

3.3. Determining Factors of the Habitat and Delimitation of Intervention Typologies

3.3.1. Relative Importance of Variables and Modeled Environmental Associations

The relative importance analysis identified the following variables as the most influential: (BIO 17), (BIO 02), (BIO 15), and (BIO 04). Among the topographic variables, slope presented the greatest relative contribution, followed by the TWI and TPI.

Table 3 shows, in percentage values, the importance/influence that the different environmental variables introduced into the model had in the climate projections and determination of the ecological niche.

Table 3. Relative importance of environmental variables.

Variable	Name	Environmental Dimension Represented	Mean Permutation-Based Importance Score *
BIO 17	Precipitation of the driest quarter	Water availability in the driest period of the year	39.17%
BIO 02	Mean diurnal temperature range	Daily thermal variation in the environment	30.90%
BIO 15	Precipitation seasonality	Temporal variation in rainfall during the year	29.92%
BIO 04	Temperature seasonality	Annual thermal variation	19.22%
SLOPE	Slope	Terrain inclination	9.39%
TWI	Topographic Wetness Index	Relative tendency toward moisture accumulation to relief	1.45%
TPI	Topographic Position Index	Relative position of a site within the relief	1.22%

* Relative importance was estimated in BIOMOD2 using a random permutation procedure. The values represent the mean permutation-based importance score obtained from 10 permutations for each predictor. Because each predictor was evaluated independently, these values are not additive or normalized contributions and are not expected to sum to 100%.

The analysis of the probability density curves reveals a marked segregation of values for the predictive variables between the areas projected to experience habitat loss and those that will allow habitat stability and/or development.

Regarding the macroclimatic variables, the ecosystem evidences a high sensitivity to water stress. On one hand, the density curve of Precipitation of the Driest Quarter demonstrates that the areas projected to experience immediate and long-term loss are overwhelmingly concentrated in regimes of extreme aridity. In contrast, stable habitat was more frequently associated with higher precipitation values showing its highest density between 35 and 45 mm. In terms of temperature, stable habitat showed its highest density within a narrower Mean Diurnal Temperature Range, with the highest density occurring between 10.5 °C and 11.5 °C, evidencing a low tolerance to extreme variations in thermal amplitude.

This behavior is even more defined in the curves of the two variables with the greatest influence, which are shown in Figure 9.

Regarding geomorphology, the model projects habitat contraction and a shift toward higher altitudes. The probability density of distribution according to altitude indicates that the net loss zones surround the lower altitudes, from 3000 to 3800 m a.s.l. Consequently, the stable habitat shifts to higher altitudes, showing its highest-density range between 4000 and 4500 m a.s.l. On the other hand, the areas categorized as expansion and establishment or delayed expansion were associated with a modeled shift toward higher-altitude areas even exceeding 4500 m a.s.l.

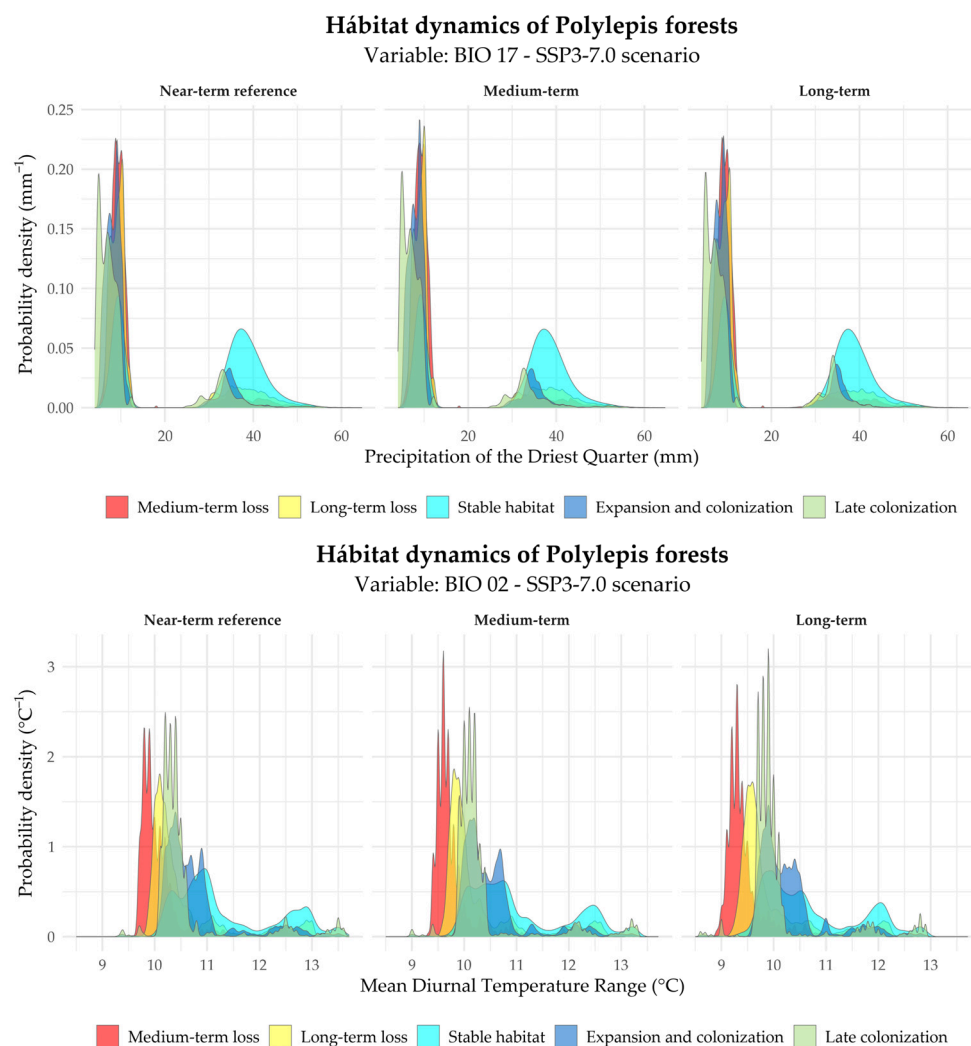


Figure 9. Kernel density distributions of Precipitation of the Driest Quarter (BIO 17, mm; **upper panel**) and Mean Diurnal Temperature Range (BIO 02, °C; **lower panel**) across habitat-dynamics categories and analysis periods under SSP3-7.0.

Additionally, the altitudinal shift is linked to an affinity for topographic complexity. The slope curve acts as a modulator, such that vulnerability to climate change is exacerbated in flat or gently inclined terrain, with loss peaks between 5° and 15°, while stable habitat was more frequently associated with steeper slopes, from 30° to 40°. This preference is corroborated by TWI, where its grouping in low values, from 5 to 7, and the coincidence with neutral values of TPI demonstrate that the habitat is configured on mid-mountain slopes, well drained, where the rugged topography buffers climatic extremes.

This pattern is observed with greater clarity in variables such as slope and altitude, whose probability density curves are shown in Figure 10.

This ecological niche characterization has been reflected in the other climate trajectories (SSP1-2.6 and SSP5-8.5), where the probability density curves express similar patterns. However, these environmental ranges represent modeled associations with projected habitat trajectories and should not be interpreted as experimentally demonstrated physiological or ecological thresholds.

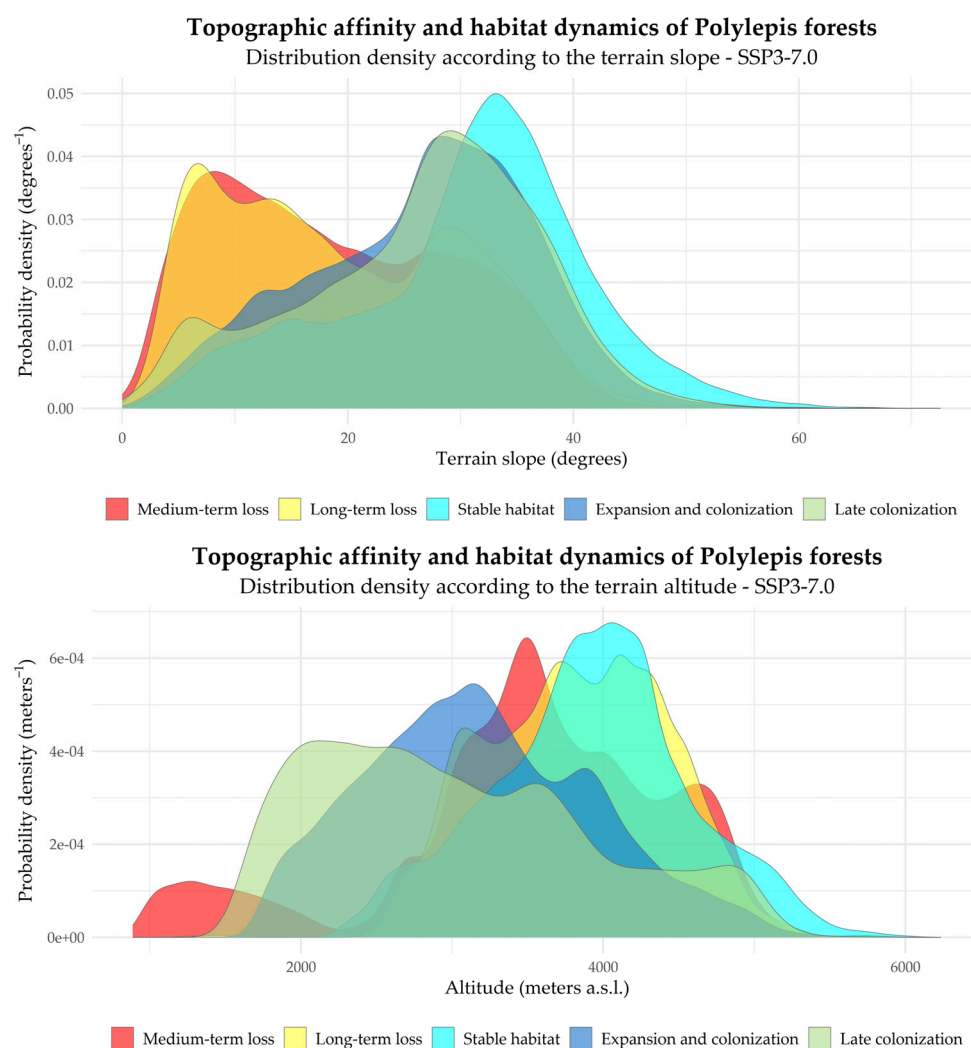


Figure 10. Kernel density distributions of terrain slope (degrees; **upper panel**) and altitude (m a.s.l.; **lower panel**) across the projected habitat-dynamics categories of *Polylepis rugulosa* under SSP3-7.0.

3.3.2. Proposal for Strategic Typologies

Based on the methodological reclassification of the spatiotemporal trajectories of the habitat, three strategic intervention typologies were obtained for the evaluated scenarios: conservation, restoration, and preventive conservation and monitoring. The surface area corresponding to each typology varied across climate scenarios, demonstrating differences in the magnitude of the areas oriented toward each type of intervention. These results are summarized in Table 4.

Table 4. Quantification of areas by strategic typology.

Scenario	Conservation (ha)	Restoration (ha)	Preventive Conservation and Monitoring (ha)
SSP1-2.6	119,395	130,792	62,276
SSP3-7.0	100,663	154,086	67,915
SSP5-8.5	65,736	137,025	35,389

4. Discussion

4.1. Model Performance and Environmental Factors

Ensemble modeling allows for reduced dependency on individual algorithms and strengthening of the robustness of the projections. In this study, EMwmeanByTSS assigned

greater weight to models with higher discrimination capacity, following consensus approaches applied in species distribution models [53]. The high performance of the final ensemble confirmed an adequate capability to differentiate between suitable and unfavorable areas, which is consistent with using TSS as a metric that integrates sensitivity and specificity [54]. The higher sensitivity observed is useful for conservation purposes because it reduces the risk of omitting marginal or ecotonal areas with potential relevance for future management or restoration actions.

The relative importance of the selected variables indicates that the potential distribution of *Polylepis rugulosa* is strongly influenced by dry-season water availability and daily thermal variability. The predominance of Precipitation of the Driest Quarter (BIO 17) likely reflects the importance of water availability during the most restrictive period of the year. In the seasonally dry environments of southern Peru, reduced precipitation during this period may intensify water limitation and hydraulic stress, thereby constraining forest regeneration and persistence. This interpretation is consistent with the high predictive importance of BIO 17 and with physiological evidence indicating that drought events affect xylem-vessel traits and drought adaptability in Peruvian *Polylepis* species [55].

The high importance of Mean Diurnal Temperature Range (BIO 02) suggests that habitat suitability is also associated with the difference between daytime and nighttime temperatures. Strong daily thermal fluctuations are characteristic of high-elevation environments and may impose contrasting thermal conditions over short periods. Similar patterns have been reported for other *Polylepis* species, with BIO 02 identified as an influential predictor of the potential distribution of Colombian *Polylepis* species [56] and as one of the principal variables explaining the current and projected distribution of *P. tarapacana* in the Altiplano [57]. Therefore, the combined importance of BIO 17 and BIO 02 suggests that the suitability of *P. rugulosa* is associated with the interaction between dry-season water limitation and daily thermal variability.

Likewise, slope, TWI, and TPI provide information regarding exposure, drainage, moisture, and landform position—factors relevant to microsite stability and the generation of favorable topoclimatic conditions [7,27,58]. In addition, density curves allowed for identifying the environmental ranges associated with the trajectories of habitat loss, stability, and gain, which helps understand under what conditions the habitat is maintained, contracts, or gains suitability, beyond merely identifying its spatial displacement [59].

4.2. Spatiotemporal Contraction of Suitable Habitat

The reclassified suitability projections show a progressive reduction in favorable habitat for *Polylepis rugulosa* forests toward the end of the century. Under SSP3-7.0, the “most suitable” category decreased from 12.12% during the near-term reference period to 0.22% in the long-term future, suggesting a severe loss of optimal climatic and ecological conditions. This trend is consistent with previous studies on *Polylepis*, which have reported reductions in suitable habitat and possible shifts toward higher elevations under climate change scenarios [8,25]. The spatiotemporal analysis reinforces this trend, as the net balance was negative under the same scenario and intensified under SSP5-8.5, indicating that areas of gain do not compensate for projected losses and suggesting a possible altitudinal compression of the habitat. In this context, the disaggregation of habitat loss, stability, and gain into more specific categories allowed the temporal dimension of change to be incorporated, differentiating trajectories occurring from the medium term from those projected toward the end of the century. This facilitates the recognition of areas requiring early attention, areas of climatic persistence, and sectors with future establishment potential, which are relevant for the spatial planning of management strategies [48,60,61].

4.3. Habitat Trajectories and Strategic Management Implications

Species distribution models are useful tools for guiding the planning of conservation and restoration strategies, as they allow for projecting current and future environmental suitability under different climate scenarios [11,48]. In this study, differentiating between areas of stability, loss, and gain permitted the interpretation of the temporal behavior of the habitat and its translation into strategic management typologies. This approach is consistent with the use of distribution models as support tools for prioritizing and planning conservation actions [48], as well as with the identification of areas of permanence and change under future climate scenarios [62].

In this regard, persistent areas can guide conservation actions due to their potential role as climate refugia [60], whereas zones with projected loss are linked to restoration, since early interventions in sites that are still usable can contribute to sustaining ecological functions and vegetation cover [63]. Finally, areas with future suitability can be oriented toward preventive conservation and monitoring, as they represent sectors that require safeguarding against pressures that could limit their subsequent establishment [64]. In this manner, planning is not based solely on generally projected climate suitability but rather incorporates a more differentiated interpretation of the projected habitat. This is useful for identifying areas of persistence, vulnerable zones, and sectors with future establishment potential—relevant criteria for guiding priority interventions [49,60].

4.4. Limitations and Future Research

Although species distribution models allow for projecting environmentally favorable areas, their results must be interpreted as estimates of potential suitability and not as a direct delimitation of areas suitable for immediate intervention. This is because SDMs are primarily based on statistical relationships between occurrence records and environmental variables; thus, they do not explicitly incorporate all ecological processes that condition actual habitat occupancy [10]. Furthermore, biotic factors such as dispersal, competition, herbivory, or mutualistic interactions can modify the effective distribution of species, even within climatically favorable areas [65].

The field surveys followed a preferential, expert-informed sampling design, which was appropriate for directing sampling effort toward areas where *P. rugulosa* was considered likely to occur [13]. While preferential presence data can theoretically retain spatial sampling bias associated with accessibility [66], this risk was inherently mitigated in our study. Because *P. rugulosa* populations have been historically restricted to steep, highly inaccessible relict patches due to anthropogenic pressure, the sampling design did not favor easily accessible routes; rather, it required high-effort field campaigns to reach these isolated environments. Furthermore, surveys were distributed across independent sampling areas separated by at least 1 km (equivalent to 10 pixels of our spatial grid) to effectively reduce local spatial clustering. Consequently, no additional post hoc corrections (such as spatial bias layers or target-group background approaches) were applied, as generating these would require systematic multi-species historical records that are currently unavailable for this rugged region. Ultimately, the combination of our high-effort field surveys and rigorous spatial thinning provides a robust representation of the species' environmental niche.

In addition, the models did not explicitly incorporate land-use change, grazing intensity, fire occurrence, human disturbance, or soil physicochemical properties. These factors can influence the degradation, regeneration, and persistence of *Polylepis* forests, even in areas with favorable climatic and topographic conditions [67,68]. Their omission may therefore lead to an overestimation of potential suitability in areas subject to intense anthropogenic pressure or unfavorable soil conditions.

Additionally, a first-order limitation of this study is the use of a single Global Circulation Model (GCM), the MPI-ESM1-2-HR. Although this high-resolution climate model is widely used and validated in the scientific literature to represent climate gradients in complex mountainous regions such as the Andes, end-of-century projections are inherently subject to high global climate variability. By relying on a single GCM, the spatial projections do not capture inter-model (inter-GCM) variance, which is typically the dominant component of long-term uncertainty. Therefore, the values presented in this study strictly reflect inter-algorithmic uncertainty (the mathematical divergence among the RF, GBM, FDA, and ANN models), and the cartographic results must be interpreted as one possible climate trajectory within a broader range of probable futures. Future research should incorporate a multi-GCM ensemble to partition and comprehensively evaluate all sources of climate uncertainty.

Additionally, we acknowledge a spatial scale mismatch among predictors. Interpolating the ~1 km CHELSA v2.1 bioclimatic data to a 100 m grid does not generate genuine microclimatic information. Consequently, the fine-scale spatial patterns observed in our suitability maps are strictly driven by the high-resolution topographic constraints from the ALOS PALSAR DEM, rather than localized climate shifts. Future modeling should integrate topoclimatic downscaling techniques to better reflect true microclimatic realities.

Finally, projected habitat gains via altitudinal expansion toward Andean summits (>4500 m) reflect purely theoretical climatic envelopes. These modeled gains ignore the hard elevational ceiling of the mountains (e.g., physical topographic limits and lack of soil substrate) as well as severe dispersal lags. Consequently, such high-altitude expansions are unlikely to represent realizable biological range shifts within the end-of-century timescale.

In this regard, the results obtained should be understood as a macroenvironmental baseline for planning, which requires local validation before guiding specific conservation or restoration actions. In the case of *Polylepis*, implementation must consider ecological field criteria, such as the availability of seed trees, seed dispersal, soil erosion, and livestock pressure—factors that can condition natural regeneration and forest establishment [69]. Regarding dispersal mechanisms, a climatically favorable zone will not necessarily be occupied by *Polylepis* if it is located far from seed trees or forest fragments, because seed arrival at the site may be limited. The natural regeneration of *Polylepis* tends to be concentrated near trees or forest edges, highlighting the importance of considering connectivity between patches before prioritizing areas for restoration [69,70]. Similarly, competition with herbaceous vegetation and herbivory or trampling associated with livestock can limit seedling establishment, even when the site presents favorable environmental conditions. These factors can affect the early stages of regeneration and reduce the natural recovery of the forest; therefore, they must be considered in field validation and the design of restoration actions [71,72].

Likewise, microsite selection is highly relevant, given that microenvironmental elements—such as the presence of rocks, altitude, land use, and local site characteristics—can influence early seedling performance [71,73]. Additionally, biological facilitation through nurse plants can reduce microenvironmental stress and favor initial survival in exposed areas [74]. In accordance with *Polylepis* restoration experiences, these actions should be accompanied by site protection, control of local pressures, and subsequent monitoring to evaluate establishment and adjust management [75].

Future research could complement this approach by incorporating more detailed biotic variables, such as natural regeneration, seed availability, mycorrhizae, or interactions with dispersing fauna, to improve the ecological interpretation of the projections [76].

5. Conclusions

- The ensemble model in BIOMOD2 showed high discrimination metrics within the adopted repeated random holdout validation framework when modeling the current and future suitability of *Polylepis rugulosa* forests in southern Peru. The potential distribution of the species was mainly influenced by seasonal water availability and thermal variability, while slope contributed to interpreting the role of topography as a local habitat modulator.
- The reclassified projections demonstrated a progressive reduction in favorable habitat for *P. rugulosa* toward the end of the century. Under the SSP3-7.0 scenario, the “most suitable” areas decreased markedly between the near-term reference period and the long-term future, whereas SSP5-8.5 showed the greatest habitat restriction.
- The spatiotemporal analysis allowed for identifying early attention areas, zones with climatic persistence, and sectors with future establishment potential for *P. rugulosa*. This differentiation provided a useful basis for formulating conservation strategies in stable areas, restoration actions in areas of projected habitat loss, and preventive conservation and monitoring in areas with future suitability.
- The proposed strategic typologies allow the translation of projected habitat trajectories of *P. rugulosa* into management criteria under climate change. However, their implementation must consider local validation and ecological field assessments, given that projected climate suitability alone does not guarantee the effective establishment or persistence of the species.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f17080894/s1>, Table S1: Pearson correlation matrix of the 24 initial environmental predictors used in the collinearity analysis.

Author Contributions: Conceptualization, A.C.-M. and B.C.-P.; methodology, S.M.-V. and K.P.d.C.-B.; software, S.M.-V.; validation, M.d.I.C.; formal analysis, S.M.-V., K.P.d.C.-B., B.C.-P., A.C.-M. and M.d.I.C.; investigation, S.M.-V. and K.P.d.C.-B.; resources, A.C.-M. and B.C.-P.; data curation, S.M.-V. and K.P.d.C.-B.; writing—original draft preparation, K.P.d.C.-B.; writing—review and editing, S.M.-V., K.P.d.C.-B., B.C.-P., A.C.-M. and M.d.I.C.; visualization, S.M.-V. and K.P.d.C.-B.; supervision, M.d.I.C.; project administration, A.C.-M. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The exact geographic coordinates of the *Polylepis* occurrences are not publicly available due to conservation concerns, as releasing precise locations could expose these highly vulnerable relict forests to further anthropogenic pressure, such as illegal logging and habitat degradation. A map showing the general spatial distribution of the records is provided in Figure 1. The R code and the dataset used for modeling are available from the corresponding author upon reasonable request.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Bellard, C.; Bertelsmeier, C.; Leadley, P.; Thuiller, W.; Courchamp, F. Impacts of Climate Change on the Future of Biodiversity. *Ecol. Lett.* **2012**, *15*, 365–377. [[CrossRef](#)] [[PubMed](#)]
2. Parmesan, C.; Yohe, G. A Globally Coherent Fingerprint of Climate Change Impacts across Natural Systems. *Nature* **2003**, *421*, 37–42. [[CrossRef](#)] [[PubMed](#)]
3. Cui, F.; Wang, B.; Zhang, Q.; Tang, H.; De Maeyer, P.; Hamdi, R.; Dai, L. Climate Change versus Land-Use Change—What Affects the Ecosystem Services More in the Forest-Steppe Ecotone? *Sci. Total Environ.* **2021**, *759*, 143525. [[CrossRef](#)] [[PubMed](#)]

4. Imfeld, N.; Sedlmeier, K.; Gubler, S.; Correa Marrou, K.; Davila, C.P.; Huerta, A.; Lavado-Casimiro, W.; Rohrer, M.; Scherrer, S.C.; Schwierz, C. A Combined View on Precipitation and Temperature Climatology and Trends in the Southern Andes of Peru. *Int. J. Clim.* **2021**, *41*, 679–698. [\[CrossRef\]](#)
5. Boza Espinoza, T.E.; Kessler, M. A Monograph of the Genus *Polylepis* (Rosaceae). *PhytoKeys* **2022**, *203*, 1–274. [\[CrossRef\]](#) [\[PubMed\]](#)
6. Cierjacks, A.; Wesche, K.; Hensen, I. Potential Lateral Expansion of *Polylepis* Forest Fragments in Central Ecuador. *For. Ecol. Manag.* **2007**, *242*, 477–486. [\[CrossRef\]](#)
7. Caballero-Villalobos, L.; Fajardo-Gutiérrez, F.; Calbi, M.; Silva-Arias, G.A. Climate Change Can Drive a Significant Loss of Suitable Habitat for *Polylepis Quadrijuga*, a Treeline Species in the Sky Islands of the Northern Andes. *Front. Ecol. Evol.* **2021**, *9*, 661550. [\[CrossRef\]](#)
8. Cuyckens, G.A.E.; Renison, D. Identification of Priority Areas for the Restoration of High Andean Mountain Forests under Climate Change: A Case Study Using Potential Distribution Models. *Restor. Ecol.* **2024**, *32*, e14193. [\[CrossRef\]](#)
9. Koç, D.E.; Ustaoglu, B.; Biltekin, D. Effect of Climate Change on the Habitat Suitability of the Relict Species *Zelkova Carpinifolia* Spach Using Ensembled Species Distribution Modelling. *Sci. Rep.* **2024**, *14*, 27967. [\[CrossRef\]](#) [\[PubMed\]](#)
10. Elith, J.; Leathwick, J.R. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annu. Rev. Ecol. Evol. Syst.* **2009**, *40*, 677–697. [\[CrossRef\]](#)
11. Thuiller, W.; Lafourcade, B.; Engler, R.; Araújo, M.B. BIOMOD—A Platform for Ensemble Forecasting of Species Distributions. *Ecography* **2009**, *32*, 369–373. [\[CrossRef\]](#)
12. Elzinga, C.L.; Salzer, D.W.; Willoughby, J.W. *Measuring & Monitoring Plant Populations*; BLM Technical Reference 1730-1; Bureau of Land Management: Denver, CO, USA, 1998.
13. Aizpurua, O.; Cantú-Salazar, L.; San Martín, G.; Biver, G.; Brotons, L.; Titeux, N. Reconciling Expert Judgement and Habitat Suitability Models as Tools for Guiding Sampling of Threatened Species. *J. Appl. Ecol.* **2015**, *52*, 1608–1616. [\[CrossRef\]](#)
14. Barbet-Massin, M.; Jiguet, F.; Albert, C.H.; Thuiller, W. Selecting Pseudo-absences for Species Distribution Models: How, Where and How Many? *Methods Ecol. Evol.* **2012**, *3*, 327–338. [\[CrossRef\]](#)
15. Li, M.; Wang, L.; Liu, H.; Sun, Y.; Li, N.; Geng, M. Spatiotemporal Distribution Shifts of *Zelkova Schneideriana* Under Climate Change: A Biomod2-Driven Modeling Framework. *Biology* **2025**, *14*, 1221. [\[CrossRef\]](#) [\[PubMed\]](#)
16. Thuiller, W.; Georges, D.; Gueguen, M.; Engler, R.; Breiner, F.; Lafourcade, B.; Patin, R.; Blancheteau, H. Biomod2: Ensemble Platform for Species Distribution Modeling. R package version 4.2-5-2; CRAN. 2012. Available online: <https://biomodhub.github.io/biomod2/> (accessed on 19 June 2026).
17. De Simone, W.; Allegranza, M.; Frattaroli, A.R.; Montecchiari, S.; Tesi, G.; Zuccarello, V.; Di Musciano, M. From Remote Sensing to Species Distribution Modelling: An Integrated Workflow to Monitor Spreading Species in Key Grassland Habitats. *Remote Sens.* **2021**, *13*, 1904. [\[CrossRef\]](#)
18. Arlot, S.; Celisse, A. A Survey of Cross-Validation Procedures for Model Selection. *arXiv* **2009**, arXiv:0907.4728. [\[CrossRef\]](#)
19. VanDerWal, J.; Shoo, L.P.; Graham, C.; Williams, S.E. Selecting Pseudo-Absence Data for Presence-Only Distribution Modeling: How Far Should You Stray from What You Know? *Ecol. Model.* **2009**, *220*, 589–594. [\[CrossRef\]](#)
20. Karger, D.N.; Chauvier, Y.; Zimmermann, N.E. Chelsa-cmip6 1.0: A Python Package to Create High Resolution Bioclimatic Variables Based on CHELSA Ver. 2.1 and CMIP6 Data. *Ecography* **2023**, *2023*, e06535. [\[CrossRef\]](#)
21. Karger, D.N.; Conrad, O.; Böhrner, J.; Kawohl, T.; Kreft, H.; Soria-Auza, R.W.; Zimmermann, N.E.; Linder, H.P.; Kessler, M. Climatologies at High Resolution for the Earth's Land Surface Areas. *Sci. Data* **2017**, *4*, 170122. [\[CrossRef\]](#) [\[PubMed\]](#)
22. Eyring, V.; Bony, S.; Meehl, G.A.; Senior, C.A.; Stevens, B.; Stouffer, R.J.; Taylor, K.E. Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) Experimental Design and Organization. *Geosci. Model Dev.* **2016**, *9*, 1937–1958. [\[CrossRef\]](#)
23. Müller, W.A.; Jungclaus, J.H.; Mauritsen, T.; Baehr, J.; Bittner, M.; Budich, R.; Bunzel, F.; Esch, M.; Ghosh, R.; Haak, H.; et al. A Higher-resolution Version of the Max Planck Institute Earth System Model (MPI-ESM1.2-HR). *J. Adv. Model. Earth Syst.* **2018**, *10*, 1383–1413. [\[CrossRef\]](#)
24. Calvin, K.; Dasgupta, D.; Krinner, G.; Mukherji, A.; Thorne, P.W.; Trisos, C.; Romero, J.; Aldunce, P.; Barrett, K.; Blanco, G.; et al. IPCC, 2023: *Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, 1st ed.; Lee, H., Romero, J., Arias, P., Bustamante, M., Elgizouli, I., Flato, G., Howden, M., Méndez-Vallejo, C., Pereira, J.J., Pichs-Madruga, R., et al., Eds.; Intergovernmental Panel on Climate Change (IPCC): Geneva, Switzerland, 2023.
25. ASF DAAC. ALOS PALSAR High Resolution Radiometric Terrain Corrected Product 2014; ASF DAAC: Fairbanks, AK, USA, 2014.
26. Amatulli, G.; Domisch, S.; Tuanmu, M.-N.; Parmentier, B.; Ranipeta, A.; Malczyk, J.; Jetz, W. A Suite of Global, Cross-Scale Topographic Variables for Environmental and Biodiversity Modeling. *Sci. Data* **2018**, *5*, 180040. [\[CrossRef\]](#) [\[PubMed\]](#)
27. Beven, K.J.; Kirkby, M.J. A Physically Based, Variable Contributing Area Model of Basin Hydrology/Un Modèle à Base Physique de Zone d'appel Variable de l'hydrologie Du Bassin Versant. *Hydrol. Sci. Bull.* **1979**, *24*, 43–69. [\[CrossRef\]](#)

28. De Reu, J.; Bourgeois, J.; Bats, M.; Zwervaeagher, A.; Gelorini, V.; De Smedt, P.; Chu, W.; Antrop, M.; De Maeyer, P.; Finke, P.; et al. Application of the Topographic Position Index to Heterogeneous Landscapes. *Geomorphology* **2013**, *186*, 39–49. [\[CrossRef\]](#)
29. Conrad, O.; Bechtel, B.; Bock, M.; Dietrich, H.; Fischer, E.; Gerlitz, L.; Wehberg, J.; Wichmann, V.; Böhner, J. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. *Geosci. Model Dev.* **2015**, *8*, 1991–2007. [\[CrossRef\]](#)
30. Pearson, R.G. Species' Distribution Modeling for Conservation Educators and Practitioners. *Lessons Conserv.* **2010**, *3*, 54–89. [\[CrossRef\]](#)
31. Hansen, S.E.; Monfils, M.J.; Hackett, R.A.; Goebel, R.T.; Monfils, A.K. Data-centric Species Distribution Modeling: Impacts of Modeler Decisions in a Case Study of Invasive European Frog-bit. *Appl. Plant Sci.* **2024**, *12*, e11573. [\[CrossRef\]](#) [\[PubMed\]](#)
32. De Marco, P.; Nóbrega, C.C. Evaluating Collinearity Effects on Species Distribution Models: An Approach Based on Virtual Species Simulation. *PLoS ONE* **2018**, *13*, e0202403. [\[CrossRef\]](#) [\[PubMed\]](#)
33. Santos, D.P.; Silva, T.S.F.; De Assis Figueiredo, F.A.M.M. Climate Change May Increase Environmental Suitability of the Babassu Complex (*Attalea* spp., Arecaceae). *J. Biogeogr.* **2025**, *52*, e70027. [\[CrossRef\]](#)
34. Rew, J.; Cho, Y.; Moon, J.; Hwang, E. Habitat Suitability Estimation Using a Two-Stage Ensemble Approach. *Remote Sens.* **2020**, *12*, 1475. [\[CrossRef\]](#)
35. Guisan, A.; Thuiller, W.; Zimmermann, N.E. *Habitat Suitability and Distribution Models: With Applications in R*, 1st ed.; Cambridge University Press: Cambridge, UK, 2017.
36. Guisan, A.; Edwards, T.C.; Hastie, T. Generalized Linear and Generalized Additive Models in Studies of Species Distributions: Setting the Scene. *Ecol. Model.* **2002**, *157*, 89–100. [\[CrossRef\]](#)
37. Hastie, T.; Tibshirani, R.; Buja, A. Flexible Discriminant Analysis by Optimal Scoring. *J. Am. Stat. Assoc.* **1994**, *89*, 1255–1270. [\[CrossRef\]](#)
38. De'ath, G.; Fabricius, K.E. Classification and Regression Trees: A Powerful Yet Simple Technique for Ecological Data Analysis. *Ecology* **2000**, *81*, 3178–3192. [\[CrossRef\]](#)
39. Pichler, M.; Hartig, F. Machine Learning and Deep Learning—A Review for Ecologists. *Methods Ecol. Evol.* **2023**, *14*, 994–1016. [\[CrossRef\]](#)
40. Breiman, L. Random Forests. *Mach. Learn.* **2001**, *45*, 5–32. [\[CrossRef\]](#)
41. Elith, J.; Leathwick, J.R.; Hastie, T. A Working Guide to Boosted Regression Trees. *J. Anim. Ecol.* **2008**, *77*, 802–813. [\[CrossRef\]](#) [\[PubMed\]](#)
42. Booth, T.H.; Nix, H.A.; Busby, J.R.; Hutchinson, M.F. Bioclim: The First Species Distribution Modelling Package, Its Early Applications and Relevance to Most Current MaxEnt Studies. *Divers. Distrib.* **2014**, *20*, 1–9. [\[CrossRef\]](#)
43. Araujo, M.; New, M. Ensemble Forecasting of Species Distributions. *Trends Ecol. Evol.* **2007**, *22*, 42–47. [\[CrossRef\]](#) [\[PubMed\]](#)
44. Fielding, A.H.; Bell, J.F. A Review of Methods for the Assessment of Prediction Errors in Conservation Presence/Absence Models. *Environ. Conserv.* **1997**, *24*, 38–49. [\[CrossRef\]](#)
45. Vistín, D.A.; Salas, E.M.; Balseca, J.E.; Lara, N.X. Distribución potencial de *Polylepis incana* en los Andes ecuatorianos para estudios de fisiología vegetal y planes de rehabilitación forestal. *Ecol. Austral* **2022**, *33*, 001–012. [\[CrossRef\]](#)
46. Zhao, G.; Cui, X.; Sun, J.; Li, T.; Wang, Q.; Ye, X.; Fan, B. Analysis of the Distribution Pattern of Chinese *Ziziphus Jujuba* under Climate Change Based on Optimized Biomod2 and MaxEnt Models. *Ecol. Indic.* **2021**, *132*, 108256. [\[CrossRef\]](#)
47. Tytar, V.; Kozynenko, I.; Pupins, M.; Škute, A.; Čeirāns, A.; Georges, J.-Y.; Nekrasova, O. Species Distribution Modeling of *Ixodes Ricinus* (Linnaeus, 1758) Under Current and Future Climates, with a Special Focus on Latvia and Ukraine. *Climate* **2024**, *12*, 184. [\[CrossRef\]](#)
48. Guisan, A.; Tingley, R.; Baumgartner, J.B.; Naujokaitis-Lewis, I.; Sutcliffe, P.R.; Tulloch, A.I.T.; Regan, T.J.; Brotons, L.; McDonald-Madden, E.; Mantyka-Pringle, C.; et al. Predicting Species Distributions for Conservation Decisions. *Ecol. Lett.* **2013**, *16*, 1424–1435. [\[CrossRef\]](#) [\[PubMed\]](#)
49. Moilanen, A.; Lehtinen, P.; Kohonen, I.; Jalkanen, J.; Virtanen, E.A.; Kujala, H. Novel Methods for Spatial Prioritization with Applications in Conservation, Land Use Planning and Ecological Impact Avoidance. *Methods Ecol. Evol.* **2022**, *13*, 1062–1072. [\[CrossRef\]](#)
50. Hu, W.; Zhang, D.; Chen, B.; Liu, X.; Ye, X.; Jiang, Q.; Zheng, X.; Du, J.; Chen, S. Mapping the Seagrass Conservation and Restoration Priorities: Coupling Habitat Suitability and Anthropogenic Pressures. *Ecol. Indic.* **2021**, *129*, 107960. [\[CrossRef\]](#)
51. Buisson, L.; Thuiller, W.; Casajus, N.; Lek, S.; Grenouillet, G. Uncertainty in Ensemble Forecasting of Species Distribution. *Glob. Change Biol.* **2010**, *16*, 1145–1157. [\[CrossRef\]](#)
52. Gomez, K.A.; Gomez, A.A. *Statistical Procedures for Agricultural Research; An International Rice Research Institute Book*, 2nd ed.; Wiley: New York, NY, USA, 1984.
53. Marmion, M.; Parviainen, M.; Luoto, M.; Heikkinen, R.K.; Thuiller, W. Evaluation of Consensus Methods in Predictive Species Distribution Modelling. *Divers. Distrib.* **2009**, *15*, 59–69. [\[CrossRef\]](#)
54. Allouche, O.; Tsoar, A.; Kadmon, R. Assessing the Accuracy of Species Distribution Models: Prevalence, Kappa and the True Skill Statistic (TSS). *J. Appl. Ecol.* **2006**, *43*, 1223–1232. [\[CrossRef\]](#)

55. Rodríguez-Ramírez, E.C.; Crispín-DelaCruz, D.B.; Ticse-Otarola, G.; Requena-Rojas, E.J. Assessing the Hydric Deficit on Two *Polylepis* Species from the Peruvian Andean Mountains: Xylem Vessel Anatomic Adjusting. *Forests* **2022**, *13*, 633. [\[CrossRef\]](#)
56. Fajardo-Gutiérrez, F.; Infante-Betancour, J.; Cabrera-Amaya, D.M. Modelización de la distribución potencial del género *Polylepis* en Colombia y consideraciones para su conservación. *Ecol. Austral* **2018**, *28*, 202–215. [\[CrossRef\]](#)
57. Cuyckens, G.A.E.; Christie, D.A.; Domic, A.I.; Malizia, L.R.; Renison, D. Climate Change and the Distribution and Conservation of the World's Highest Elevation Woodlands in the South American Altiplano. *Glob. Planet. Change* **2016**, *137*, 79–87. [\[CrossRef\]](#)
58. Toivonen, J.; Gonzales-Inca, C.; Bader, M.; Ruokolainen, K.; Kessler, M. Elevational Shifts in the Topographic Position of *Polylepis* Forest Stands in the Andes of Southern Peru. *Forests* **2017**, *9*, 7. [\[CrossRef\]](#)
59. Austin, M. Species Distribution Models and Ecological Theory: A Critical Assessment and Some Possible New Approaches. *Ecol. Model.* **2007**, *200*, 1–19. [\[CrossRef\]](#)
60. Keppel, G.; Stralberg, D.; Morelli, T.L.; Bátori, Z. Managing Climate-Change Refugia to Prevent Extinctions. *Trends Ecol. Evol.* **2024**, *39*, 800–808. [\[CrossRef\]](#) [\[PubMed\]](#)
61. Michalak, J.L.; Lawler, J.J.; Roberts, D.R.; Carroll, C. Distribution and Protection of Climatic Refugia in North America. *Conserv. Biol.* **2018**, *32*, 1414–1425. [\[CrossRef\]](#) [\[PubMed\]](#)
62. Maxwell, S.L.; Reside, A.; Trezise, J.; McAlpine, C.A.; Watson, J.E. Retention and Restoration Priorities for Climate Adaptation in a Multi-Use Landscape. *Glob. Ecol. Conserv.* **2019**, *18*, e00649. [\[CrossRef\]](#)
63. Volis, S. Conservation-Oriented Restoration—A Two for One Method to Restore Both Threatened Species and Their Habitats. *Plant Divers.* **2019**, *41*, 50–58. [\[CrossRef\]](#) [\[PubMed\]](#)
64. Barrows, C.W.; Ramirez, A.R.; Sweet, L.C.; Morelli, T.L.; Millar, C.I.; Frakes, N.; Rodgers, J.; Mahalovich, M.F. Validating Climate-change Refugia: Empirical Bottom-up Approaches to Support Management Actions. *Front. Ecol. Environ.* **2020**, *18*, 298–306. [\[CrossRef\]](#)
65. Araújo, M.B.; Luoto, M. The Importance of Biotic Interactions for Modelling Species Distributions under Climate Change. *Glob. Ecol. Biogeogr.* **2007**, *16*, 743–753. [\[CrossRef\]](#)
66. Phillips, S.J.; Dudík, M.; Elith, J.; Graham, C.H.; Lehmann, A.; Leathwick, J.; Ferrier, S. Sample Selection Bias and Presence-only Distribution Models: Implications for Background and Pseudo-absence Data. *Ecol. Appl.* **2009**, *19*, 181–197. [\[CrossRef\]](#) [\[PubMed\]](#)
67. Kessler, M.; Toivonen, J.M.; Sylvester, S.P.; Kluge, J.; Hertel, D. Elevational Patterns of *Polylepis* Tree Height (Rosaceae) in the High Andes of Peru: Role of Human Impact and Climatic Conditions. *Front. Plant Sci.* **2014**, *5*, 194. [\[CrossRef\]](#) [\[PubMed\]](#)
68. Hoyos, Y.D.; Vargas, N.; Sanchez, A. Different Functional Responses in Populations of *Polylepis* Quadrijuga (Rosaceae) as a Consequence of Anthropogenic Disturbance. *Front. For. Glob. Change* **2024**, *7*, 1488389. [\[CrossRef\]](#)
69. Torres, R.C.; Renison, D.; Hensen, I.; Suarez, R.; Enrico, L. *Polylepis Australis*' Regeneration Niche in Relation to Seed Dispersal, Site Characteristics and Livestock Density. *For. Ecol. Manag.* **2008**, *254*, 255–260. [\[CrossRef\]](#)
70. Morales, L.V.; Sevillano-Rios, C.S.; Fick, S.; Young, T.P. Differential Seedling Regeneration Patterns across Forest–Grassland Ecotones in Two Tropical Treeline Species (*Polylepis* spp.). *Austral Ecol.* **2018**, *43*, 514–526. [\[CrossRef\]](#)
71. Cáceres, Y.; Schrieber, K.; Lachmuth, S.; Auge, H.; Argibay, D.; Renison, D.; Hensen, I. Effects of Altitude, Land Use and Microsites on Early Life Performance of a High Mountain Tree: Insights from an in Situ Sowing Experiment. *Divers. Distrib.* **2019**, *25*, 1537–1550. [\[CrossRef\]](#)
72. Teich, I.; Cingolani, A.M.; Renison, D.; Hensen, I.; Giorgis, M.A. Do Domestic Herbivores Retard *Polylepis Australis* Bitt. Woodland Recovery in the Mountains of Córdoba, Argentina? *For. Ecol. Manag.* **2005**, *219*, 229–241. [\[CrossRef\]](#)
73. Victoria Lien, L.; Juan Manuel, C.; Cuyckens, G.A.E. Influencia Del Micrositio y El Ambiente En La Instalación de *Polylepis* Tarapacana En Los Altos Andes. *Neotrop. Biodivers.* **2021**, *7*, 135–145. [\[CrossRef\]](#)
74. Kleier, C.; Lambrinos, J.G. The Importance of Nurse Associations for Three Tropical Alpine Life Forms. *Arct. Antarct. Alp. Res.* **2005**, *37*, 331–336. [\[CrossRef\]](#)
75. Christmann, T.; Aranda, M.L.; Recharte, J. Restoration of Andean Forests Using a Socioecological Approach: Case Study from the Aquia Mountain Community in Peru. *Mt. Res. Dev.* **2025**, *45*, D1–D13. [\[CrossRef\]](#)
76. Wisz, M.S.; Pottier, J.; Kissling, W.D.; Pellissier, L.; Lenoir, J.; Damgaard, C.F.; Dormann, C.F.; Forchhammer, M.C.; Grytnes, J.; Guisan, A.; et al. The Role of Biotic Interactions in Shaping Distributions and Realised Assemblages of Species: Implications for Species Distribution Modelling. *Biol. Rev.* **2013**, *88*, 15–30. [\[CrossRef\]](#) [\[PubMed\]](#)

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