Climate change and tree cover loss affect on the habitat suitability of *Cedrela angustifolia*: Evaluating climate vulnerability and conservation in Andean Montane Forests

Fressia N. Ames-Martínez[1]*, Ivan Capcha[2], Anthony Guerra[2], Janet Inga[3], Harold Rusbelth Quispe-Melgar[4,5], Esteban Galeano[6], Ernesto C. Rodríguez-Ramírez[7]

[1]Laboratorio de Biotecnología y Biología Molecular, Universidad Continental, Av. San Carlos 1980, Huancayo, Junín, Peru.

[2]Facultad de Ciencias Forestales y del Ambiente, Universidad Nacional del Centro del Perú, El Tambo, Huancayo, Junín, Peru.

[3]Laboratorio de la Anatomía e Identificación de la Madera, Universidad Continental, Av. San Carlos 1980, Huancayo, Junín, Peru.

[4]Programa de Ecología y Diversidad, Asociación ANDINUS, Sicaya, Huancayo, Junín, Peru.

[5]Facultad de Ciencias de la Salud, Universidad Continental, Av. San Carlos 1980, Huancayo, Junín, Peru.

[6]Department of Forestry, College of Forest Resources, Mississippi State University, Mississippi, United States

[7]Laboratorio de Dendrocronología, Universidad Continental, Av. San Carlos 1980, Huancayo, Peru

*Corresponding author:

Fressia N. Ames Martínez

22 Huancayo, Junin, Peru, CP: 12000

23 Email address: fames@continental.edu.pe

24 **ORCID**

25 Fressia N. Ames–Martínez: https://orcid.org/0000-0003-2840-3154

26 Anthony Guerra: https://orcid.org/0000-0002-9830-8550

27 Janet Inga: https://orcid.org/0000-0002-2321-8518

28 Harold R. Quispe Melgar: https://orcid.org/0000-0001-6676-0879

29 Esteban Galeano: https://orcid.org/0000-0002-8330-8240

30 Ernesto C. Rodríguez–Ramírez: https://orcid.org/0000-0001-6206-8615

Abstract

Background

Because of illegal logging, habitat fragmentation, and high-value timber, Andean Montane Forest *Cedrela* species (such as *Cedrela angustifolia*) are endangered in Central and South America. Studying the effects of climate change and tree cover loss on the distribution of *C. angustifolia* will help us understand the climatic and ecological sensitivity of this species and suggest conservation and restoration strategies.

Methods

Using ecological niche modeling with two algorithms (MaxEnt and Random Forest) under climatic variation approach, we generated 16,920 models with different combinations of variables and parameters. We identified suitable areas for *C. angustifolia* trees under present and future climate scenarios (2040, 2070, and 2100 with SSP 3-7.0 and SSP 5-8.5), tree cover loss, and variables related to soil and topography.

Results

The potential present distribution was estimated to be 13,080 km^2 with tree cover loss and 16,148.5 km^2 without tree cover loss, and we demonstrated that from 2040 to 2100, the species distribution will decrease (from -22.16% to -36.88% with tree cover loss variation). The current habitat availability and climate change from the two algorithms combined were estimated to range from -20.28% to -42.36%. Only 24.28% of the current potential distribution is within PAs and is likely reduced to 25-30% by 2100. The results indicate that Bolivia displayed greater habitat suitability than did Ecuador, Peru, and Argentina. Finally, we recommend developing conservation management strategies that consider both

protected and unprotected areas, as well as the impact of land-use changes, to improve the persistence of *C. angustifolia* in the future.

Keywords

Cedrela species; climatic refugia; species distribution models; habitat suitability; deforestation; ecological biogeography.

Introduction

Climate change has had a significant impact on reducing Andean tree populations and even on the extinction of endemic species (Tejedor Garavito et al., 2015; Urrutia and Vuille, 2009). Similarly, anthropic activities such as habitat destruction and illegal logging, can lead to the extinction of threatened species (Pievani, 2014). Climate variability influences autecological processes and environmental fluctuations (Anderson and Song, 2020). For example, temperature and precipitation oscillations influence specific wood anatomical plasticity, phenology, climatic resilience, geographic range, productivity, and disruption of inter- and intraspecific relationships in tree species (Araújo and Rahbek, 2006; Fonti et al., 2010; Piao et al., 2019). Therefore, understanding the fate of tree species in response to climate change is necessary to provide viable conservation and management strategies for endangered Andean montane tree species (Urrutia and Vuille, 2009).

Bioclimatic niche modeling shows various applications in this paradigm of climate change in endangered areas, and researchers highly appreciate its anthropic use (Urrutia and Vuille, 2009). Andean countries have increasingly sought to align their efforts in climate change adaptation and mitigation since 2011, with a growing consensus and demand for synergies (Llambí and Garcés, 2020). The integration of ecological information

into niche modeling provides a relationship between ecological processes in response to climate change. Understanding the montane ecological niche and its response to future climate change will lead to greater recognition and prioritization of efforts in Andean ecosystems. This knowledge will encourage sustainable resource management, particularly in fragile ecosystems (Llambí and Garcés, 2020; Urrutia and Vuille, 2009).

Andean Montane Forests (AMFs; Bush et al., 2007) constitute a significant part of the tropical Andes biodiversity hotspot (Myers et al., 2000). AMFs provide a stable balance within communities of organisms in which genetic, species and ecosystem diversity remain subject to gradual changes through natural succession, high species richness, and ecosystem services to both the high- and lowland moisture areas of the Andes (Cuesta et al., 2009; Myers et al., 2000). Forest fires, tree cover loss, and climate change have influenced major changes in montane ecosystems over the past century, such as ecosystem fragmentation and loss of diversity (Feeley and Silman, 2010; Gaglio et al., 2017; Rolando et al., 2017). Hence, establishing sustainable management policies for threatened Andean Mountain tree species is of multinational interest. Therefore, it is important to understand how climate change affects these species.

The arboreal genus *Cedrela* L. (Meliaceae) is a protected tree species (CITES and IUCN; Pennington and Muellner, 2010) comprising 19 species widely distributed from North America to the South American Mountains, where it inhabits steep ravines (Köcke et al., 2015; Muellner et al., 2010; Palacios et al., 2019; Pennington and Muellner, 2010). *Cedrela angustifolia* Moc. & Sessé ex DC. (VU; as indicated by Hills (2021) on the IUCN Red List; www.iucnredlist.org/) is ecologically important as a pioneer and codominant species associated with *Oreopanax*, *Podocarpus*, and *Weinmania* (Pennington and

98 Muellner, 2010). Additionally, it plays a significant role in providing essential ecosystem
99 services, including firewood, timber, particleboards, furniture, flooring veneers, and
100 railway ties (Pennington and Muellner, 2010; SERFOR, 2020).

101 The species distribution model (SDM) is an important tool for identifying climatic
102 refugia in areas with changing environmental variables and abiotic conditions, such as
103 those of *Cedrela* species. Based occurrence and environmental data, SDMs are used as
104 tools to estimate the extent of a species' range in the future or in the past (Peterson et al.,
105 2011). Similarly, tropical forests are susceptible to the pressures of logging, deforestation,
106 and tree cover loss, particularly in regions previously characterized by colder climates
107 (Gaglio et al., 2017; Sarmiento, 2002). The conversion of forests into agricultural lands,
108 particularly for livestock and crops such as avocado or granadilla, is an unregulated logging
109 activity that is often driven by global demands for timber, further exacerbating forest loss
110 (Bax and Francesconi, 2018; Cuenca et al., 2016).

111 These alterations are intrinsically linked to the acceleration of atmospheric CO_2
112 concentrations on both regional and global scales, mainly caused by anthropogenic sources,
113 in particular the burning of fossil fuels and deforestation (Friedlingstein et al., 1999). At the
114 physiological level, elevated CO_2 levels further influence climatic conditions by
115 modulating transpiration rates, this is attributed to enhanced water use efficiency, which
116 subsequently diminishes stomatal conductance while promoting plant growth (Kleidon et
117 al., 2000; Longobardi et al., 2016). It is therefore necessary to understand how climate
118 change and forest cover loss will affect the distribution of *C. angustifolia*.

119 In this study, we hypothesized that the most suitable habitats for *C. angustifolia* would
120 be negatively affected by climate change and tree cover loss by 2100; thus, enhancing the

121 effectiveness of protected areas and suitable sites for restoration efforts and ecological
122 refugia to maintain viable populations in South America. The findings of this study may be
123 used to establish natural protected areas and conservation-based areas for *C. angustifolia*
124 and provide information relevant to the listing status in the IUCN Red List category.

125 Our objectives were to (1) identify the environmental variables responsible for the
126 present and future potential distribution of *C. angustifolia*; (2) assess the climate variation
127 and tree cover loss effect on *C. angustifolia* by comparing the present and future potential
128 distributions (2011-2040, 2041-2070, and 2071-2100; SSP 3-7.0, and 5-8.5 scenarios); (3)
129 assess the effect of tree cover loss on the potential distribution of *C. angustifolia* in present
130 and future scenarios up to 2100; and (4) determine the potential refugia for climate change
131 and conservation of *C. angustifolia*, relating natural protected areas (NPAs), land use
132 change, present, and future potential distribution data. This study aimed to evaluate the
133 response of *Cedrela angustifolia* to climate pressure and to provide recommendations and
134 conservation strategies that will significantly impact countries in mega-diverse tropical
135 regions.

136 **1. Materials and Methods**

137 *1.1. Study area*

138 The study area comprises the Andean Montane Forest region (Ecuador, Peru, Bolivia, and
139 Argentina; Fig. 1), with elevations ranging from 1,800 to 3,300 m asl (Pennington and
140 Muellner, 2010). The study was delimited by Tungurahua Province, Ecuador, in the north
141 (1° S), and Catamarca Province, Argentina, in the south (28° S), at approximately 3–900
142 km.

1.2. Data sampling

Geographic distribution data for *Cedrela angustifolia* were obtained from the Tropicos database (https://tropicos.org/home; Missouri Botanical Garden, 2022) and the Global Biodiversity Information Facility database (https://gbif.org/; GBIF secretariat, 2022), and scientific publications (i.e., Inza et al., 2012; Paredes-Villanueva et al., 2016; Pennington and Muellner, 2010; Wong and Reynel, 2021) ~~obtained~~ 310 occurrences. Additionally, we checked and excluded outlier georeferenced points (records outside the study range and habitat), and herbarium accessions with missing location data. Furthermore, we used geographic distances to narrow our datasets while accounting for environmental variation. Based on the environmental heterogeneity of the ecosystems in which *C. angustifolia* occurs, such as montane forests and inter-Andean valleys, we selected differential distances greater than ~1 km to filter the sites and avoid duplicate records of the species. In total, 104 records were retained from Ecuador, Peru, Bolivia, and Argentina (89 GBIF and Tropicos.org and 15 scientific studies) (Fig. 2).

1.3. Data preparation

We used 37 environmental variables: 22 bioclimatic variables for present and future conditions, elevation, 10 soil raster layers, one NDVI raster and three forest change data rasters (Table 1). Under the assumption that it influences the climatic change scenario (Peterson et al., 2011), the climate variation of *Cedrela angustifolia* is related to its present and future distributions (2040, 2070, and 2100 mean periods). We obtained raster-model bioclimatic data from the CHELSA database, with a spatial resolution of 1.0 km^2 (https://chelsa-climate.org/; Karger et al., 2022) for present and future scenarios. In the present and future models, we consider 19 raster-model bioclimatic variables and potential

166 evapotranspiration (PET), climate moisture index (CMI), and near surface relative humidity
167 (HURS) (Table 1).

168 To evaluate the projection of bioclimatic variables to three different periods in the
169 future, we used the Coupled Model Intercomparison Project Phase 6 (CMIP6), which is
170 part of the Working Group on Coupled Modeling (WGCM) (Eyring et al., 2016). We
171 considered the model projections because the models are given a common set of future
172 concentrations of greenhouse gases, aerosols and other climate forcing to project what
173 might happen in the future (Eyring et al., 2016).

174 We selected two future climate scenarios (shared socioeconomic pathways; SSP 3-
175 7.0 and SSP 5-8.5) for the five models to derive future climate projections (Table S1). We
176 assume that SSP 3-7.0 is a less chaotic scenario because it represents a smaller reduction
177 than SSP 5-8.5 in global greenhouse gas concentrations by 2100, which is the highest
178 carbon emissions scenario and the most pessimistic view of the future. We considered a
179 digital elevation model (DEM) variable (Karger et al., 2022) to assess the elevation effects
180 (Fig. 2).

181 In addition, we obtained 11 soil raster layers from SoilGrid (https://soilgrids.org/;
182 Batjes et al., 2020), with a 250 m spatial resolution. Moreover, we obtained global forest
183 change data (from 2000 to 2022) from Global Forest Watch, with approximately 30 m per
184 pixel (https://www.globalforestwatch.org/map/; Hansen et al., 2013). Additionally, we used
185 the normalized difference vegetation index (NDVI), which indicates vegetation coverage
186 and spatial distribution of vegetation, calculated as the mean annual NDVI from 2000–
187 2020, using data provided by Earth Explorer with a 1 km^2 spatial resolution
188 (https://earthexplorer.usgs.gov/). Finally, the downloaded soil, topographic, and forest

189 change layers were resampled to match the spatial resolution of the bioclimatic layers (1
190 km^2) using the *crop* function (cropping the layer to the area of the 4 countries), *mask*
191 function (creating a new layer from the cropped layer with the same boundaries of the 4
192 countries) and *resample* function (projecting the values of the new layer to the same spatial
193 resolution of the bioclimatic layers) via the *raster* package (Hijmans, 2023) in R software v.
194 4.3.1 (R Core Team, 2022).

195 *1.4. Data analysis*

196 We determined the appropriate selection of bioclimatic variables to perform
197 statistical and ecological parameter analyses of suitable models according to Ames-
198 Martínez et al. (2022). We selected variables with multicollinearity based on measures such
199 as principal component analysis (PCA), inflation factor value (VIF), sampling bias, and
200 pairwise Pearson's correlation (*r*), from this preview selection, we selected non-correlated
201 (Pearson <0.7) variables that made significant contributions and had greater biological
202 significance, according to the experience of the authors. Our approach involved the use of
203 the *sdm* (*calibration* function; Naimi and Araújo, 2016), *fuzzySim* (*corSelect* function;
204 Barbosa, 2015), *regclass* (*VIF* function; Petrie, 2020), *FactoMineR* (*PCA* function; Husson
205 et al., 2023) and *virtualspecies* packages (*removeCollinearity* function; Leroy et al., 2019)
206 (Fig. 2).

207 Finally, after the process of variable selection, we selected 16 environmental
208 variables: isothermality (BIO3), temperature seasonality (BIO4), minimum temperature of
209 the cold month (BIO6), mean temperature of the warmest quarter (BIO10), precipitation
210 seasonality (BIO15), precipitation of the warmest quarter (BIO18), precipitation of the
211 coldest quarter (BIO19), climate moisture index (CMI), altitude (ALT), soil organic carbon

stock (SOCS), organic carbon density (OCD), silt content (SILT), clay content (CC), deforestation (DEF), forest loss (LF), and NDVI. For tree cover loss analysis, we used the loss forest raster in some models and other models without this raster to compare forest loss in present and future scenarios, given that the same current rate of tree cover loss will continue into the future.

1.5. Modeling and validation

MaxEnt modeling assessment

MaxEnt was used to fit the complex responses to only the occurrence data (Phillips et al., 2017). We generated bias files using the Gaussian kernel density of sampling localities tools to increase the weight of presence data points using SDMToolbox in ArcGIS (Brown et al., 2017). We used noncollinear variables and only occurrence data from MaxEnt v. 3.4.1 implemented in *the kuenm* package (*kuenm_cal* and *cal_eval* functions; Cobos et al., 2019; Phillips et al., 2017) to calibrate the parameter values, evaluate candidate models, and make future projections. We tested 8,460 candidate models derived from all combinations of three feature classes (linear, quadratic, and product), five regularization multipliers (0.25, 0.50, 1.00, 1.50, and 2.00), and 564 sets of environmental variables (in groups of 6-12 variables). We trained the model sets with 70% of the occurrence data and evaluated them with the remaining 30%. The potential distribution of the best model was obtained from the average of 30,000 background points using bootstrap replicates of 500 iterations each and allowed for free model extrapolation.

Finally, we selected the scenario and candidate models from the "best" variable set using the selected parameters. To reduce the uncertainty, we generated 10 replicate runs of

cross-validation, the last results are the average of these replicates, and finally, they were used to build the present and future models (Fig. 2).

Random forest modeling assessment

We used the Random Forest (RF) regression algorithm to model species distributions with discrimination capacity in the presence and absence of data (Liu et al., 2012). We obtained 10,000 pseudoabsence data points with the geographic distance method and assumed that any points were located at least 10 km from the presence data to avoid pseudoabsence data because of dispersal (Evans et al., 2011).

We examined the relative importance of each predictor by employing the determination coefficient (R^2) in conjunction with the mean squared error (MSE). We implemented a 100-fold cross-validation procedure repeated 10 times to construct the RF models with default settings. Notably, the number of trees (5000), sets of predictor variables at each split (564), and minimum size of terminal nodes (50) were key parameters influencing the performance of the RF models.

The dataset, which encompassed both presence and pseudoabsence data, was randomly partitioned into ten equal subsets. Our modeling strategy involves training the RF model on nine of these subsets and validating it on the remaining subset. It is essential to highlight that we generated 100 RF models to cross-validation model, and the outcomes were derived by aggregating the results from these models. We used *the randomForest* package (*randomForest* function; Liaw and Wiener, 2022) to generate pseudoabsence data and RF models (Fig. 2).

1.6. Comprehensive evaluation

We derived the potential distribution from the best model and assessed the relative importance of each variable using the average performance evaluation indicators corresponding to the area under the curve (AUC), the partial receiver operating characteristic (ROC) curve, the omission rate, the Akaike information criterion corrected (AICc; as the optimal complexity parameter), the Akaike information criterion (W AICc), and the Bayesian information criterion (BIC) (Hirzel et al., 2006; Peterson and Soberón, 2012; Jiménez and Soberón, 2020). The partial ROC curve was used on 50% occurrence data for bootstrap resampling, 100 iterations, and omission rate error (5%, maximum permissible omission error) (Cobos et al., 2019). The success rate curve was further used to assess the performance of the MaxEnt and RF models in predicting the species distribution for validation of the models (Rahmati et al., 2016). Finally, Schoener's D index was used to compare the similarity of the suitable distribution maps between the MaxEnt and RF models using the *ENMTools* package. (*enmtools.maxent* and *enmtools.rf* function; Warren et al., 2021).

All distribution maps were converted to binary data (0-1) using a logistic threshold for the presence of 10% of the data using the lowest distribution probability (Radosavljevic and Anderson, 2014). The maps were averaged to generate spatial information on the present and future presence probabilities across all *Cedrela* species. We followed the ODMAP protocol for the modeling process (Overview, Data, Model, Assessment, and Prediction; Table S1; Zurell et al., 2020).

We determined the surface area variation in each climatic model (km^2) between the present and future scenarios (Table 1). The final shapes were obtained using MaxEnt with maps edited in QGIS v. 3.18.3 (QGIS.org, 2021). We analyzed the mean temperature,

annual precipitation, and tree loss variation during the present and three future periods using the *ggdist* (Kay and Wiernik, 2023), *gghalves* (Tiedemann, 2022), and *ggplot2* packages (*ggplot2* function; Wickham et al., 2021). We performed two-way ANOVA and *post hoc* Tukey's test to compare the means using the *rstatix* package (*anova_test* and *tukey_hsd* functions; Kassambara, 2023) (Fig. 2).

1.7. Predicted refuges to climate change

We linked the present and future potential of the *Cedrela angustifolia* distribution with predicted refugia to climate change by identifying appropriate grids under the SSP3-7.0 and SSP5-8.5 scenarios. We used the consensus model between the present and future models, land cover (Hansen et al., 2013), and protected natural areas (PNA; UNEP-WCMC and IUCN, 2023) to recognize and estimate remnant patches outside the PNA. We performed a spatial distribution bias correction to avoid overadjusting future projections. We included 10,000 bias files and bioclimatic variables to assess potential refuges for climate change analysis. We implemented a Gaussian Kernel analysis using the *kernel* function in QGIS software to avoid sampling bias and identify the greatest potential refuges for climate change (Fig. 2).

2. Results

2.1. Model evaluation and contribution of predictor variables

All candidates for the MaxEnt and RF models were generated and compared, withonly a single model of each period and algorithm meeting the criteria of significance, predictive ability, fitting, and complexity (Table S2). Our results showed that the MaxEnt and RF models both showed excellent performance, with average AUC ratio values and thresholds,

301 which decreased when assessed using the independent testing dataset. Nonetheless, the
302 Maxent model demonstrated a greater AUC; however, RF displayed a better predictive
303 performance than Maxent (Table S2).

304 For the present and future models, the relative contribution of each predictor
305 variable to the SDMs was assessed by visualizing the percentage contribution and
306 permutation importance (Table 2). In our analysis of the present and future models, we
307 identified ten environmental variables as the most important factors for fitting the model.
308 These variables were precipitation seasonality (BIO15), soil organic carbon stock (SOCS),
309 normalized difference vegetation index (NDVI), temperature seasonality (BIO4), organic
310 carbon density (OCD), precipitation of the warmest quarter (BIO18), silt content (SILT),
311 clay content (CC), loss forest (LF), and isothermality (BIO3). These variables showed a
312 high percentage contribution to the model for both the present and future scenarios, as well
313 as for the three periods (Table 2).

314 *2.2. Present potential distribution*

315 The potential distribution area affected by tree cover loss in *C. angustifolia* was
316 approximately 13,080 km^2 (MaxEnt and RF values mean; SD ± 671.75 km^2), and
317 Schoener's D index between the RF model and the MaxEnt model was 0.857. Nevertheless,
318 without the tree cover loss effect, the total distribution of 16,148.5 km^2 (± 847.82 km^2) was
319 16,148.5 km2, and Schoener's D index was 0.749. Finally, areas in Peru and Bolivia were
320 suitable for *C. angustifolia* according to the current records (Fig. 3).

321 With respect to the tree cover loss effect, the distributions detected were 798 km^2 (±
322 59.4 km^2) in Ecuador, 1,947 km^2 (± 52.33 km^2) in Peru, 9,591 km^2 (± 579.83 km^2) in

323 Bolivia, and 744 km^2 (± 84.85 km^2) in Argentina. Without a tree cover loss effect, we
324 detected 948.5 km^2 (± 130.81 km^2) in Ecuador, 2,579 km^2 (± 487.9 km^2) in Peru, 11,400.5
325 km^2 (± 427.79 km^2) in Bolivia, and 1,220.5 km^2 (± 65.90 km^2) in Argentina (Fig. 2).

326 We found that the presence of *C. angustifolia* probably mainly affected for this
327 environmental variables: BIO3 at 5.3-6 °C, BIO4 at 20 °C to 31 °C, BIO18 at 100–200
328 mm, BIO15 at 750-830 mm, SOCS at 0-5%, NDVI at 0.95-1.00 units, OCD at 0-5%, slit at
329 0-10%, CCF at 0-10%, and LF at 55%.

330 *2.3. Future potential distribution*

331 We detected a decrease in the distribution range of SSP 3-7.0 and 5-8.5 during the three
332 periods (Fig. 3). For 2040, we estimated an extension equivalent of 8,934 km^2 (± 1,131.37
333 km^2, SSP 3-7.0) and 9,094 km^2 (± 851.36 km^2, SSP 5-8.5), with a Schoener D index of
334 0.759 (Fig. 4A). Nevertheless, without the tree cover loss effect, we detected 11,424 km^2 (±
335 841.46 km^2, SSP 3-7.0) and 11,078 km^2 (± 744.58 km^2, SSP 5-8.5), indicating 29.26% and
336 31.40% tree cover loss, respectively, with a Schoener D index of 0.786 (Fig. 4B).

337 During 2070, our models predicted decreases of 29.91% and 30.53% in SSP3-7.0
338 and SSP5-8.5, respectively, without the tree cover loss effect and 33.93% and 42.32%,
339 respectively, with the influence of tree cover loss, and Schoener's D index was 0.846.
340 Finally, for the 2100 period, the area decreased by 30.43% (SSP 3-7.0) and 33.33% (SSP 5-
341 8.5) without the tree cover loss effect; however, the tree cover loss effect decreased by
342 27.40% and 38.47%, respectively, in the total distribution, with a Schoener D index of
343 0.872 (Fig. 4AB).

The mean temperatures to 2040 in the SSP 3–7.0 and SSP 5–8.5 scenarios showed no significant differences among countries (Fig. 5A-D); however, Argentina and Bolivia exhibited statistically significant differences during the 2070 . Similarly, both countries displayed similar mean temperature values (~20.5 °C and ~18.7 °C, respectively) for the period 2010–2040 (Fig. 5ab). Ecuador and Peru showed similar mean annual temperature values (~15.2 °C and 16.3 °C, respectively) between the present and 2011–2040 periods (Fig. 5c, d). In the four countries, 2100 year presented statistically significant differences compared to the other periods (Fig. 5A-D). In contrast, the annual precipitation did not significantly differ among the four periods and countries (Fig. 5E-H).

2.4. Tree cover loss effect in the present and future

The relationships between the predictor and response variables show how tree cover loss influences model predictions. Thus, we further analyzed how the predicted probability of species occurrence changed with tree cover loss via the marginal responses of the probability of presence suitability (Fig. 6A). We found that 30.59% of the total area was the most suitable habitat without tree cover loss; nevertheless, Peru, Ecuador, and Argentina showed variations in the increase in tree cover loss area in 2040, 2070, and 2100 (Fig. 6B). For example, Ecuador and Argentina decreased by 51.25% and 14.08%, respectively, with the influence of tree cover loss (Fig. 6B) or total distribution, and Bolivia increased by more than 30% of the area distribution in all periods without tree cover loss. Finally, Peru and Argentina will decrease by 70% by 2070.

2.5. Potential refuges to climate change

Our analysis revealed variations in the habitat suitability distribution areas of *C. angustifolia (*9,449 $km^2 \pm 574$ km^2) in the four countries. Ecuador (724 $km^2 \pm 123$ km^2), Peru (1,784 $km^2 \pm 193$ km^2), and Argentina (683 $km^2 \pm 76$ km^2) exhibited high potential for refuge from climate change; however, Bolivia (6,258 $km^2 \pm 456$ km^2) displayed decreasing habitat (Fig. 7). Only 24.28% of the current potential distribution is within PAs and is likely reduced to 25-30% by 2100.

The predictions of the core distribution regions obtained from the MaxEnt and RF models showed greater heterogeneity and stronger gradients. In addition, our analysis identified Azuay and Zamora Cinchipe as refugees to Ecuador; Cajamarca, Junín, Apurimac, and Cusco as refugees to Peru; Cochabamba, Chuquisaca, and Tarija as refugees to Bolivia; and Salta and Tucumán to Argentina as potential refuges to climate change.

3. Discussion

The impact of climate change and tree cover loss on Andean Montane Forests has been acknowledged for a considerable period, but the precise influence of climate change on the distribution of specific pioneer tree species remains unclear (Bax et al., 2021; Balthazar et al., 2015; Bush et al., 2007). Our findings suggest that the distribution of *C. angustifolia* will decrease in the future owing to climate change projections for 2040, 2070, and 2100.

3.1. Potential climate variation

In previous studies, the predictive effectiveness of random forest (RF) and maximum entropy (MaxEnt) models was systematically evaluated through automated parameter optimization (Cotrina et al., 2021; Mi et al., 2017; Zhao et al., 2022). While the RF model typically provides robust and accurate predictions using default configurations (Freeman et

al., 2015), the MaxEnt model often requires parameter refinement (Feng et al., 2019; Jiménez and Soberón, 2020). Therefore, in this investigation, we carefully selected optimal feature class amalgamations and regularization parameters for MaxEnt and subsequently compared the predictive ability of the fine-tuned MaxEnt model with that of the RF model. Consistent with previous literature, both the RF and optimized MaxEnt models exhibited commendable predictive accuracies; however, the RF model exhibited marginal superiority, which was evident in both cross-validation and external dataset evaluations. This is consistent with the findings of Mi et al. (2017) and Čengić et al. (2020), who described the improved performance of RF over standard MaxEnt configurations in species distribution prediction.

The distribution of *C. angustifolia* was influenced by seasonal variations in precipitation and temperature, and the model performance was excellent (AUC > 0.98), indicating the efficiency and accuracy of the model (Warren and Seifert, 2011). These populations exhibit tolerance to colder temperatures and higher humidity and maintain their evolutionary climatic conditions, as detected by Muellner et al. (2010) and Koecke et al. (2013). Our analysis suggested that Bolivian montane forests offer more favorable conditions (81% present model) and ecosystem conservation for *C. angustifolia* (Pennington and Muellner, 2010), with more than half of these species recorded within the all NPAs.

3.2. Effect of future climate change

The distribution patterns of different species are influenced by various ecological and evolutionary factors that enable them to survive in specific environments within varied landscapes (Rahbek et al., 2019). Despite this, Tejedor Garavito et al. (2015) argued that

land-use change, particularly deforestation of tropical montane ecosystems, would be more detrimental to biodiversity than climate change and could lead to the loss of endemic tree species worldwide (Feeley and Silman, 2010).

Based on the evaluated scenarios, an increase in mean annual temperature from 4.1 °C to 5 °C in the present temperature record is expected to 2100. This would result in a significant reduction in suitable habitats in Bolivia (>20.26%) and Argentina (>28.99%). By 2100, the *Cedrela* species will not be able to find optimal sites, as the thermal limit is exceeded (~ 21.8 °C). However, Peru and Ecuador exhibit favorable climatic conditions that allow *C. angustifolia* to migrate to warmer areas, ~~which suggests that these species can acclimate o adapt to the environment~~ and persist through rapid changes in climate (Pearson, 2006). This confirms the climatic vulnerability of *C. angustifolia* (Cotrina et al., 2021; Koecke et al., 2013; Rodríguez-Ramírez et al., 2022). Similar results have been reported for *C. odorata* (Sampayo-Maldonado et al., 2023) and other *Cedrela* species (Cotrina et al., 2021; Koecke et al., 2013).

We have demonstrated that tree cover loss will have an impact on more than 30% of the range of *C. angustifolia*, which is a crucial factor contributing to the reduction in *C. angustifolia* in the four countries. If the current rate of deforestation continues or increases, it will result in a decrease in distribution (Hansen et al., 2013). This could be explained by the fact that because of the low CO_2 absorption that would be generated by the reduction of trees by 2100, the greenhouse effect will intensify due to the increase in surface temperature, decreased absorption of solar radiation, and evapotranspiration (Kleidon et al., 2000; Longobardi et al., 2016). Similarly, tree cover loss increases the risk of soil erosion, leading to reduced soil fertility and increased sedimentation in the water bodies of these

forests (Bax and Francesconi, 2018; Cuenca et al., 2016; Tapia-Armijos et al., 2015). Therefore, the climatic impact of deforestation on AMF weakens the relationship between atmospheric circulation and the hydrological cycle (Longobardi et al., 2016).

3.3. Potential habitat suitability and refugia

Suitable habitats for *C. angustifolia* will be maintained in all four countries; however, habitat suitability will decrease in all countries evaluated in the present and future models. In Bolivia, there were higher rates of illegal logging and forest fires than in the other three countries, making it more vulnerable to climate change and less likely to maintain a suitable habitat for this species (Hansen et al., 2013). In contrast, Ecuador, Peru, and Argentina exhibited areas with better habitat suitability than the present model, suggesting that unexplored forests with similar climatic conditions allow the species to adapt through natural or active restoration (i.e., *C. angustifolia* plantations in inter-Andean valleys; SERFOR 2020).

Additionally, their presence increased in NPAs, as described by Pennington and Muellner (2010). This shows that NPAs function as biodiversity reserves and buffers against the effects of changing climatic conditions, allowing the formation of refugia and providing ecological corridors for species to adapt to or migrate over the long term (Cuesta et al., 2009; Geldmann et al., 2013). In contrast, 75.72% of habitat suitability was detected outside the NPAs, indicating that it is necessary to develop forest management and monitoring strategies to protect these forests because they are more susceptible to selective logging and timber overexploitation, (Cotrina et al., 2021; SERFOR, 2020).

4. Conclusions

Our study demonstrated that *Cedrela angustifolia* is susceptible to future climate change, indicating variations in suitable habitats between Central and South America. Moreover, we suggest designating a climate sanctuary for *Cedrela* species that is connected to NPAs to buffer against land-use transformations. Consequently, it is crucial to collaborate with local communities residing near forests to protect endangered and vulnerable CITES and IUCN species, as well as their habitats, both within and outside NPAs.

Finally, why is *C. angustifolia* ecologically important? Because this tree has several ecological implications, such as biodiversity support because it provides habitat and food for various species, its root system helps prevent soil erosion, maintains soil structure and fertility, and can influence the local microclimate by providing shade and reducing temperature fluctuations, and its valuable timber can promote sustainable management practices (Pennington and Muellner, 2010).

Nongovernmental organizations (NGOs), ~~which~~ and different environmental legacy institutions, are recommended to use the findings and boundaries established by the species distribution model (SDM) both currently and in the future to safeguard and preserve the species under investigation. Therefore, it is crucial to emphasize the outcomes of our study, considering the need to initiate conservation efforts for *C. angustifolia* (as an umbrella species), including the establishment of new protected areas, habitat restoration, and the creation of ecological corridors that benefit other related species.

A coordinated effort at the local, national, and international levels is needed to combat deforestation and climate change in the Andes. The distinctive ecosystems of the AMF and the well-being of its inhabitants must be preserved through the implementation of conservation programs, sustainable land-use plans, and climate change mitigation

initiatives. To ensure the effective regulation of *Cedrela* logging, development propagation, and restoration programs, it is crucial to assist local authorities in comprehending the ecological significance of these practices. Furthermore, we suggest conducting additional research on other aspects, such as phenology, functional ecology, and spatiotemporal patterns, to provide a more in-depth understanding of how tree species in the Andean-Montane forest (AMF) respond to the impacts of climate change and human activities.

Acknowledgments

We thank the Servicio Nacional Forestal y de Fauna Silvestre-SERFOR, which approved the research outside Protected Natural Areas through the General Management Resolution RDG 007-2020-MINAGRI-SERFOR-DGGSPFFS.

References

Ames-Martínez, F.N., Luna-Vega, I., Dieringer, G., Rodríguez-Ramírez, E.C., 2022. The effect of climate change on Arcto-Tertiary Mexican beech forests: Exploring their past, present, and future distribution. Ecol. Evol. 12, 1–12. https://doi.org/10.1002/ece3.9228

Anderson, J.T., Song, B.-H., 2020. Plant adaptation to climate change—Where are we? J. Syst. Evol. 58, 533–545. https://doi.org/10.1111/jse.12649

Araújo, M.B., Rahbek, C., 2006. How does climate change affect biodiversity? Science 313, 1396–1397. https://doi.org/10.1126/science.1131758

Balthazar, V., Vanacker, V., Molina, A., Lambin, E. F., 2015. Impacts of forest cover change on ecosystem services in high Andean mountains. Ecol. Indic. 48, 63-75. https://doi.org/10.1016/j.ecolind.2014.07.043

500 Barbosa, A.M., 2015. fuzzySim: Applying fuzzy logic to binary similarity indices in
501 ecology. Methods Ecol. Evol. 6, 853–858. https://doi.org/10.1111/2041-210X.12372

502 Batjes, N.H., Ribeiro, E., Van Oostrum, A., 2020. Standardized soil profile data to support
503 global mapping and modeling (WoSIS snapshot 2019). Earth Syst. Sci. Data 12, 299–
504 320. https://doi.org/10.5194/essd-12-299-2020

505 Baumgartner, J.B., Esperón-Rodríguez, M., Beaumont, L.J., 2018. Identifying in situ
506 climate refugia for plant species. Ecography 41, 1850-1863.
507 https://doi.org/10.1111/ecog.03431

508 Bax, V., Castro-Nunez, A., Francesconi, W., 2021. Assessment of potential climate change
509 impacts on montane forests in the peruvian andes: Implications for conservation
510 prioritization. Forests 12, 375. https://doi.org/10.3390/f12030375Bax, V., Francesconi,
511 W., 2018. Environmental predictors of forest change: An analysis of natural
512 predisposition to deforestation in the tropical Andes region, Peru. Appl. Geogr. 91,
513 99–110. https://doi.org/10.1016/j.apgeog.2018.01.002

514 Briscoe, N. J., Kearney, M. R., Taylor, C. A., Wintle, B. A., 2016. Unpacking the
515 mechanisms captured by a correlative species distribution model to improve
516 predictions of climate refugia. Glob. Change Biol. 22, 2425–
517 2439. https://doi.org/10.1111/gcb.13280

518 Brown, J.L., Bennett, J.R., French, C.M., 2017. SDMtoolbox 2.0: The next generation
519 Python-based GIS toolkit for landscape genetic, biogeographic and species
520 distribution model analyses. PeerJ 5, e4095. https://doi.org/10.7717/peerj.4095

521 Bush, M.B., Hanselman, J.A., Hooghiemstra, H., 2007. Andean montane forests and

522 climate change. Trop. Rainfor. Responses to Clim. Chang. 35–60.
523 https://doi.org/10.1007/978-3-642-05383-2_2

524 Čengić, M., Rost, J., Remenska, D., Janse, J.H., Huijbregts, M.A.J., Schipper, A.M., 2020.
525 On the importance of predictor choice, modeling technique, and number of
526 pseudoabsences for bioclimatic envelope model performance. Ecol. Evol. 10, 12307–
527 12317. https://doi.org/10.1002/ece3.6859

528 Cobos, M.E., Peterson, A.T., Barve, N., Osorio-Olvera, L., 2019. Kuenm: An R package
529 for detailed development of ecological niche models using Maxent. PeerJ 7, 1–15.
530 https://doi.org/10.7717/peerj.6281

531 Cotrina, A., Rojas, N.B., Bandopadhyay, S., Ghosh, S., Torres, C., Oliva, M., Guzman,
532 B.K., Salas, R., 2021. Biogeographic distribution of *Cedrela* spp. Genus in Peru using
533 maxent modeling: A conservation and restoration approach. Diversity 13.
534 https://doi.org/10.3390/d13060261

535 Cuenca, P., Arriagada, R., Echeverría, C., 2016. How much deforestation do protected
536 areas avoid in tropical Andean landscapes? Environ. Sci. Policy 56, 56–66.
537 https://doi.org/10.1016/j.envsci.2015.10.014

538 Cuesta, F., Peralvo, M., Valarezo, N., 2009. Los bosques montanos de los Andes
539 Tropicales. Programa Regional ECOBONA-Intercooperation.

540 DIVA-GIS, 2017. Free Spatial Data by Country. http://www.diva-gis.org/gdata (Accessed
541 12 November 2023)

542 Evans, J., Murhpy, M., Holden, Z., Cushman, S., 2011. Modeling species distribution and
543 change using Random Forest, in: Predictive Species and Habitat Modeling in

Landscape Ecology: Concepts and Applications. pp. 139–159. https://doi.org/10.1007/978-1-4419-7390-0

Eyring, V., Bony, S., Meehl, G.A., Senior, C.A., Stevens, B., Stouffer, R.J., Taylor, K.E., 2016. Overview of the coupled model intercomparison project phase 6 (CMIP6) experimental design and organization. Geosci. Model Dev. 9, 1937–1958. https://doi.org/10.5194/gmd-9-1937-2016

Feeley, K.J., Silman, M.R., 2010. Land-use and climate change effects on population size and extinction risk of Andean plants. Glob. Chang. Biol. 16, 3215–3222. https://doi.org/10.1111/j.1365-2486.2010.02197.x

Feng, X., Park, D.S., Liang, Y., Pandey, R., Papeş, M., 2019. Collinearity in ecological niche modeling: Confusions and challenges. Ecol. Evol. 9, 10365–10376. https://doi.org/10.1002/ece3.5555

Fonti, P., Von Arx, G., García-González, I., Eilmann, B., Sass-Klaassen, U., Gärtner, H., Eckstein, D., 2010. Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. New Phytol. 185, 42–53. https://doi.org/10.1111/j.1469-8137.2009.03030.x

Freeman, E.A., Moisen, G.G., Coulston, J.W., Wilson, B.T., 2015. Random forests and stochastic gradient boosting for predicting tree canopy cover: Comparing tuning processes and model performance. Can. J. For. Res. 46, 323–339. https://doi.org/10.1139/cjfr-2014-0562

Friedlingstein, P., Joel, G., Field, C.B., Fung, I.Y., 1999. Toward an allocation scheme for global terrestrial carbon models. Glob. Chang. Biol. 5, 755–770.

https://doi.org/10.1046/j.1365-2486.1999.00269.x

Gaglio, M., Aschonitis, V.G., Mancuso, M.M., Puig, J.P.R., Moscoso, F., Castaldelli, G., Fano, E.A., 2017. Changes in land use and ecosystem services in tropical forest areas: A case study in Andes mountains of Ecuador. Int. J. Biodivers. Sci. Ecosyst. Serv. Manag. 13, 264–279. https://doi.org/10.1080/21513732.2017.1345980

GBIF secretariat, 2022. *Cedrela angustifolia* Moc. & Sessé ex DC. in GBIF Backbone Taxonomy. https://doi.org/https://doi.org/10.15468/39omei

Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M., Burgess, N.D., 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biol. Conserv. 161, 230–238. https://doi.org/10.1016/j.biocon.2013.02.018

Hansen, M.C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. Science 850, 850–854. https://doi.org/10.1126/science.1244693

Harris, N.L., Gibbs, D.A., Baccini, A., Birdsey, R.A., de Bruin, S., Farina, M., Fatoyinbo, L., Hansen, M.C., Herold, M., Houghton, R.A., Potapov, P. V., Suarez, D.R., Roman-Cuesta, R.M., Saatchi, S.S., Slay, C.M., Turubanova, S.A., Tyukavina, A., 2021. Global maps of twenty-first century forest carbon fluxes. Nat. Clim. Chang. 11, 234–240. https://doi.org/10.1038/s41558-020-00976-6

Hijmans, R.J., 2023. raster: geografic data analysis and modeling https://rspatial.org/raster (accessed 11 November 2023).

588 Hills, R., 2021. *Cedrela angustifolia*. The IUCN Red List of Threatened Species 2021.
589 e.T61794858A61794860 https://dx.doi.org/10.2305/IUCN.UK.2021-
590 3.RLTS.T61794858A61794860.en. (accessed 27 October 2023).

591 Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of
592 habitat suitability models to predict species presences. Ecol. Model. 199, 142–152.
593 https://doi.org/10.1016/j.ecolmodel.2006.05.017

594 Husson, F., Josse, J., Le, S., J, M., 2023. FactoMineR: multivariate exploratory data
595 analysis and data mining http://factominer.free.fr (accessed 11 November 2023).

596 Inza, M. V., Zelener, N., Fornes, L., Gallo, L.A., 2012. Effect of latitudinal gradient and
597 impact of logging on genetic diversity of *Cedrela lilloi* along the Argentine Yungas
598 Rainforest. Ecol. Evol. 2, 2722–2736. https://doi.org/10.1002/ece3.336

599 Jiménez, L., Soberón, J., 2020. Leaving the area under the receiving operating
600 characteristic curve behind: An evaluation method for species distribution modeling
601 applications based on presence-only data. Methods Ecol. Evol. 11, 1571–1586.
602 https://doi.org/10.1111/2041-210X.13479

603 Karger, D., Lange, S., Chantal, H., Reyer, C., Zimmermann, N., 2022. CHELSA-W5E5
604 v1.0: W5E5 v1.0 reducido con CHELSA v2.0. Repos. ISIMIP.
605 https://doi.org/https://doi.org/10.48364/ISIMIP.836809.1

606 Kassambara, A., 2023. rstatix: Pipe-friendly framework for basic statistical test
607 https://rpkgs.datanovia.com/rstatix/(accessed 10 November 2023).

608 Kay, M., Wiernik, B., 2023. ggdist: Visualizations of Distributions and Uncertainty.
609 https://doi.org/https://doi.org/10.5281/zenodo.3879620 (accessed 10 November 2023).

610 Kleidon, A., Fraedrich, K., Heimann, M., 2000. A green planet versus a desert world:
611 estimating the maximum effect of vegetation on the land surface climate. Clim.
612 Chang. 44, 471–493. https://doi.org/https://www.doi.org/10.1023/A:1005559518889

613 Köcke, A. V., Muellner-Riehl, A.N., Cáceres, O., Pennington, T.D., 2015. *Cedrela ngobe*
614 (Meliaceae), a new species from Panama and Costa Rica. Edinburgh J. Bot. 72, 225–
615 233. https://doi.org/10.1017/S0960428615000098

616 Koecke, A.V., Muellner-Riehl, A.N., Pennington, T.D., Schorr, G., Schnitzler, J., 2013.
617 Niche evolution through time and across continents: The story of Neotropical *Cedrela*
618 (Meliaceae). Am. J. Bot. 100, 1800–1810. https://doi.org/10.3732/ajb.1300059

619 Leroy, B., Meynard, C., Bellard, C., Courchamp, F., Delsol, R., Gaul, W., 2019.
620 virtualspecies: e Generation of Virtual Species Distributions.
621 https://borisleroy.com/virtualspecies/(accessed 10 November 2023).

622 Liaw, A., Wiener, M., 2022. randomForest: Breiman and Cutler's Random Forests for
623 classification and regression.
624 https://doi.org/https://www.stat.berkeley.edu/~breiman/RandomForests/(accessed 11
625 November 2023).

626 Llambí, L.D., Garcés, A., 2020. Adaptación al cambio climático en los Andes: Vacíos y
627 prioridades para la gestión del conocimiento. CONDESAN, Quito-Ecuador.

628 Longobardi, P., Montenegro, A., Beltrami, H., Eby, M., 2016. Deforestation induced
629 climate change: Effects of spatial scale. PLoS One 11, e0153357..
630 https://doi.org/10.1371/journal.pone.0153357

631 Mi, C., Huettmann, F., Guo, Y., Han, X., Wen, L., 2017. Why choose Random Forest to

predict rare species distribution with few samples in large undersampled areas? Three Asian crane species models provide supporting evidence. PeerJ 5, e2849. https://doi.org/10.7717/peerj.2849

Missouri Botanical Garden, 2022. *Cedrela angustifolia* Moc. & Sessé ex DC. https://www.tropicos.org/(accessed 30 October 2023).

Muellner, A.N., Pennington, T.D., Koecke, V.A., Renner, S.S., 2010. Biogeography of *Cedrela* (Meliaceae, Sapindales) in Central and South America. Am. J. Bot. 97, 511–518. https://doi.org/10.3732/ajb.0900229

Myers, N., Mittermeier, R., Mittermeier, C., da Fonseca, G., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 858. https://doi.org/10.1038/468895a

Naimi, B., Araújo, M.B., 2016. Sdm: A reproducible and extensible R platform for species distribution modeling. Ecography (Cop.). 39, 368–375. https://doi.org/10.1111/ecog.01881

Palacios, W.A., Santiana, J., Iglesias, J., 2019. A new species of *Cedrela* (Meliaceae) from the eastern flanks of ecuador. Phytotaxa 393, 84–88. https://doi.org/10.11646/phytotaxa.393.1.8

Paredes-Villanueva, K., López, L., Navarro Cerrillo, R.M., 2016. Regional chronologies of *Cedrela fissilis* and *Cedrela angustifolia* in three forest types and their relation to climate. Trees - Struct. Funct. 30, 1581–1593. https://doi.org/10.1007/s00468-016-1391-8

Pennington, T.D., Muellner, A.N., 2010. A monograph of *Cedrela* (Meliaceae). Books, DH, Sherborne, UK.

654 Peterson, A.T., Soberón, J., 2012. Species distribution modeling and ecological niche
655 modeling: Getting the Concepts Right. Nat. a Conserv. 10, 102–107.
656 https://doi.org/10.4322/natcon.2012.019

657 Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura,
658 M., Araújo, M.B., 2011. Ecological Niches and Geographic Distributions (MPB-49).
659 Princeton University Press, New Jersey, USA.

660 Petrie, A., 2022. regclass: tools for an introductory class in regression and modeling.
661 https://titles.cognella.com/introduction-to-regression-and-modeling-with-r-
662 9781631892509 (Accessed 12 November 2023)

663 Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the
664 black box: an open-source release of Maxent. Ecography 40, 887–893.
665 https://doi.org/10.1111/ecog.03049

666 Piao, S., Liu, Q., Chen, A., Janssens, I.A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., Zhu,
667 X., 2019. Plant phenology and global climate change: Current progresses and
668 challenges. Glob. Chang. Biol. 25, 1922–1940. https://doi.org/10.1111/gcb.14619

669 Pievani, T., 2014. The sixth mass extinction: Anthropocene and the human impact on
670 biodiversity. Rend. Lincei 25, 85–93. https://doi.org/10.1007/s12210-013-0258-9

671 QGIS.org, 2021. QGIS Geographic Information System. OSGeo, 3(4), 10. https://qgis.org/

672 R Core Team, 2022. R: A language and environment for statistical computing.
673 https://www.r-project.org/

674 Radosavljevic, A., Anderson, R.P., 2014. Making better Maxent models of species

distributions: Complexity, overfitting and evaluation. J. Biogeogr. 41, 629–643. https://doi.org/10.1111/jbi.12227

Rahbek, C., Borregaard, M.K., Colwell, R.K., Dalsgaard, B., Holt, B.G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R.J., Fjeldså, J., 2019. Humboldt's enigma: What causes global patterns of mountain biodiversity? Science 365, 1108–1113. https://doi.org/10.1126/science.aax0149

Rahmati, O., Pourghasemi, H.R., Melesse, A.M., 2016. Application of GIS-based data driven random forest and maximum entropy models for groundwater potential mapping: A case study at Mehran Region, Iran. Catena 137, 360–372. https://doi.org/10.1016/j.catena.2015.10.010

Rodríguez-Ramírez, E.C., Ferrero, M.E., Acevedo-Vega, I., Crispin-DelaCruz, D.B., Ticse-Otarola, G., Requena-Rojas, E.J., 2022. Plastic adjustments in xylem vessel traits to drought events in three *Cedrela* species from Peruvian Tropical Andean forests. Sci. Rep. 12, 1–14. https://doi.org/10.1038/s41598-022-25645-w

Rolando, J.L., Turin, C., Ramírez, D.A., Mares, V., Monerris, J., Quiroz, R., 2017. Key ecosystem services and ecological intensification of agriculture in the tropical high-Andean Puna as affected by land-use and climate changes. Agric. Ecosyst. Environ. 236, 221–233. https://doi.org/10.1016/j.agee.2016.12.010

Sampayo-Maldonado, S., Ordoñez-Salanueva, C.A., Mattana, E., Way, M., Castillo-Lorenzo, E., Dávila-Aranda, P.D., Lira-Saade, R., Téllez-Valdés, O., Rodríguez-Arévalo, N.I., Flores-Ortiz, C.M., Ulian, T., 2023. Potential distribution of *Cedrela odorata* L. in Mexico according to its optimal thermal range for seed germination

under different climate change scenarios. Plants 12, 150. https://doi.org/10.3390/plants12010150

Sarmiento, F., 2002. Anthropogenic Change in the Landscapes. Geogr. Rev. 92, 213–234.

Stark, J. R., Fridley, J. D., 2022. Microclimate-based species distribution models in complex forested terrain indicate widespread cryptic refugia under climate change. Glob. Ecol. Biogeogr. 31, 562-575. https://doi.org/10.1111/geb.13447

SERFOR, 2020. Estado situacional del género *Cedrela* en Perú. Lima, Perú.

Tapia-Armijos, M.F., Homeier, J., Espinosa, C.I., Leuschner, C., De La Cruz, M., 2015. Deforestation and forest fragmentation in south Ecuador since the 1970s - Losing a hotspot of biodiversity. PLoS One 10, 1–18. https://doi.org/10.1371/journal.pone.0133701

Tejedor Garavito, N., Newton, A.C., Golicher, D., Oldfield, S., 2015. The relative impact of climate change on the extinction risk of tree species in the montane tropical Andes. PLoS One 10, 1–19. https://doi.org/10.1371/journal.pone.0131388

Tiedemann, F., 2022. gghalves: Compose half-half plots using your favorite geoms. https://github.com/erocoar/gghalves (accessed 11 November 2023).

UNEP-WCMC, IUCN, 2023. Protected Planet: The World Database on Protected Areas (WDPA). https://www.iucnredlist.org/

Urrutia, R., Vuille, M., 2009. Climate change projections for the tropical Andes using a regional climate model: Temperature and precipitation simulations for the end of the 21st century. J. Geophys. Res. Atmos. 114, 1–15.

https://doi.org/10.1029/2008JD011021

Warren, D.L., Matzke, N.J., Cardillo, M., Baumgartner, J.B., Beaumont, L.J., Turelli, M., Glor, R.E., Huron, N.A., Simões, M., Iglesias, T.L., Piquet, J.C., Dinnage, R., 2021. ENMTools 1.0: an R package for comparative ecological biogeography. Ecography 44, 504–511. https://doi.org/10.1111/ecog.05485

Warren, D.L., Seifert, S., 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol. Appl. 21, 335–342. https://doi.org/https://doi.org/10.1890/10-1171.1

Wickham, H., Chang, W., Henry, L., Pedersen, T.L., Takahashi, K., Wilke, C., K., W., Yutani, H., Dunnington, D., 2021. Package ggplot2: Create elegant data visualizations using the grammar of graphics. https://ggplot2.tidyverse.org (accessed 12 November 2023)

Wong, A., Reynel, C., 2021. Venación foliar de tres especies de *Cedrela* (Meliaceae) de los andes del Perú. Rev. For. del Perú 36, 227–246. https://doi.org/10.21704/rfp.v36i2.1800

Zhao, Z., Xiao, N., Shen, M., Li, J., 2022. Comparison between optimized Maxent and random forest modeling in predicting potential distribution: A case study with *Quasipaa boulengeri* in China. Sci. Total Environ. 842, 156867. https://doi.org/10.1016/j.scitotenv.2022.156867

Zurell, D., Franklin, J., König, C., Bouchet, P.J., Dormann, C.F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J.J., Leitão, P.J., Park, D.S., Peterson, A.T., Rapacciuolo, G., Schmatz, D.R., Schröder, B., Serra-Diaz, J.M.,

Thuiller, W., Yates, K.L., Zimmermann, N.E., Merow, C., 2020. A standard protocol for reporting species distribution models. Ecography 43, 1261–1277. https://doi.org/10.1111/ecog.04960