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How do climate change and tree cover loss affect the habitat suitability of *Cedrela angustifolia*? Evaluating climate vulnerability and conservation in Andean Montane Forests

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Background Because of illegal logging, habitat fragmentation, and high value timber of endangered Andean Montane Forest *Cedrela* species (such as *Cedrela angustifolia*) from 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 conservation and restoration strategies.

Methods Using ecological niche modeling with two algorithms (MaxEnt and Random Forest) under the ecological niche conservatism 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 linked 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 protected areas and is likely to be reduced to 25-30% by 2100. The results indicate that Bolivia displayed higher habitat suitability than 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.

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Abstract

Background

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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

Andean Montane Forests (AMFs; Bush et al., 2007) constitute a significant part of the Tropical Andes biodiversity hotspot (Myers et al., 2000). The AMFs provide an ecological balance, high species richness, and ecosystem services to both the high- and lowland moisture areas of the Andes (Myers et al., 2000; Cuesta, Peralvo & Valarezo, 2009). Forest fires, tree cover loss, and climate change have influenced major changes in montane ecosystems over the past century (Feeley & 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.

Climate change has a significant impact on the reduction of Andean forest-tree populations and even in the extinction of species restricted to a limited range (Urrutia & Vuille, 2009; Tejedor Garavito et al., 2015). Likewise, anthropic activities as habitat destruction and illegal logging can lead to the extinction of threatened species (Pievani, 2014). Nonetheless, climatic oscillations and tree cover loss can directly influence on autecological processes and environmental fluctuations (Anderson & Song, 2020). For example, temperature and precipitation variations affect specific wood anatomical plasticity, phenology, climatic resilience, geographic range, productivity, and disruption of inter- and intraspecific relationships in tree species (Araújo & Rahbek, 2006; Fonti et al., 2010; Piao et al., 2019). To provide viable conservation and management strategies for endangered Andean montane tree species, it is necessary to understand how tree species respond to climate change (Urrutia & Vuille, 2009).

In this paradigm of climate change in insect species, bioclimatic niche modeling has various tools, and researchers highly value its anthropological applications (Urrutia & Vuille, 2009). From 2011, the Andean countries have aligned their efforts in adapting to climate change and mitigating it, with a growing consensus and demand for synergies (Llambí & Garcés, 2020). By integrating ecological information into niche modeling, a relationship can be established between ecological processes and climate change. Understanding the montane ecological niche and its response to future climate change will contribute to the recognition and prioritization of efforts in Andean ecosystems. In particular, in fragile ecosystems, this will promote sustainable resource management (Urrutia & Vuille, 2009; Llambí & Garcés, 2020).

The arboreal genus *Cedrela* L. (Meliaceae) is a protected Andean montane tree species (CITES and IUCN; Pennington and Muellner, 2010), comprising 19 species widely distributed from North America to the South American mountains, where it occurs in steep ravines (Muellner et al., 2010; Pennington & Muellner, 2010; Köcke et al., 2015; Palacios, Santiana & Iglesias, 2019). In particular, *Cedrela angustifolia* Moc. & Sessé ex DC. (VU; as indicated by Hills (2021) on the IUCN Red List; www.iucnredlist.org/). This species is ecologically important as a pioneer and co-dominant species associated with *Oreopanax*, *Podocarpus*, and *Weinmania* (Pennington & Muellner, 2010). Additionally, it plays a significant role in providing essential ecosystem services, including firewood, timber, particleboards, furniture, flooring veneers, and railway tires (Pennington & Muellner, 2010; SERFOR, 2020).

The Species Distribution Model (SDM) is an important tool for identifying climatic refugia in areas with changing environmental variables and abiotic conditions, such as those of *Cedrela* species occur. Using incidence and environmental data, they frequently used SDMs as tools for estimating the extent of a species range in the future or in the past (Peterson et al., 2011). Likewise, tropical forests are susceptible to the pressures of logging, deforestation, and tree cover loss, particularly in regions previously characterized by colder climates (Sarmiento, 2002; Gaglio et al., 2017).

The conversion of forests into agricultural lands, particularly for livestock and avocado or granadilla crops, is an unregulated logging activity, often driven by global demands for timber, which further exacerbate forest loss (Cuenca, Arriagada & Echeverría, 2016; Bax & Francesconi, 2018). These changes are directly related to the increase in atmospheric CO_2 concentrations on both regional and global levels. This is mainly because of modifications in the exchange of energy, and momentum exchanges between different subsystems, and energy reservoirs (Friedlingstein et al., 1999). Elevated levels of CO_2 can affect climatic conditions by influencing transpiration rates. This is because of increased water use efficiency, which reduces stomatal conductance while promoting plant growth (Kleidon, Fraedrich & Heimann, 2000; Longobardi et al., 2016). Therefore, it is important to investigate how climate change and forest cover loss will impact the distribution of *C. angustifolia*.

In this study, we hypothesized that the most suitable habitats for *C. angustifolia* would be negatively affected by climate change and tree cover loss by 2100; therefore, it is necessary to identify the effectiveness of protected areas and suitable sites for restoration efforts and ecological refugia to maintain viable populations in South America. The findings of this study may be used to establish Natural Protected Areas and conservation-based areas for *C. angustifolia* and provide information relevant to the listing status in the IUCN Red List category.

This study evaluated the response of *Cedrela angustifolia* to climate pressure and to provide recommendations and conservation strategies that will significantly impact countries in a mega-diverse tropical region. Our aims were to: (1) identify environmental variables responsible for the present and future potential distribution of *C. angustifolia*; (2) assess the climate sensitivity and tree cover loss effect on *C. angustifolia* by comparing the present and future potential distribution (2011-2040, 2041-2070, and 2071-2100 periods; SSP 3-7.0, and 5-8.5 scenarios); (3) evaluate the tree cover loss effect on the *C. angustifolia* potential distribution in present and future scenarios up to 2100; and (4) determine the *C. angustifolia* potential refugia for climate change and conservation, relating Natural Protected Areas (NPAs), land use change, present, and future potential distribution data.

Material and Methods

Study area

The study area comprised the Andean Montane Forest region (Ecuador, Peru, Bolivia, and Argentina; Fig. 1), with elevations ranged from 1,000 to 3,300 m asl. The study was delimited by Tungurahua Province, Ecuador, in the north (1° S), and Catamarca Province, Argentina, in the south (28° S), at approximately 3–900 km.

Data sampling

Geographic distribution data for *Cedrela angustifolia* was obtained from the Tropicos database (https://tropicos.org/home; Missouri Botanical Garden, 2022), Global Biodiversity Information Facility database (https://gbif.org/; GBIF secretariat, 2022), and scientific publications (i.e., Pennington & Muellner, 2010; Inza et al., 2012; Paredes-Villanueva, López & Navarro Cerrillo, 2016; Wong & Reynel, 2021)(Pennington & Muellner, 2010; Inza et al., 2012; Paredes-Villanueva, López & Navarro Cerrillo, 2016; Wong & Reynel, 2021), obtained 310 occurrences. Additionally, we analyzed and excluded georeferenced points that were incorrect, outliers, duplicates, and herbarium accessions with missing location data. Moreover, we used geographic distances to narrow our datasets while accounting for environmental variation. Based on environmental heterogeneity, we selected differential distances to filter sites. Finally, we obtained 104 records were obtained from Ecuador, Peru, Bolivia, comprising 89 records from GBIF and Tropicos.org, and 15 records from scientific studies.

Environmental variables

We used 36 environmental variables: 19 bioclimatic and three climatic variables for present and future conditions, 10 soil raster layers, one NDVI raster and three forest change data rasters (Table 1). The climate sensitivity of *Cedrela angustifolia* is related to its present and future distributions (2011-2040, 2041-2070, and 2071-2100 periods) under the assumption that it influences the niche conservatism scenario (Peterson et al., 2011). 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 both present and future models, we consider three raster-model bioclimatic variables, including potential evapotranspiration (PET), climate moisture index (CMI), and near-surface relative humidity (HURS).

To assess the projection of bioclimatic variables in the future, we utilized the 'Coupled Model Intercomparison Project Phase 6' (CMIP6) from the 'Working Group on Coupled Modelling' (WGCM) for three different time periods (Eyring et al., 2016). Two future climate scenarios

(Shared Socioeconomic Pathways; SSP 3-7.0 and 5-8.5) were selected for the five models to derive future climate projections (Table 1). We assume that SSP 3-7.0 is a less chaotic scenario because it represents a smaller reduction than SSP 5-8.5 in global greenhouse gas concentrations by 2100, which is the highest carbon emissions scenario and the most pessimistic view of the future. To assess the elevation effects, we utilized a Digital Elevation Model (DEM) variable (Karger et al., 2022).

Besides, we obtained 11 soil raster layers from SoilGrid (https://soilgrids.org/; Batjes et al., 2020), with 250 m of spatial resolution. Moreover, we obtained global forest change data (land cover, tree cover loss, loss and gain of forest raster layers from 2000 to 2022) of Global Forest Watch, with 30 m per pixel approximately (https://www.globalforestwatch.org/map/; Hansen et al., 2013). Additionally, we used the Normalized Difference Vegetation Index (NDVI) to determine vegetation coverage and spatial distribution, calculated as the mean NDVI annual to 2000-2020 using data from Earth Explorer with a spatial resolution of 1 km^2 (https://earthexplorer.usgs.gov/). Finally, the soil, topographic, and forest change layers were resampled to match the spatial resolution of the bioclimatic layers (1 km^2) using the *raster* package (Hijmans, 2023) in R software v. 4.3.1 (R Core Team, 2022).

The bioclimatic variables were selected appropriately for statistical and ecological parameter analysis of suitable models, following the methodology of Ames-Martínez et al. (2022). Variables with multicollinearity were selected based on measures, such as principal component analysis (PCA), inflation factor value (VIF), Sampling Bias, and pairwise Pearson's correlation (r). Our approach involved using *sdm* (Naimi & Araújo, 2016), *fuzzySim* (Barbosa, 2015), and *FactoMineR* (Husson et al., 2023) and *virtualspecies* packages (Leroy et al., 2019).

Finally, after the process of variable selection, we selected 19 environmental variables: isothermality (BIO3), temperature seasonality (BIO4), minimum temperature of the cold month (BIO6), mean temperature of the warmest quarter (BIO10), precipitation seasonality (BIO15), precipitation of the warmest quarter (BIO18), precipitation of the 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. To analyze tree cover loss, we used loss forest raster in some models and compared it to other models without this raster to determine forest loss in present and future scenarios, assuming the same current rate of tree cover loss continues into the future.

MaxEnt modeling assessment

MaxEnt was used to fit the complex responses to only the occurrence data. 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, Bennett & French, 2017). We used noncollinear variables and only occurrence data from MaxEnt v. 3.4.1 implemented in *the kuenm* package (Phillips et al., 2017; Cobos et al., 2019) 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 final results are the average of these replicates, which were used to build the present and future models.

Random forest modeling assessment

The Random Forest (RF) regression algorithm was utilized to model species distribution with discrimination capacity in the presence and absence of data. To avoid pseudo-absence data due to the dispersal capacity, we performed 10,000 pseudo-absence data using the geographic distance method and excluded any points located within 10 km of the presence data (Evans et al., 2011).

The relative importance of each predictor was examined using the determination coefficient (R^2) in conjunction with the Mean Squared Error (MSE). To construct the RF models with default settings, a 100-fold cross-validation procedure was implemented and repeated 10 times. It is worth noting that the performance of the RF models was influenced by key parameters such as the number of trees (5000), sets of predictor variables at each split (564), and minimum size of terminal nodes (50).

The dataset included both presence and pseudo-absence data and was randomly divided into ten equal subsets. Our modeling strategy consisted of training the RF model on nine of these subsets and validating it on the remaining subset. It is important to note that we generated 100 RF models, and the results were aggregated from these models. To generate pseudo-absence data and RF models, we used *the random forest* package (Liaw & Wiener, 2022).

Models’ evaluation

The potential distribution was derived from the best model. The relative importance of each variable was assessed using several performance evaluation indicators, including the ‘Area Under Curve’ (AUC), the partial ‘Receiver Operating Characteristic’ (ROC), Omission Rate, the Akaike Information Criterion corrected (AICc; as optimal complexity parameter), Akaike weights (W AICc), and Bayesian Information Criteria (BIC) (Hirzel et al., 2006; Peterson and Soberón, 2012; Jiménez and Soberón, 2020). The partial ROC 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, Pourghasemi & Melesse, 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 (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 & Anderson, 2014). Spatial information on present and future presence probabilities across *Cedrela* species was generated by averaging the maps. 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 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 & Wiernik, 2023), *gghalves* (Tiedemann, 2022), and *ggplot2* packages (Wickham et al., 2021). We performed a two-way ANOVA and *post-hoc* Tukey's test to compare the means using the *rstatix* package (Kassambara, 2023).

Predicted refuges to climate change

We linked the present and future potential of *Cedrela angustifolia* potential distribution with predicted refuges to climate change, identifying suitable grids in scenarios SSP 3-7.0 and SSP 5-8.5 scenarios. To recognize and estimate remnant patches outside the PNA, we used the consensus model between the present and future models, land cover (Hansen et al., 2013), and Protected Natural Areas (PNA; UNEP-WCMC & IUCN, 2023). We performed a spatial distribution bias correction to avoid over-adjusting future projections. We included 10,000 bias files and bioclimatic variables to assess potential refugees for climate change analysis. We implemented a Gaussian Kernel analysis using the QGIS software to avoid sampling bias and identify the highest potential refuges for climate change.

Results

Model evaluation and contribution of predictor variables

All candidates for MaxEnt and RF models were generated and compared, with only 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, which decreased when assessed using the independent testing dataset. Nonetheless, the MaxEnt model showed a higher AUC ratio, however RF better predictive performance than MaxEnt (Table S2).

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

Present potential distribution

The potential distribution maps with tree cover loss effect of *C. angustifolia* was approximately 13,080 km^2 (MaxEnt and Random Forest values mean; SD ± 671.75 km^2), and Schoener's D index between RF model and MaxEnt model was 0.857. Nevertheless, without the tree cover loss effect was 16,148.5 km^2 (± 847.82 km^2) in total distribution, with Schoener's D index was 0.749. Notably, areas in Peru and Bolivia were suitable for *C. angustifolia* under the current records (Fig. 2).

With tree cover loss effect, the distribution detected was 798 km^2 (± 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 Bolivia, and 744 km^2 (± 84.85 km^2) in Argentina. Notwithstanding, without tree cover loss effect, we detected that in Ecuador exhibited 948.5 km^2 (± 130.81 km^2), Peru with 2,579 km^2 (± 487.9 km^2), Bolivia with 11,400.5 km^2 (± 427.79 km^2), and Argentina 1,220.5 km^2 (± 65.90 km^2) (Fig. 2).

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We found that the presence of *C. angustifolia* probably affected the 5.3-6 °C of BIO3, BIO4 variation from 20 °C to 31 °C, decreasing BIO18 values from 100–200 mm, BIO15 from 750-830 mm, 0-5% of SOCS, NDVI of 0.95-1.00 units, 0-5% of OCD, 0-10% of slit, 0-10% of CCF, and 55% of LF.

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Future potential distribution

We detected a decrease in the distribution range of SSP 3-7.0 and 5-8.5 during the three periods (Fig. 2). For 2011-2040, we estimated an extension equivalent to 8,934 km^2 (± 1,131.37 km^2, SSP 3-7.0) and 9,094 km^2 (± 851.36 km^2, SSP 5-8.5), with Schoener's D index of 0.759 (Fig. 3A). Nevertheless, without the tree cover loss effect, we detected 11,424 km^2 (± 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 31.40% tree-cover loss, respectively, with Schoener's D index of 0.786 (Fig. 3B).

During 2041-2070, our models predicted a decrease in area of 29.91% and 30.53%in SSP 3-7.0 and SSP 5-8.5, respectively, without the tree-cover loss effect, and 33.93% and 42.32% with the tree-cover loss influence, and Schoener's D index was 0.846. Finally, for the 2071-2100 period, the area decreased by 30.43% (SSP 3-7.0), and 33.33% (SSP 5-8.5) without the tree cover loss effect; however, with the tree cover loss effect decreasing by 27.40% and 38.47% in the total distribution, with Schoener's D index of 0.872 (Fig. 3AB).

The mean temperatures from 2011 to 2040 in the SSP 3–7.0 and SSP 5–8.5 scenarios showed no significant differences among countries (Fig. 4A-D); however, Argentina and Bolivia exhibited statistically significant differences during the 2041–2070 period. Similarly, both countries displayed similar mean temperature values (~20.5 °C and ~18.7 °C, respectively) for the period 2010–2040 (Fig. 4ab). 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. 4c, d). In the four countries, the period 2071–2100 presented statistically significant differences compared to the other periods (Fig. 4A-D). In contrast, annual precipitation showed no significant differences among the four periods and countries (Fig. 4E-H)

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 species occurrence probability changed with tree cover loss by marginal responses of the presence suitability probability (Fig. 5A). We found that 30.59% of the total area was the most suitable habitat without the tree cover loss effect; nevertheless, Peru, Ecuador, and Argentina showed variations in the gain of tree cover loss area in 2040, 2070, and 2100 (Fig. 5B). For example, Ecuador and Argentina decreased by 51.25% and 14.08%, respectively, with the influence of tree cover loss (Fig. 5B) or total distribution, and Bolivia increased by more than 30% of the area distribution in all periods without tree cover loss. Nevertheless, Peru and Argentina will decrease by 70% in 2070.

Potential refuges to climate change

Our analysis showed variations in the habitat suitability distribution areas of *C. angustifolia* (9,449 $km^2 \pm 574\ km^2$) in the four countries. Nonetheless, 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 a high potential for refuge from climate change; however, Bolivia (6,258 $km^2 \pm 456\ km^2$) displayed a decreasing habitat (Fig. 6). Only 24.28% of the current potential distribution is within protected areas, and is probably reduced to 25-30% in 2100.

The predictions of the core distribution regions obtained from the MaxEnt and RF models showed a higher 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 refugees to climate change.

Discussions

The impact of climate change and tree cover loss on Andean Montane Forests has been acknowledged for a considerable period; however, the precise influence of climate change on the distribution of specific pioneer relict tree species remains unclear. Our findings suggest that the distribution of *Cedrela angustifolia* will decrease in the future owing to climate change projections for 2011-2040, 2041-2070, and 2071-2100. During these periods, high temperatures and CO_2 concentrations significantly affected the distribution of species (Eyring et al., 2016).

Present potential climate sensitivity

In previous studies, the predictive effectiveness of random forest (RF) and maximum entropy (MaxEnt) models has been 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 & Soberón, 2020). In this investigation, we carefully selected optimal feature class amalgamations and regularization parameters for MaxEnt. When then compared the predictive ability of the fine-tuned MaxEnt with the RF model. Both 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.

Seasonal variations in precipitation and temperature influenced the distribution of *C. angustifolia*. The model performed with excellent efficiency and accuracy (AUC > 0.98), as indicated by (Warren & Seifert, 2011). Populations of *C. angustifolia* 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). According to our analysis, Bolivian montane forests provide a more favorable ecological assemblage (81% according to the present model) and ecosystem conservation for *C. angustifolia* (Pennington & Muellner, 2010). More than half of the records of these species are within the PAs.

Effect of climate change in the future

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 strict-endemic tree species worldwide (Feeley & Silman, 2010).

Based on the evaluated scenarios, an increase in temperature from 4.1 °C to 5 °C in the present temperature record is expected. 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). Nonetheless, Peru and

Ecuador offer favorable climatic conditions that would allow *C. angustifolia* to migrate to warmer areas through the "thermophilization phenomenon' (Fadrique et al., 2018). This confirms the climatic vulnerability of *C. angustifolia* (Koecke et al., 2013; Cotrina Sánchez et al., 2021; 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 the 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, Fraedrich & Heimann, 2000; Longobardi et al., 2016). Likewise, tree cover loss increases the risk of soil erosion, leading to reduced soil fertility and increased sedimentation in water bodies of these forests (Tapia-Armijos et al., 2015; Cuenca, Arriagada & Echeverría, 2016; Bax & Francesconi, 2018). Therefore, the climatic impact of deforestation in AMF weakens the relationship between atmospheric circulation and hydrological cycle (Longobardi et al., 2016).

Potential habitat suitability and refuges

Suitable habitats for *C. angustifolia* will be maintained in all four countries; however, habitat suitability will decrease in all countries, in contrast to the present and future models evaluated. In Bolivia, showed the higher rates of illegal logging and forest fires than 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 has 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, Peralvo & Valarezo, 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 as they are more susceptible to selective logging and timber overexploitation as we demonstrated by our results (Cotrina et al., 2021; SERFOR, 2020).

Conclusions

Our study demonstrates that *Cedrela angustifolia* is vulnerable to future climate change, indicating differences in suitable habitats between Central and South America. Moreover, recommend the establishment of climate refugee for *Cedrela* species that is connected to NPAs and land-use changes. 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.

Non-Governmental Organizations (NGOs) and different environmental legacy institutions are recommended to use the potential findings and boundaries established by the Species Distribution Model (SDM) both currently and in the future to safeguard and preserve the species under investigation. Habitat suitability is stable and has a significant conservation value.

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.

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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.

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Table 1(on next page)

Information about the present and future models.

The table shows the model names, spatial resolutions, periods, and literature sources.

Table 1. Information about the present and future models. The table shows the model names, spatial resolutions, periods, and literature sources.

Time	**Model name**	**Spatial resolution**	**Period**	**Source**
Present	Present	1 km^2	1980-2010	CHELSA (Karger et al. 2022)
Future (SSP 3-7.0 and 5-8.5 scenarios)	GFDL-ESM4 IPSL-CM6A-LR MPI-ESM1-2-HR MRI-ESM2-0 UKESM1-0-LL	1 km^2	2011-2040 2041-2070 2071-2100	

Table 2 (on next page)

Percent contribution and permutation importance for present and future models in the two scenarios.

The table shows the periods of time, model names, variables, percent contribution, and permutation importance. PR = present model, a = SSP 3-7.0 scenario of future model, b = SSP 5-8.5 scenario of future model

Table 2. Percent contribution and permutation importance for present and future models in the two scenarios. The table shows the periods of time, model names, variables, percent contribution, and permutation importance. PR = present model, a = SSP 3-7.0 scenario of future model, b = SSP 5-8.5 scenario of future model

Variables	**Percent contribution in MaxEnt (%)**							**Increment of node purity in RF**						
	PR	2040		2070		2100		PR	2040		2070		2100	
		a	b	a	b	a	b		a	b	a	b	a	b
BIO15	26.3	11.3	12.6	24.6	14.6	16.4	24.6	46.1	23.9	33.4	28.6	24.6	26.5	24.5
SOCS	20.3	21.6	15.8	15.3	15.8	17.9	26.7	40.6	36.1	29.4	34.3	37.4	37.6	32.4
NDVI	11.7	15.3	24.3	29.3	11.3	12.3	15.9	36.8	32.2	35.7	35.7	29.4	30.5	29.1
BIO4	8.5	4.6	13.4	14.6	16.3	6.2	11.3	34.8	34.8	35.3	29.7	40.4	37.2	29.9
OCD	7.4	7.10	8.9	11.6	15.9	4.6	14.2	28.9	20.9	21.1	20.8	19.6	21.1	18.9
BIO18	6.2	24.7	7.6	4.9	7.6	7.6	8.4	25.1	18.3	18.4	17.9	16.6	26.9	21.9
SILT	4.8	11.3	4.3	5.8	2.4	4.9	9.5	24.3	26.6	26.3	25.2	24.9	27.3	28.1
CC	3.7	2.8	5.6	6.7	6.4	3.8	7.6	18.1	19.3	19.7	19.1	17.1	17.6	19.4
DEF	2.4	7.6	4.9	12.6	3.9	6.4	9.3	19.1	14.3	15.3	15.6	13.7	12.7	14.3
BIO3	2.3	4.9	2.6	7.3	6.9	3.7	6.7	14.7	20.6	18.7	19.6	21.3	17.4	18.2

Figure 1

Study area for *Cedrela angustifolia* climate sensitivity analysis in the Andean Montane Forests.

(a) Current distribution of *C. angustifolia* forest in Ecuador, Peru, Bolivia, and Argentina; (b) *C. angustifolia* dasometric features: 1=tree, 2=leaves, 3=fruit; and (c) tree cover loss of this species categorized by country, corresponding to the year 2021 (Hansen et al., 2013; Harris et al., 2021) .

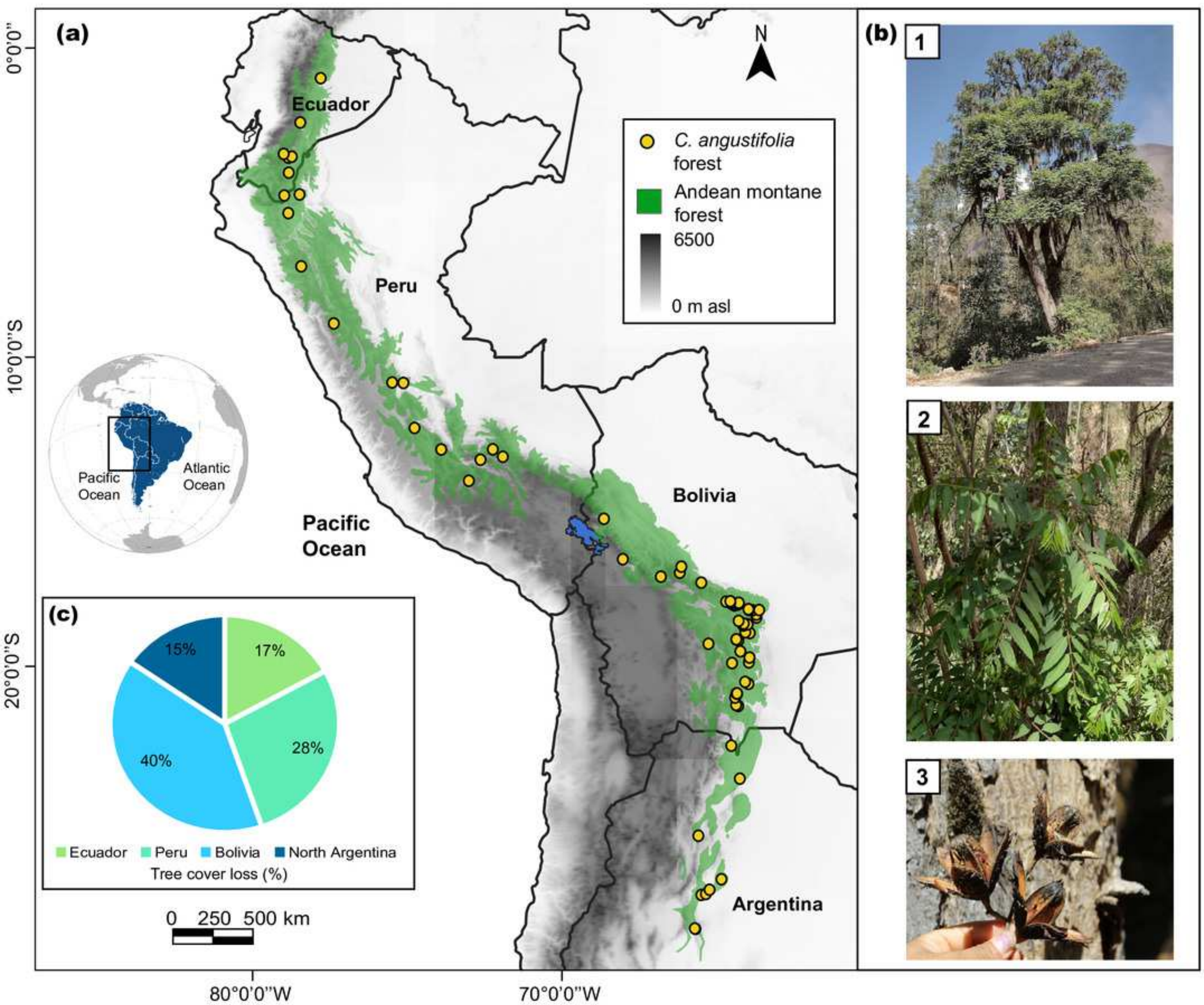


Figure 2

Present and future models (SSP 3-7.0 and 5-8.5), and area coverage percentage for each country and model, in 1980-2010 (present), 2011-2040, 2041-2070, and 2071-2100 periods.

tcl = tree cover loss raster in the model, wtcl = without tree cover loss raster in the model.

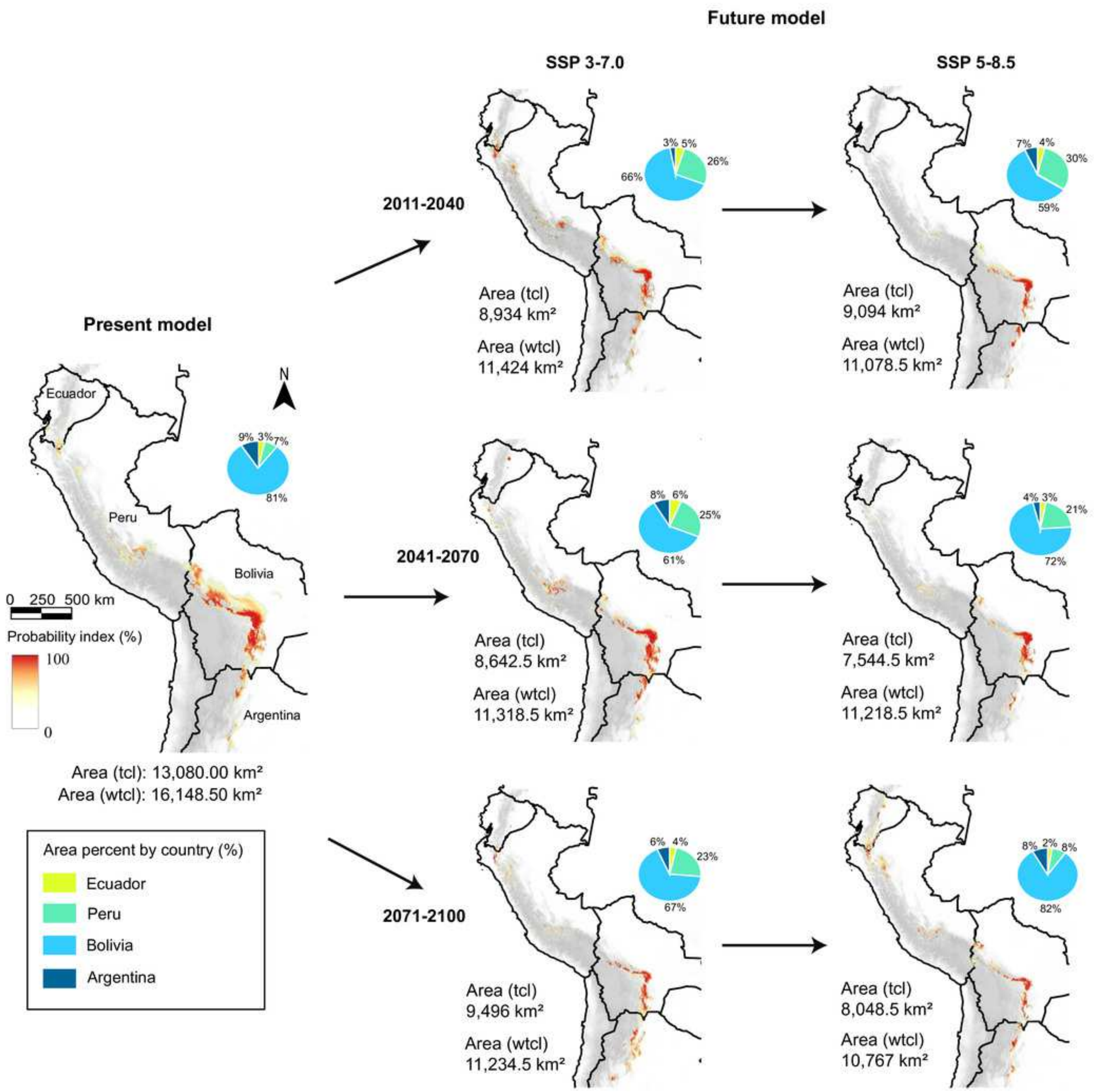
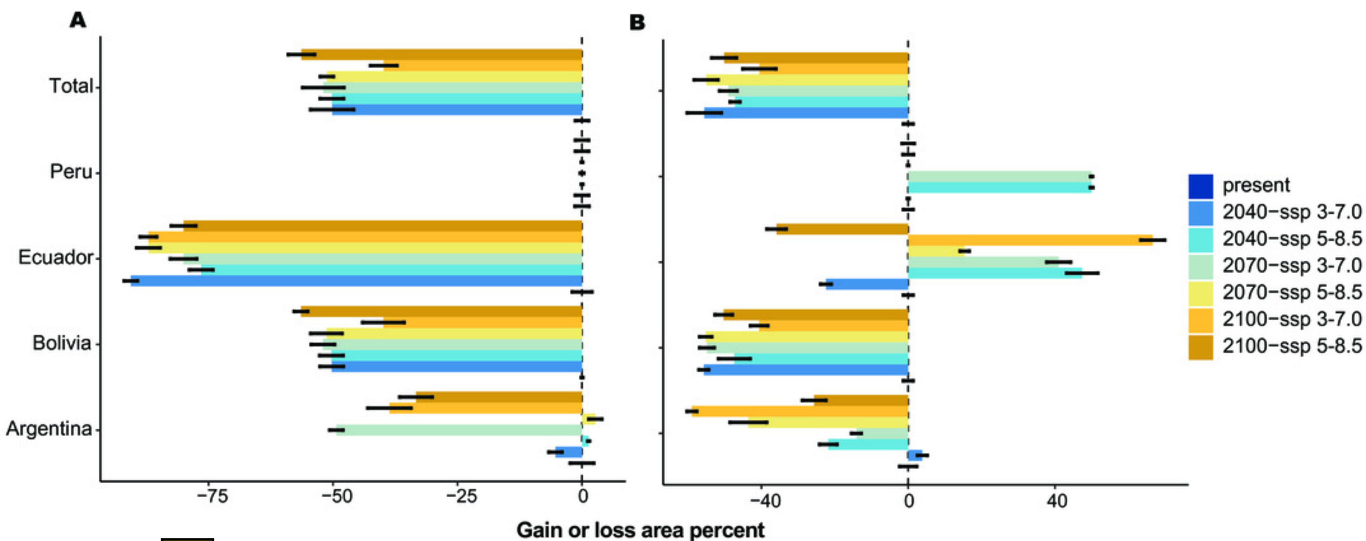

Future model
SSP 3-7.0
SSP 5-8.5
2011-2040
2041-2070
2071-2100
Present model
Ecuador
Peru
Bolivia
Argentina
N
0 250 500 km
Probability index (%)
100
0
Area (tcl): 13,080.00 km²
Area (wtcl): 16,148.50 km²
Area percent by country (%)
Ecuador
Peru
Bolivia
Argentina
9% 3% 7% 81%
Area (tcl) 8,934 km²
Area (wtcl) 11,424 km²
3% 5% 26% 66%
Area (tcl) 9,094 km²
Area (wtcl) 11,078.5 km²
7% 4% 30% 59%
Area (tcl) 8,642.5 km²
Area (wtcl) 11,318.5 km²
8% 6% 25% 61%
Area (tcl) 7,544.5 km²
Area (wtcl) 11,218.5 km²
4% 3% 21% 72%
Area (tcl) 9,496 km²
Area (wtcl) 11,234.5 km²
6% 4% 23% 67%
Area (tcl) 8,048.5 km²
Area (wtcl) 10,767 km²
8% 2% 8% 82%

Figure 3

Gain or loss area percentage for present and future periods, with two scenarios for each country in the present and SSP 3-7.0 and SSP 5-8.5 future scenarios for three periods.

(A) with forest loss effect, (b) without forest loss effect.



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3/22/2024
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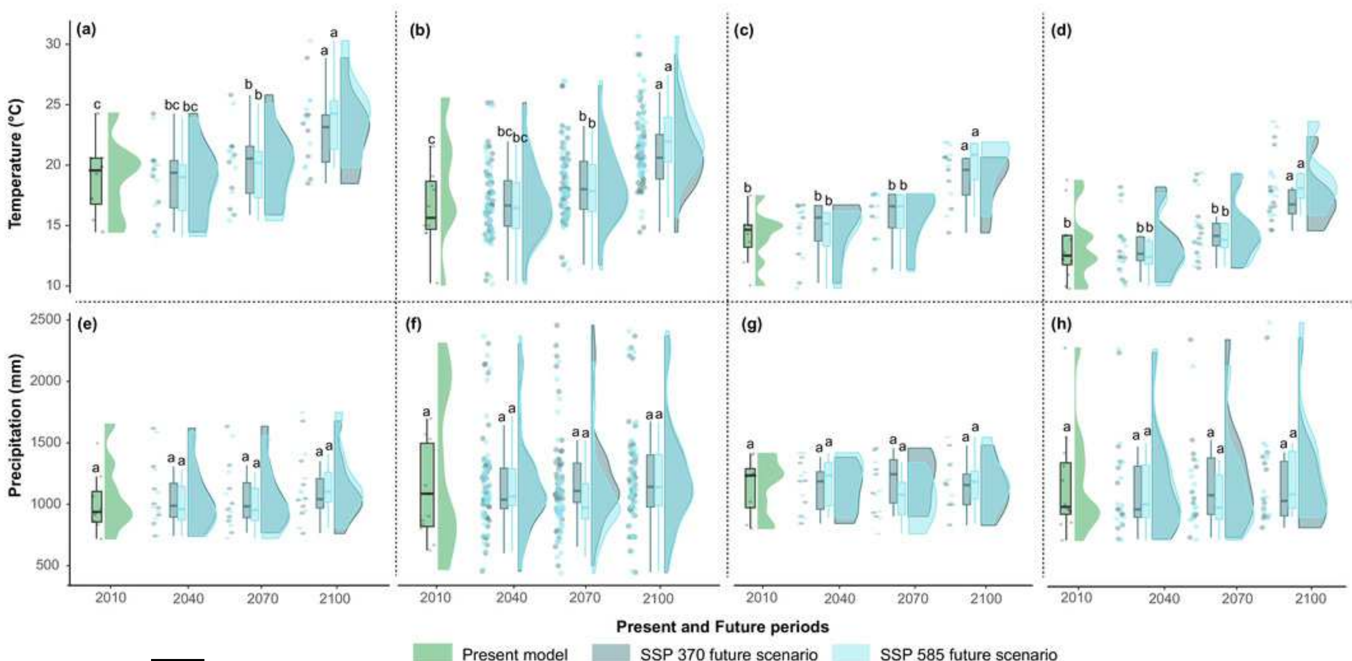
Figure 4

Raincloud plots for mean annual temperature (°C) (a, b, c, d) and annual precipitation (mm) (e, f, g, h) (y-axis) by present and future periods (x-axis) for each country.

(a, e) Argentina, (b, f) Bolivia, (c, g) Ecuador, and (d, h) Peru. The green rainclouds correspond to the present model, the gray rainclouds correspond to the SSP 3-7.0 future scenario, and the light blue rainclouds correspond to the SSP 5-8.5 future scenario. Each rain cloud has a corresponding boxplot (left side). The letters over each boxplot indicate statistically significant ($p < 0.05$) differences between the years 2010, 2040, 2070, and 2100.



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3/22/2024
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Figure 5

Tree cover loss effect for present and future periods (x-axis), with two scenarios for each country.

(a) Suitability probability of *C. angustifolia* presence, (b) gain or loss area percentage for each country.

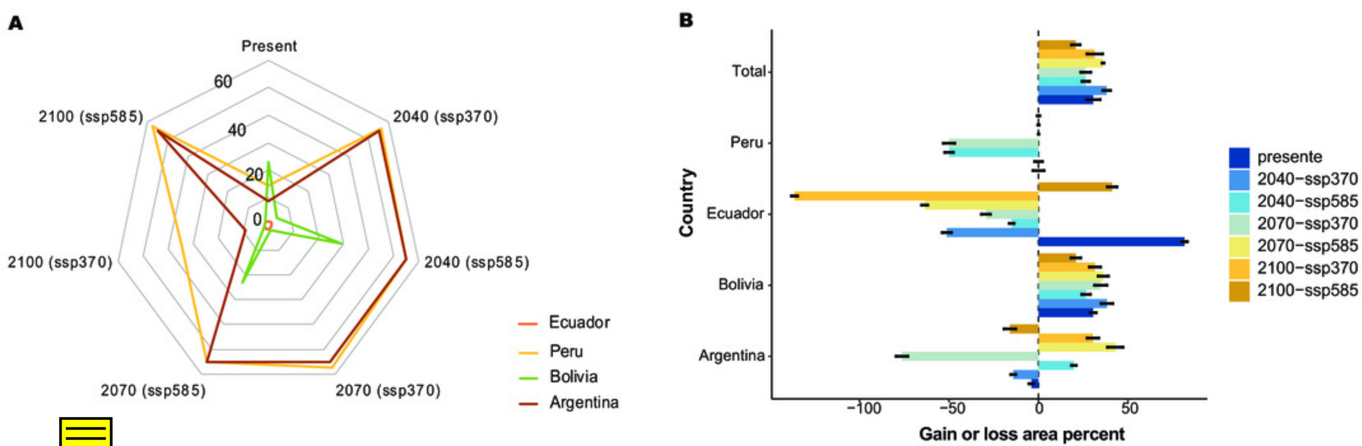

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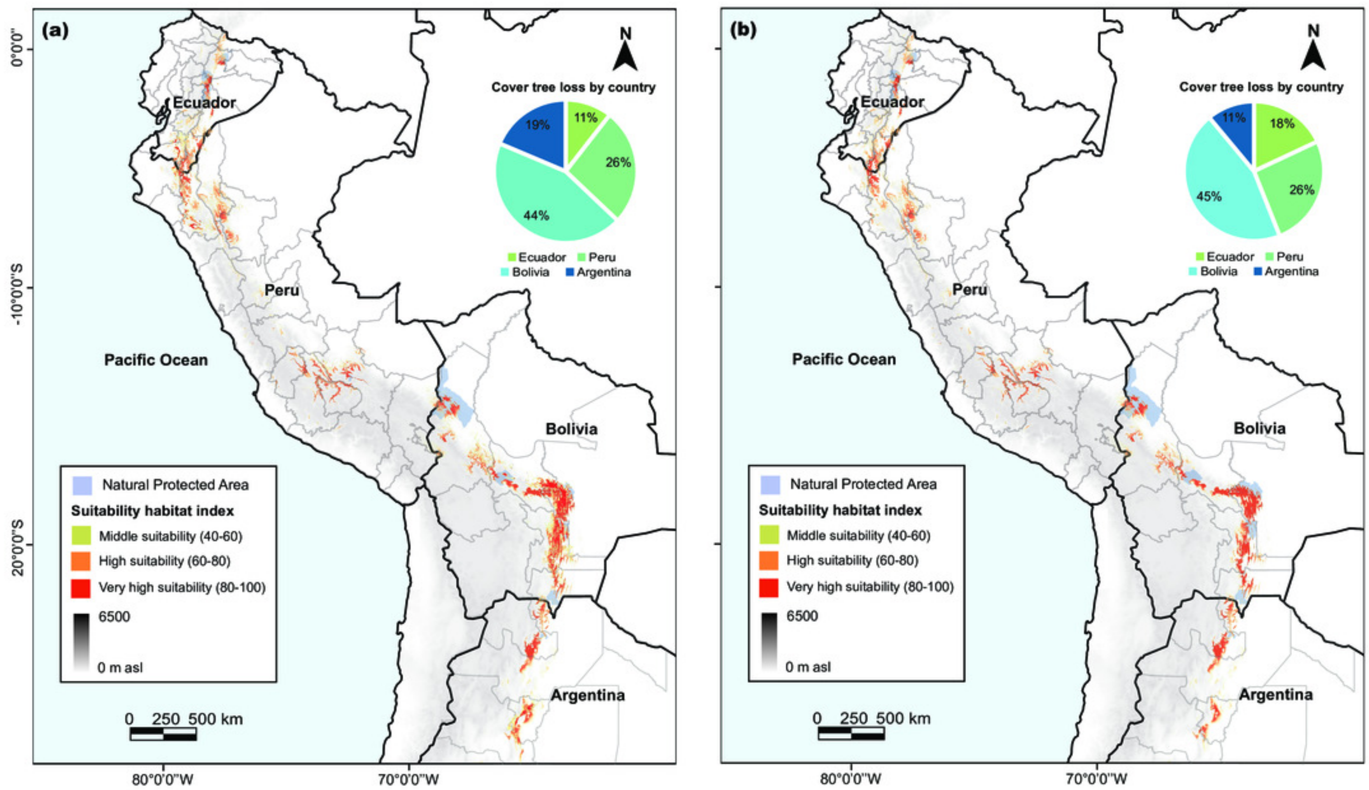
Figure 6

Cedrela angustifolia suitability habitat by country and for specific protected areas in the different countries, under combined of present and future climate change scenarios, and cover tree loss percent for two algorithms.

(a) MaxEnt model (b) Random Forest model.



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How do climate change and tree cover loss affect the habitat suitability of Cedrela angustifolia ? Evaluating climate vulnerability and conservation in Andean Montane Forests (# 96346) Structure and Criteria

Raw, Criteria

01 Ellen Quinlan Page 8

22/3/2024 0:54

What does this mean?

02 Ellen Quinlan Page 8

22/3/2024 0:54

03 Ellen Quinlan Page 8

22/3/2024 0:55

Like what?

04 Ellen Quinlan Page 8

22/3/2024 0:54

05 Ellen Quinlan Page 8

22/3/2024 0:55

What does this mean? Needs more explanation.

06 Ellen Quinlan Page 8

22/3/2024 0:56

The wording of this sentence is confusing.

07 Ellen Quinlan Page 8

22/3/2024 0:55

08 Ellen Quinlan Page 8

22/3/2024 0:56
Why?

09 Ellen Quinlan Page 8

22/3/2024 0:56

10 Ellen Quinlan Page 8

22/3/2024 0:56

11 Ellen Quinlan Page 8

22/3/2024 0:57
such as

12 Ellen Quinlan Page 8

22/3/2024 0:57

13 Ellen Quinlan Page 8

22/3/2024 0:57
delete

14 Ellen Quinlan Page 8

22/3/2024 0:58
^such as

15 Ellen Quinlan Page 8

22/3/2024 0:57

16 Ellen Quinlan Page 8

22/3/2024 0:57

17 Ellen Quinlan Page 9

22/3/2024 0:58
define what you mean by "relict"

18 Ellen Quinlan Page 9

22/3/2024 0:58

19 Ellen Quinlan Page 9

22/3/2024 0:58

"Since"

20 Ellen Quinlan Page 9

22/3/2024 0:58

21 Ellen Quinlan Page 9

22/3/2024 1:05

How?

22 Ellen Quinlan Page 9

22/3/2024 1:05

23 Ellen Quinlan Page 9

22/3/2024 1:06

Not a complete sentence

24 Ellen Quinlan Page 9

22/3/2024 1:06

25 Ellen Quinlan Page 10

22/3/2024 1:10

This paragraph could use more background.

26 Ellen Quinlan Page 10

22/3/2024 1:09

This paragraph and the one above seem very disjunct.

27 Ellen Quinlan Page 10

22/3/2024 1:09

who is "they"?

28 Ellen Quinlan Page 10

22/3/2024 1:09

29 Ellen Quinlan Page 10

22/3/2024 1:10

Please expand on this

30 Ellen Quinlan Page 10

22/3/2024 1:10

31 Ellen Quinlan Page 10

22/3/2024 1:13

How? The connection is not clear to me.

32 Ellen Quinlan Page 10

22/3/2024 1:11

33 Ellen Quinlan Page 10

22/3/2024 1:13

Don't understand what this means.

34 Ellen Quinlan Page 10

22/3/2024 1:13

35 Ellen Quinlan Page 10

22/3/2024 1:14

This entire paragraph is very confusing.

36 Ellen Quinlan Page 10

22/3/2024 1:16

Did you do this? This reads like it was an aim of this study.

37 Ellen Quinlan Page 10

22/3/2024 1:16

38 Ellen Quinlan Page 11

22/3/2024 1:18

Use the full scientific name once at the beginning of of the paper and then C. angustifolia consistently throughout.

39 Ellen Quinlan Page 11

22/3/2024 1:17

Delete.

40 Ellen Quinlan Page 11

22/3/2024 1:17

41 Ellen Quinlan Page 11

22/3/2024 1:17

42 Ellen Quinlan Page 11

22/3/2024 1:19

Define.

43 Ellen Quinlan Page 11

22/3/2024 1:19

44 Ellen Quinlan Page 11

22/3/2024 1:20

Why did you select this cut off? Is it of biological relevance?

45 Ellen Quinlan Page 11

22/3/2024 1:19

46 Ellen Quinlan Page 12

22/3/2024 1:20

Delete.

47 Ellen Quinlan Page 12

22/3/2024 1:20

48 Ellen Quinlan Page 12

22/3/2024 1:21
how was this determined?

49 Ellen Quinlan Page 12

22/3/2024 1:20

50 Ellen Quinlan Page 12

22/3/2024 1:21
explain more how you did this

51 Ellen Quinlan Page 12

22/3/2024 1:21

52 Ellen Quinlan Page 12

22/3/2024 1:21
Replace with "In total"

53 Ellen Quinlan Page 12

22/3/2024 1:21

54 Ellen Quinlan Page 12

22/3/2024 1:23
I would replace with "retained". You obtained many more records but only 104 were retained after filtering.

55 Ellen Quinlan Page 12

22/3/2024 1:22
delete, repetitive

56 Ellen Quinlan Page 12

22/3/2024 1:22

57 Ellen Quinlan Page 12

22/3/2024 1:22

58 Ellen Quinlan Page 12

22/3/2024 1:24

The organization of this section in generally confusing.

59 Ellen Quinlan Page 12

22/3/2024 1:23

What is the difference between a "bioclimatic" and "climatic" variable?

60 Ellen Quinlan Page 12

22/3/2024 1:23

61 Ellen Quinlan Page 12

22/3/2024 1:25

How/why were these 19 selected? Why are just 3 listed here?

62 Ellen Quinlan Page 12

22/3/2024 1:24

63 Ellen Quinlan Page 13

22/3/2024 1:27

Delete. Begin with "We"

64 Ellen Quinlan Page 13

22/3/2024 1:27

65 Ellen Quinlan Page 13

22/3/2024 1:28

"from"

66 Ellen Quinlan Page 13

22/3/2024 1:28

67 Ellen Quinlan Page 14

22/3/2024 1:30

This is only 16 variables, not 19

68 Ellen Quinlan Page 14

22/3/2024 1:31
What is this?

69 Ellen Quinlan Page 14

22/3/2024 1:30

70 Ellen Quinlan Page 14

22/3/2024 1:31

71 Ellen Quinlan Page 14

22/3/2024 1:31
cite

72 Ellen Quinlan Page 14

22/3/2024 1:31

73 Ellen Quinlan Page 15

22/3/2024 1:31
cite

74 Ellen Quinlan Page 15

22/3/2024 1:31

75 Ellen Quinlan Page 15

22/3/2024 1:33
Remove. Start with "The"

76 Ellen Quinlan Page 15

22/3/2024 1:32

77 Ellen Quinlan Page 17

22/3/2024 1:34
Define acronym the first time it is used.

78 Ellen Quinlan Page 17

22/3/2024 1:34

79 Ellen Quinlan Page 18

22/3/2024 1:36

wording doesn't make sense.

80 Ellen Quinlan Page 18

22/3/2024 1:36

81 Ellen Quinlan Page 18

22/3/2024 1:39

Why is this notable?

82 Ellen Quinlan Page 18

22/3/2024 1:37

83 Ellen Quinlan Page 18

22/3/2024 1:40

Delete. Begin with "Without"

84 Ellen Quinlan Page 18

22/3/2024 1:40

85 Ellen Quinlan Page 19

22/3/2024 1:42

Wording is extremely confusing.

86 Ellen Quinlan Page 19

22/3/2024 1:41

87 Ellen Quinlan Page 20

22/3/2024 1:44

Remove. The word does not add anything and makes statement less clear.

88 Ellen Quinlan Page 20

22/3/2024 1:43

89 Ellen Quinlan Page 20

22/3/2024 1:44

Delete. Same thing as above.

90 Ellen Quinlan Page 20

22/3/2024 1:44

91 Ellen Quinlan Page 21

22/3/2024 1:45

"refuges" not "refugees"

92 Ellen Quinlan Page 21

22/3/2024 1:45

93 Ellen Quinlan Page 21

22/3/2024 1:46

Need citations to back up this statement and place in context.

94 Ellen Quinlan Page 21

22/3/2024 1:45

95 Ellen Quinlan Page 21

22/3/2024 1:46

What does this mean?

96 Ellen Quinlan Page 21

22/3/2024 1:46

97 Ellen Quinlan Page 21

22/3/2024 1:47

Again, be consistent with use of either C. angustifolia or full scientific name.

98 Ellen Quinlan Page 21

22/3/2024 1:46

99 Ellen Quinlan Page 21

22/3/2024 1:48

Was this explicitly tested in the model? I don't think it was.

100 Ellen Quinlan Page 21

22/3/2024 1:47

101 Ellen Quinlan Page 21

22/3/2024 1:49

would combine these sentences to "...MaxEnt, and then compared..."

102 Ellen Quinlan Page 21

22/3/2024 1:48

103 Ellen Quinlan Page 22

22/3/2024 1:49

"as indicated by Warren & Seifert (2011)"

104 Ellen Quinlan Page 22

22/3/2024 1:49

105 Ellen Quinlan Page 22

22/3/2024 1:50

What does this mean? Maybe just "more favorable conditions"?

106 Ellen Quinlan Page 22

22/3/2024 1:50

delete

107 Ellen Quinlan Page 22

22/3/2024 1:50

108 Ellen Quinlan Page 22

22/3/2024 1:50

109 Ellen Quinlan Page 22

22/3/2024 1:52

Just Bolivian or all NPAs?

110 Ellen Quinlan Page 22

22/3/2024 1:51

this

111 Ellen Quinlan Page 22

22/3/2024 1:51

112 Ellen Quinlan Page 22

22/3/2024 1:52

113 Ellen Quinlan Page 22

22/3/2024 1:52

What does this mean?

114 Ellen Quinlan Page 22

22/3/2024 1:52

115 Ellen Quinlan Page 22

22/3/2024 1:52

What is this referring to? MAT?

116 Ellen Quinlan Page 22

22/3/2024 1:52

117 Ellen Quinlan Page 22

22/3/2024 1:53

Over what time period?

118 Ellen Quinlan Page 22

22/3/2024 1:53

119 Ellen Quinlan Page 23

22/3/2024 1:54

Don't think this applies here. Thermophilization refers to community shifts towards warm-adapted species and Fadrique et al. 2018 is not the right attribution.

120 Ellen Quinlan Page 23

22/3/2024 1:53

121 Ellen Quinlan Page 23

22/3/2024 1:56

I don't think you showed/tested this and I don't think this is the primary driver of their range reduction.

122 Ellen Quinlan Page 23

22/3/2024 1:55

123 Ellen Quinlan Page 23

22/3/2024 1:57

Not sure what this means. How can you say that habitat suitability will decrease but its in contrast with your models? I thought this is what you showed?

124 Ellen Quinlan Page 23

22/3/2024 1:57

125 Ellen Quinlan Page 24

22/3/2024 1:58

delete

126 Ellen Quinlan Page 24

22/3/2024 1:58

127 Ellen Quinlan Page 24

22/3/2024 1:58

"Moreover, we..."

128 Ellen Quinlan Page 24

22/3/2024 1:58

129 Ellen Quinlan Page 24

22/3/2024 1:59

"to buffer against land use changes"

130 Ellen Quinlan Page 24

22/3/2024 1:59

131 Ellen Quinlan Page 24

22/3/2024 2:00

"and"

132 Ellen Quinlan Page 24

22/3/2024 2:00

133 Ellen Quinlan Page 24

22/3/2024 2:00

delete

134 Ellen Quinlan Page 24

22/3/2024 2:00

135 Ellen Quinlan Page 24

22/3/2024 2:01

Not sure what this means

136 Ellen Quinlan Page 24

22/3/2024 2:01

137 Ellen Quinlan Page 25

22/3/2024 2:02

I suggest adding a paragraph somewhere in this section re-establishing why Cedrela is ecologically important, why NGOs and governments should care about its conservation.

138 Ellen Quinlan Page 43

22/3/2024 2:06

x-axes are different scales between panels A&B. This makes the panels look more similar than they are.

139 Ellen Quinlan Page 44

22/3/2024 2:08

I can't differentiate between the two colors of blue on this figure.

140 Ellen Quinlan Page 45

22/3/2024 2:08

This needs a better caption/explanation

141 Ellen Quinlan Page 46

22/3/2024 2:09

Can you show which areas experience the most change?