iForest
Biogeosciences and Forestry

Research Article
doi: 10.3832/ifor4880-018
vol. 19, pp. 1-8

Ensemble modeling of *Pinus cembroides* Zucc. distribution under future CMIP6 climate scenarios in northern Mexico

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This study employed ensemble species distribution models (SDMs) using the "biomod2" package and different General Circulation Models (GCMs) to assess the impacts of climate change on the potential distribution of *Pinus cembroides* in Mexico. Using presence and pseudo-absence data, along with bioclimatic variables from CHELSA v2.1, future habitat suitability was projected for the near future (2041-2060) and far future (2061-2080) under two CMIP6 scenarios (SSP245 and SSP585). Our results predict that under future climate conditions, *P. cembroides* will likely undergo substantial range contractions, with losses of approximately 65%-85% of the current suitable habitat and no colonization of novel areas. Temperature-related predictors, particularly Bio8 (mean temperature of the wettest quarter) and Bio9 (mean temperature of the driest quarter) were identified as the primary drivers of the species' distribution. These results suggest that under warming scenarios, *P. cembroides* will be confined to high elevation refugia, thereby increasing fragmentation and reducing its adaptive capacity. Overall, our findings provide a critical baseline for adaptive forest management strategies, such as assisted migration and the conservation of high elevation refugia, to mitigate the impacts of climate change on *P. cembroides*.

Keywords: Biomod2, CHELSA, CMIP6, *Pinus cembroides*, Potential Distribution

Introduction

Climate change is altering forest ecosystems by modifying temperature and precipitation regimes (Khan & Verma 2022). Consequently, species are migrating to higher latitudes and elevations to find suitable climatic conditions (Pecl et al. 2017). Moreover, more frequent droughts, wildfires, and pest outbreaks are driving widespread tree mortality and ecosystem degradation, thereby threatening biodiversity and key ecosystem services, including carbon sequestration and water regulation (Anderegg et al. 2020, Hartmann et al. 2022). Thus, forecasting species' responses to climate-driven changes is essential for ecologists and land managers (Bellard et al. 2012).

Mexico is particularly vulnerable to these climatic alterations. Mean annual temperatures have increased by approximately 0.7 °C over the past 50 years, accompanied by increased precipitation variability (Cavazos et al. 2020, Murray-Tortarolo 2021). Projections under high-emissions scenarios indicate an additional warming of up to 4.5 °C by 2100, and a decline in soil moisture (Almazroui et al. 2021). Such changes have already increased mortality rates and suppressed radial growth in conifer forests at their xeric margins (Manzanilla-Quijada et al. 2024).

Pinus cembroides Zucc., commonly known as Mexican pinyon, occurs on dry, rocky soils throughout the Sierra Madre Oriental, Sierra Madre Occidental, and Trans-Mexican Volcanic Belt (Constante-García et al. 2009, Martínez-Sifuentes et al. 2020). *P. cembroides* reaches up to 15 m in height and 30-70 cm in diameter (Herrera-Soto et al. 2018). Nutrient limitations, particularly nitrogen and phosphorus, can restrict both root development and crown expansion in this species (Constante-García et al. 2009). Individual trees typically establish on mildly acidic substrates (mean pH: 5.3; $H^+ \approx 25\%$ of exchangeable cations) under warm xerophytic temperate climates, predominantly occupying ecotones between arid desert scrub and humid montane forests (Rzedowski 1978). Although *P. cembroides* exhibits exceptional drought tolerance, its distribution is primarily limited by temperature extremes during the wettest (Bio 8) and driest (Bio 9) quarters (Martínez-Sánchez et al. 2023). Under future warming scenarios, models project range contractions exceeding 75%, confining populations to isolated high-elevation refugia and threatening genetic diversity and connectivity (Romero-Sánchez et al. 2017).

Species distribution models (SDMs) correlate species occurrences with environmental predictors, such as temperature, precipitation, and elevation, to estimate current habitat suitability and forecast future range shifts (Elith et al. 2006, Guisan et al. 2013). Algorithms include parametric regression (generalized linear models, generalized additive models), machine-learning methods (random forests, boosted regression trees, artificial neural networks), presence-only techniques (MaxEnt, surface range envelopes), and mechanistic models integrating species-specific physiology. These methods have been successfully applied to diverse taxa, including conifers in

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Received: Apr 14, 2025 - Accepted: Sep 02, 2025

Citation: Martínez-Sánchez JN, Cavazos T, Gárate-Escamilla H, De Luna M, Cuéllar-Rodríguez G (2026). Ensemble modeling of *Pinus cembroides* Zucc. distribution under future CMIP6 climate scenarios in northern Mexico. iForest 19: 1-8. – doi: 10.3832/ifor4880-018 [online 2026-01-10]

Communicated by: Maurizio Marchi

Tab. 1 - The bioclimatic variables analyzed to quantify changes in the potential distribution of *P. cembroides*.

Variable	Description
Bio 2	Mean diurnal range
Bio 3	Isothermality
Bio 7	Temperature annual range
Bio 8	Mean temperature of wettest quarter
Bio 9	Mean temperature of driest quarter
Bio 12	Annual precipitation
Bio 14	Precipitation of driest month
Bio 18	Precipitation of warmest quarter
Bio 19	Precipitation of coldest quarter

Mexico (Sáenz-Romero et al. 2017, Gómez-Pineda et al. 2020), and provide critical projections to inform adaptive forest management, such as assisted migration and conservation of high-elevation refugia, to mitigate climate change impacts (Bower et al. 2024).

However, each SDM entails uncertainties arising from the methodology, data quality, and assumptions underlying future climate scenarios (Araújo et al. 2019). To address these challenges, ensemble modeling approaches integrate predictions from multiple SDMs and general circulation models (GCMs), thereby enhancing the robustness of projections and reducing uncertainty (Thuiller et al. 2019, Valavi et al. 2022).

In this study, we assessed the impacts of climate change on the distribution of *P. cembroides* in Mexico. We first identified the key climatic drivers of its current range, and then projected habitat suitability under two climate scenarios (SSP245 and SSP585) for the periods 2041-2060 and 2061-2080 using an ensemble modeling framework. Finally, we mapped areas of habitat loss, stability, and potential gain. Employing multiple algorithms reduces model uncertainty and increases confidence in future suitability predictions.

Methodology

Species presence records

Occurrence records for *P. cembroides* were obtained from the National Forest and Soil Inventory and the National Biodiversity Information System (CONABIO 2020). Duplicate records were removed to match the spatial resolution of the climate data and prevent model overfitting. Overall, 1696 occurrence records were obtained.

Environmental data

We analyzed 19 bioclimatic variables representing current and future climate conditions to quantify changes in the potential distribution of *P. cembroides*. Climate layers were derived from CHELSA v. 2.1, which integrates surface observations, satellite data, and the ERA5 reanalysis at approximately 1-km spatial resolution. (Karger et al. 2017). To reduce multicollinearity, we retained predictors with VIF<10 (Kaky et al. 2020 - Tab. 1). We focused on climate drivers, since broad-scale temperature and precipitation gradients determine range limits. In contrast, static factors (*e.g.*, soil, topography) cannot be projected under future scenarios (Zamora-Maldonado et al. 2025). This climate-only framework isolates the effects of climate change on habitat suitability (Pearson & Dawson 2003). We then projected suitability for 2041-2060 (near future) and 2061-2080 (far future) under the SSP2-4.5 and SSP5-8.5 scenarios (Eyring et al. 2016) using the Python package "chelsa-cmip6" ver. 1.0 (Karger et al. 2023). To address GCM uncertainty, we generated a multi-model ensemble (MME) by comparing monthly temperature and precipitation outputs against CRU observations (Harris et al. 2014). We evaluated model performance using the normalized standard deviation, centered root-mean-square error, Taylor skill score, pattern correlation coefficient, and mean bias (Harris et al. 2014, Goberville et al. 2015). These metrics guided the selection of models that best capture regional climate variability (Knutti et al. 2017).

Ensemble modelling

We implemented ensemble distribution modeling in R using the "BIOMOD2" v. 4.2-2 package (R Core Team 2020). We included nine correlative modeling algorithms: Generalized Linear Models (GLM – McCullagh & Nelder 1989), a parametric regression framework; Generalized Additive Models (GAM – Hastie & Tibshirani 1990), which use spline-based smoothing; Generalized Boosted Models (GBM – Ridgeway 1999), a gradient-boosted ensemble of decision trees; Classification Tree Analysis (CTA – Breiman 2001), based on CART; Flexible Discriminant Analysis (FDA – Hastie et al. 1994), discriminant analysis with non-parametric smoothing; Artificial Neural Networks (ANN – Ripley 1996), feed-forward neural networks; Maximum Entropy (MaxEnt – Phillips et al. 2006), a presence-only maximum-entropy method; Random Forest (RF – Breiman 2001), a bootstrap-aggregated decision-tree ensemble; and, Surface Response Envelopes (SRE – Busby 1991), a climatic-envelope model based on predictor ranges. Each model was trained on 75% of the data and evaluated on the remaining 25% (Phillips et al. 2006). We generated 10,000 random pseudo-absences for each model using a random cross-validation strategy (Guisan et al. 2017). Default algorithm parameters were used to minimize overfitting. To enhance robustness, each algorithm was run three times (Khan & Verma 2022). We assessed performance using the area under the ROC curve (AUC, 0-1), partial AUC (pAUC, FPR ≤ 0.10), and True Skill Statistic (TSS, -1 to 1), retaining only models with TSS > 0.8 for ensemble integration (Fielding & Bell 1997, Lobo et al. 2008, Kaky et al. 2020). The AUC indicates relatively good to excellent model performance when values exceed 0.8 and 0.9, respectively (Fielding & Bell 1997). pAUC provides a firmer foundation for evaluating predictions from ecological niche models (Peterson et al. 2008). TSS combines sensitivity (true positive rate) and specificity (true negative rate) to assess a model's ability to predict presence and absence. The closer the TSS is to 1, the higher the prediction accuracy (Allouche et al. 2006). Only models with TSS > 0.8 were retained for ensemble integration. Finally, we used BIOMOD_EnsembleModelling to generate two consensus projections: EMmean (unweighted mean) and TSS-weighted mean to reduce model-specific uncertainty (Huang et al. 2024).

Variable importance

To quantify the relative influence of each

Tab. 2 - Mean and standard deviation evaluation metrics by algorithm for P. cembroides: True Skill Statistic (TSS), Area Under the Curve (AUC), and partial AUC (pAUC).

Algorithm	TSS mean	TSS std	AUC mean	AUC std	PAUC mean	PAUC std
ANN	0.740	0.001	0.914	0.047	0.662	0.097
CTA	0.736	0.014	0.882	0.013	0.692	0.004
FDA	0.728	0.012	0.919	0.005	0.678	0.002
GAM	0.735	0.020	0.930	0.005	0.734	0.001
GBM	0.758	0.012	0.946	0.004	0.821	0.002
GLM	0.772	0.022	0.942	0.004	0.779	0.002
MAXENT	0.780	0.024	0.947	0.005	0.841	0.018
RF	0.711	0.034	0.957	0.003	0.924	0.091
SRE	0.524	0.004	0.762	0.005	0.500	0.000
EMmean	0.775	0.018	0.948	0.004	0.885	0.021
EMwmean	0.777	0.016	0.949	0.004	0.890	0.019

bioclimatic predictor on the distribution of *P. cembroides*, we employed the permutation-importance method (Elith et al. 2005). Each predictor was permuted in turn while holding all other variables constant; we then quantified the reduction in model predictions relative to the original output. We then corrected this reduction by accounting for the correlation between permuted and original predictions (Ahmad et al. 2019). Larger corrected reductions indicate greater variable importance, whereas a zero reduction denotes no contribution.

Tab. 3 - Mean variable importance scores of the selected bioclimatic variables for each algorithm: Artificial Neural Networks (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Model (GAM), Generalized Boosted Model (GBM), Generalized Linear Model (GLM), Maximum Entropy (MAXENT), Random Forest (RF), Surface Range Envelope (SRE).

Variable	ANN	CTA	FDA	GAM	GBM	GLM	MAXENT	RF	SRE
Bio 2	0.335	0.000	0.205	0.238	0.000	0.520	0.042	0.045	0.039
Bio 3	0.008	0.045	0.051	0.049	0.028	0.700	0.085	0.043	0.041
Bio 7	0.000	0.000	0.177	0.163	0.000	0.887	0.088	0.132	0.081
Bio 8	0.292	0.322	0.212	0.215	0.181	0.357	0.474	0.114	0.002
Bio 9	0.713	0.738	0.614	0.495	0.280	0.287	0.111	0.072	0.063
Bio 12	0.145	0.063	0.105	0.265	0.058	0.230	0.250	0.051	0.101
Bio 14	0.134	0.000	0.001	0.066	0.005	0.053	0.024	0.044	0.043
Bio 18	0.027	0.000	0.035	0.036	0.006	0.014	0.020	0.049	0.036
Bio 19	0.041	0.000	0.023	0.004	0.004	0.052	0.033	0.041	0.062

Spatial distribution

We computed the Habitat Suitability Index (HSI) for each model as the predicted probability of species occurrence. We derived the ensemble HSI by averaging predictions from the EMmean and EMwmean methods. We then normalized raw HSI values (0-1000) to a scale of 0-1. Suitability classes were defined as highly suitable (HIS ≥ 0.8), moderately suitable (0.6 ≤ HIS < 0.8), marginally suitable (0.4 ≤ HIS < 0.6), and unsuitable (HIS < 0.4 – Sun et al. 2024).

Results

Model evaluation

The final ensemble models EMmean and EMwmean achieved average AUC values of 0.948 and 0.949 across replicates (Tab. 2). During calibration, AUCs were 0.987 for EMmean and 0.999 for EMwmean. On independent validation data, AUCs were 0.954 and 0.955, with TSS of 0.775 and 0.777, demonstrating high predictive accuracy for *P. cembroides*. Among individual algorithms, MaxEnt achieved the highest TSS (0.780), followed by GLM (0.772) and GBM (0.758). RF showed the highest AUC (0.957), followed by MaxEnt (0.947). The SRE model performed least favorably (AUC = 0.762; TSS = 0.524), indicating limited discrimination between presence and absence of the species. ANN (TSS = 0.740, AUC = 0.914) and CTA (TSS = 0.736, AUC = 0.882) demonstrated moderate performance. pAUC (FPR ≤ 0.10) for single algorithms ranged from 0.50 (SRE) to 0.99 (RF), with intermediate values for CTA (0.74), FDA (0.71), GLM (0.81), MaxEnt (0.84), ANN (0.75), GBM (0.81), and GAM (0.76). These results demonstrate that integrating multiple algorithms into an ensemble enhances the reliability of species distribution predictions.

Variable importance

Tab. 3 summarizes the mean importance scores for nine bioclimatic predictors across the nine algorithms, revealing substantial variability. Temperature predictors were the most influential: Bio 8 (mean temperature of the wettest quarter) ranged from 0.181 in GBM to 0.474 in MaxEnt (ensemble = 0.321); Bio 9 (mean temperature of the driest quarter) varied from 0.280 in GBM to 0.738 in CTA (ensemble = 0.171); Bio 3 (isothermality) scored 0.700 in GLM (ensemble = 0.277); and Bio 7 (annual temperature range) peaked at 0.887 in GLM (ensemble = 0.340). In contrast, precipitation predictors showed lower importance: Bio 2 (mean diurnal range, ensemble = 0.201), Bio 12 (annual precipitation, 0.184),

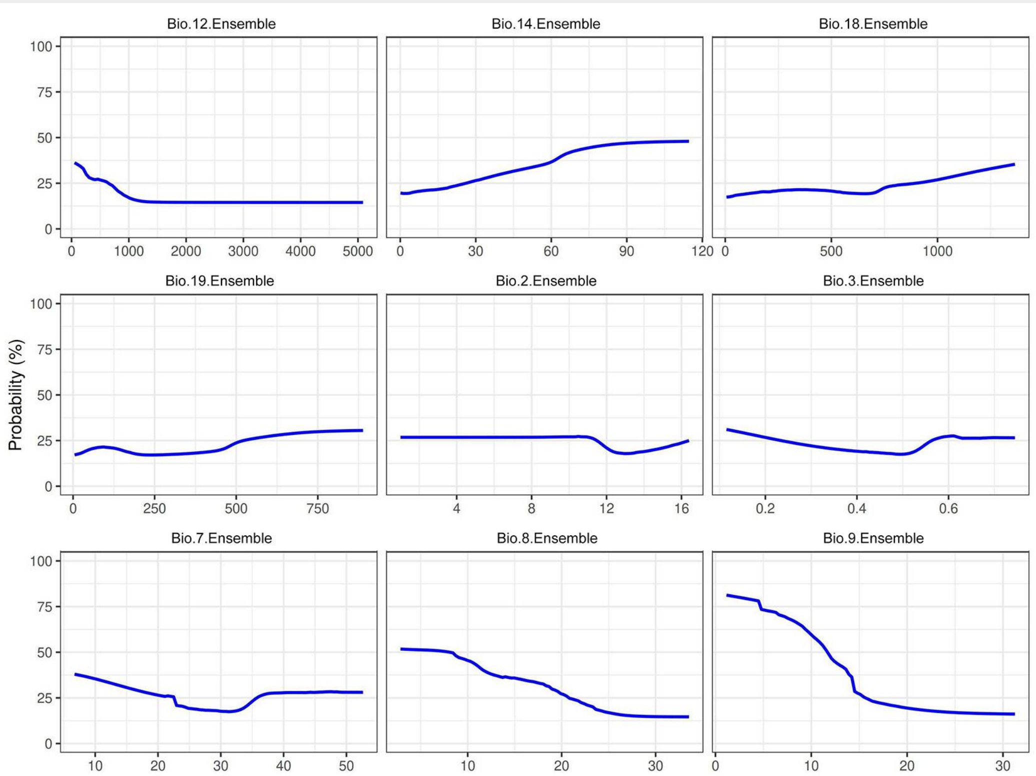

Fig. 1 - Response curve of the EMwmean for Bio 12 (annual precipitation), Bio 14 (precipitation of driest month), Bio 18 (precipitation of warmest quarter), Bio 19 (precipitation of coldest quarter), Bio 2 (mean diurnal range), Bio 3 (isothermality), Bio 7 (temperature annual range), Bio 8 (mean temperature of wettest quarter) and Bio 9 (mean temperature of driest quarter).

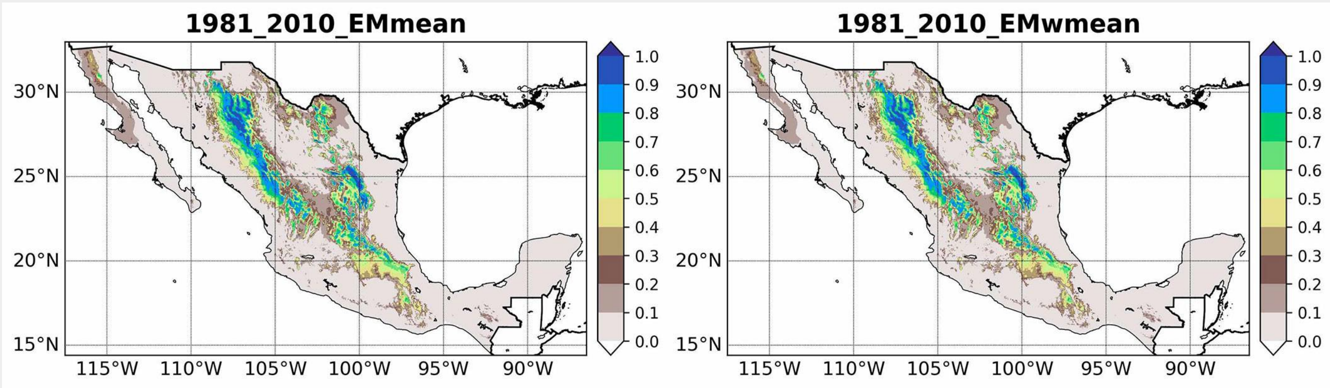

Fig. 2 - Current potential distribution of *P. cembroides* based on ensemble predictions derived from committee averaging (EMmean) and weighted mean (EMwmean) methods.

Bio 14 (precipitation of the driest month, 0.043), Bio 18 (precipitation of the warmest quarter, 0.026), and Bio 19 (precipitation of the coldest quarter, 0.045). These results confirm that seasonal temperature extremes and variability (Bio 3, Bio 7, Bio 8, and Bio 9) primarily determine the distribution of *P. cembroides*, whereas precipitation variables play a subordinate role.

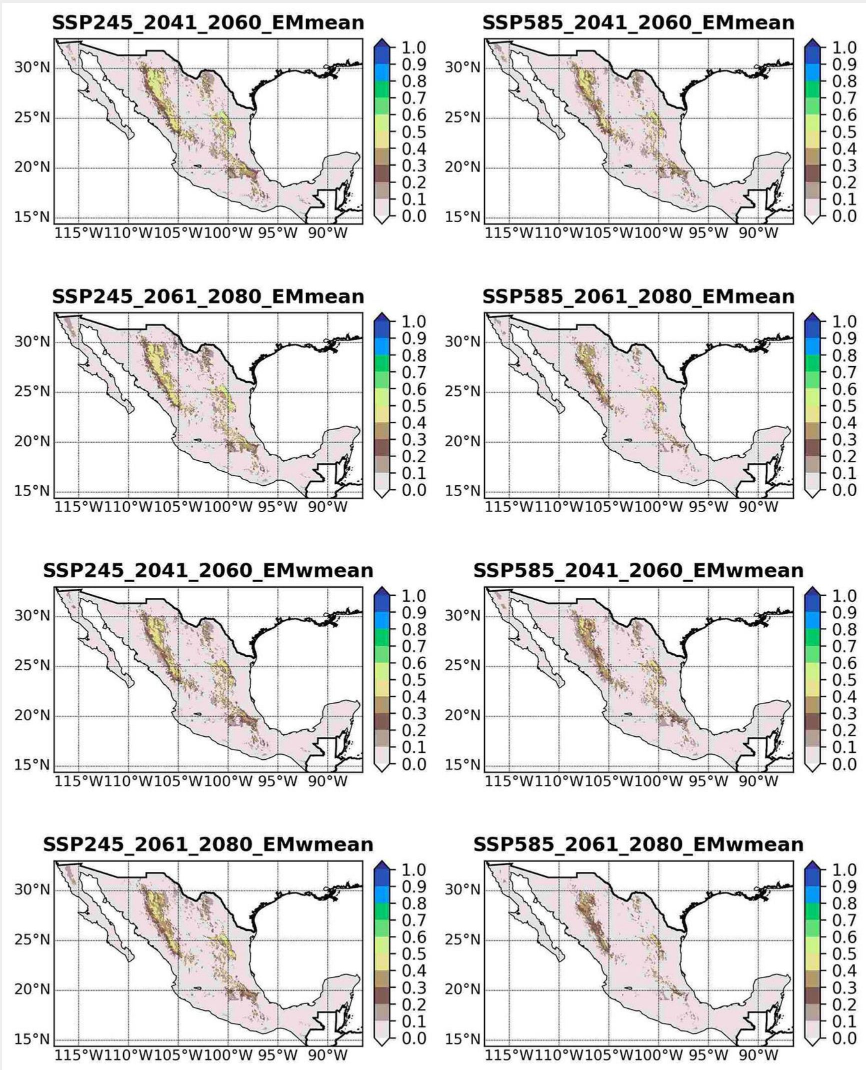

Fig. 3 - Projected future distribution of *P. cembroides* under climate change scenarios SSP245 and SSP585 for the periods 2041-2060 and 2061-2080, based on ensemble predictions derived from committee averaging (EMmean) and weighted mean (EMwmean) methods.

Response curves

Seasonal temperature extremes (Bio 2, Bio 3, Bio 7, Bio 8, and Bio 9) primarily limit the suitability of *P. cembroides*. Suitability declines sharply for the mean temperature of the wettest quarter (Bio 8) and the driest quarter (Bio 9) above 20 °C. Still, it remains at or above 0.6 between 15 °C and 20 °C (Fig. 1). We also observed moderate effects of isothermality (Bio 3) and annual temperature range (Bio 7), with suitability falling once Bio 7 exceeds roughly 25-30 °C.

In contrast, precipitation predictors have a secondary influence. Habitat suitability persists under the semi-arid regimes typical of the species' range and declines only modestly with reductions in annual or seasonal precipitation. These findings demonstrate that, despite its drought tolerance, *P. cembroides* remains vulnerable to elevated temperatures and reduced moisture, factors likely to constrain its distribution under future warming scenarios.

Current and future distribution

Under current climate conditions (1981-2010), the ensemble models EMmean and EMwmean identify *P. cembroides* primarily in mountainous regions (Fig. 2). Both approaches consistently indicate high suitability in the Sierra Madre Oriental and Sierra Madre Occidental, in particular, in the regions of Chihuahua, Durango, and Nuevo León, and along the Trans-Mexican Volcanic Belt. Total suitable area is estimated at 5.4×10^5 km^2 for EMmean and 5.2×10^5 km^2 for EMwmean. Although EMwmean extends slightly further into the southwestern Sierra Madre Occidental, both models converge on these mountain ranges as key refugia.

Under SSP245 (2041-2060), high-elevation areas retain moderate to high suitability (HIS ≥ 0.6) but occur in more fragmented patches than during the baseline period (Fig. 3). By 2061-2080, continuity of suitable habitat declines further, particularly in the central Sierra Madre Occidental, where areas with HIS ≥ 0.8 shrink sharply. Under the more extreme SSP585 scenario, losses intensify, and by 2061-2080, only isolated pockets of moderate suitability (HIS = 0.4-0.6) persist across northern and central Mexico. Although EMwmean occasionally predicts slightly larger clusters of moderate suitability, both ensembles agree on a pronounced contraction in the range.

Range-change statistics (Tab. 4) reveal severe losses under all scenarios. For 2041-2060, EMmean projects a 65.6% decline under SSP245 and 74.1% under SSP585; EMwmean estimates losses of 67.8% and 76.7%, respectively. The most extreme contractions occur during 2061-2080 under SSP585, with projected losses of 84.6% (EMmean) and 85.9% (EMwmean). No scenario predicts net habitat gain. These changes are particularly pronounced in northern Mexico, along both the Sierra Madre Oriental and Sierra Madre Occidental, where the current range is projected to decline significantly.

Fig. 4 shows that the stable category is most extensive between 22° and 26 °N and at elevations of 1500-2500 m a.s.l. Habitat gains remain marginal, accounting for less than 5% of the landscape, and are restricted to latitudes below 20° N and mid-elevations (1000-1500 m). Under SSP245 (2041-2060), approximately 25% of stable habitat is lost, whereas under SSP585 (2061-2080) losses exceed 50%, reflecting a pronounced contraction of the species' current range.

Tab. 4 - Summary of the range change statistics (in 10^5 km^2) for *P. cembroides* under SSP245 and SSP585 scenarios in 2041-2060 and 2061-2080.

Scenario	Ensemble	Loss	Stable	Gain	Loss (%)	Gain (%)	Change (%)
SSP245_2041_2060	EMmean	3.6	1.9	0.0	65.6	0.0	-65.6
SSP245_2041_2060	EMwmean	3.6	1.7	0.0	67.8	0.0	-67.8
SSP585_2041_2060	EMmean	4.0	1.4	0.0	74.1	0.0	-74.1
SSP585_2041_2060	EMwmean	4.0	1.2	0.0	76.7	0.0	-76.7
SSP245_2061_2080	EMmean	3.7	1.8	0.0	67.5	0.0	-67.4
SSP245_2061_2080	EMwmean	3.7	1.6	0.0	70.6	0.0	-70.6
SSP585_2061_2080	EMmean	4.6	0.8	0.0	84.6	0.0	-84.6
SSP585_2061_2080	EMwmean	4.5	0.7	0.0	85.9	0.0	-85.9

Discussion

Ensemble modeling and model performance

SDMs are essential tools for understanding the biogeographic patterns and potential future ranges of forest species, particularly under scenarios of rapid climate change (Elith & Franklin 2013). In Mexico, SDMs for *Pinus* have often relied on a single algorithm, such as MAXENT (Phillips et al. 2006), due to its strong performance with presence-only data (Cruz-Cárdenas et al. 2016, Martínez-Sifuentes et al. 2020). Nonetheless, predictions generated from individual models are vulnerable to algorithmic biases, which can lead to an underestimation of overall model uncertainty (Araújo et al. 2019).

Our study demonstrates that the ensemble framework implemented in BIOMOD2 (Thuiller et al. 2025) yields robust and consistent projections by integrating multiple SDMs and GCMs. Averaging or weighting these projections effectively captures intermodel variability, thereby refining final habitat suitability maps (Goberville et al. 2015, Thuiller et al. 2019).

The consensus models achieved high evaluation metrics, with TSS values of 0.775 and 0.777 and AUC values of 0.945 and 0.949 for EMmean and EMwmean, respectively. These results are consistent with previous studies employing similar multi-model frameworks (Montoya-Jiménez et al. 2022). Among individual models, MAXENT, GLM, GBM, and RF showed the highest predictive performance, whereas SRE, CTA, and FDA consistently underperformed in terms of TSS, AUC, and pAUC metrics (Kaky et al. 2020, Khan & Verma 2022, Montoya-Jiménez et al. 2022).

Although ensemble approaches do not consistently yield improved predictive accuracy, our results underscore their value for species with narrow ecological tolerances, where even minor prediction errors can undermine conservation outcomes (Araújo & Guisan 2006).

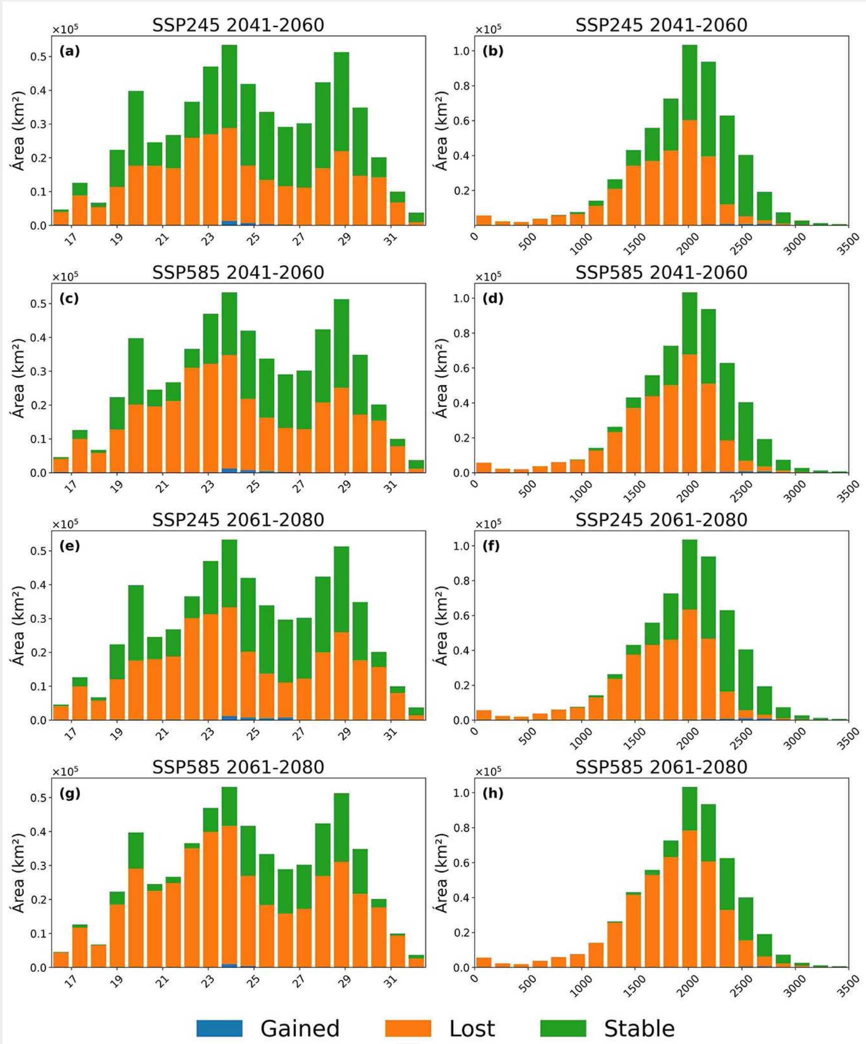

Fig. 4 - Latitudinal and elevational distributions of potential habitat area for *P. cembroides*, showing area gained (blue), lost (orange), and stable (green) under SSP245 and SSP585 scenarios for 2041-2060 (top two rows) and 2061-2080 (bottom two rows) for EMmean (a-d) and EMwmean (e-h).

Environmental predictors

Seasonal temperature extremes emerged as the primary drivers of *P. cembroides* suitability. Bio 8 (mean temperature of the wettest quarter) and Bio 9 (mean temperature of the driest quarter) together accounted for the largest share of the variation in our ensemble models. This result is consistent with studies on Mexican conifers (Aceves-Rangel et al. 2018, García-Aranda et al. 2018, Gómez-Pineda et al. 2020, Martínez-Sánchez et al. 2023), which also emphasize the key role of seasonal temperature variability in defining distributional limits.

Habitat suitability declined markedly when mean temperatures in the wet and dry quarters exceeded 20 °C, indicating thermal thresholds that delimit the climatic niche of *P. cembroides*. In contrast, precipitation variables exerted only marginal effects on suitability, indicating that, despite their tolerance of semi-arid regimes, temperature extremes impose a greater constraint than moisture availability. This finding aligns with previous studies demonstrating that seasonal temperature variability exerts a more decisive influence than precipitation in determining pine distributions (Aceves-Rangel et al. 2018).

Although macroclimatic drivers govern distribution patterns at broad spatial scales, local edaphic factors, such as soil depth, aspect, and nutrient availability, become critical at finer resolutions by modulating microclimatic conditions in heterogeneous landscapes.

Future distribution

Climate change poses a significant threat to coniferous forests in topographically complex regions such as Mexico. Previous projections based on WorldClim and CMIP5 scenarios indicated moderate to substantial habitat contraction for temperate, tropical, and semi-arid species (Gómez-Díaz et al. 2011, Cruz-Cárdenas et al. 2016).

Our study employed high-resolution CHELSA v. 2.1 data and updated CMIP6 Shared Socioeconomic Pathway scenarios, predicting a 65%-85% reduction in suitable habitat for *P. cembroides* by 2080-2100. Losses are most severe under SSP585, which is characterized by elevated greenhouse gas emissions and intensified warming (Almazroui et al. 2021). These contractions suggest that remaining populations will be confined to fragmented, high-elevation refugia in the Sierra Madre ranges. Although local microclimates may allow persistence or even limited expansion in some areas (Romero-Sánchez et al. 2017), at regional to national scales, *P. cembroides* is expected to contract to elevations of 1500-2500 m and latitudes of 22°-26° N (Romero-Sánchez et al. 2017, Bower et al. 2024). Projected altitudinal shifts of 300-500 m and habitat reductions of 60%-75% have been reported for *Pinus hartwegii* and *Abies religiosa* (Alfaro-Ramírez et al. 2020, Martínez-Sifuentes et al. 2020). *Pseudotsuga menziesii* may lose over 80% of its Mexican range, persisting only in isolated high-elevation refugia (Martínez-Sifuentes et al. 2020). In contrast, *Pinus oocarpa* could gain a modestly novel habitat (Gómez-Pineda et al. 2020). These patterns demonstrate the importance of elevational connectivity and assisted migration for conserving genetic diversity under future warming, and highlight the role of scale-dependent processes in species distribution modelling.

Conservation implications and future research

The projected contraction of *P. cembroides* habitat under high-emission scenarios presents critical conservation challenges. Range reduction will exacerbate fragmentation and erode genetic diversity, a vulnerability already documented in Mexican conifer populations under climate-induced stress (Sáenz-Romero et al. 2012).

Assisted migration facilitates the translocation of vulnerable populations into regions projected to remain climatically suitable (Gustafson et al. 2023). Establishing ecological corridors further enhances connectivity among isolated stands, mitigating demographic risks associated with small populations.

Our emphasis on macroclimatic drivers underscores the importance of incorporating non-climatic factors into future Species Distribution Models (SDMs), including land-use change, soil properties, and species-specific biotic interactions (Santos-Hernández et al. 2021). Such integrated models would produce more realistic projections, ultimately guiding more effective conservation interventions.

As occurrence records and high-resolution climate projections continue to improve, ongoing model recalibration will support adaptive forest management. This iterative framework will inform prioritization efforts and help secure the long-term persistence of *P. cembroides* and Mexico's pine ecosystems under intensifying climatic stressors.

Conclusions

This study employed SSP245 and SSP585 projections from CHELSA v. 2.1 within a BIOMOD2 ensemble framework to assess the future distribution of *P. cembroides*. Both ensemble approaches (EMmean and EMwmean) and MAXENT consistently demonstrated high predictive accuracy, reinforcing their effectiveness in modeling semi-arid-adapted species.

Although the species exhibits considerable resilience, *P. cembroides* is anticipated to experience a marked range contraction with an estimated 65%-85% loss of its current habitat by the end of the century. High-elevation refugia are likely to remain climatically suitable, while the potential for new habitat emergence is minimal. These results highlight urgent conservation priorities. The severe loss and fragmentation of suitable areas will likely diminish genetic diversity and limit adaptive capacity. Proactive measures are essential, including assisted migration to more humid lowlands, protection of montane refugia, and establishment of ecological corridors to maintain connectivity. Overall, this study demonstrates the utility of ensemble SDMs for capturing climate-driven range dynamics and emphasizes the critical need for adaptive management strategies to mitigate the rapid impacts of climate change on *P. cembroides.*

Acknowledgements

JNM-S and GC-R thank SECIHTI (*Secretaría de Ciencia, Humanidades, Tecnología e Innovación*, Mexico City, MX) for the scholarships granted.

References

Aceves-Rangel LD, Méndez-González J, García-Aranda MA, Nájera-Luna JA (2018). Distribución potencial de 20 especies de pinos en México [Potential distribution of 20 pine species in Mexico]. Agrociencia 52: 1043-1057. [in Spanish]

Ahmad R, Khuroo AA, Charles B, Hamid M, Rashid I, Aravind NA (2019). Global distribution modelling, invasion risk assessment and niche dynamics of *Leucanthemum vulgare* (Ox-eye Daisy) under climate change. Scientific Reports 9: 476-485. - doi: 10.1038/s41598-019-47859-1

Alfaro-Ramírez FU, Ramírez-Albores JE, Vargas-Hernández JJ, Franco-Maass S, Pérez-Suárez M (2020). Potential reduction of Hartweg's pine (*Pinus hartwegii* Lindl.) geographic distribution. PLoS One 15 (2): e0229178. - doi: 10.1371/journal.pone.0229178

Allouche O, Tsoar A, Kadmon R (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43: 1223-1232. - doi: 10.1111/j.1365-2664.2006.01214.x

Almazroui M, Islam MN, Saeed F, Saeed S, Ismail M, Ehsan MA, Diallo I, O'Brien E, Ashfaq M, Martínez-Castro D, Cavazos T, Cerezo-Mota R, Tippett MK, Gutowski Jr WJ, Alfaro EJ, Hidalgo HG, Vichot-Llano A, Campbell JD, Kamil S, Rashid IU, Sylla MB, Stephenson T, Taylor M, Barlow M (2021). Projected changes in temperature and precipitation over the United States, Central America, and the Caribbean in CMIP6 GCMs. Earth Systems and Environment 5: 1-24. - doi: 10.1007/s41748-021-00199-5

Anderegg WR, Trugman AT, Badgley G, Anderson CM, Bartuska A, Ciais P, Cullenward D, Field CB, Freeman J, Goetz SJ, Hicke JA, Huntzinger D, Jackson RB, Nickerson J, Pacala S, Randerson JT (2020). Climate-driven risks to the climate mitigation potential of forests. Science 367 (6485): 1027-1031. - doi: 10.1126/science.aaz7005

Araújo MB, Guisan A (2006). Five (or so) challenges for species distribution modelling. Journal of Biogeography 33: 1677-1688. - doi: 10.1111/j.1365-2699.2006.01584.x

Araújo MB, Anderson RP, Barbosa AM, Beale CM, Dormann CF, Early R, Garcia RA, Guisan A, Maiorano L, Naimi B, O'Hara RB, Zimmermann NE, Rahbek C (2019). Standards for distribution models in biodiversity assessments. Science Advances 5: eaat4858. - doi: 10.1126/sciadv.aa t4858

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012). Impacts of climate change on the future of biodiversity. Ecology Letters 15 (4): 365-377. - doi: 10.1111/j.1461-0248.2011.01736.x

Bower AD, Frerker KL, Pike CC, Labonte NR, Palik BJ, Royo AA, Anderson SM, Ferreira AR, Brandt LA (2024). A practical framework for applied forestry assisted migration. Frontiers in Forests and Global Change 7: 1454329. - doi: 10.3389/ffgc.2024.1454329

Breiman L (2001). Random forests. Machine Learning 45: 5-32. - doi: 10.1023/A:1010933404324

Busby JR (1991). BIOCLIM - a bioclimate analysis and prediction system. In: "Nature Conservation: Cost Effective Biological Surveys and Data Analysis" (Margules CR, Austin MP eds). CSIRO, Melbourne, Australia, pp. 64-68.

Cavazos T, Luna-Niño R, Cerezo-Mota R, Fuentes-Franco R, Méndez M, Pineda-Martínez LF, Valenzuela E (2020). Climatic trends and regional climate models intercomparison over the CORDEX-CAM (Central America, Caribbean, and Mexico) domain. International Journal of Climatology 40: 1396-1420. - doi: 10.1002/joc.6276

CONABIO (2020). Sistema Nacional de Información sobre Biodiversidad. Registros de ejemplares [National Information System on Biodiversity. Specimen Records]. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad – CONABIO, Ciudad de México, México, website. [in Spanish] [online] URL: http://www.snib.mx/ejemplares/descarga/

Constante-García V, Villanueva-Díaz J, Cerano-Paredes J, Cornejo-Oviedo EH, Valencia-Manzo S (2009). Dendrocronología de *Pinus cembroides* Zucc. y reconstrucción de precipitación estacional para el sureste de Coahuila [Dendrocronology of *Pinus cembroides* Zucc. and reconstruction of seasonal precipitation for southern Coahuila]. Revista Mexicana de Ciencias Forestales 34: 17-39. [in Spanish]

Cruz-Cárdenas G, López-Mata L, Silva JT, Bernal-Santana N, Estrada-Godoy F, López-Sandoval JA (2016). Potential distribution model of Pinaceae species under climate change scenarios in Michoacán. Revista Chapingo Serie Ciencias Forestales y del Ambiente 22: 135-148. - doi: 10.5154/r.rchscfa.2015.06.027

Elith J, Ferrier S, Huettmann F, Leathwick J (2005). The evaluation strip: a new and robust method for plotting predicted responses from species distribution models. Ecological Modelling 186: 280-289. - doi: 10.1016/j.ecolmodel.2004.12.007

Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Huettmann JJ, Leathwick JR, Lehmann S, Li F, Loiselle SA (2006). Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129-151. - doi: 10.1111/j.2006.0906-7590.04596.x

Elith J, Franklin J (2013). Species distribution modelling. In: "Encyclopedia of Biodiversity" (Levin S ed). Academic Press, Waltham, MA, pp. 692-705.

Eyring V, Bony S, Meehl GA, Senior CA, Stevens B, Stouffer RJ, Taylor KE (2016). Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. Geoscientific Model Development 9: 1937-1958. - doi: 10.5194/gmd-9-1937-2016

Fielding AH, Bell JF (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24: 38-49. - doi: 10.1017/S0376892997000088

García-Aranda MA, Méndez-González J, Hernández-Arizmendi JY (2018). Potential distribution of *Pinus cembroides*, *Pinus nelsonii* and *Pinus culminicola* in northeastern Mexico. Ecosistemas y Recursos Agropecuarios 5: 3-13. - doi: 10.19136/era.a5n13.1396

Goberville E, Beaugrand G, Hautekete C, Piquot Y, Luczak C (2015). Uncertainties in the projection of species distributions related to general circulation models. Ecology and Evolution 5 (5): 1100-1116. - doi: 10.1002/ece3.1411

Gómez-Díaz JD, Monterroso-Rivas AI, Tinoco-Rueda JA, Toledo-Medrano ML, Conde-Alvarez C, Gay-García C (2011). Assessing current and potential patterns of 16 forest species driven by climate change scenarios in México. Atmósfera 24: 31-52.

Gómez-Pineda E, Sáenz-Romero C, Ortega-Rodríguez JM, Blanco-García A, Madrigal-Sánchez X, Lindig-Cisneros R, Lopez-Toledo L, Pedraza-Santos ME, Rehfeldt GE (2020). Suitable climatic habitat changes for Mexican conifers along altitudinal gradients under climatic change scenarios. Ecological Applications 30 (2): e02041. - doi: 10.1002/eap.2041

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AI, Regan TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C, Martin TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney MR, Possingham HP, Buckley YM (2013). Predicting species distributions for conservation decisions. Ecological Letters 16 (12): 1424-1435. - doi: 10.1111/ele.12189

Guisan A, Thuiller W, Zimmermann NE (2017). Habitat suitability and distribution models with applications in R. Cambridge University Press, Cambridge, UK, pp. 462. [online] URL: http://books.google.com/books?id=rYswDwAAQBAJ

Gustafson EJ, Kern CC, Kabrick JM (2023). Can assisted tree migration today sustain forest ecosystem goods and services for the future? Forest Ecology and Management 529: 120723. - doi: 10.1016/j.foreco.2022.120723

Harris I, Jones PD, Osborn TJ, Lister DH (2014). Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 dataset. International Journal of Climatology 34 (3): 623-642. - doi: 10.1002/joc.3711

Hartmann H, Bastos A, Das AJ, Esquivel-Muelbert A, Hammond WM, Martínez-Vilalta J, McDowell NG, Powers JS, Pugh TAM, Ruthrof KX, Allen CD (2022). Climate change risks to global forest health: emergence of unexpected events of elevated tree mortality worldwide. Annual Review of Plant Biology 73: 673-702. - doi: 10.1146/annurev-arplant-102820-012804

Hastie TJ, Tibshirani RJ (1990). Generalized additive models. Chapman and Hall, New York, USA, pp. 352.

Hastie T, Tibshirani R, Buja A (1994). Flexible discriminant analysis by optimal scoring. Journal of the American Statistical Association 89: 1255-1270. - doi: 10.1080/01621459.1994.10476866

Herrera-Soto G, González-Cásares M, Pompa-García M, Camarero JJ, Solís-Moreno R (2018). Growth of Pinus cembroides Zucc. in response to hydroclimatic variability in four sites forming the species latitudinal and longitudinal distribution limits. Forests 9 (7): 440. - doi: 10.3390/f9070440

Huang Y, Li T, Chen W, Zhang Y, Xu Y, Guo T, Wang S, Liu J, Qin Y (2024). Analysis of the distribution pattern of *Phenacoccus manihoti* in China under climate change based on the BIOMOD2 model. Biology 13 (7): 538. - doi: 10.3390/biology13070538

Kaky E, Nolan V, Alatawi A, Gilbert F (2020). A comparison between ensemble and MaxEnt species distribution modelling approaches for conservation: a case study with Egyptian medicinal plants. Ecological Informatics 60: 101150. - doi: 10.1016/j.ecoinf.2020.101150

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Wilber R, Zimmermann NE, Linder HP, Kessler M (2017). Climatologies at high resolution for the Earth's land surface areas. Scientific Data 4 (1): 1-20. - doi: 10.1038/sdata.2017.122

Karger DN, Chauvier Y, Zimmermann NE (2023). Chelsa-cmip6 1.0: a Python package to create high-resolution bioclimatic variables based on CHELSA Ver. 2. 1 and CMIP6 Data. Ecography 2023 (6): e06535.

Khan S, Verma S (2022). Ensemble modeling to predict the impact of future climate change on the global distribution of Olea europaea subsp. cuspidata. Frontiers in Forests and Global Change 5: 977691. - doi: 10.3389/ffgc.2022.977691

Knutti R, Sedláček J, Sanderson BM, Lorenz R, Fischer EM, Eyring V (2017). A climate model projection weighting scheme accounting for performance and interdependence. Geophysical Research Letters 24: 4529-4538. - doi: 10.1002/2016GL072012

Lobo JM, Jiménez-Valverde A, Real R (2008). AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17 (2): 145-151. - doi: 10.1111/j.1466-8238.2007.00358.x

Manzanilla-Quijada GE, Osuna-Vallejo V, Zacarías-Correa AG, Gómez-Pineda E, Gallardo-Salazar JL, Sáenz-Romero C (2024). Zonas de transferencia de semillas para la reforestación en la Reserva de la Biosfera Mariposa Monarca y la Meseta Purépecha ante el cambio climático [Seed transfer zones for reforestation in the Monarch Butterfly Biosphere Reserve and the Meseta Purépecha facing climate change]. Revista Chapingo Serie Ciencias Forestales y del Ambiente 30 (2): 1-21. [in Spanish] - doi: 10.5154/r.rchscfa.2023.11.056

Martínez-Sánchez JN, Cuéllar Rodríguez LG, Yerena Yamallel JI, Cavazos Pérez MT, Gárate Escamilla HA (2023). Comparación de bases de datos climáticos en la modelación de distribución potencial de *Pinus cembroides* Zucc. [Comparison of climatic databases in modeling the potential distribution of Pinus cembroides Zucc.]. Revista Mexicana de Ciencias Forestales 14 (79): 135-158. [in Spanish] - doi: 10.29298/rmcf. v14i79.1350

Martínez-Sifuentes AR, Villanueva-Díaz J, Manzanilla-Quiñones U, Becerra-López JL, Hernández-Herrera JA, Estrada-Avalos J, Velázquez-Pérez AH (2020). Spatial modeling of the ecological niche of *Pinus greggii* Engelm. (Pinaceae): a species conservation proposal in Mexico under climatic change scenarios. iForest 13: 426-434. - doi: 10.3832/ifor3491-013

McCullagh P, Nelder JA (1989). Generalized linear models (2nd edn). Chapman and Hall, London, UK, pp. 532.

Montoya-Jiménez JC, Valdez-Lazalde JR, Angeles-Perez G, De Los Santos-Posadas HM, Cruz-Cárdenas G (2022). Predictive capacity of nine algorithms and an ensemble model to determine the geographic distribution of tree species. iForest 15: 363-371. - doi: 10.3832/ifor4084-015

Murray-Tortarolo GN (2021). Seven decades of climate change across Mexico. Atmósfera 34 (2): 217-226. - doi: 10.20937/ATM.52803

Pearson RG, Dawson TP (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12(5): 361-371. - doi: 10.1046/j.1466-822X.2003.00042.x

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen C, Clark TD, Colwell RK, Danielsen F, Evengård B, Falconi L, Ferrier S, Frusher S, Garcia RA, Griffis RB, Hobday AJ, Janion-Scheepers C, Jarzyna MA, Jennings S, Williams SE (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 355 (6332): eaai9214. - doi: 10.1126/science.aai9214

Peterson AT, Papeş M, Soberón J. (2008). Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecological Modelling 213: 63-72. - doi: 10.1016/j.ecolmodel.2007.11.008

Phillips SJ, Anderson RP, Schapire RE (2006). Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231-259. - doi: 10.1016/j.ecolmodel.2005.03.026

R Core Team (2020). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [online] URL: http://www.r-project.org/

Ripley BD (1996). Pattern recognition and neural networks. Cambridge University Press, Cambridge, UK, pp. 403.

Romero-Sánchez ME, González-Hernández A, Pérez-Miranda R, Velasco-Bautista E, Moreno-Sánchez F (2017). Efecto del cambio climático a nivel local en la distribución potencial de cuatro especies de la cuenca Río Bravo-San Juan, Coahuila, México [Effect of climate change at local level on the potential distribution of four forest species in the Río Bravo-San Juan Basin, Coahuila, México]. Agroproductividad 10: 42-47. [in Spanish]

Ridgeway G (1999). The state of boosting. Computing Science and Statistics 31: 172-181.

Rzedowski J (1978). Vegetación de México [Vegetation of Mexico]. Limusa, Ciudad de México, MX, pp. 432. [in Spanish]

Sáenz-Romero C, Rehfeldt GE, Duval P, Lindig-Cisneros RA (2012). *Abies religiosa* habitat prediction in climatic change scenarios and implications for monarch butterfly conservation in Mexico. Forest Ecology and Management 275: 98-106. - doi: 10.1016/j.foreco.2012.03.004

Sáenz-Romero C, Lamy JB, Ducousso A, Musch B, Ehrenmann F, Delzon S, Cavers S, Chalupka W, Dagdas S, Hansen JK, Lee SJ, Liesebach M, Rau HM, Psomas A, Schneck V, Steiner W, Zimmermann NE, Kremer A (2017). Adaptive and plastic responses of *Quercus petraea* populations to climate across Europe. Global Change Biology 23 (7): 2831-2847. - doi: 10.1111/gcb.13576

Santos-Hernández AF, Monterroso-Rivas AI, Granados-Sánchez D, Villanueva-Morales A, Santacruz-Carrillo M (2021). Projections for Mexico's tropical rainforests considering ecological niche and climate change. Forests 12: 119. - doi: 10.3390/f12020119

Sun Y, Zhang H, Jiang K, Xiang D, Shi Y, Huang S, Li Y, Han H (2024). Simulating the changes of habitat suitability of chub mackerel (*Scomber japonicus*) in the high seas of the North Pacific Ocean using ensemble models under medium to long-term future climate scenarios. Marine Pollution Bulletin 207: 116873. - doi: 10.1016/j.marpolbul.2024.116873

Thuiller W, Guéguen M, Renaud J, Karger DN, Zimmermann NE (2019). Uncertainty in ensembles of global biodiversity scenarios. Nature Communications 10 (1): 1-9. - doi: 10.1038/s41467-019-09519-w

Thuiller W, Georges D, Gueguen M, Engler R, Breiner F, Lafourcade B, Patin R, Blancheteau H (2025). BIOMOD2: ensemble platform for species distribution modeling. CRAN, R package version 42:6-2, website. [online] URL: http://CRAN.R-project.org/package=biomod2

Valavi R, Guillera-Arroita G, Lahoz-Monfort JJ, Elith J (2022). Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. Ecological Monographs 92 (1): e01486. - doi: 10.1002/ecm.1486

Zamora-Maldonado HC, Avila-Foucat VS, Sánchez-Sotomayor VG (2025). Modeling climate change impacts on the potential distribution of bighorn sheep in Mexico. Frontiers in Climate 7: 1386632. - doi: 10.3389/fclim.2025.1386632