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Research article

Sequence in the distribution of mistletoe under climate change: *Laxaxalpan* River sub-basin, state of *Puebla*
Secuencia en la distribución de muérdago enano ante el cambio climático: subcuenca Río *Laxaxalpan*, *Puebla*

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Abstract

Parasitic plants are a contributing factor to the decline in forest health, and their distribution has expanded in recent years due to climate change. The objective of this study was to determine the distribution of current and future suitability, under climate change scenarios, of *Arceuthobium globosum* in temperate forests of the *Laxaxalpan* River sub-basin, state of *Puebla*, Mexico. The MaxEnt algorithm was used, and model performance was evaluated using the *AUC* and partial *ROC* indices for the current period. The General Circulation Models (GCMs) CanESM5-CanOE and GFDL-ESM4 were also considered under the SSP126 and SSP370 scenarios for the period 2041-2060. *Chi*-square tests with Monte Carlo simulation were applied to evaluate changes in suitability categories. The current distribution showed a predominance of areas with low and no suitability for mistletoe. Overall, climate change scenarios indicated an increase in areas with no suitability and the disappearance of those with high suitability, while the areas with medium and low suitability decreased significantly. The *chi*-square analysis showed a significant reduction in medium and high suitability areas, with a transition to low and no suitability categories. The results suggest that future climatic conditions in the study area will no longer be suitable for the distribution of dwarf mistletoe, highlighting the high sensitivity of this parasitic species to climate change.

Keywords: *Arceuthobium globosum* Hawksw. & Wiens, suitable areas, temperate forest, climate change, pines, parasitic plants.

Resumen

Las plantas parásitas constituyen un factor de deterioro para la salud de los bosques, y en los últimos años su distribución se ha extendido debido a las alteraciones climáticas. El objetivo del presente estudio fue determinar la distribución de la idoneidad actual y futura, bajo escenarios de cambio climático, de *Arceuthobium globosum* en bosques de templados de la subcuenca río Laxaxalpan, Puebla, México. Se utilizó el algoritmo *MaxEnt* y se evaluó el desempeño del modelo mediante los índices *AUC* y *ROC* parcial para el periodo actual. Asimismo, se consideraron los Modelos de Circulación General (MCG): CanESM5-CanOE y GFDL-ESM4 bajo los escenarios SSP126 y SSP370 para el periodo 2041-2060. Se aplicaron pruebas de X^2 con simulación de Monte Carlo para evaluar los cambios en las categorías de idoneidad. La distribución actual mostró una predominancia de áreas con idoneidad baja y nula para el muérdago. En general, los escenarios de cambio climático indicaron un aumento de las áreas con idoneidad nula y la desaparición de las altas, mientras que la superficie con idoneidad media y baja se redujeron significativamente. El análisis X^2 mostró una reducción significativa de las áreas media y alta, con transición hacia las categorías baja y nula. Los resultados sugieren que las condiciones climáticas futuras en el área de estudio dejarán de ser idóneas para la distribución del muérdago enano, lo que evidencia la alta sensibilidad de esta especie parásita ante el cambio climático.

Palabras clave: *Arceuthobium globosum* Hawksw. & Wiens, áreas idóneas, bosque templado, cambio climático, pinos, plantas parásitas.

Introduction

Pests affect both plants and animals (Secretaría de la Convención Internacional de Protección Fitosanitaria [CIPF]; 2018). In the forestry sector, a pest is defined as a living organism capable of causing damage to trees, forests, or forest products. These include insects, spiders, nematodes, fungi, bacteria, viruses, herbaceous plants, mammals, birds, parasitic plants, and other organisms (Nair, 2007). In Mexico, the area affected by pests in 2024 was 87 645 ha, distributed among the causal agents of damage caused by: parasitic plants (66.4 %), bark beetles (19.2 %), defoliating insects (9.0 %), bark beetles (2.2 %), diseases (2.0 %), and other pests (1.2 %) (Comisión Nacional Forestal [Conafor], 2025). Among the main effects caused by these pests are reduced growth, weakening, and death of the plant; they also facilitate attacks by other biotic agents.

Climate change is one of the main factors influencing the fluctuation and geographic redistribution of populations (Cambrón-Sandoval et al., 2018), since modifications

in temperature and precipitation patterns alter plant metabolic processes, generate physiological stress, and favor the development of pests. Therefore, it is important to determine the risk level of these pathogens, especially for the implementation of mitigation measures.

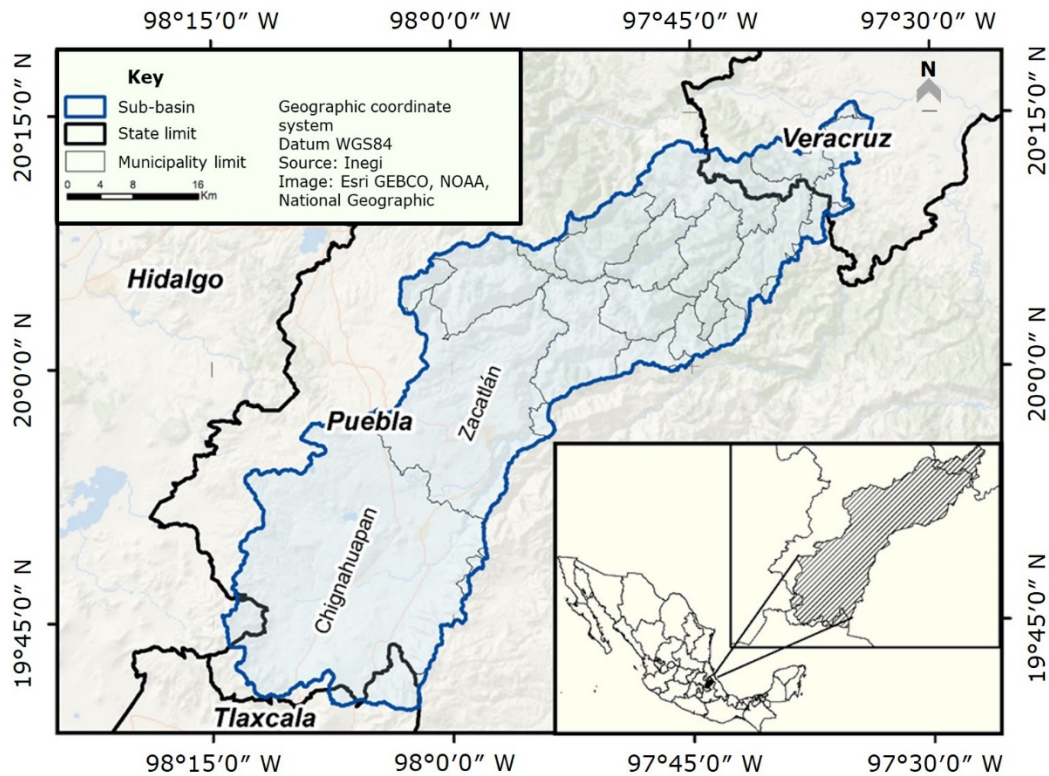
The *Laxaxalpan* River sub-basin, located in the *Sierra Norte* of *Puebla*, is of forestry and hydrological importance. However, as in most of the country's forest ecosystems, pine forests have been affected by various pests, including bark beetles (Curculionidae) and parasitic plants (Santalaceae) (Cibrián-Tovar, 2011). Dwarf mistletoe, *Arceuthobium globosum* subsp. *grandicaule* Hawksw. & Wiens, occurs on 14 pine species; it is one of the most widespread parasitic plants in Mexico and primarily affects the growth and commercial value of wood (Cibrián-Tovar *et al.*, 2007). Its life cycle is similar to other species, comprising a prolonged endophytic phase within the tree tissue and a short aerial phase, in which it develops reproductive structures. The shoots can be green or yellow, averaging 18 to 50 cm in length, but can reach up to 70 cm in height. It obtains water and minerals from its host through specialized structures called haustoria (Cibrián-Tovar *et al.*, 2007).

In this context, monitoring forest health becomes essential for the prevention and control of potential mass infestations. The application of species distribution models is fundamental for identifying areas at risk of pest presence, for developing monitoring and management strategies, and thus contributing to the preservation of the health of forest ecosystems. Therefore, this study aimed to determine the current and future suitability distribution, under climate change scenarios, of *Arceuthobium globosum* Hawksw. & Wiens in temperate forests of the *Laxaxalpan* River sub-basin, state of *Puebla*, Mexico.

Materials and Methods

Study Area

The *Laxaxalpan* River sub-basin, located in the *Necaxa* and *Tecolutla* basins, lies between 20°15'34.567" and 19°39'54.631" N and 98°14'25.232" and 97°33'31.084" W. It primarily encompasses the *Sierra Norte* range of the state of *Puebla* and, to a lesser extent, the states of *Hidalgo*, *Tlaxcala* and *Veracruz*; it covers an area of 1 608.95 km² (Instituto Nacional de Estadística y Geografía [Inegi], 2018) (Figure 1).



Chignahuapan = *Chignahuapan* municipality; *Zacatlán* = *Zacatlán* municipality.
Sources: Inegi (2018) and Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Conabio, 2011).

Figure 1. Location map of the study area.

The sub-basin is located between the Trans-Mexican Volcanic Belt and the *Sierra Madre Oriental* physiographic provinces. It has an altitudinal range from 15 m in *Veracruz* to 3 489 m in *Puebla*. The terrain is primarily composed of mountains and hills, with a small proportion of plains (Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2001). The predominant climates are warm humid Am(f) and Af(m), semi-warm humid (A)C(fm), temperate humid C(m) and C(fm), temperate sub-humid C(w₁)(w) and C(w₂), semi-cold sub-humid C(E)(w₂)(w), and semi-cold sub-humid C(E)(w₂) (García & Conabio, 1998). The total annual precipitation of the sub-basin ranges from 2 600 to 3 500 mm, and the average annual temperature varies from 12 to 24 °C (García & Conabio, 1998). The predominant vegetation types are pine forests (*Pinus* spp.), pine-oak forests (*Pinus-Quercus*) and mountain mesophyll forests (Inegi, 2021).

Current predictive bioclimatic data and variables

Georeferenced presence records of *A. globosum* were integrated from phytosanitary technical reports and open access biodiversity repositories (Global Biodiversity Information Facility [GBIF], 2025; iNaturalist, 2024). Twenty-three predictor variables were used: 19 bioclimatic variables derived from temperature and precipitation data from historical climate data from the WorldClim platform (Fick & Hijmans, 2017), three topographic variables (altitude, aspect, and slope) generated from processing the Mexican Elevation Continuum (CEM) available from the Inegi platform (Inegi, 2023), and one Lang's humidity index (Álvarez, 1992) (Table 1). All land cover data were adjusted to the same resolution (approximately 926 m²), the geographic coordinate system, and the WGS 1984 datum. A statistical evaluation of the predictor variables was performed using Pearson's correlation analysis ($r \leq \pm 0.8$) (Manzanilla-Quñones *et al.*, 2019), in the Niche Toolbox module of RStudio® (Osorio-Olvera *et al.*, 2020).

Table 1. Bioclimatic variables from WorldClim.

Code	Bioclimatic variable	Units	Source
BIO1	Average annual temperature	°C	Fick and Hijmans (2017)
BIO2	Diurnal temperature range	°C	
BIO3	Isothermality $\left(\frac{BIO1}{BIO7} \times 100\right)$	-	
BIO4	Temperature seasonality	%	
BIO5	Maximum temperature of the warmest period	°C	
BIO6	Minimum temperature of the coldest period	°C	
BIO7	Annual temperature range ($BIO5 - BIO6$)	°C	
BIO8	Average temperature in the wettest quarter	°C	
BIO9	Average temperature in the driest quarter	°C	
BIO10	Average temperature in the warmest quarter	°C	
BIO11	Average temperature in the coldest quarter	°C	
BIO12	Annual precipitation	mm	
BIO13	Precipitation in the wettest period	mm	
BIO14	Precipitation in the driest period	mm	
BIO15	Precipitation seasonality	%	
BIO16	Precipitation in the wettest quarter	mm	
BIO17	Precipitation in the driest quarter	mm	
BIO18	Precipitation in the warmest quarter	mm	
BIO19	Precipitation in the coldest quarter	mm	
20	Altitude	m	Inegi (2023)
21	Exposure	N, S, E, W	
22	Slope	%	
23	Humidity index (<i>HI</i>)	Dimensionless	Álvarez (1992)

Bioclimatic variables predicting climate change scenarios

The bioclimatic variables of the two General Circulation Models (GCM): (1) CanESM5-CanOE (Canadian Earth System Model v.5-"Canadian Ocean Ecosystem Model") and (2) GFDL-ESM4 (Geophysical Fluid Dynamics Laboratory-Earth System Model version 4.1), were obtained from the WorldClim website (WorldClim, 2023), for the SSP126 and SSP370 climate change scenarios, for the 2041-2060 time horizon. SSP126 represents an intensive mitigation scenario with low emissions, while SSP370 corresponds to a higher emissions scenario; their inclusion allows for limiting the range of variation in climate suitability and comparing the species' sensitivity to different levels of forcing.

Modeling Methods

The pest species' suitability distributions were generated using the algorithm MaxEnt 3.4.4 (Phillips, 2010) was used, incorporating the pest presence record database and environmental variables. The following options were selected: "Create response curves" to visualize the response patterns of the variables; "Make pictures of predictions" to generate geographic projections of the model results; and "Do Jackknife to measure variable importance", which allows for analysis of each variable's contribution to the final model characteristics. The output format was logistic regression. In the MaxEnt parameters, 75 % of the presence data was used for model training and 25 % for validation, with 500 interactions using cross-validation. For the distribution of suitability under climate change scenarios, the variables for each GCM were added to the "Projection layers directory file" section (Conabio, 2023; Phillips, 2010).

Model evaluation and cutoff threshold

The predictive capacity of the distribution models was evaluated using the Area Under the Curve (*AUC*) metric from Receiver Operating Characteristic (*ROC*) analysis to measure the performance of the classification models (Peterson et al., 2011). For this purpose, NicheToolBox from the R language package was used with an omission error of 0.05 (Peterson et al., 2008).

The output maps generated by MaxEnt correspond to probability of presence data according to the logistic threshold; these were reclassified into quartiles based on the suggestion of Chakraborty et al. (2016), in four suitability categories: none (0-25 % probability of occurrence), low (25-50 %), medium (50-75 %), and high (75-100 %). Subsequently, the reclassified distribution maps were cropped using the polygons of temperate forests (pine, mixed: oak-pine, and pine-oak) in different successional stages, where the parasitic plant under study thrives. For this purpose, the land use layer, vegetation Series VI (Inegi, 2021), was used.

***Chi*-square analysis of temporal changes**

A *chi*-square (X^2) analysis was performed using the statistical software R 4.4.1 (R Core Team, 2025), considering a contingency table with the frequencies corresponding to the suitability classes (none, low, medium and high) for the periods 1970-2000 and 2041-2060, under the scenarios. Because the frequency distributions did not meet the normality assumptions, the significance of the X^2 statistic was estimated using a Monte Carlo simulation with 10 000 permutations, which allowed for a robust estimate of the null distribution of the X^2 statistic. This procedure

consisted of randomizing the observed frequencies among the categories and periods. In each iteration, the χ^2 value was calculated, and the empirically generated maximum and minimum values were compared (Van Geert *et al.*, 2012).

Results

Validation of the distribution model of *A. globosum* suitability

AUC values of 0.973 were obtained for the training data and 0.957 for the model validation test. The partial *ROC* test was 1.956, indicating reliable statistical performance. The variables that most influenced the model construction were the mean annual temperature (*BIO1*) and the Lang humidity index (*HI*).

Distribution of *A. globosum* current suitability

The results show that areas with high current suitability are located mainly in the southern zone, above 3 200 m altitude. The medium suitability category is located between 2 900 and 3 200 m altitude, while the low suitability category is located below 2 900 m (Figure 2).

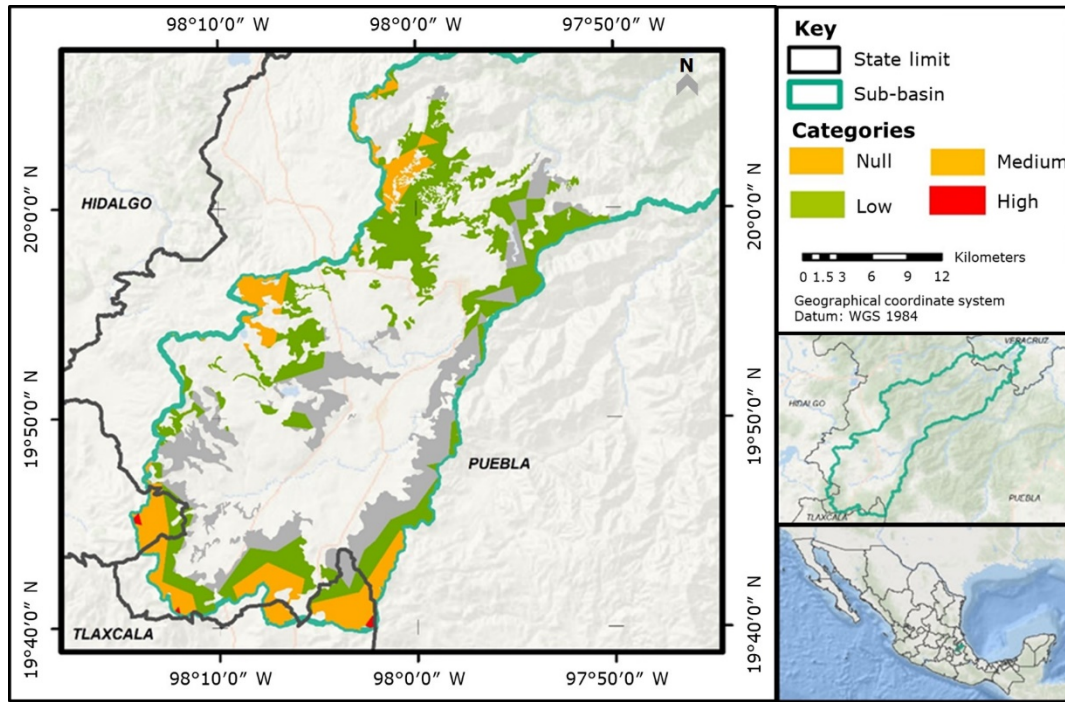


Figure 2. Distribution of current suitability of *Arceuthobium globosum* Hawksw. & Wiens using the Maxent method.

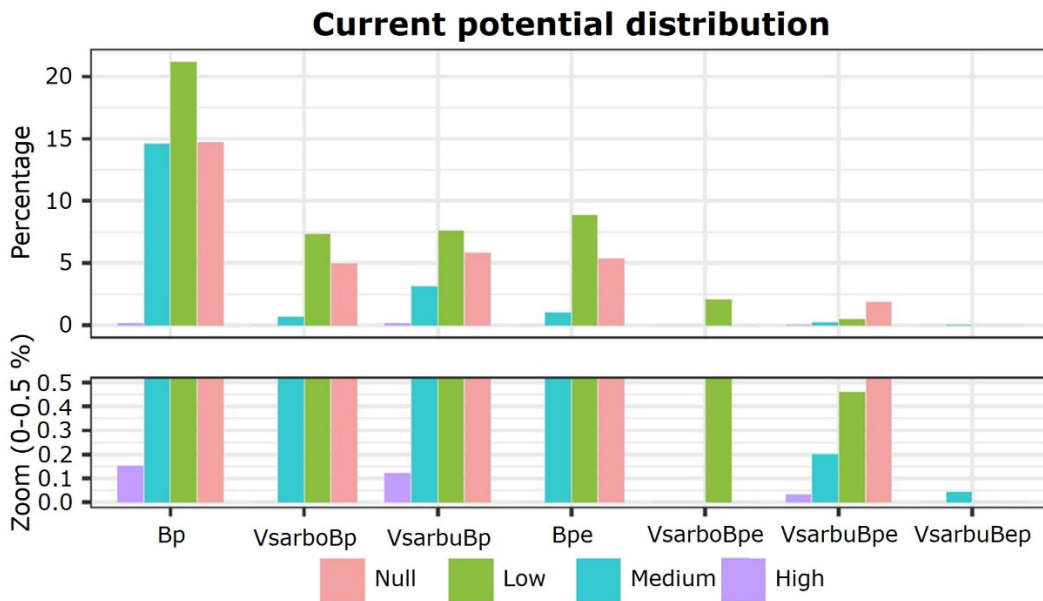
The areas with suitable distribution categories for *A. globosum* in the sub-basin are detailed in Table 2.

Table 2. Area and percentage by current suitability category of *Arceuthobium globosum* Hawksw. & Wiens in the *Laxaxalpan* sub-basin.

Category	Area in km ²	Area in %
High	1.23	0.30
Medium	81.05	19.59
Low	196.05	47.40
Null	135.22	32.69
Total	413.55	100.00

It can be observed that the combined high, medium, and low distribution of the species covers the largest area of the study area (67.28 %), while the low category alone is the most extensive; in contrast, the high category represents less than 0.5 %.

The current distribution of the parasitic plant by vegetation succession type can be seen in Figure 3. The data indicate that 54.69 % of the area (high, medium and low) of the study area is located in different types of pine forest successions, and 12.60 % in mixed forest successions. 35.90 % of the pest's distribution (high, medium and low) is found in primary pine forest, followed by 21.6 % in disturbed pine and mixed forests, and 9.79 % in primary mixed forest.



Bp = Pine forest; Vsarbo = Secondary tree vegetation; Vsarbu = Secondary shrub vegetation; Bpe = Pine-oak forest; Bep = Oak-pine forest.

Figure 3. Percentage of each category in the current suitability distribution of *Arceuthobium globosum* Hawksw. & Wiens by vegetation type.

Distribution of suitability under climate change scenarios

The predicted distributions of the pest in the future with the CanESM5-CanOE and GFDL-ESM4 models are presented in Figure 4. In general, both climate change scenarios show a spatial contraction of the environmental suitability of the species under study, compared to the current distribution.

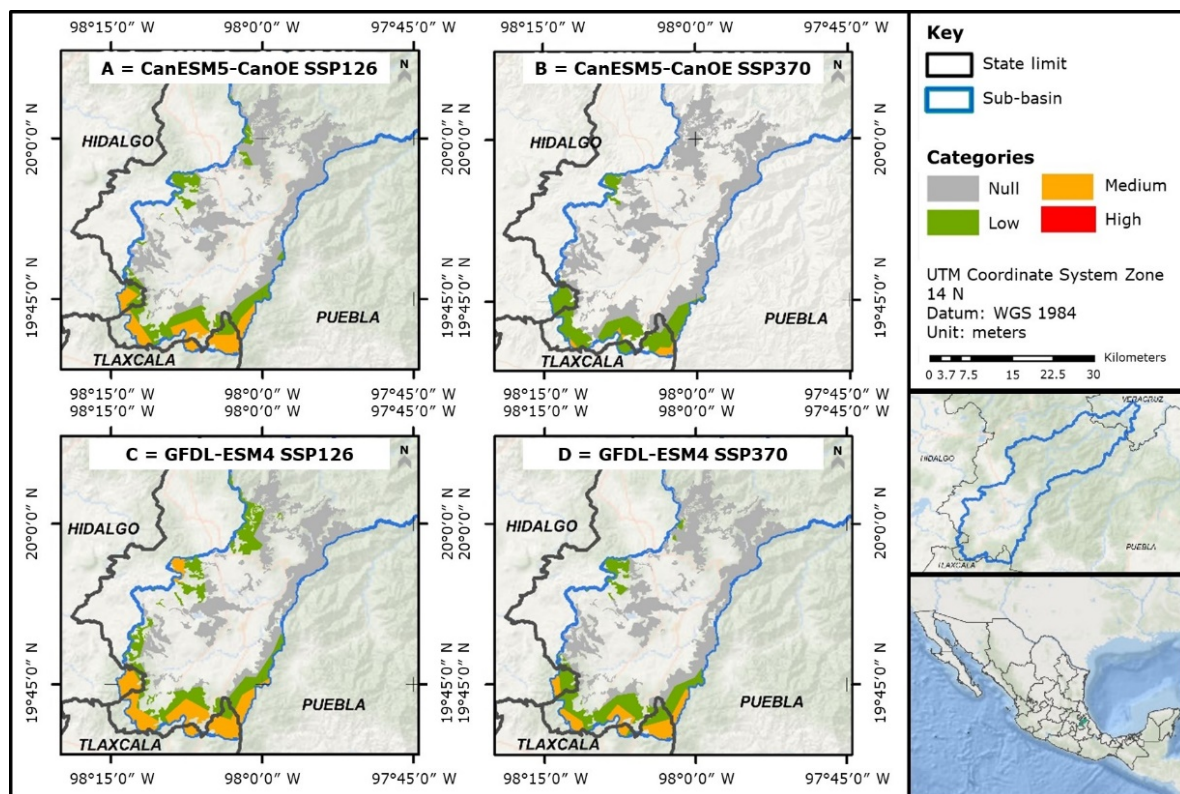


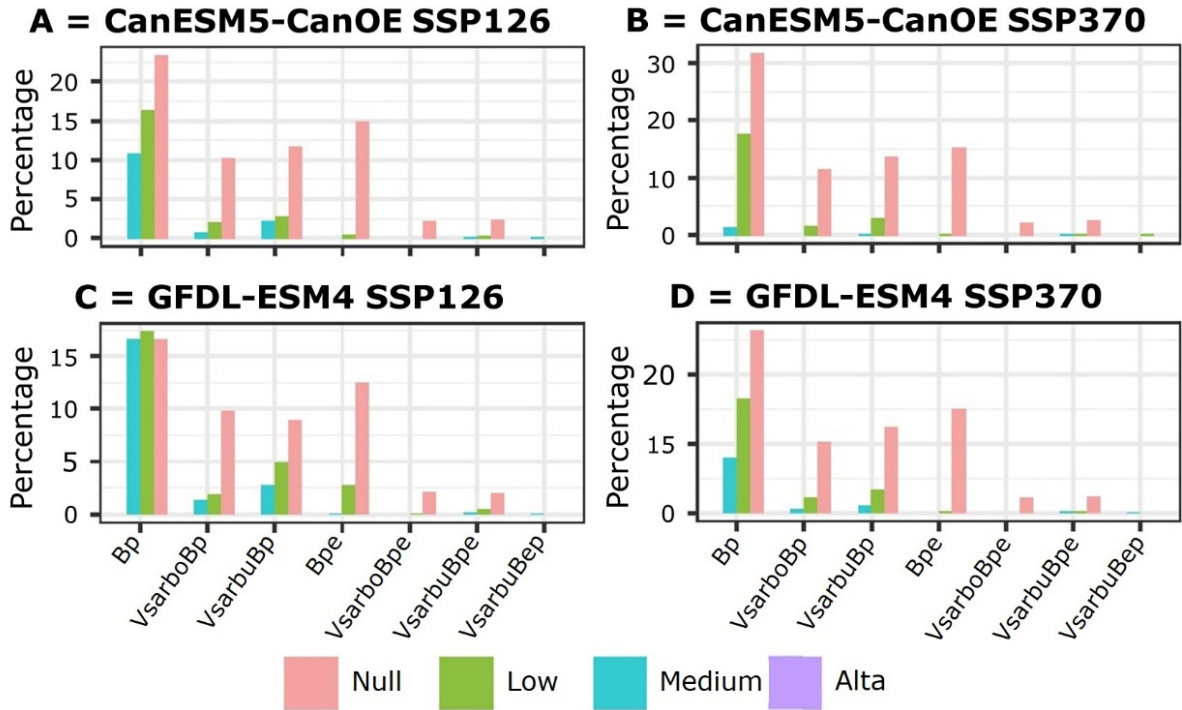
Figure 4. Suitability distribution maps of *Arceuthobium globosum* Hawksw. & Wiens with two general circulation models and two climate scenarios.

Figure 4A shows the SSP126 scenario, where the spatial configuration shifts Southward and to higher altitudes compared to the current distribution. The medium category is located above 2 800 m altitude, the low category between 2 600 and, in some areas, 3 000 m, and the high category disappears from the basin.

In Figure 4B, corresponding to the SSP370 scenario, the mistletoe configuration is reduced to a greater extent compared to the SSP126 scenario. The greater contraction observed in SSP370 suggests a more severe effect of climate forcing on the pest's suitability distribution. The medium category rises above 3 200 m altitude, the low category between 2 800 and 3 200 m, and the high category disappears. This indicates a marked restriction of the mistletoe's ecological niche under higher-emission scenarios.

The distributions using the GFDL-ESM4 general circulation model are presented in Figures 4C and 4D. In Figure 4C, corresponding to the SSP126 scenario, the projected mistletoe area is reduced and concentrated in the higher and Southern parts of the basin, compared to the current distribution. The medium category shifts above 2 800 m altitude, the low category between 2 600 and 2 800 m, and the high category is no longer present in the basin. In Figure 4D of SSP370, the mistletoe distribution is further reduced than in the SSP126 scenario, with shifts toward the higher elevations compared to the current distribution. The medium category is located above 2 900 and 3 000 m altitude, the low category between 2 700 and 2 800 m, and the high category disappears from the basin.

Figure 5A shows the percentage differences in distribution areas; the results of the CanESM5-CanOE model, in the SSP126 scenario, showed that pine forest accounts for 34.93 % of the distribution and mixed forest for 0.71 %. In comparison, these values represent a reduction of 19.76 % and 11.89 %, respectively, with respect to the current distribution.



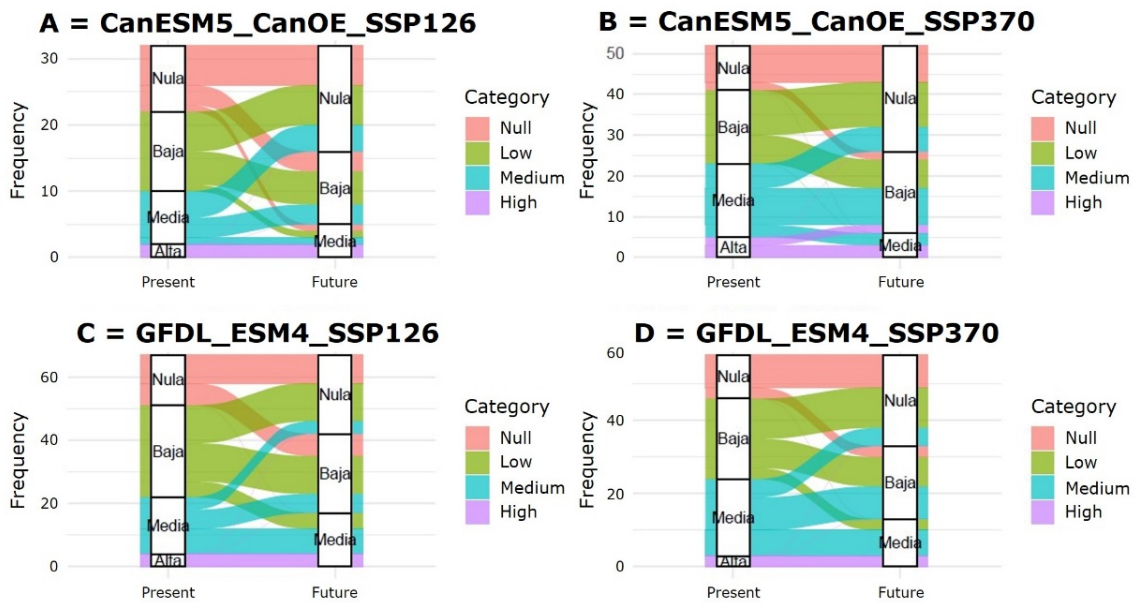
Bp = Pine forest; Vsarbo = Secondary tree vegetation; Vsarbu = Secondary shrub vegetation; Bpe = Pine-oak forest; Bep = Oak-pine forest.

Figure 5. Percentage by category of the suitability distribution of *Arceuthobium globosum* Hawksw. & Wiens with two general circulation models and two climate scenarios, by vegetation type.

In Figure 5B, the results of the CanESM5-CanOE model, SSP370 scenario, by vegetation type, show that pine forest accounts for 23.43 % of the distribution and mixed forest for 0.20 %. These values represent a reduction of 31.24 % and 12.40 %, respectively, compared to the current distribution. The results in Figure 5C, corresponding to the GFDL-ESM4 GCM and the SSP126 scenario, show that, by vegetation type, pine forest accounts for 44.78 % of the distribution and mixed forest for 3.33 %. These values represent a reduction of 9.91 % and 9.27 %, respectively, compared to the current distribution. In Figure 5D, the results of the SSP370 scenario show that pine forest accounts for 31.25 % of the distribution.

Contingency analysis of suitability distribution

Chi-square tests with Monte Carlo simulation showed, in all four climate models, a significant trend of decreasing favorable conditions for *A. globosum*. A progressive transition from medium and high categories to low and none is observed, predicting a consistent loss of suitable areas in the future period (2041-2060) (Figure 6). CanESM5–CanOE SSP370 shows an intensification of this process under more severe scenarios, with a marked decrease in areas with intermediate suitability, which shift to the low category (Figure 6B). In contrast, GFDL–ESM4 retains a higher proportion of areas in intermediate categories, suggesting a less severe response to projected environmental changes (Figure 6). This likely represents a relative tolerance to temperature conditions, which keeps certain areas within their estimated climatic niche. The greater suitability projected by the GFDL-ESM4 model, compared to CanESM5-CanOE, can be attributed to the former's tendency to preserve intermediate climatic conditions in regions where *A. globosum* finds favorable environmental ranges. Likewise, a general trend toward increased low and null suitability is observed in the future under the SSP370 scenario.



Nula = Null; *Baja* = Low; *Media* = Medium; *Alta* = High. CanESM5-CanOE-SSP126: $X^2=184.32, p<0.0001$; CanESM5-CanOE-SSP370: $X^2=203.71, p<0.0001$; GFDL-ESM4-SSP126: $X^2=193.55, p<0.0001$; GFDL-ESM4-SSP370: $X^2=222.11, p<0.0001$. A = CanESM5-CanOE SSP126; B = CanESM5-CanOE SSP370; C = GFDL-ESM4 SSP126; D = GFDL-ESM4 SSP370.

Figure 6. Transitions between present and future suitability levels (2041-2060) for *Arceuthobium globosum* Hawksw. & Wiens under two general circulation models and two climate scenarios.

In general, the SSP370 scenario with the GFDL-ESM4 GCM projects the greatest loss of suitability, with dominant transitions toward null and low categories; that is, there is a lower risk of *A. globosum* presence in the temperate forests of the study area. In contrast, the SSP126 scenario with CanESM5-CanOE shows more moderate changes, with some persistence in medium and high categories; in other words, it represents an increased risk for the forests.

Discussion

The suitability distribution model validation, according to Peterson *et al.* (2011), shows that the *AUC* values for the training data (0.973) and for the model validation (0.957) are considered good predictors. The *ROC* test (1.956) indicates reliable statistical performance, according to Peterson *et al.* (2008). Regarding the current distribution, Endara-Agramont *et al.* (2023) indicate that the altitudinal range in which *A. globosum* occurs is between 2 450 and 4 000 m.

The similarity between the distribution patterns projected by the GCMs CanESM5-CanOE and GFDL-ESM4 demonstrates that the observed trends are robust against variability among climate models (Eyring *et al.*, 2016). However, the greater proportion of areas with suitable distribution projected by GFDL-ESM4, compared to CanESM5-CanOE, may be due to differences in the representation of climatic gradients in mountainous areas of the study region, where mistletoe finds favorable microclimatic conditions, since there are spaces that could function as climate refugia (Kearney & Porter, 2009).

The projected changes in the distribution of suitability for *Arceuthobium* *sp.* under climate change scenarios, compared to the current distribution, indicate that the species is closely associated with specific altitude and climate ranges, particularly the mean annual temperature and the length of the growing season, which limits its presence outside of suitable environmental conditions (Ramírez-Dávila & Porcayo-Camargo, 2009). Several studies have documented that changes in temperature and precipitation induce altitudinal shifts in mistletoe towards cooler, higher elevations, as a response to the loss of optimal climatic conditions at lower elevations (Nickrent, 2002). According to Sosa-Díaz *et al.* (2018), among climatic variables, the average minimum temperature during the coldest period of the year was the most relevant for the distribution of dwarf mistletoe in the country. The reduction observed under climate change scenarios (9.91 % and 9.27 %) compared to the current distribution,

with the highest proportion in pine forests, suggests relatively more favorable conditions for mistletoe establishment (Körner, 2007).

In the contingency analysis of changes in the species' distribution, the χ^2 tests with Monte Carlo simulation showed a decrease in favorable conditions for *A. globosum* in the sub-basin. This suggests that climate change would reduce the spread of this parasitic plant, potentially posing a lesser threat to its hosts between 2041 and 2060 (Kearney & Porter, 2009). The loss of suitability with dominant transitions (none and low) in the SSP370 scenario with the GFDL-ESM4 GCM indicates a lower risk of *A. globosum* presence in the temperate forests of the study area, as this scenario corresponds to higher CO₂ emissions and high deforestation. Conversely, the more moderate changes, with some persistence in the medium and high categories under the SSP126 scenario with CanESM5-CanOE, show an increased risk for these forests, as this scenario considers mitigation measures for CO₂ emissions and greater control over deforestation, among other factors (Intergovernmental Panel on Climate Change [IPCC], 2021).

Conclusions

The species suitability distribution models are primarily determined by the bioclimatic variables mean annual precipitation and humidity index. The generated models predict that areas of high, medium, and low suitability for *A. globosum* are concentrated mainly in the higher altitude zones of the sub-basin. Future climate scenarios indicate that areas with medium suitability tend to decrease and high suitability tend to disappear, while areas with low and no suitability increase. Overall, the projected models suggest that the suitability distribution of *A. globosum* will be significantly altered in the future, with a reduction in favorable conditions for its presence in the temperate forests of the *Laxaxalpan* River sub-basin.

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Conflict of interest

The authors declare no conflict of interest.

Contribution by author

Ramiro Pérez Miranda: research organization, results analysis, and discussion; Victor Javier Arriola Padilla: writing and technical review; Leticia Bonilla Valencia: statistical analysis and interpretation of results; Ángel Emmanuel Cruz Estrada: manuscript review and corrections; Norma Fernández Alejo: literature review, writing and results analysis; Martha Elena Domínguez Hernández: text review.

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