

Geographical and ecological distribution analysis of *Dalbergia calderonii* Standl. (Fabaceae): implications for the conservation of this critically endangered rosewood

Manuel Medina-Amaya

Universidad de Ciencias y Artes de Chiapas

Clara Luz Miceli-Méndez

Universidad de Ciencias y Artes de Chiapas

Miguel A. Pérez-Farrera

Universidad de Ciencias y Artes de Chiapas

Sergio López

sergio.lopez@unicach.mx

Universidad de Ciencias y Artes de Chiapas

Octavio Rojas-Soto

Instituto de Ecología

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Abstract

Dalbergia is economically essential for its high-quality rosewood wood in fine furniture. Thus, there is a high demand for wood, which has led to illegal logging. *Dalbergia calderonii* Standl. is associated with tropical deciduous forests, where there is a high rate of deforestation, leading to the decline of the species' natural populations. The knowledge of its potential areas of presence and associated environments can contribute to species conservation. Here, we modeled the potential distribution of *D. calderonii* and identified areas with remnants. We found that the potential distribution model for *D. calderonii* predicts two geographically separate areas, one in southern Mexico and the other in northern Central America; thus, we also modeled them as two independent populations and compared their ecological niches. We transferred all models into the Last Interglacial, the Last Glacial Maximum, and the mid-Holocene climatic scenarios to understand the species' recent biogeographic history. We found that 65% of the species' potential distribution comprises sites with sparse vegetation and bare soil; besides, we found no significant differences between the niches of the Mexican and Central American populations. The transferences to the past scenarios showed that the potential history of the species distribution had been characterized by dynamics of expansions and contractions describing commonly geographical isolations but also including stages of continuum distributions. We suggest that future conservation strategies prioritize both populations independently, based on their disjunct distribution.

Introduction

The species of the genus *Dalbergia* L.f. also known as rosewoods are widely distributed globally, with approximately 250, and centers of diversity in Central and South America, Africa, Madagascar, and Asia (Klitgaard & Lavin, 2005). However, some studies have recorded 269 species worldwide (Wu et al., 2022). Despite the morphological variability and diverse habitat preferences of *Dalbergia* species, which makes it challenging to classify New and Old-World species into natural groups (Bentham, 1860; Prain, 1904; de Carvalho, 1989), the group is suggested to be monophyletic and originated in America. However, there is no complete correlation between geography and phylogeny, but it is possible that several long-distance dispersal events are responsible for the pantropical distribution (Vatanparast et al., 2013; Rahaingoson et al., 2022). Recent studies have shed light on the evolutionary history and biogeography of the genus, providing valuable insights into its diversification and global distribution (Vatanparast et al., 2013; Rahaingoson et al., 2022; Sotuyo et al., 2022).

The wood of Dalbergias, due to its density, fine texture and bending behaviour (Karlinasari et al., 2012) as well as its hardness and durability, make it suitable for carving, which is why it is used in cabinetmaking and in the production of fine furniture (Pittier, 1922; Lewis et al., 2005; Jenkins et al., 2012; Winfield et al., 2016) and musical instruments (De la Paz Pérez et al., 2002; Karlinasari et al., 2012; Cervantes-Maldonado, 2016; Herrera-Castro et al., 2019); that is why they are a so-called precious wood species. It is also used in traditional medicine (Lee et al., 2013; Wang et al., 2014) and its applications in the pharmaceutical (Zhao et al., 2020) as antimicrobial (Rutiaga-Quñones et al., 2010; Saha et al., 2013), antifungal (Rutiaga et al., 1995; Barragán-Huerta et al., 2004), antibiotic, antioxidant, and cytotoxic agents (Hamburger et al., 1987; Lianhe et al., 2011; Gutierrez & Baez, 2013). In addition, *Dalbergia* species have been reported to establish symbiotic relationships with rhizobia for nitrogen fixation, playing an important role in ecosystems, improving soil fertility (Rasolomampianina et al., 2005) and even food industries applications (Gutiérrez-Zúñiga et al., 2014) are being explored.

The timber of *Dalbergia* species has been traded internationally for at least 300 years (Richter et al., 1996). Its value is so high that the amount of global seizures far exceeds the combined seizures of ivory, rhino horn and big cats (Zhu, 2020). Since 2010, there has been an increase in demand for many Dalbergias worldwide (Treanor, 2015); this market is fuelled by the illegal harvest and trade of numerous species, with the majority coming from direct harvesting of natural populations (Jenkins et al., 2012; Camino & Morales, 2013; Cervantes-Maldonado, 2016; Cervantes et al., 2019; Linares & Martínez-Salas, 2020; Rahaingoson et al., 2022). Such severe overexploitation is affecting to its associated to ecosystems loss due to the expansion and growth in demand for tropical hardwoods, of which China is the main consumer (Zhu, 2020; Pedraza Ortega et al., 2022).

In Mexico, there are about 15–20 species (Sousa et al., 2001; Linares & Sousa, 2007; Ricker et al., 2013; Villaseñor, 2016; Cervantes et al., 2019), and in Central America, the genus comprises 14 species (Chamberlain et al., 2022) grouped in the clades *Dalbergia ecastaphyllum*, *D. glabra*, *D. granadillo* and *D. glomerata*. The latter clade includes *Dalbergia calderonii* Standl. (Sotuyo et al., 2022) a species of interest in the present study, whose type specimen was recorded in El Salvador in 1928 and subsequently in different years from 1994 to 2021; in Guatemala, there are records from 1942 and 2021, Honduras in 1975, and Mexico in 1950, 1974 and 2009 (Teisher, 2024). According to Standley (1922), *D. calderonii* is typically found in tropical deciduous forests and medium deciduous forests, also defined by other authors as low deciduous forests and medium sub-deciduous forests (Miranda & Hernández, 1963), tropical deciduous forests and medium sub-deciduous forests (Rzedowski & Huerta, 1978), semi-humid deciduous forests and semi-dry deciduous forests (Lauer, 1966) and tropical and subtropical dry forests (Olson & Dinerstein, 2002). These forests are under threat due to land use changes such as

agriculture, logging, urbanization, and livestock grazing (Miles et al., 2006; Díaz-Gallegos et al., 2010; Rosete-Vergés et al., 2014), leading to high rates of deforestation. As a result, *D. calderonii* is now considered critically endangered by the IUCN (Linares & Martínez-Salas, 2020) and is included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2023).

Ecological Niche and Species Distribution Models (ENM/SDM) allow the prediction of the potential areas of presence of species based on the correlation between the species' presence records associated with environmental characteristics, starting from the reconstruction of ecological niches (i.e., environmental spaces) through the use of mathematical and computer algorithms (Hijmans & Graham, 2006; Phillips et al., 2006; Elith et al., 2011). MaxEnt is a maximum entropy-based machine learning algorithm that is widely used to model and predict species distributions by examining species-environment correlations based on occurrence data and their environmental covariates (Phillips et al., 2006). Diverse studies have demonstrated the use of ENM/SDM in plant conservation worldwide (e.g., Raes et al., 2009; Trisurat et al., 2011; Zhang et al., 2012). Due to the anthropogenic pressure to which tree species are subjected, it has been recommended to evaluate their diversity, modeling potential distribution, extinction risk, and estimating phylogenies particularly in the group of legumes, prioritizing some genera such as *Bauhinia* L., *Dalbergia* L.f., *Desmodium* Desv., *Mucuna* Adans., and *Vigna* Savi (Yahara et al., 2013). Among the evaluation proposals is the use of SDM, which are considered key methods to evaluate the status and trends of species at a spatial level for a better comprehension of the plant habitats to enable more effective strategies to safeguard them (Margules & Pressey, 2000; Watts et al., 2009; Trisurat et al., 2011; Zhang et al., 2012). Some research has been carried out in this sense, in Africa with *Dalbergia vacciniifolia* Vatke (Ngarega, Gikonyo, et al., 2022), in China with several species of *Dalbergia* (Liu et al., 2019; Yuheng et al., 2021) and in Nepal with *Dalbergia latifolia* Roxb. (Mahatara et al., 2021). However, no related studies have been found for Mesoamerican species.

The main goals of this study were to describe the potential distribution of *D. calderonii* by identify the climatic and edaphic variables that best fit the distribution models; to analyze if the two allopatric populations from Mexico and Central America possess similar environments; and to understand the dynamyc of the species' past potential distribution. Finally, as a conservation goal, we identified areas with remmanent of vegetation in the suitable areas currently predicted by the models.

Methods

Occurrence records

A set of records of *D. calderonii* was compiled from a large part of the Mesoamerican region, specifically in southern Mexico in the States of Oaxaca and Chiapas and in Central America in Guatemala, El Salvador, and Honduras. Species occurrence data were obtained from the Global Biodiversity Information Facility (GBIF.Org User, 2022) The Tropicos database of the Missouri Botanical Garden, the herbaria of Mexico (MEXU and CHIP), the herbaria of El Salvador (LAGU and MHES), records of the project "Generación de Capacidades y Lineamientos Técnicos de Manejo para Elaborar Dictámenes de Extracción no Perjudicial Orientados a las Especies del Género *Dalbergia* en Guatemala, El Salvador y Honduras" (MARN, 2020) and records from fieldwork carried out from 2021 to 2022 (years).

Of the 301 records compiled, misidentified and duplicate records were eliminated. To reduce spatial autocorrelation and improve the performance of the models (Boria et al., 2014), spatial filtering was applied when the distance between two or more records was less than 1 km and only one of the records was retained.

Environmental variables

Environmental variables were obtained from the CHELSA V2.1 project. (Karger et al., 2017), and initially the 19 available bioclimatic variables were taken, which have spatial information of temperatures and precipitation in digital format at a resolution of 30 seconds (~1 km² at the equator), and with a temporality of 29 years (1981-2010). Of these variables, four that combine temperature and precipitation information within the same layer (i.e., Bio8, Bio9, Bio18, and Bio19) were eliminated, as they potentially present spatial anomalies in the form of odd discontinuities between neighboring pixels for the study area (Booth, 2022). In addition, we included Potential Evapotranspiration (ET0) and Global Aridity Index (IA_ET0) variables (Trabucco & Zomer, 2019) and 17 variables related to soil physical and chemical properties obtained from the SoilGrids v2.0 database of *ISRIC-World Soil* Information (Hengl et al., 2017) at a resolution of 30 seconds. Soil is an important factor in the geographic distribution of plants (Linder et al., 2005; Giraldo-Kalil et al., 2023). Therefore, edaphic variables have been recommended for more adequate modeling (Velazco et al., 2017).

The selection of the variables to characterize the ecological niche of the species followed the performance of several tests, including a Jackknife analysis, a principal component analysis (PCA), a variance inflation factor analysis (VIF) and finally, a Spearman correlation

analysis (Cobos et al., 2019). Those variables matching the criteria of the highest significance for Jackknife analysis and PCA, with a VIF value <10 and a correlation value <0.8 were selected. All these selection methods were applied as this allows the identification of an adequate set of variables that improves the performance of the models (Cobos et al., 2019). The final variables selected are summarized in Table 1.

Table 1. Climatic and edaphic variables used to create the models of potential distribution and ecological niche of *D. calderonii*.

Type of variables	Variable	Description
Climate	Bio4 *	Temperature seasonality (°C)
	Bio6 ±	Mean daily minimum air temperature of the coldest moth (°C)
	Bio7 *	Annual range of air temperature (°C)
	Bio10 *	Mean daily mean air temperatures of the warmest quarter (°C)
	Bio14 ±*	Precipitation amount of the driest month (kg m ⁻²)
	Bio15 ±*	Precipitation seasonality (Kg m ⁻²)
	Bio16 *	Mean monthly precipitation amount of the wettest quarter (Kg m ⁻²)
	Bio17 *	Mean monthly precipitation amount of the driest quarter (Kg m ⁻²)
	ET0 ±	Potential evapotranspiration (mm yr ⁻¹)
Edaphic	BDTICM ±	Absolute depth to bedrock (cm)
	BDRICM ±	Depth to bedrock (R horizon) up to 200 cm
	CECSOL ±	Cation exchange capacity of soil in cmolc/kg
	ORCDRC ±	Soil organic carbon content (fine earth fraction) in g per kg
	PHIKCL ±	Soil pH x 10 in KCl
	SLTPPT ±	Silt content (2-50 micrometer) mass fraction in %

± Variables used in the general model and characterization of the niche; *variables used in the models projected into the past.

Calibration area

Maxent is an algorithm that requires a calibration area to model species distribution, since it requires a background to characterize the ecological niches from the presence records. The BAM diagram (Soberón & Peterson, 2005; Soberón, 2007) is a conceptual framework for interpreting the interactions between the three main factors that determine species distribution: biotic factors (B), abiotic factors (A), and the accessible area (M). In this context, the calibration area is represented by M and corresponds to those areas that the species has been able to access in a given historical period, which is compatible with the biogeographic history of the species (Soberón & Peterson, 2005; Barve et al., 2011). Based on the suggestions by Rojas-Soto et al. (2024) the delimitation of the calibration area was defined by selecting the areas coinciding with the records of presence with biogeographic units, which in this case were the biogeographic regions of the Neotropics (Morrone et al., 2022). Once the regions were selected, the areas were shortened by applying a spatial restriction or buffer of 100 km to the occurrences (Figure 1). When the analysis of Mexico (Mmx) and Central America (Mca) populations were established (see below), two areas of accessibility were again created following the same procedure.

Species distribution models (SDM)

For the development of the distribution models of *D. calderonii* (general model) and its two population models (see below), we used the Maxent V3.4.1 algorithm (Phillips & Dudík, 2008), which performs well with small sample sizes (Pearson et al., 2007). The modeling process was carried out with the package kuenm (Cobos et al., 2019), which allows testing different regularization values, which in this case were 17 values tested (from 0.1 to 1 incrementing every 0.1, and from 2 to 8 incrementing every 1) and only three types of relationships: linear, quadratic and their combination (l, q and lq) to reduce the complexity of the model.

The overall model was calibrated with 70% of the presence data and 30% for validation; 10 replicates were performed with a limit of 1000 iterations, and the *Bootstrap* type resampling method was used. The candidate models were evaluated on the basis of the statistical significance of the partial ROC curve (Peterson et al., 2008), the omission rate (<0.05%) and the lowest value of the Akaike's information criterion (AIC) corrected for small sample sizes (Warren et al., 2010; Warren & Seifert, 2011; Morales et al., 2017).

The final overall model was constructed from the median of the ten replicates based on the best combination of parameters evaluated. The resulting map in continuous format was converted to a binary map (presence/absence) using the probability value from the tenth percentile of the calibration data as a threshold. Pixels with probability values below the threshold were classified as absences and pixels with probability values above the threshold were classified as presences.

Considering that the general model predicted suitable environments in two geographically separate regions, two independent models were developed for each of the regions. The first was for the Chiapas and Oaxaca occurrence records, defined as the Mexican population model (Mmx), and the second was for the El Salvador, Guatemala and Honduras records, which was called the Central American population model (Mca). For this, exactly the same steps of the process used for the general model and described previously were followed, varying only the calibration areas (Figure 1).

As part of the interest in the potential areas of the historical presence of the species (general model) and of each of the two populations (Mmx and Mca), transferences were made into the past. Due to the non-existence of edaphic and evapotranspiration (ET0) variables in the past, for this historical analysis, we used only the climatic variables from CHELSA (Karger et al., 2017) (Table 1). Each model's transferences were made to the mid-Holocene (MH ~8,000 yr; Fordham et al., 2017), Last Glacial Maximum (LGM ~21,000 years; Karger et al., 2021) and Last Interglacial (LIG ~130,000 yr; Otto-Bliesner et al., 2006) all variables with 2.5 minute resolution (~5km), this resolution was chosen as it is the finest available for the LGM.

Estimated current loss of area of D. calderonii

Areas with sparse or absent vegetation in the potential area of presence of the species were estimated according to the general model; for this purpose, the Global Forest Cover (GFC) was used at a resolution of 30 meters (Hansen et al., 2013). The GFC was cut using the map from the general model as a mask and then resampled with the bilinear interpolation method at a resolution of 250 meters. The GFC values were recategorized following the classification proposed by Moncada et al. (2022) as detailed in Table 2. Considering the extent and the resolution according to the general model, areas with <40% forest cover within the suitable area were considered sites where the species is unlikely to be found due to the sparse vegetation in these areas.

Table 2. Categories established for the reclassification of the CFG in the regions were predicted to be suitable by the general model.

Category	Range %	Description.
1	0 - 20	Dry bare soil area
2	20 - 40	Areas with sparse vegetation and bare soil.
3	40 - 60	Areas with sparse vegetation
4	60 - 100	Area with dense vegetation

Source: Adapted from (Moncada et al., 2022).

Comparison of niche between Mexican and Central American populations

To provide evidence from an environmental perspective on a potential differentiation between Mexican and Central American populations, we compared their use of environmental space using two different approaches. The first approach was a test of niche similarity (Broennimann et al., 2012; Di Cola et al., 2017) with Shoener's (D) and Hellinger's (H) indices. (Warren et al., 2008). Environmental variation was ordered using principal component analysis (PCA), and then the densities of presences of the two populations and the density of environmental conditions on the first two axes of the PCA were calculated with the kernel density function (Broennimann et al., 2012). The similarity between the niches of the two populations was assessed by assuming that the niche of the Mexican (Nmx) and the niche of the Central American (Nca) populations were more similar than a random model (Warren et al., 2008). For this process, 1000 permutations were made, and the statistical significance of the niche overlap was assessed (Di Cola et al., 2017).

The second approach consisted of creating minimum volume ellipsoids (Farber & Kadmon, 2003) to characterize the niches of the Mexican and the Central American populations. Environmental variables were converted to principal components (PC), and models were

constructed based on the centroid and covariance matrix of the variables at a 95% significance level. The two niches were compared, and the null hypothesis that the two ellipsoids fitted to the actual observations overlapped at least as much as the random data type was tested. For this, we used an ellipsoid envelopes test, in which we measured the overlap between the ellipsoids. We performed 1,000 replicates with a 5% confidence limit. The analyses were performed using the routines implemented in the package *ellipsenm* (Cobos et al., 2022).

Results

Evaluation of the models

67 presence records of *D. calderonii* were compiled. The model with the best performance was the response type "lq" and the regularization value of 0.2, so it was selected as the general model. The model performance parameters were AUC ratio = 1.7, omission rate = 0.0 and AICc = 1497. Table 3 summarizes the performance values of the final models obtained.

Table 3. Performance statistics for the best models of the general model and the Mexican and Central American populations.

Model	Type of response	Regularization value	AUC Ratio	Omission rates 5%.	AICc
General model	lq	0.2	1.7	0.00	1497
Mmx	q	5	1.5	0.25	298
Mca	lq	8	1.5	0.12	1103

Contribution of environmental variables

Based on estimates of the relative contributions of environmental variables to the general model and the Jackknife test, precipitation of the driest month (Bio14) was the main variable for the *D. calderonii* distribution model (general model). It was followed in greatest contribution by the minimum temperature of the coldest month (Bio6), cation exchange capacity (CECSOL) and absolute depth to bedrock (BDTICM), all four being the most important variables. Considering the binary map, *D. calderonii* is associated with environments where the precipitation of the driest month ranges between 0 and 250 mm and a minimum temperature of the coldest month between 28 and 29.7°C. For Mmx populations, the most important variables were Bio14, BDTICM and BDRICM. For Mca the most important variables were CECSOL, Bio14 and Bio15. Bio14 was consistently one of the most important variables in all models.

Model prediction

The general model predicted areas of potential presence in two discontinuous regions. The northernmost is located in southern Mexico, in the states of Oaxaca and Chiapas. From the eastern end of the South Coast, continuing in the Isthmus Plain and extending through the Sierra Sur, the Central Depression to the southern region of the Chiapas Highlands. The second area corresponds to the Central American Pacific, particularly in the central region of the Crystalline Highlands and to the east of the Volcanic Highlands of Guatemala, continuing through the southern cordillera of Honduras, and almost the entire northern, central region and the western and eastern coasts of El Salvador (Figure 2a).

The total suitable area of the overall model was estimated to be 57,797 pixels, of which according to CFG. (Hansen et al., 2013) areas with sparse vegetation or bare soil comprise 37,568 pixels; that is, a reduction in the extent of the potential distribution of 65% (Figure 2b). When we modeled each of the populations independently, in comparison to the general model that included all species' records (Figure 2a), it is note wothy that the predictes areas increases in Mexican population area (Figure 2c) and, conversely, decreases in the Central America population (Figure 2d). The Mmx population presented suitable areas mainly in the Pacific region of Oaxaca, Chiapas, and extending into a small region of Guatemala (Figure 2c). In contrast, for the Mca population, suitable areas were predicted mainly in El Salvador, extending in small regions to the north into Honduras and to the west into Guatemala (Figure 2d).

Environmental ranges between Mexico and Central America populations

In addition to the differences in the predictions of the geographic areas, the values of the environmental variables also differ between the populations of Mexico and Central America (Figure 3). For example, it is observed that in the Mca population the ranges of the Bio6 and Bio14 variables are almost completely restricted to higher and lower values with respect to the Mmx population (Figure 3a). For the

variables Bio15 and ET0 the Mca population is restricted to the intermediate and upper ranges in relation to the ranges of the Mmx population (Figure 3b). In the edaphic variables the tendency is similar in CECSOI, ORCDRC and SLTPPT which in the Mca population are limited to the lower values (CECSOL and ORCDRC) and higher in SLTPPT with respect to the Mmx population, the exception is the BDTICM variable that presents very similar ranges between the two populations (Figure 3c-d).

Transferences into the past

Past transferences of the *D. calderonii* models show that its potential distribution has undergone changes. The general model for the Middle Holocene (MH) shows that the geographic distribution was very similar to the present (Figure 4a), but in the Last Glacial Maximum (LGM) period the distribution was further south than its present distribution, being limited only to Central America, mainly in the Pacific region of Nicaragua (Figure 4b). It is noteworthy that there were no current environmental combinations in the climate of the Interglacial period (LIG), since there are no predicted area for that period.

The transferences made with the populations of Mexico for the MH show two suitable areas in southern Mexico and part of Central America (Figure 4c). In the LGM period, the suitable areas in southern Mexico are again lost, occurring only in Central America (Figure 4d). For the LIG period, the extent of its projected distribution in Central America was reduced, but suitable areas appear again in southern Mexico, it is also important to highlight the discontinuity of the distribution in this period (Figure 4e).

Population transferences for Central America predict only suitable conditions for MH with very restricted and fragmented distribution in the southern regions of Mexico, El Salvador and Nicaragua (Figure 4f). For LGM the potential distribution was limited to a very small Pacific region of Costa Rica (Figure 4f), and did not present suitable areas for LIG. Finally, a consensus model was created by summing all transferences to the past, to identify regions of climate stability where environmental suitability has been constant under the different scenarios. These include Oaxaca (Mexico), El Salvador and some neighboring regions of Guatemala and Honduras. But it is in Nicaragua where the species most frequently presented suitable regions (Figure 4h).

Niche similarity

The niche similarity test between Nmx and Nca showed a value of 0.11 in Shoener's index and 0.27 in Hellinger's index, although in both cases were non-significant (p value = 0.1) so there was no difference between the niches of the two populations (Figure 5). On the other hand, the volume of the ellipsoidal ecological niche for Nmx was smaller (31.2 dimensionless units), with respect to Nca (47.7 dimensionless units). The total overlap between the two niches was 0.25%; however, it was not possible to reject the null hypothesis that the niche of the Mexican population (Nmx) and the niche of the Central American population (Nca) are more similar than a random model (Figure 6).

Discussion

Contribution of environmental variables

According to the general model, the most important factor in determining the potential distribution of *D. calderonii* is the precipitation amount of the driest month (Bio 14). The species prefers sites with precipitation levels of less than 250 mm, which coincides with the vegetation reported for the species, namely deciduous forests. These forests are characterized by a long dry season lasting for 4–7 months, during which they receive less than 100 mm of monthly rainfall. This information is supported by several studies (Holdridge et al., 1971; Walter, 1971; Murphy & Lugo, 1986; Gentry, 1995; Graham & Dilcher, 1995; Bandar et al., 2016).

Model prediction

The general model's predicted area aligns with the information provided on *D. calderonii*'s distribution, which is associated with deciduous forests (Standley, 1922). According to Bandar et al. (2016), who defined floristic groups based on the Neotropical dry forest's floristic relationships, *D. calderonii* is related to the floristic groups of Mexico and Central America-North South America. Along with the Antilles and northern inter-Andean valleys, these groups form the northern upper clade.

The general model predicted two suitable sites, which are geographically separate. The variation in the rainfall regime between these two areas, which ranges from 1800 to 3500 mm annually, is the likely reason for this disjunction. It is worth noting that *D. calderonii* is typically found in deciduous forests where the precipitation ranges from 1000 to 2000 mm per year. This condition is probably the main factor responsible for the separation of the potential distribution of the species. Additionally, the models for the Mexican (Mmx) and

Central American (Mca) populations predict potential distribution areas that are also geographically separated. This supports the idea that the two geographically isolated populations also possessed slight environmental variations, despite we found no significant differences. Another low but still possibility, is that there are no records in the intermediate region where some populations might exist. Something to highlight is that, in comparison to the general model, when we modeled each of the populations independently, the predicted areas increases in Mexican population area and decreases in the Central America population. This apparent contradictory model outputs could be a consequence of the differences in the number of records used and the environmental variation included in each of the extent of the calibration areas (M) in each population. Where there is an evident inequity between them, being higher records in the Central America population and more diverse environments in the Mexican population.

It's important to note that 65% of *D. calderonii*'s potential distribution is located in areas classified as sparse vegetation or bare soil due to deforestation processes (Hansen et al., 2013). This has significantly reduced and fragmented its potential distribution (Díaz-Gallegos et al., 2010; Rosete-Vergés et al., 2014). Land-use change and population growth have been identified as the leading causes of forest species extinction, and therefore (de Wasseige et al., 2013), it's unlikely that the species will be able to continue in these highly fragmented and degraded areas.

Transferences into the past

Transferences from the general model show that the potential distribution of the species has remained similar between the present and the MH (mid-Holocene) but shifted towards the south (Pacific of Nicaragua) during the LGM (Last Glacial Maximum). The LGM was a major climatic event that directly impacted the species' distribution. Several studies suggest that changes in species ranges are associated with Quaternary climatic oscillations, including Ramos et al. (2007), Novaes et al. (2010, 2013), Viana & Lovato (2010), and Collevatti et al. (2012, 2014).

It is worth noting that while the general model suggested a discontinuous distribution of *D. calderonii* in the past, the projection from the Mmx model showed that the species had a continuous distribution during the Last Glacial Maximum (LGM) but that it fragmented in the Middle Holocene (MH). Some studies suggest that changes in species ranges are linked to Quaternary climatic oscillations and are significant factors that drive strong phylogeographic structure and high genetic divergence among tree populations. (Ramos et al., 2007, 2009; Novaes et al., 2010, 2013; Viana & Lovato, 2010; Collevatti et al., 2012, 2014). This may partly explain the geographic separation of the potential distribution and the considerable niche difference between the two populations.

According to the consensus model based on past transferences of *D. calderonii*, the species had consistently suitable environments, mainly in the Pacific region of Nicaragua and occasionally in El Salvador, certain parts of Guatemala, Honduras, and southern Mexico (Oaxaca). The results indicate that during the projected periods, the species experienced changes in its suitable areas, moving from southern Mexico to northern Costa Rica. Additionally, the projected distribution of the species has fragmented at least twice as evidenced by the Mmx model. Despite the results, we must consider that the lack of sufficient records in both populations (particularly in the Mexican population) and their absence in the intermediate area between both populations, could be limiting the adequate reconstruction of the species' ecological niche. This lack could be the result of natural or anthropogenic local extinctions that are obscuring the recovery of current and past distribution patterns during modelling and transfer exercises.

Niche overlap

When niches between the Mexican (Mmx) and Central American (Mca) populations were compared, they showed a relatively low environmental values in the similarity test; however, this observed value was non-significant (i.e, it could be obtained also randomly). Similar result was obtained when the comparison was measured by niche overlap using ellipsoids. Although both tests were not significant, the differences observed when analyzing some variables independently, could be linked to the varying environments they are exposed to; suggesting that the current geographic isolation between both populations can represents a primary differentiation stage that may lead to a divergence in physiological and ecological tolerances. Despite we could not find statistical differences neither similitude between the populations of *D. calderonii*, low niche similarity is common in closely related species; for instance, it has been found in five species of the family Myristicaceae (Shivaprakash et al., 2022) and in genera such as *Zaluzania* Comm. ex Gaertn. (Suárez-Mota & Villaseñor, 2020) and *Damburneya* Raf. (Giraldo-Kalil et al., 2023).

Other studies indicate that the geographic differences contribute to the differentiation of niches between closely related species (Suárez-Mota & Villaseñor, 2020; Shivaprakash et al., 2022; Giraldo-Kalil et al., 2023). This separation in geography and environment could also imply a genetic separation, as seen in *Dalbergia nigra* (Vell.) Allemão ex Benth., where three genetically different and latitudinally separated groups were identified across its geographic distribution (Ribeiro et al., 2011). Although genetic analyses were not included in

this study, given the evident geographic isolation and slight differences in environment between the Mexican and Central American populations.

The result here exposes and provides critical information for the conservation state and population trend of *D. calderonii*. Determining geographical and environmental range size is critically important for species conservation and management and for developing restoration and conservation mechanisms (Raes et al., 2009; Zhang et al., 2012; Yahara et al., 2013; Barbosa et al., 2019; de Mello et al., 2019; Liu et al., 2019; Adjonou et al., 2020; Lima & Calado, 2020; Semu et al., 2021; Mahatara et al., 2021; Dimobe et al., 2022; Ngarega, Gikonyo, et al., 2022; Ngarega, Nzei, et al., 2022). For example, our results help establish prioritized areas for conservation, mechanisms to regulate their trade, and management plan preparation. Considering these geographic and environmental differences, it is possible that the two populations constitute two distinct management systems. Therefore, we suggest that all different management and conservation efforts should prioritize both populations.

Declarations

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Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

No ethical statement is reported.

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Author contributions

Conceptualization: Manuel Medina-Amaya, Octavio Rojas-Soto, Sergio López. Data curation: Manuel Medina-Amaya. Formal analysis: Manuel Medina-Amaya, Octavio Rojas-Soto, Sergio López. Investigation: Manuel Medina-Amaya, Clara Luz Miceli-Méndez, Miguel A. Pérez-Farrera, Octavio Rojas-Soto, Sergio López. Methodology: Manuel Medina-Amaya, Miguel A. Pérez-Farrera, Octavio Rojas-Soto, Sergio López. Resources: Manuel Medina-Amaya, Clara Luz Miceli-Méndez, Miguel A. Pérez-Farrera. Writing –original draft: Manuel Medina-Amaya. Writing –review & editing: Manuel Medina-Amaya, Miguel A. Pérez-Farrera, Octavio Rojas-Soto, Sergio López, Clara Luz Miceli-Méndez

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Figures

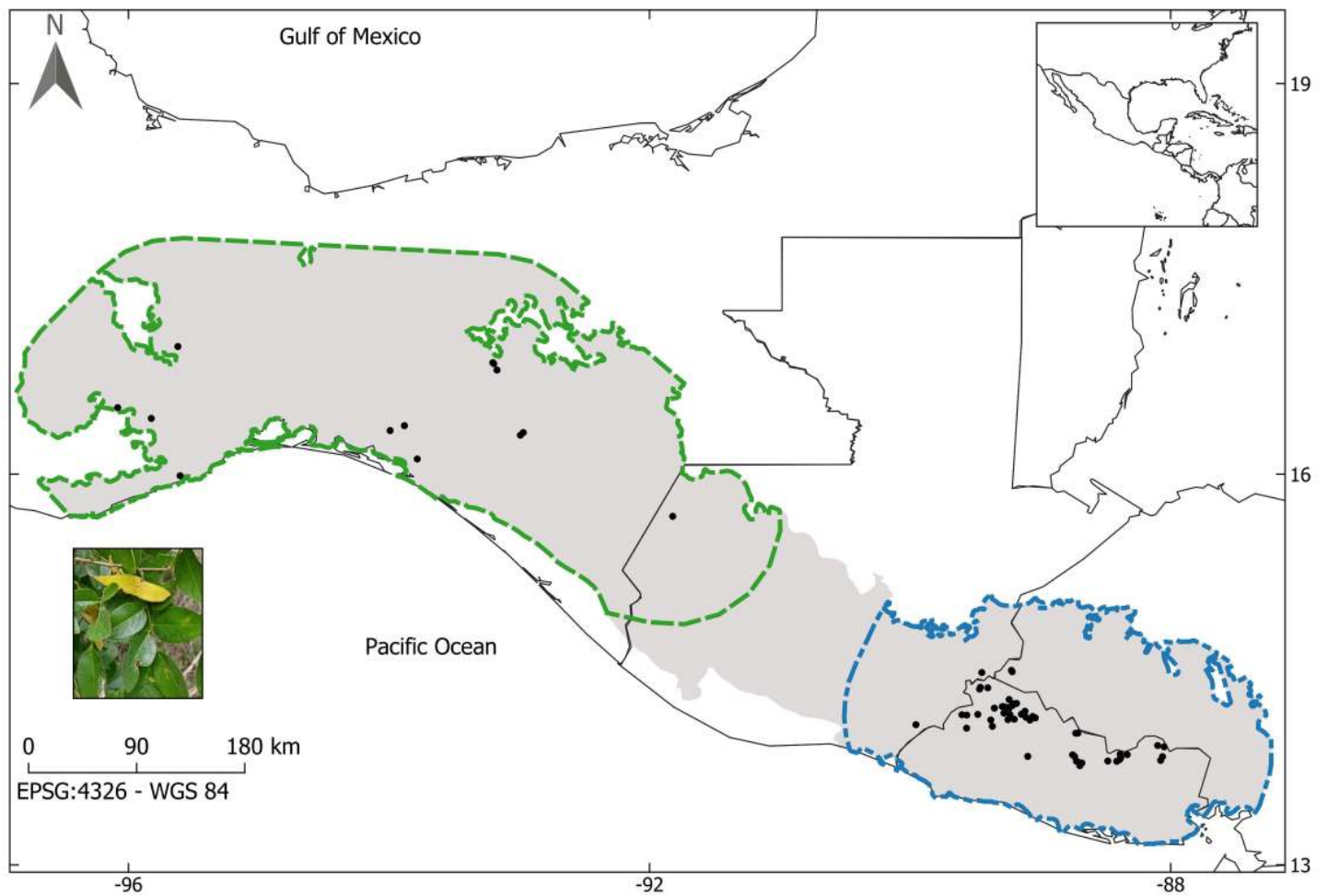


Figure 1

Records of presence of *Dalbergia calderonii* (black dots), and model calibration areas representing the accessible areas (M) for the species' general model (gray polygon), and for the Mexican population model (green line) and Central American population model (blue line).

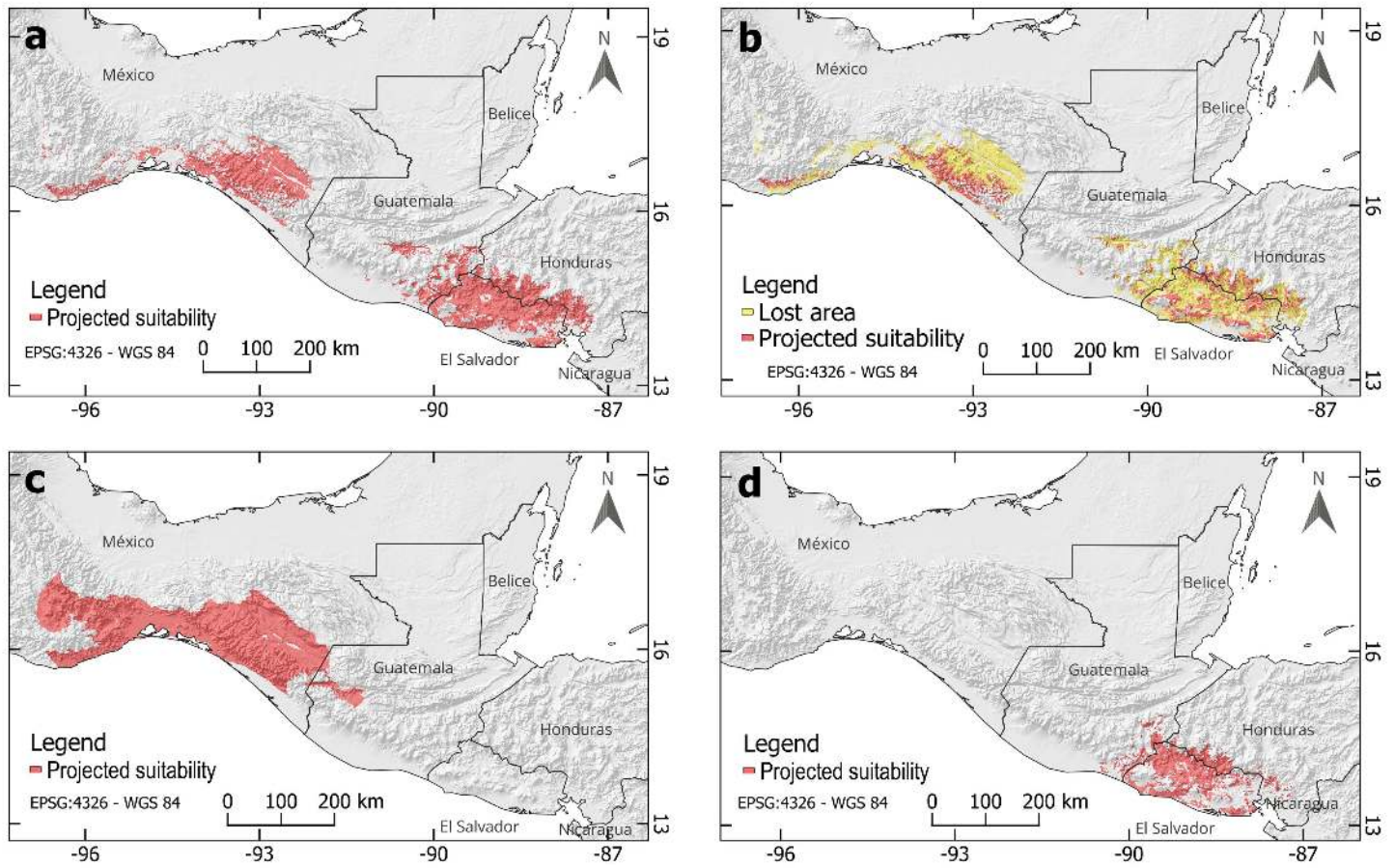


Figure 2

Areas of potential distribution of *Dalbergia calderonii* (red areas): a) general model; b) general model eliminating areas with sparse vegetation and bare soil (yellow areas); c) model of the Mexican population (Mmx); and d) model of the Central American population (Mca).

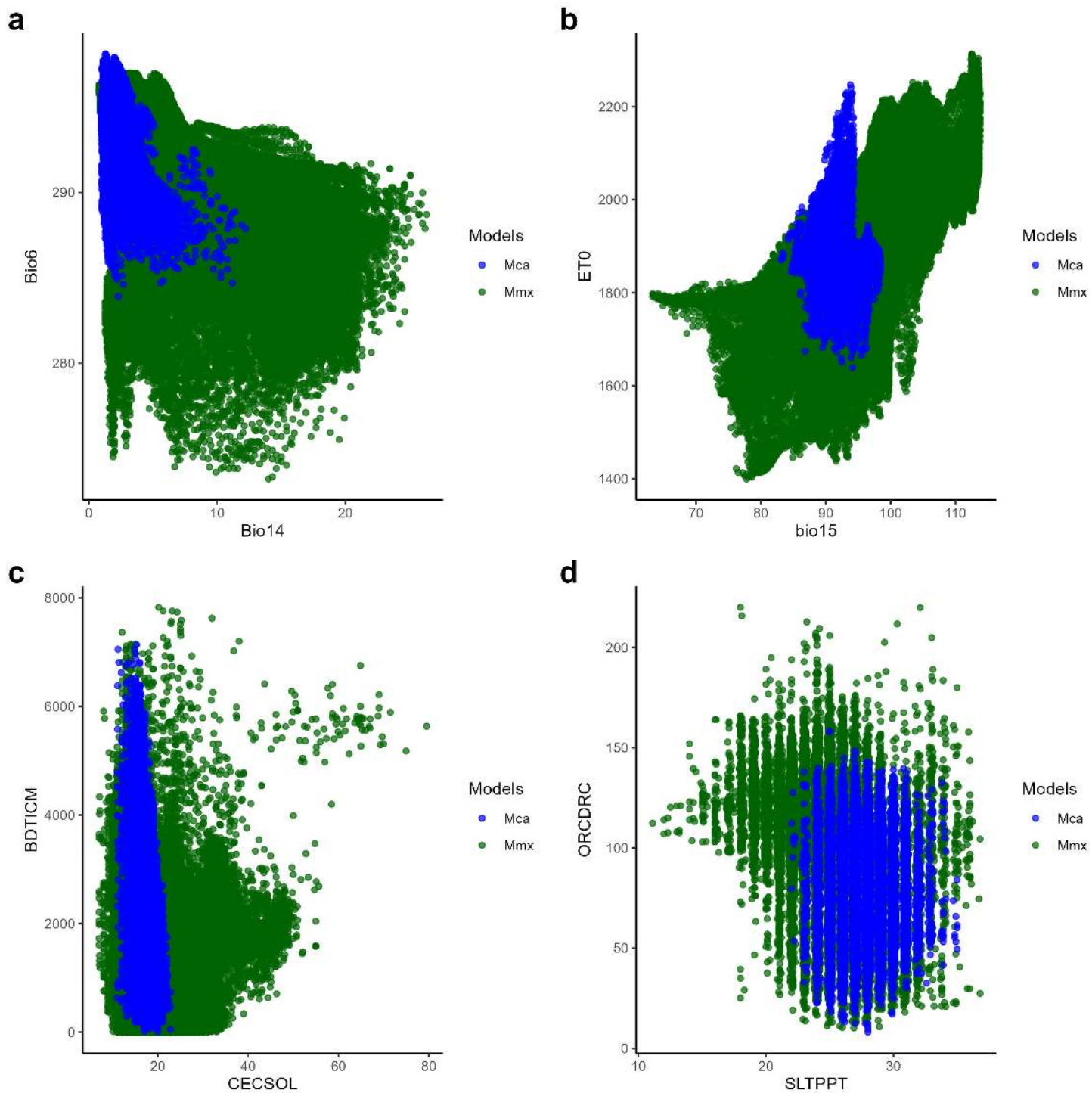


Figure 3

Comparison in two-dimensional environmental spaces of some of the most important variables predicted by the models for Mmx and Mca populations.

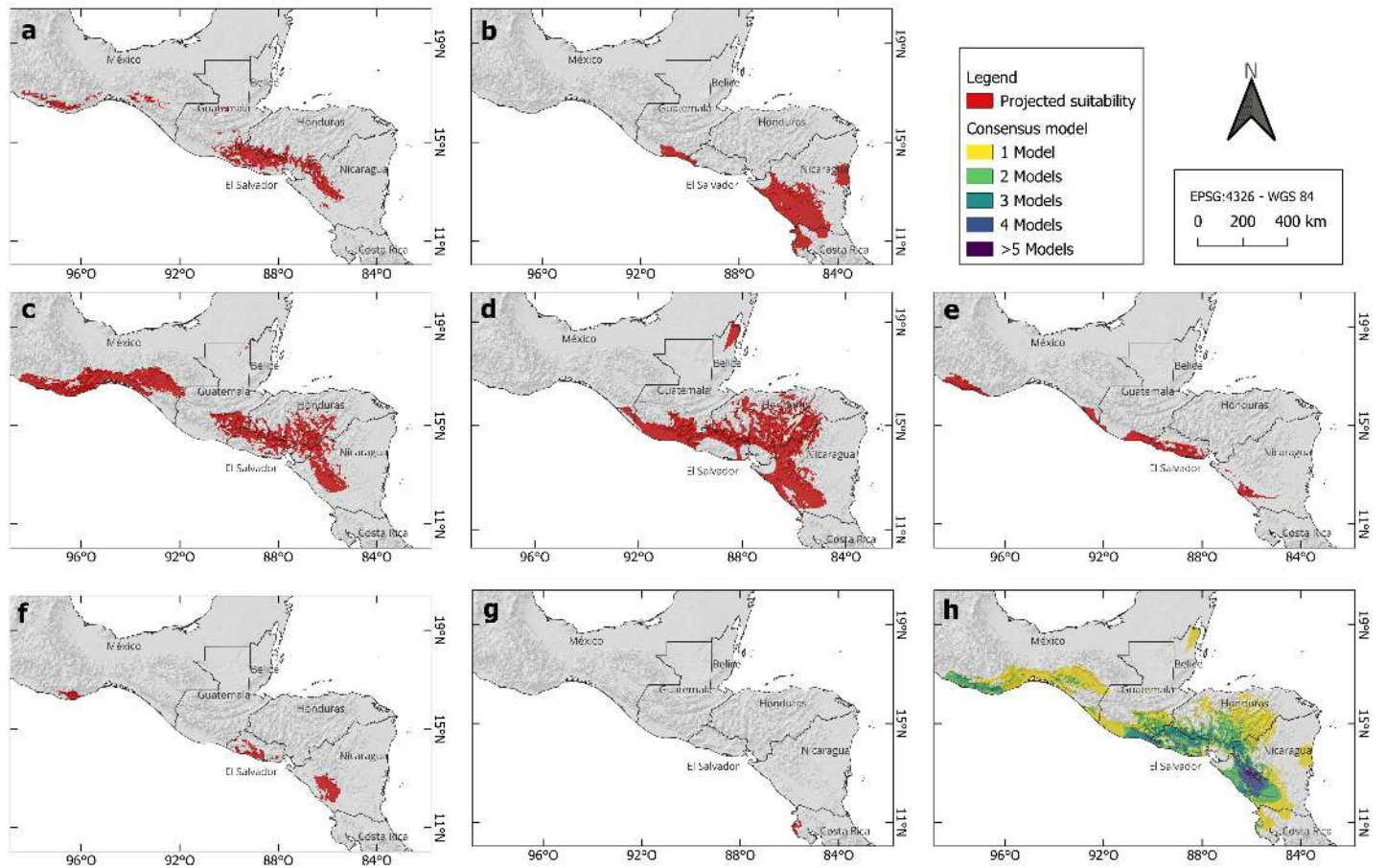


Figure 4

Changes in the potential distribution of *Dalbergia calderonii* and its projected populations from the present to different scenarios in the past: a) General model towards the Middle Holocene; b) General model towards the Last Glacial Maximum; c) Population of Mexico towards the Middle Holocene; d) Population of Mexico towards the Last Glacial Maximum; e) Population of Mexico towards the Last Interglacial; f) Population of Central America towards the Middle Holocene; g) Population of Central America towards the Last Glacial Maximum; h) Consensus among all models.

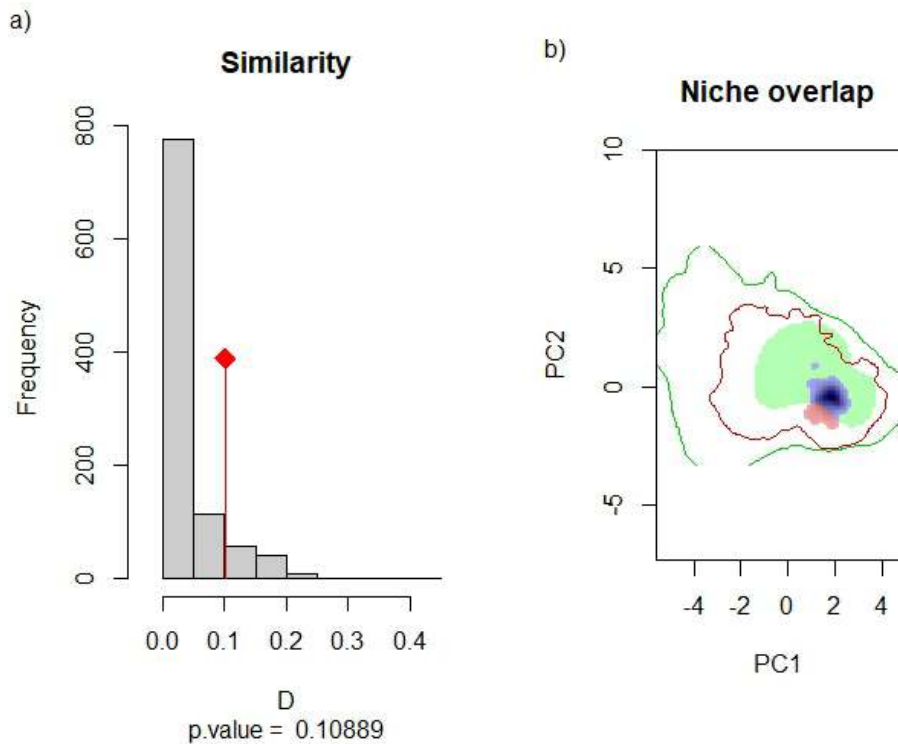


Figure 5

Niche comparison results. a) Niche similarity test; b) niche overlap of the Mexican and the Central American populations.

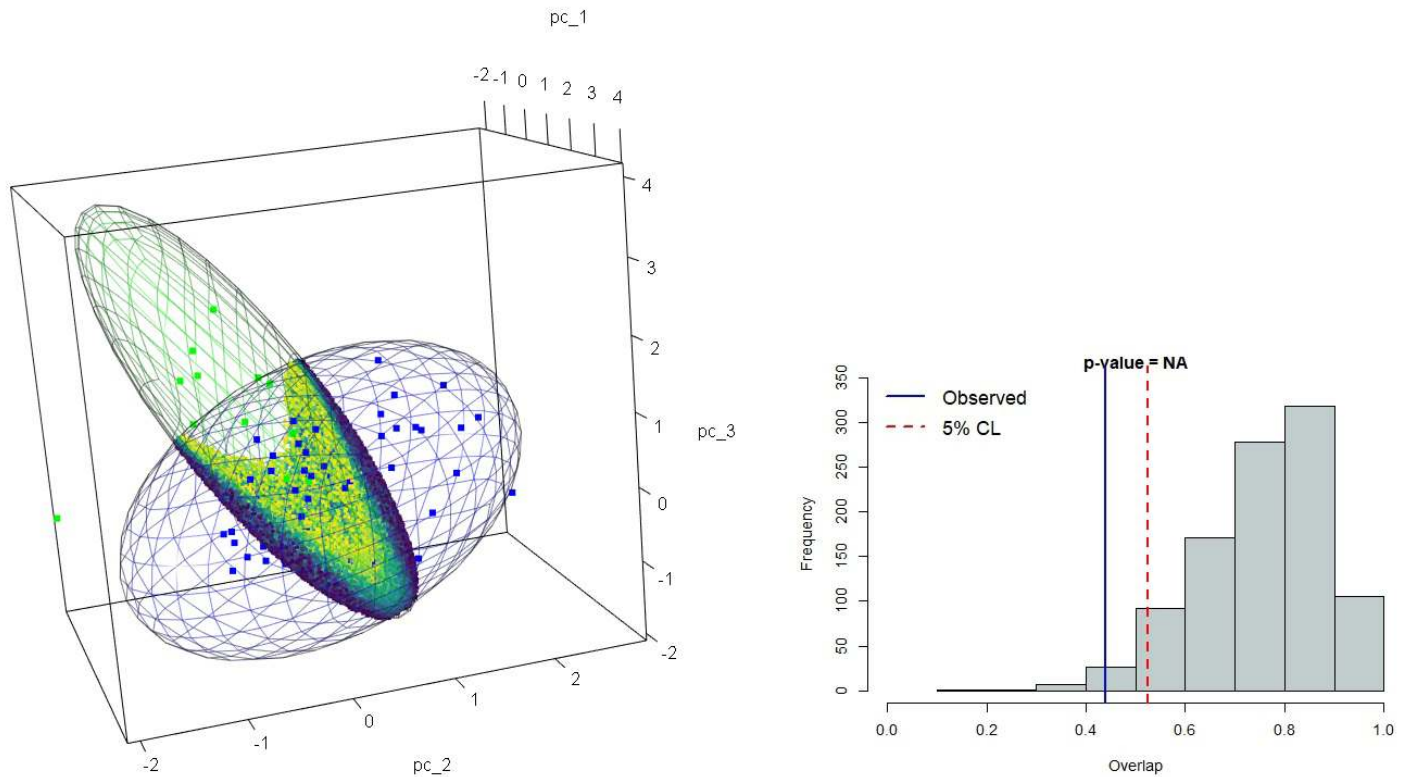


Figure 6

Comparison of niche overlap using ellipsoid and principal component models. Left: green ellipsoid corresponds to the Mexican population and blue ellipsoid corresponds to the Central American population. Right: Comparison of the observed values of overlap with the random niches of 1000 replicates. Solid blue line shows the observed value. Dashed red line shows the 5% confidence interval.

