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Beyond protected areas: spatial conservation priorities for an endemic and endangered orchid species in Mexico using species distribution models

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Introduction: Identifying geographic areas with suitable environmental
conditions for endangered and endemic species is crucial to enhancing
conservation efforts. *Oncidium incurvum* is a rare epiphytic orchid endemic to
Mexico. Like its relatives, it faces human-related pressures that threaten its
survival. This study aimed to identify geographic areas that are environmentally
suitable for this species and to propose priority zones for its conservation.

Methods: Occurrence data were obtained from herbarium collections and field
observations. The data were verified and cleaned to identify distribution patterns.
MaxEnt was used to model the species distribution using 18 environmental
variables. The resulting model was overlaid on a map of Mexico's biogeographic
provinces for clarity. The model was overlaid on layers of the human impact index,
protected natural areas, and priority conservation sites to identify areas
for conservation.

Results: The species is distributed across southern and southeastern Mexico,
occurring in montane cloud forests, evergreen tropical forests, and coniferous
and oak forests. Factors influencing its potential distribution include temperature
seasonality, elevation, annual precipitation, precipitation during humid months,
and annual evapotranspiration. The proposed priority conservation areas are the
Sierra Madre del Sur, the Chiapas Highlands, and the Veracruz Province within the
portion corresponding to the state of Chiapas.

Discussion: This study identified suitable areas that support the presence of
O. incurvum beyond known hotspots and protected areas. The findings provide
crucial information to guide conservation efforts for *O. incurvum* and highlight the
importance of integrating areas of medium suitability environmental into the
environmental as climatic refuges for rare and endemic species.

KEYWORDS

ecological niche modeling, epiphytes, mountain cloud forests, *Oncidium*,
Orchidaceae, rare species

1 Introduction

For over a century, ecologists have studied the historical and current factors that shape the spatial patterns of species distributions. However, the ongoing loss of biodiversity driven by global changes and human-driven landscape modifications (Ceballos et al., 2015) has made these questions more urgent than ever. Conservation biology faces two major challenges: understanding the factors that generate biodiversity (Keil and Chase, 2019) and identifying key geographic hotspots to ensure its conservation (Maxwell et al., 2020). Understanding the geographic ranges of species and the environmental factors that shape them is crucial for supporting global diversity patterns, assessing extinction risk, and informing conservation plans (Svahnström et al., 2025). The absence of this knowledge hampers our ability to identify geographic areas that require protection.

Understanding current and potential distributions of species, particularly for endemic or at-risk species, helps identify habitat features and provides valuable insights for their conservation or adjusting spatial distributions (Meza-Rangel et al., 2014). This is important because the habitats and distribution areas of species are changing due to climate change, human activities, and natural disturbances (Chen et al., 2011).

Advances in bioinformatics have created new opportunities to analyze species presence or absence, supporting the development of conservation strategies through species distribution models (Plischoff and Fuentes-Castillo, 2011). Analyzing species presence records alongside environmental variables enables us to predict potential areas with suitable conditions for species establishment and to explore less-studied areas that could be vital for the recovery and persistence of their populations (Mateo et al., 2011). This is particularly significant because species distribution models are valuable tools for identifying climate refugia for rare and endangered species (Kolanowska, 2023). Thus, ecological niche (EN) and species distribution models (SDM) are effective tools for conserving vulnerable taxonomic groups and their habitats (Cotrina et al., 2021).

Orchidaceae is one of the largest families of flowering plants worldwide, comprising approximately 31,000 species (Freudenstein, 2025). Around 50% are threatened, and only 7% are listed in the IUCN Red List (Vitt et al., 2023), leaving the vast majority without legal protection and vulnerable. Given that the IUCN criteria for assessing the extinction risk of a species include the geographic distribution (IUCN, 2024), various studies have utilized ecological niche and species distribution models to contribute valuable information by identifying suitable habitats for conservation, thereby facilitating inference of species distributions aligned with conservation targets (Babanezhad and Naqinezhad, 2025).

Regarding orchids, Wang et al. (2015) conducted a notable study where data on *Spiranthes parksii* Correll guides future research toward areas with high likelihood of presence and helps identify areas for conservation. Another study worth highlighting is that of Pica et al. (2024), who identified environmental factors influencing the distribution and suitable habitat areas that provide refuge for three orchid species, ensuring their survival. More research has been carried out about this topic; however, most

studies have focused on terrestrial orchids, being less common in epiphytes. Among the studies with epiphytic orchids are *Laelia speciosa* (Kunth) Schltr. in Mexico (Flores-Tolentino et al., 2020), *Vanda thwaitesii* Hook.f. in India (Decruse, 2023), and *Corybas taliensis* Tang & F.T.Wang in China (Liu et al., 2024), where distribution models were used for conservation purposes, demonstrating their usefulness.

In Mexico, approximately 1,300 orchid species have been recorded (Castillo-Pérez et al., 2018), of which 40% are endemic to the country (Hágsater et al., 2005). As in other parts of the world, the main causes of their decline are poaching of wild populations and illegal trade, driven by the visual appeal of their flowers (Hinsley et al., 2018), collection for religious and cultural ceremonies, and habitat loss and fragmentation (Reiter et al., 2016). This is compounded by the limited distribution ranges of most species, their naturally small and isolated populations, and their highly specialized pollination strategies (Bohman et al., 2014), which can push them into an extinction vortex.

Oncidium incurvum Barker ex Lindl. (Figure 1) is an epiphytic orchid restricted to certain evergreen tropical forests and mountain cloud forests in southern and southeastern Mexico (Soto-Arenas and Solano-Gómez, 2007a). Given to its limited geographic range, this species can be considered rare sensu Rabinowitz (1981). Small geographic ranges are key indicators of a species' extinction risk, as highlighted by Purvis et al. (2000), making this understanding crucial.

This species is classified as threatened under Mexican law (NOM-059-SEMARNAT-2010; SEMARNAT, 2010), due to illegal trade driven by its ornamental appeal, characterized by inflorescences with numerous purple flowers and curved petals (Beutelspacher, 2013), as well as its ceremonial use (Flores-Palacios and Valencia-Díaz, 2007; Álvarez-Mora et al., 2016). However, at the international level, it lacks an assessment of its conservation status. In the face of the ongoing increase in deforestation and land-use change, the fragmentation of its natural habitats has threatened isolated populations (Sánchez-Ramos and Dirzo, 2014; Martínez-Ramos et al., 2016), making a preliminary assessment of its conservation status urgent and the incorporation of this assessment into international legislation in the short term.

Given this critical scenario, understanding spatial distribution patterns and the environmental factors that shape them is crucial for developing effective management plans for orchid conservation. This is particularly important for epiphytic orchids, which are sensitive to environmental changes (Zotz and Hietz, 2001; Fay and Chase, 2009). Some studies have documented the general effects of environmental variables on their distribution patterns (Gaskett and Gallagher, 2018; Evans et al., 2020). Hence, contributing to this knowledge is essential.

Changing climate conditions further threaten the survival of epiphytic orchids; therefore, identifying critical geographic areas, both current and potential, with suitable environmental conditions for conserving *O. incurvum* is crucial. Taking the above into account, the following research questions were posed: What are the distribution patterns, and what environmental variables influence the distribution of *O. incurvum*? What is the current conservation status of the species? Which geographic areas present



FIGURE 1

Oncidium incurvum: (A, B) in situ. (C) flower detail. Photographs by J. Andrés Vázquez-Benito.

suitable environmental conditions for its possible establishment? Which of these suitable geographic areas are critical and effective for the species conservation? In this context, the objectives of this study were a) to understand the current distribution patterns of *O. incurvum*, b) to assess the relative importance of environmental variables in the species distribution, c) to identify geographic areas with habitat suitability for the species, d) to explore the preliminary conservation status of the species based on criterion B of the IUCN guidelines, and e) to analyze and propose key geographic zones for the protection of *O. incurvum*. We discuss the preliminary conservation status of *O. incurvum* and the current and future threats to its persistence.

2 Materials and methods

2.1 Occurrence data

Occurrence records were compiled from herbarium specimens and direct field collections. Specimens from the following botanical collections were examined: AMO, CHAP, CHAPA, CHIP, CIB, CNS-UT, COLO:V, ENCB, FMNH, HUAP, IEB, JCJB, MEXU, MO, MSC, OAX, SEL, SERO, UAMIZ, and XAL (acronyms according to Thiers, 2026). The data span the period from 1971 to 2015. From this review, 147 records with geospatial information were selected, excluding those lacking geographic coordinates. The geographic coordinates for all records were verified using Google Earth Pro v.7.3.6 (Google, 2023). After verification, 41 valid records remained.

Field expeditions to locate, document, and updated records of the species' presence were conducted from April 2023 to August 2024 (Figure 1). The routes spanned the known distribution range

of *O. incurvum* in the tropical evergreen forests and mountain cloud forests across the Mexican states of Chiapas, Oaxaca, Puebla, and Veracruz. As a result of these expeditions, 36 new georeferenced records were obtained, bringing the total number of valid and verified presence records to 77. Because the species is protected under Mexican law NOM-059-SEMARNAT-2010 (SEMARNAT, 2010), only one complete specimen was collected, and has been deposited as a voucher (CHAPA156997) in the CHAPA herbarium collection (Thiers, 2026) of the Colegio de Postgraduados.

The 77 records were subjected to numerical and geospatial reduction analysis to minimize spatial autocorrelation, utilizing the spThin package in R (Aiello-Lammens et al., 2015). A critical distance of 5 km between records was determined heuristically, given that *O. incurvum* is an endemic, numerically rare species with a distribution limited to the mountain cloud and tropical evergreen forests of Chiapas, Puebla, Oaxaca, and Veracruz. After spatial reduction, 34 presence records without autocorrelation remained and were used in the modeling.

2.2 Current distribution patterns

To analyze the current distribution patterns of the species across Mexican states, a 0.5° latitude × 0.5° longitude polygon mesh was created using QGIS v3.32.3 (QGIS.org, 2024). This mesh was used to count occurrence records, which were then overlaid on the state political division layer at a scale of 1:250000 (INEGI, 2024) using ArcGIS v.10.8 (ESRI, 2021).

To describe the topography associated with the distribution of *O. incurvum*, the Physiographic Provinces in Mexico layer (INEGI, 2001) was used. Additionally, the Land Use and Vegetation of Mexico layer, Series VII (National Continuum), from INEGI (2021) was used to identify patterns in the vegetation types inhabited by

the species. Climate information associated with the vegetation and its nomenclatural equivalents was obtained as described by Rzedowski (2006).

Using the elevation data (m a.s.l.) from the herbarium labels, along with data collected directly in the field, we analyzed the altitudinal distribution of the species with the support of InfoStat (Di Rienzo et al., 2011). Presence records were grouped into 500 m intervals, and we counted the number of records in each interval.

2.3 Environmental variables

The 19 bioclimatic variables were downloaded from WorldClim (<https://www.worldclim.org/data/worldclim21.html>; Fick and Hijmans, 2017) and then clipped to a dissolved polygon of the Mexican Republic in QGIS v3.32.3 (<https://www.qgis.org/QGIS.org>, 2024). The output rasters were configured to have the same number of rows and columns and saved in ASCII format. Of these 19 environmental variables, only five were selected (Table 1) as being potentially linked to the geographic distribution of *O. incurvum*. In addition, ten environmental variables were selected based on Cruz-Cárdenas et al (2014; Table 1). This set of variables was chosen based on the epiphytic habit of *O. incurvum* and was clipped to the vegetation types where this species occurs, using QGIS v3.32.3. Under these same considerations, three additional covariates were calculated due to their importance for epiphytic species. These variables include: relative humidity of the humid months (RHH), calculated as the sum of precipitation from May to October divided by the total annual precipitation (BIO12) (Mociño

and García, 1974); relative humidity of the dry months (RHS), calculated as the precipitation from November to April divided by BIO12; and the percentage of winter precipitation (LLINV) estimated by summing the precipitation from November, December, and January then dividing by BIO12. Therefore, a total of 18 environmental variables were used in the distribution model of *O. incurvum*.

Both the generated and selected covariables are derived from data sets that exhibit multicollinearity or a high degree of correlation among the variables. Multicollinearity can inflate the variances of the predicted values and the estimated parameters, leading to a misleading relationship between the explanatory variables and the response variable (Guerrero, 2017). Therefore, it is crucial to ensure that all environmental covariates are mutually independent or orthogonal.

The multicollinearity problem was addressed by applying Principal Component Analysis (PCA) to the 18 environmental variables using ArcGIS v.10.8 (ESRI, 2021). One of the outstanding properties of PCA is that the resulting Principal Components (PCs) are orthogonal, meaning they are independent of each other. This property allows the PCs to be used as independent environmental covariates in species distribution modeling. Additionally, PCA serves various purposes, including dimensionality reduction, which involves decreasing the number of predictive variables while still retaining a high percentage of the variance from the original data (Tabachnick and Fidell, 2007). The first resulting PC explains the maximum percentage of variance recorded in the generated covariates, the second PC explains the maximum percentage of the remaining variance, and so on until the last PC

TABLE 1 Environmental covariates and factor loadings in the first two principal components (PCs) cumulatively explain 92.18% of the total variance observed.

Acronym	Covariate	PC1 (76.14%)	PC2 (16.03%)
¹ BIO1	Annual mean temperature	-0.00647	0.03904
¹ BIO3	Isothermality	0.00386	-0.00218
¹ BIO4	Temperature seasonality	0.93316*	0.13490
¹ BIO12	Annual precipitation	-0.22689*	0.24163*
¹ BIO15	Precipitation seasonality	-0.00065	-0.00552
² ETRA	Real annual evapotranspiration	-0.14824	0.17069*
² ETRAH	Real evapotranspiration of the humid months (May to October)	-0.12221	0.11303
² ETRAS	Real evapotranspiration of the dry months (November to April)	-0.02806	0.06939
² PPH	Precipitation of the humid months (May to October)	-0.19771*	0.16379
² PPS	Precipitation of the dry months (November to April)	-0.02918	0.07164
² TH	Mean temperature of the humid months (May to October)	0.00011	0.00328
² TS	Mean temperature of the dry months (November to April)	-0.00155	0.00360
² Elevation	Digital elevation model (altitude data m a.s.l.)	-0.00514	-0.91823*
² IVN _H	Humid months of year normalized index	-0.00009	0.00004
² IVN _S	Dry months of year normalized index	-0.00008	0.00007
³ RHH	Relative humidity of the humid months (May to October)	-0.00003	-0.00004
³ RHS	Relative humidity of the dry months (November to April)	0.00003	0.00004
³ LLINV	Percentage of winter precipitation (November to January)	0.00002	0.00003

¹Covariates selected from WorldClim. ²Covariates provided by Cruz-Cárdenas et al. (2014). ³Covariates generated in this study based on Mociño and García (1974). *Values with the greatest contribution to each PC (% variance).

(Tabachnick and Fidell, 2007). Dimensionality reduction is achieved by selecting a ranked number of PCs that explain a high percentage of the variation recorded in the original data. The number of PCs selected is a function of the variance percentage that meets the standards of the research conducted. In this case, among the 18 resulting PCs, the first two accounted for 92.18% of the total variance in the data (Table 1).

2.4 Species distribution model

The model was calibrated using the Kuenm v.1.1.1 statistical package for R (Cobos et al., 2019). During this process, 14 regularization multipliers and seven feature class combinations were evaluated. Parameters exhibiting a 5% omission rate and the corrected Akaike information criterion (AICc) were selected. The resulting model used a regularization factor of 0.1 and the combination of linear (L) and quadratic (Q) classes to configure the MaxEnt v3.4.4 algorithm (Phillips et al., 2023). MaxEnt estimates the species' probability distribution using the near-uniform or maximum entropy distribution, constrained by the set of incomplete occurrence records for *O. incurvum*.

The mobility area (*M*) of *O. incurvum* was delimited based on the updated and expanded distribution of its occurrence records. The assessment used the Biogeographic Provinces of Mexico as outlined by Morrone (2019) and incorporated the species' latest occurrence data.

To generate the species distribution model (SDM), the MaxEnt algorithm was employed. This algorithm requires only the presence records of the species and a set of predictive environmental covariates (Phillips et al., 2006). The 34 records of *O. incurvum*, free of geospatial autocorrelation, along with the two principal components from the PCA, were utilized in the modeling process. Because MaxEnt is a non-parametric algorithm, it can incorporate interactions among variables, producing continuous suitability maps (Elith et al., 2006).

The selected MaxEnt configuration was activated by enabling the do Jackknife modules to assess the relative importance of each variable and do figures for each variable with a logistic output from the model. Seventy-five percent of the presence records were selected to train the model. The remaining 25% was used to validate it (Phillips and Dudík, 2008). The extrapolate and do clamping modules were disabled.

Model performance was evaluated using omission rates and Receiver Operating Characteristic (ROC) curves (Hernández et al., 2018). In ROC analysis, values close to or equal to 1 for the Area Under the Curve (AUC) are considered excellent, while those ranging from 0.85 to 0.95 are deemed good. Meanwhile, AUC values near 0.5 should be disregarded as they indicate a random model (Elith, 2000).

Using the mean and one standard deviation from the Maxent results, the output was reclassified into three categories. Class 1 was defined as the "unsuitable class" and included values ≥ 0.5 . Class 2 was the "medium suitable class" with values between 0.51 and 0.69, and Class 3, namely the "highly suitable class", included values ≥ 0.7 . Class 3 contains areas with environmental conditions favorable

for the permanent, stable, and indeterminate persistence of *O. incurvum*, in contrast to Class 1, which lacks the environmental conditions for its indefinite presence. Conversely, Class 2 includes areas with moderately suitable habitat conditions that support the species' presence, albeit in an unstable or intermittent manner.

Attributes related to areas in the high (≥ 0.7) and medium (0.51 – 0.69) suitability classes were extracted from the MaxEnt model using the Extract by Attributes tool in ArcGIS v10.8 (ESRI, 2021). This process created an ASCII layer showing areas classified within those suitability categories. The layer was then overlaid with the Biogeographic Provinces of Mexico layer (Morrone, 2017; Morrone, 2019) to clip the suitable areas based on the area *M* used in the model. Zonal statistics were calculated from the resulting layers using the Spatial Analyst Tools and Field Calculator in ArcGIS v10.8.

2.5 Preliminary conservation status

To assess the species' conservation status, a preliminary evaluation was conducted using IUCN criteria and categories (IUCN, 2024) based on geographic data (Criterion B) and the GeoCAT program (Bachman et al., 2011). Conservation information was supplemented with literature and distribution model results.

2.6 Identification of priority areas for conservation of *O. incurvum*

After obtaining the final SDM, we analyzed and identified priority areas for *O. incurvum* conservation by considering the CONABIO (2019) index of human impact on terrestrial biodiversity. This index ranges from 0 to 1, with 0 indicating no impact and 1 indicating the maximum impact. Additionally, to identify potential threats to the species' preservation in suitable areas identified by the model, we overlaid the layers previously generated by biogeographic province, which include high and medium environmental suitability areas, with the Land Use and Vegetation of Mexico layer (INEGI, 2021). The resulting information was used to calculate zonal statistics in hectares for each environmental suitability class and land use by biogeographic province, as previously described in ArcGIS.

To identify suitable areas, particularly those classified as high and medium suitability, we examined two layers of information within Mexico's protected regions: the federal Natural Protected Areas (NPAs) (CONANP, 2024) and the Priority Terrestrial Sites (PTS) designated for Biodiversity Conservation (CONABIO et al., 2007). To identify priority areas for the conservation of *O. incurvum*, the following criteria were considered: 1) areas classified as high or medium suitability according to the MaxEnt model, 2) the presence and extent of vegetation types where the species thrives, 3) locations with a human impact index close to 0, and 4) high and medium suitability zones within NPAs or PTS that have been recognized as extreme or high priority for conservation efforts in the country. By focusing on these areas, we can significantly enhance our conservation strategies and ensure the sustainability of this species.

3 Results

3.1 Current distribution patterns

Oncidium incurvum is a species whose distribution is limited to southern and southeastern of Mexico, specifically in four of the 32 states that make up the country. The areas with the highest number of recorded sightings of this species are central Veracruz (39%),

northern Oaxaca (26%), northern Puebla (16%), and eastern Oaxaca (10%). The lowest presence of the species was recorded in southern Veracruz (4%), and in northwestern and southwestern Chiapas, both at 5% (Figure 2A).

In Mexico, the physiographic provinces show varying levels of species presence. The eastern part of the Neo-Volcanic Axis has the highest percentage at 41%. This is followed by the southeastern section of the Sierra Madre del Sur at 26%, the eastern part of the

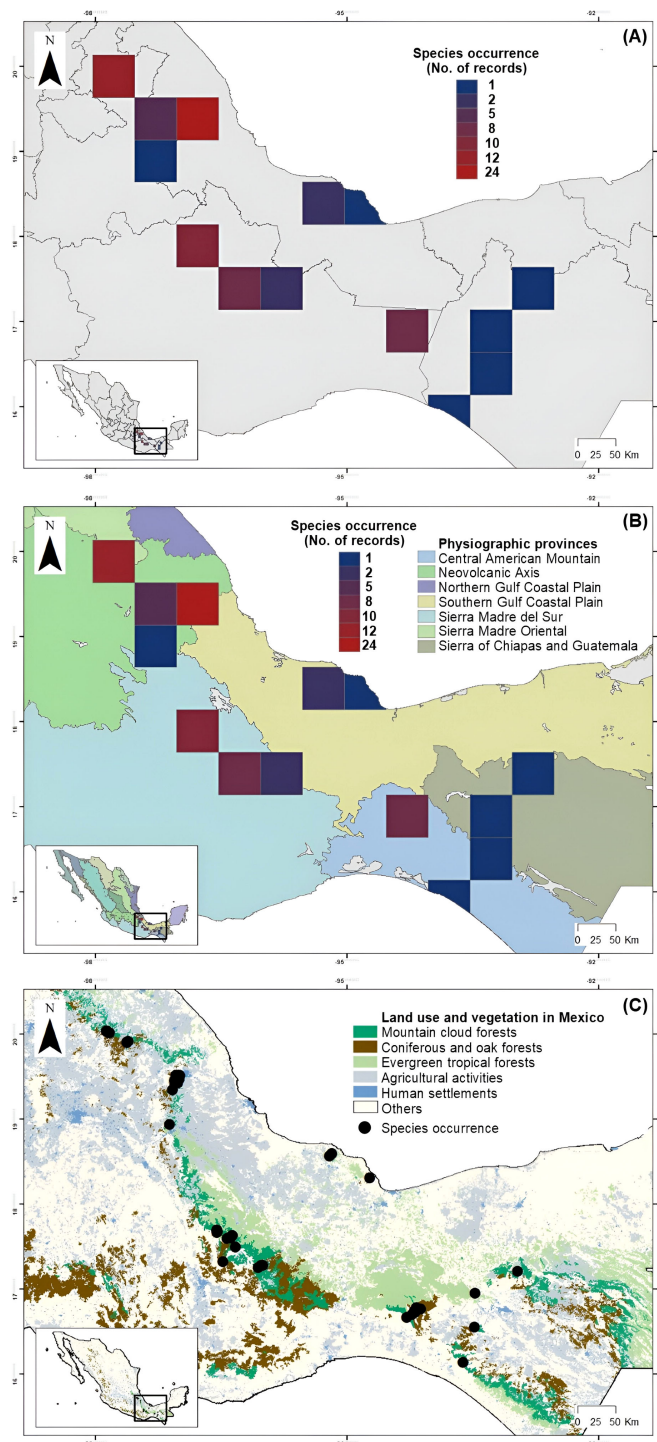


FIGURE 2
Distribution of *Oncidium incurvum* by: (A) Political Division (INEGI, 2024). (B) Physiographic Provinces (INEGI, 2001). (C) Land Use and Vegetation in Mexico (INEGI, 2021). Maps by J. Andrés Vázquez-Benito.

Central American Mountain Range at 13%, and the southern region of the Sierra Madre Oriental at 12%. In contrast, the Sierra de Chiapas and Guatemala exhibit the lowest species presence, at 3% (Figure 2B).

Regarding vegetation types, 73% of this orchid's occurrences are found in mountain cloud forests (MCF), followed by coniferous and oak forests (COF) at 22%, which are associated with humid temperate and subhumid climates, respectively. The species occasionally occurs in evergreen tropical forests (ETF), which make up 5% of its distribution (Figure 2C).

Altitudinal distribution analysis of *O. incurvum* indicates that this species occurs at elevations from 775 to 2,246 m. Occurrences increase between 1,000 and 1,500 m, which account for 36% of total observations. The highest occurrence is found between 1,501 and 2,000 m (46%). In contrast, occurrences decrease at the extremes of its altitudinal range, with 5% at 500–1,000 m and 13% between 2,000 and 2,500 m.

3.2 Environmental variables

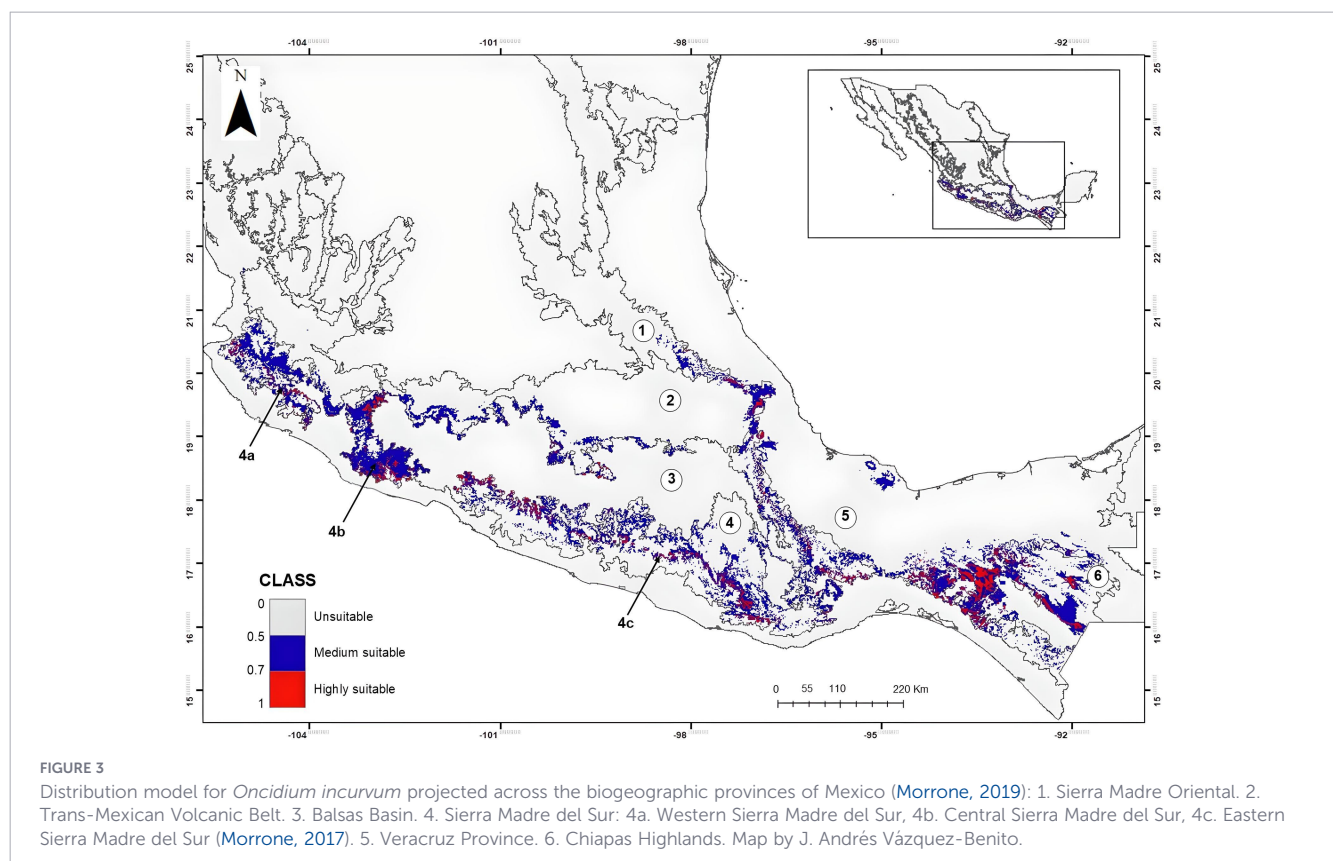
The results from the first two PCs indicate that temperature seasonality (BIO4) in PC1 and total annual precipitation (BIO12), precipitation in humid months (PPH), and real evapotranspiration (ETRA) are the most significant climatic variables determining the distribution of *O. incurvum*. However, in PC2, the digital elevation model (elevation) was the most important geographic factor structuring climatic variables (Table 1).

3.3 Species distribution model

The ROC analysis showed that the AUC for the training was 0.911, indicating that the resulting model is good. According to the model generated by MaxEnt (Figure 3), 2.99% of area *M* had a probability ≥ 0.7 of having potentially suitable environmental conditions for the establishment of *O. incurvum*, indicating a highly suitable class. Additionally, the medium suitability class, with a probability ranging from 0.51 to 0.69, covered 10.71% of area *M*.

The areas with the largest surface areas suitable for both the high and medium classes for the occurrence of the species are located in the Sierra Madre del Sur biogeographic province, covering 500,129.78 ha and 2,669,806.1 ha, respectively. The Eastern Sierra Madre del Sur subprovince, particularly along the Balsas Basin, slope between the states of Guerrero and Oaxaca, contains the largest area in the highly suitable class. Meanwhile, the northwest region of the Sierra Madre del Sur, the Central Sierra Madre del Sur, and Western Sierra Madre del Sur subprovinces have the highest proportion of areas classified as medium suitable class. This region encompasses parts of the states of Michoacán, Colima, and Jalisco.

Following the Veracruz Province in terms of environmentally suitable surface, which has 305,547.68 ha of highly suitable and 664,429.7 ha of medium suitable habitats, bordering the Trans-Mexican Volcanic Belt and to the south with the Chiapas Highlands. This latter province stands out for having large areas



suitable for hosting the species (highly suitable class = 268,763 ha, medium suitability class = 694,140.1 ha). Meanwhile, the Trans-Mexican Volcanic Belt, in its convergence with the Balsas Basin, the Veracruz Province, and the Sierra Madre del Sur, was the second province with the largest medium suitable area, totaling 706,369.4 ha, only below the SMS (Figure 3). Other areas that show a high suitability class, but with surface areas under 300,000 ha, are located in the southern part of the Sierra Madre Oriental along its borders with the Veracruz Province (Table 2).

3.4 Conservation status

According to the IUCN (2024) Red List categories and criteria, *O. incurvum* can be classified as endangered (EN) under B2ab(iii) (v). The species' area of occupancy (AOO) was < 500 km² (188 km²), and its distribution is restricted to certain regions of Puebla, Veracruz, Chiapas, and Oaxaca. Additionally, its habitats, the MCF, COF, and ETF, are among the most threatened vegetation types in the country (Sánchez-Ramos and Dirzo, 2014; Martínez-Ramos et al., 2016; Alvarado-Rosales et al., 2024). The decline of *in-situ* populations is exacerbated by illegal poaching of mature individuals of the species (Flores-Palacios and Valencia-Díaz, 2007; Álvarez-Mora et al., 2016). In addition, the SDM indicated that areas potentially suitable for the conservation of *O. incurvum* account for less than 1% and 3% of the national territory, corresponding to

high and medium suitability, respectively. Taken together, these factors highlight the species' vulnerability.

3.5 Identification of priority areas for conservation of *O. incurvum*

Based on SDM results, the largest expanses of highly suitable habitat occur in the Eastern Sierra Madre del Sur subprovince of the Sierra Madre del Sur and at the convergence of two biogeographic provinces: the Veracruz Province and the Chiapas Highlands. Together, these areas are significant because they contain the largest expanses of MCF along the Mexican Pacific coast. These areas account for 1,009,272.7 ha of highly suitable habitat (Figure 4A; Table 2). Of this area, only 7.56% belongs to MCF and 18.45% to COF, located in regions with an index impacted by human activities < 0.3 (Figure 4B). According to the Land Use and Vegetation map, in environmentally suitable areas with forest cover, agricultural activities and human settlements are the leading causes of impact, with values close to 1. This human influence reduces suitable areas by 25% within the species' suitable habitats. Consequently, the effective area of suitable habitat for *O. incurvum* is estimated to be 37,576.3 ha of MCF and 131,324.7 ha of COF in the Eastern Sierra Madre del Sur subprovince, 27,870.7 ha of MCF and 52,435.7 ha of COF at the Chiapas Highlands, and 10,908.1 ha of MCF and 2,536 ha of COF located south of the Veracruz Province (Table 2).

TABLE 2 Area in hectares (ha) of highly and medium suitability classes regions according to the potential distribution model for *Oncidium incurvum*, based on Land Use and Vegetation in the biogeographic provinces of Mexico (Morrone, 2019).

Biogeographic province	Suitable area	Land use (ha)					
	(ha)	MCF	COF	ETF	AA	HS	Others
Highly suitable class							
Sierra Madre Oriental	115291.2	40674.7	20337.4	0	54279.1	0	0
Trans-Mexican Volcanic Belt	157574.3	21256.8	5530.9	0	76612.6	17774.4	36399.6
Sierra Madre del Sur	500129.7	44011.4	137185.6	4051.1	67917.6	1700.4	245263.6
Eastern Sierra Madre del Sur	434962.0	37576.3	131324.7	4038.1	51939.8	1506.2	208576.9
Central Sierra Madre del Sur	35644.9	0	0	0	0	0	35644.9
Western Sierra Madre del Sur	29522.8	6412.2	5846.8	0	15954.3	193.8	1115.7
Chiapas Highlands	268763.0	27870.7	52435.7	6584.7	60874.8	1424.4	119572.7
Veracruz Province	305547.7	10908.1	2536.0	69023.2	110088.8	4949.9	108041.7
Total	1847435.6						
Medium suitability class							
Sierra Madre Oriental	79459.6	20064.1	12738.6	0	36943.0	1831.1	7882.8
Trans-Mexican Volcanic Belt	706369.4	48386.3	101221.5	0	314913.8	16344.7	225503.1
Sierra Madre del Sur	2669806.0	179781.7	745366.8	20831.7	373747.6	8119.1	1341959.1
Eastern Sierra Madre del Sur	1687489.1	117500.0	203317.9	20831.7	0	3880.3	1341959.1
Central Sierra Madre del Sur	915796.5	0	542048.9	0	373747.6	0	0
Western Sierra Madre del Sur	66520.4	62281.7	0	0	0	4238.7	0
Chiapas Highlands	694140.1	133607.9	126949.2	28978.2	240889.2	6638.3	157077.3
Veracruz Province	664429.9	13966.4	6576.3	214764.3	287924.0	8363.0	132835.9
Total	7484011.0						

Mountain cloud forests (MCF), coniferous and oak forests (COF), evergreen tropical forests (ETF), agricultural activities (AA), human settlements (HS).

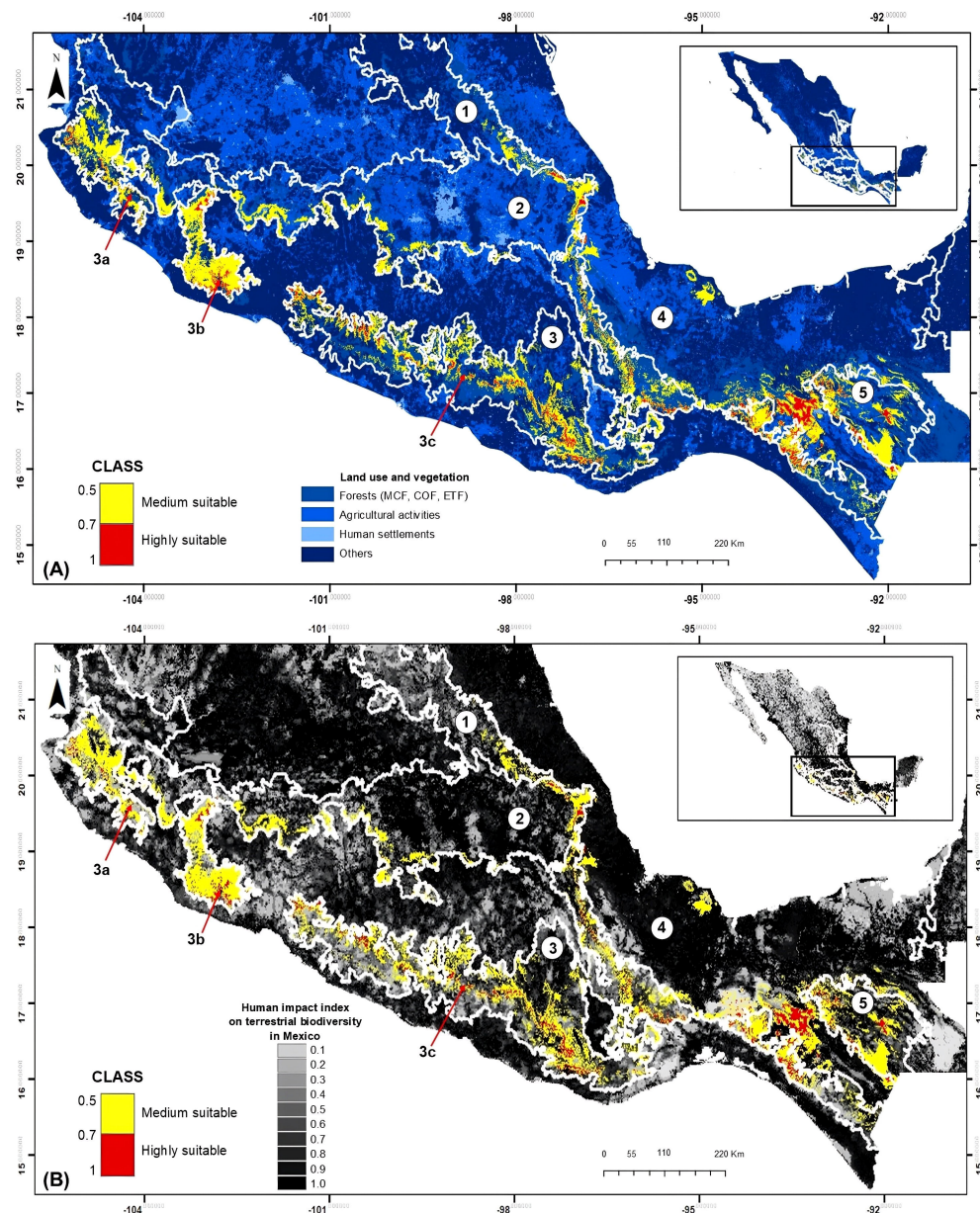


FIGURE 4

Distribution model for *Oncidium incurvum* projected across: (A) Land Use and Vegetation (INEGI, 2021). (B) Human Impact Index on Terrestrial Biodiversity in Mexico (CONABIO, 2019). Biogeographic provinces of México (Morrone, 2019): 1. Sierra Madre Oriental. 2. Trans-Mexican Volcanic Belt. 3. Sierra Madre del Sur: 3a. Western Sierra Madre del Sur, 3b. Central Sierra Madre del Sur, 3c. Eastern Sierra Madre del Sur (Morrone, 2017). 4. Veracruz Province. 5. Chiapas Highlands. Maps by J. Andrés Vázquez-Benito.

Areas within the highly suitable class located in some NPAs were identified (Figure 5A). These include: Sierra Tecuani in the Sierra Madre del Sur, Selva El Ocote and Sumidero Canyon in the Veracruz Province, and the La Sepultura, the El Triunfo, and the Forest Protection Zone in Chiapas (municipalities of La Concordia, Ángel Albino Corzo, Villa Flores, and Jiquipilas) in the Chiapas Highlands. In total, five areas have been categorized as extreme conservation priority (Figure 5B).

The suitable medium class covers the largest surface area located to the west of the Sierra Madre del Sur, where it meets the Trans-Mexican Volcanic Belt (Western Sierra Madre del Sur subprovince), to the south of the Trans-Mexican Volcanic Belt, and where it intersects with both the Veracruz Province and the Chiapas

Highlands. Overall, these areas account for 2,131,459.8 ha of suitable land (Figure 4A; Table 2). Of this, only 12% is classified as MCF and 11% as COF. According to the human impact index, these forests are situated in areas with an index value below 0.3 (Figure 4B). Consequently, the effective suitable habitat for the medium suitability class comprises 62,281.7 ha of MCF and zero hectares of COF in the Western Sierra Madre del Sur subprovince, 48,386.3 ha of MCF and 101,221.5 ha of COF in the Trans-Mexican Volcanic Belt, 133,607.9 ha of MCF and 126,949.2 ha of COF in the Chiapas Highlands, and 13,966.4 ha of MCF and 6,576.3 ha of COF in the Veracruz Province (Table 2).

Additionally, notable areas within the medium suitability class include: the Sierra de Manantlán and the Río Blanco Canyon in the

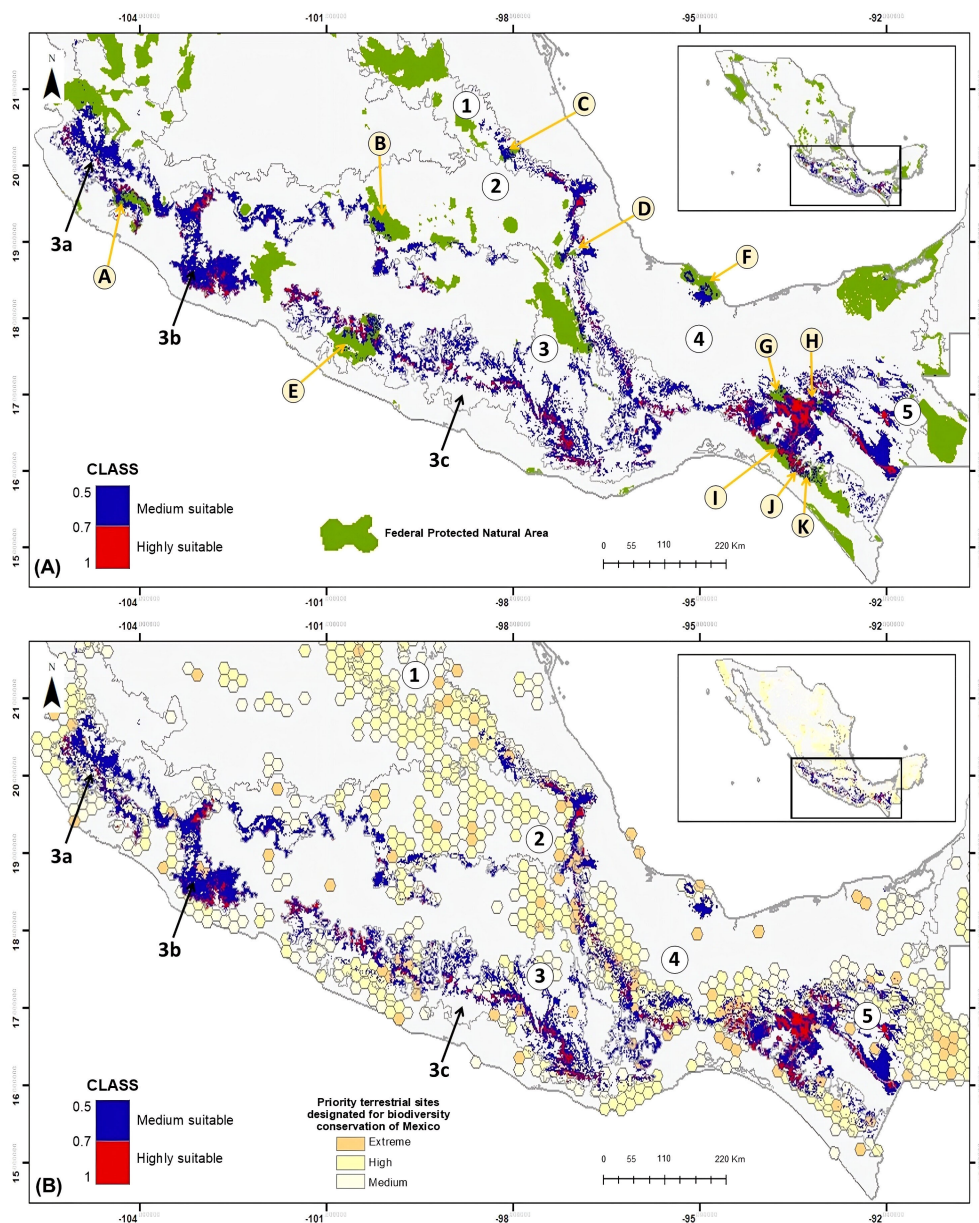


FIGURE 5

Distribution model for *Oncidium incurvum* projected across: (A) Federal Protected Natural Areas (NPAs; CONANP, 2024). (B) Priority Terrestrial Sites designated for Biodiversity Conservation of Mexico (CONABIO et al., 2007). Biogeographic provinces of México (Morrone, 2019): 1. Sierra Madre Oriental. 2. Trans-Mexican Volcanic Belt. 3. Sierra Madre del Sur. 3a. Western Sierra Madre del Sur, 3b. Central Sierra Madre del Sur, 3c. Eastern Sierra Madre del Sur (Morrone, 2017). 4. Veracruz Province. 5. Chiapas Highlands. Federal Protected Natural Areas (CONANP, 2024) A. Sierra de Manantlán. B. Forest Protection Zone of the lands constituting the basins of the Valle de Bravo, Malacatepec, Tilostoc, and Temascaltepec rivers. C. Forest Protection Zone of the Necaxa River Hydrographic Basin. D. Río Blanco Canyon. E. Sierra Tecuani. F. Tuxtla Biosphere Reserve. G. Selva el Ocote. H. Sumidero Canyon. I. the La Sepultura. J. Forest Protection Zone (state of Chiapas: municipalities of La Concordia, Ángel Albino Corzo, Villa Flores, and Jiquipilas). K. the El Triunfo. Maps by J. Andrés Vázquez-Benito.

Sierra Madre del Sur, the Forest Protection Zone of the lands in the basins of the Valle de Bravo, Malacatepec, Tilostoc, and Temascaltepec rivers in the Trans-Mexican Volcanic Belt, the Forest Protection Zone of the Necaxa River Hydrographic Basin in the Sierra Madre Oriental, and the Tuxtla Biosphere Reserve in the Veracruz Province (Figure 5A). Furthermore, 16 priority areas for extreme conservation overlap with medium suitability areas. All are located within the provinces of Sierra Madre del Sur, Trans-Mexican Volcanic Belt, Chiapas Highlands, and Veracruz Province (Figure 5B).

4 Discussion

4.1 Current distribution patterns

The distribution of *O. incurvum* is restricted to a small area in Mexico. Although its presence in the southern states was previously reported (Soto-Arenas and Solano-Gómez, 2007a), this research has expanded and refined the known distribution and the environmental conditions associated with this species.

Our results indicate that the highest proportion of individuals occurs in Veracruz and Oaxaca, two states that rank among the top three in Orchidaceae species richness in the country (Salazar, 2012). In contrast, areas such as the Sierra Madre in Chiapas and the Sierra Norte of Puebla have the fewest occurrences. This pattern is likely due to insufficient collection efforts in these regions and the species' natural rarity (Soto-Arenas and Solano-Gómez, 2007a; Romero-Santamaría et al., 2024), rather than a true decline in the species' presence.

The species exhibits a strong preference for mountainous areas, particularly in the eastern of the Neo-Volcanic Axis physiographic province and the southeastern part of the Sierra Madre del Sur, where the highest concentration of individuals is found (67%). This data aligns with findings by Aragón-Parada et al. (2021), who indicate that variation in relief, climate, and vegetation across both physiographic provinces supports the presence of orchids.

Both physiographic provinces are notable for containing a significant portion of the MCFs, which extend from the Sierra Madre Oriental to the north and northeast of Oaxaca and occur as patches of mountain ranges in Chiapas (Gual and González-Medrano, 2014). The MCF is the preferred vegetation type for *O. incurvum* and other taxa of this genus (Guerra and Huamani, 1995), where environmental conditions favor its presence (Hágsater et al., 2005).

The presence of *O. incurvum* in the COF was particularly significant because it was the second most common vegetation type to host this species. The orchid's occurrence in this vegetation had not been previously recorded. This discovery expands its distribution to another vegetation type and, consequently, its geographic and environmental range. This distribution reflects *O. incurvum*'s adaptation to lower environmental humidity, driven primarily by elevation, and by annual and winter precipitation (Guerrero-Hernández et al., 2019). Additionally, *O. incurvum* prefers the genus *Quercus* L. as a phorophyte, whose species are dominant components of these forests, along with some conifers.

The findings indicate that the ETF recorded the fewest occurrences of this species, representing only 5%. In ETFs, temperature and humidity are high, and they are usually distributed between 0 and 1,000 m a.s.l (Rzedowski, 2006). Although these conditions favor orchid species diversity (Morales-Linares et al., 2015), *O. incurvum* exhibits a contrasting pattern. The climate of the ETF corresponds to the lower altitudinal limit, characterized by high temperatures and relative humidity, which contrast with the moderately warm and cooler environments of the MCF and COF, respectively.

The Sierra Madre del Sur is characterized by elevations that typically exceed 1,000 m, with the highest elevations occurring in the states of Oaxaca and Guerrero (Morrone, 2017; Aragón-Parada et al., 2021). In the eastern transition region where the Neo-Volcanic Axis physiographic province meets the Sierra Madre del Sur, specifically between Veracruz and Oaxaca, elevations range from 1,000 to 2,000 m. This region provides favorable environmental conditions for the dispersal, establishment, and reproduction of orchids (Solano-Gómez et al., 2016). The highest concentrations of *O. incurvum* individuals have been observed in

northern Oaxaca and central Veracruz. This distribution pattern is also observed in other taxa of the genus *Oncidium* (Jiménez, 2016) and in several species within the subfamily Epidendroideae (Kolanowska, 2014).

4.2 Environmental variables

The distribution of *O. incurvum* is strongly correlated with the temperature seasonality and elevation. Temperature seasonality, measured by the standard deviation of temperature, indicates how much temperatures vary around their mean. Elevation is closely related to precipitation, temperature, and relative humidity, making it a key geographic factor for analyzing the distribution of epiphytic orchids. Both influence seed germination, phenology, and population density (Timsina et al., 2021; Aini et al., 2022).

Epiphytic plants rely heavily on atmospheric moisture (Foster, 2001), making them sensitive to even slight changes in humidity. This sensitivity underscores the importance of total annual precipitation, humidity during the wet months, and annual evapotranspiration for the species' survival. The results align with *O. incurvum*'s preference for moderate-to-intermediate relative humidity, which corresponds to elevation gradients within its modeled distribution.

The total annual precipitation, the percentage of winter precipitation in the MCF and COF, elements of the mountain cloud forest flora, and the contribution of fog to relative humidity (Guerrero-Hernández et al., 2019) are also critical variables. In the MCF, factors such as cloud and fog, abundant precipitation, high water condensation (relative humidity), and low evapotranspiration rates in the early dry season (Bruijnzeel et al., 2011; Aparecido et al., 2018) are critical for the distribution of *O. incurvum*. In contrast, forested areas of COF that generate ecotones with the MCF above 1,500 m elevation (i.e., intermediate elevations) (Gual and González-Medrano, 2014) have a lower occurrence of this species.

These environmental variables are strongly associated with MCF (López-Mata et al., 2012; Toledo-Garibaldi and Williams-Linera, 2014) and influence the forests and host dynamics (Zuleta et al., 2016), directly affecting the distribution and presence of the species by influencing fundamental physiological and reproductive processes (Gil et al., 2020). The same variables are often correlated with the distribution of several orchid species (Kolanowska et al., 2017; Crain and Fernandez, 2020), affecting all stages of the life cycle of *O. incurvum*, and influencing its occurrence in different ways.

4.3 Species distribution model

Plant distribution is fundamentally influenced by the availability of suitable habitats. It is common practice to prioritize highly suitable sites (> 0.8) when using SDMs (Washaya et al., 2025). However, for endemic and rare plants, particularly those with limited geographic ranges, this preference can further restrict their distribution because of their narrow habitat specificity (Rabinowitz, 1981; Maciel-Mata et al., 2015). These species typically exhibit low tolerance to abiotic conditions and rely on a limited

range of resources, making them particularly vulnerable to environmental changes and human-induced disturbances (Villaseñor et al., 2024). In this research, areas and geographic regions classified as suitable for the persistent establishment of *O. incurvum* were those with probabilities greater than 0.5, corresponding to the highly and medium suitable classes.

The Sierra Madre del Sur biogeographic province was notable for having the highest number of areas suitable for *O. incurvum* distribution, particularly in the Eastern Sierra Madre del Sur subprovince. However, within this province, there are areas (Central Sierra Madre del Sur and Western Sierra Madre del Sur subprovinces) where the presence of the species has not been recorded, despite the habitats being classified as medium and highly suitable. This may reflect a lack of botanical knowledge in western Mexico (Olson and Dinerstein, 2002; Martínez-Cruz and Ibarra-Manríquez, 2012), rather than a genuine absence of the species. This interpretation is supported by the presence of other species of the same genus, including *O. brachyandrum* Lindl., *O. graminifolium* (Lindl.) Lindl., and *O. stelligerum* Rchb.f., which have been reported in these states (Hågsater and Salazar, 1990; Soto-Arenas and Solano-Gómez, 2007b). To verify these findings, further botanical exploration is needed in the mountainous regions of the central and western Sierra Madre del Sur, particularly in the states of Colima, Guerrero, Michoacán, and Jalisco.

The suitability pattern observed in the Sierra Madre del Sur is driven by climatic factors, including ambient humidity, which increases significantly toward the east of the province. This pattern aligns with high species richness reported in other studies (Aragón-Parada et al., 2021). The Sierra Madre del Sur province is located at elevations above 1,000 m a.s.l (Morrone, 2017; 2019), and is characterized by a predominance of temperate forests, especially coniferous, pine-oak, and mountain cloud forests, with *Quercus* as a dominant genus. According to Marshall and Liebherr (2000), the Sierra Madre del Sur shows biotic affinities with the Trans-Mexican Volcanic Belt, based more on climatic than historical similarities (Blancas-Calva et al., 2010). This close climatic and biotic relationship is evident in the presence of large areas classified as medium suitability in the Trans-Mexican Volcanic Belt, particularly along its border with the Sierra Madre del Sur.

On the other hand, Veracruz Province is closely associated with the Chiapas Highlands. This region is characterized by high humidity, with annual precipitation exceeding 1,000 mm. Vegetation is dominated by humid tropical forests, coniferous and oak forests, and mountain cloud forests. These conditions are especially prevalent in the Chiapas Valley (Morrone, 2019), where a large area of suitable habitat has been identified, along with medium-suitable areas where *O. incurvum* has been documented (Soto-Arenas and Solano-Gómez, 2007a).

4.4 Preliminary conservation status

Oncidium incurvum is not currently listed on the International Union for Conservation of Nature (IUCN) Red List. However, an exploratory analysis of its conservation status under IUCN criterion B (IUCN, 2024) classified the species as endangered (EN). This classification largely reflects its preference for mountain cloud

forests, which are among the most vulnerable vegetation types in Mexico and worldwide (Foster, 2001; CONABIO, 2010). These forests are characterized by high structural complexity and extraordinary biological diversity, hosting a high species richness and numerous endemic and threatened species (CONABIO, 2010). According to Aragón-Parada et al. (2021), only some MCF species are shared with the COF; this may be the case for *O. incurvum* in the SMS. Mexico's COF is the most diverse in the world, but it is estimated that between 37% and 67% of its original surface area has been transformed, making it one of the most threatened (Rzedowski, 2006).

The primary threats driving *O. incurvum* toward a critical conservation status (Soto-Arenas and Solano-Gómez, 2007a) are poaching of mature individuals for illegal trade and ceremonial use (Flores-Palacios and Valencia-Díaz, 2007; Álvarez-Mora et al., 2016), along with habitat loss and fragmentation, which have resulted in an archipelagic distribution of the species. Additionally, *O. incurvum*'s reliance on mature oak hosts and its specific environmental requirements further exacerbate its vulnerability.

Our results indicate that less than 1% of the national territory and less than 3% of its mobility area (*M*) offer highly suitable environmental conditions for *O. incurvum*. Moreover, only about 3% of the territory and 11% of the area *M* show a medium suitable probability, ranging from 0.51 to 0.69. These data underscore the urgent need to identify priority conservation areas and to monitor populations to prevent local extinction. Including *O. incurvum* on the IUCN Red List would be a crucial first step in raising awareness of the urgent need to protect this species and in developing effective conservation strategies. The urgency of this matter is further supported by the findings of Svahnström et al. (2025), who note that some epiphytic orchid lineages with limited distribution are underrepresented on the IUCN Red List. We agree with their recommendation to prioritize the inclusion of such species.

4.5 Identification of priority areas for conservation of *O. incurvum*

A key component of effective orchid conservation plans is areas with optimal conditions for their survival. In this regard, large areas in the Sierra Madre del Sur are highlighted as priority areas for the conservation of *O. incurvum*. Specifically, the Eastern Sierra Madre del Sur subprovince contains the largest area of suitable habitat. This subprovince is predominantly located in the state of Oaxaca (Aragón-Parada et al., 2021), which hosts the second-largest population of this species.

The Western Sierra Madre del Sur and Central Sierra Madre del Sur subprovinces, which cover Jalisco, Colima, Guerrero, and Michoacán, are also recommended as priority areas for conservation. In these subprovinces, the largest area falls within the medium suitable class, where the probability of suitable conditions for the species exceeds 0.5. These regions should be explored and potentially included in conservation planning because of the endemism and geographical rarity (Rabinowitz, 1981; Maciel-Mata et al., 2015; Svahnström et al., 2025) of *O. incurvum*. The medium suitable class regions represent extensive areas of potential habitat and may serve

as critical refuges for the species' long-term persistence, helping it escape unfavorable conditions within its current distribution. Therefore, protecting the forests in these subprovinces is essential, as they provide vital habitats for epiphytic orchids and other species.

Next in order of priority for conservation is the Chiapas Highlands and its convergence with the Veracruz Province, which primarily corresponds to the state of Chiapas. Previous studies have consistently identified this state as a critical region for orchid conservation (Solano-Gómez et al., 2016).

The proposed areas are based on important regions covered by MCF, COF, and ETF, all of which maintain low human impact indices (< 0.3). This could enhance the viability of *O. incurvum*, ensuring the population's survival. Additionally, beyond their environmental and ecological suitability, these conservation areas are vital for preserving regional biodiversity. In this context, 60% of the suitable areas within the Sierra Madre del Sur are located in regions identified as extreme in terms of conservation priorities, reinforcing their significance.

We identified six areas classified as highly suitable and five as medium suitable, within an NPA. These findings are important because NPAs benefit from government protection and biodiversity conservation measures, which could support the species' future reintroduction. However, it is essential to acknowledge the fragile state of many NPAs, which face significant human-induced deterioration. This raises concerns about their long-term capacity to conserve the biodiversity they are meant to protect (Maldonado-Villalpando et al., 2018).

In this context, it should be noted that in areas with high human impact (> 0.5), conservation efforts may not effectively ensure species conservation, as is the case at the Los Tuxtlas Biosphere Reserve in the state of Veracruz (Von Thaden et al., 2020). Thus, pursuing conservation initiatives in heavily impacted areas could lead to ineffective strategies for the species. Interestingly, the highest concentration of *O. incurvum* individuals is in the central part of Veracruz, at the borders of Veracruz Province and the Trans-Mexican Volcanic Belt, an area without NPAs that has nonetheless allowed the species' persistence.

The results indicate that the suitable habitats for *O. incurvum* are inadequately protected within the current NPA system. This suggests that the contribution of formally protected areas to conserving this orchid may remain limited in the future, depending on the extent of suitable habitats safeguarded by the National Commission of Natural Protected Areas-CONANP (Swart, 2019). Given this scenario, one alternative is to consider areas outside the NPAs to create corridors that facilitate connectivity between them, thereby strengthening regional conservation and promoting ecological integrity (Riemann et al., 2011).

In orchids, the specificity of these interactions is a key factor. According to Ackerman et al. (2023), approximately 76% of species depend on pollinators for reproduction, which influences their distribution and conservation. Unfortunately, to date, no research has examined the organisms with which *O. incurvum* interacts. Given the current threats to pollinators, it is urgent to focus research efforts on this topic. Therefore, future studies should

consider biotic interactions and integrate them into models used to plan orchid conservation actions.

Our findings call for reassessing planning decisions to protect not only *O. incurvum* but also epiphytic orchids as a group. This is based on the idea that orchids serve as umbrella and flagship species that can guide habitat conservation efforts in the areas where they grow (Gale et al., 2018). This is especially important in areas of high conservation value, such as the Sierra Madre del Sur, the Chiapas Highlands, and the area where they intersect with the Veracruz Province in Mexico.

In conclusion, as human impact on biodiversity continues to escalate, there is an increasing need to allocate the limited financial resources available for conservation. Key factors such as reproductive biology, pollinators, species interactions, propagation, and socioeconomic aspects must be taken into account to ensure that these plans are viable and effective in terms of time, location, and economic sustainability.

Our model identified critical suitable habitats that support *O. incurvum* occurrence outside known hotspots and protected areas. The findings of this work highlight the importance of considering climatic and geographic factors when developing effective management plans for orchid conservation. It is essential to increase collection efforts in the central and western regions of the Sierra Madre del Sur, focusing on the states of Colima, Guerrero, Michoacán, and Jalisco, to document their presence and provide heuristic validation of the accuracy of the modeling results. The results presented have significant implications for orchid conservation in Mexico and can serve as a reference dataset to identify key locations of vascular plants throughout the country, as well as contribute to understanding the potential to integrate medium suitable class areas as climate refuges in spatial planning for species conservation.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

JV-B: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Visualization, Writing – original draft, Writing – review & editing. MB-H: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing. LL-M: Formal analysis, Methodology, Resources, Software, Validation, Writing – original draft, Writing – review & editing. IG-E: Funding acquisition, Supervision, Writing – review & editing. MM-R: Supervision, Writing – review & editing. XA-D: Supervision, Writing – review & editing.

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