

POTENTIAL DISTRIBUTION OF *CROTON GUATEMALENSIS*:
A MODEL WITH REPRODUCTIVE BIOLOGY DATA
DISTRIBUCIÓN POTENCIAL DE *CROTON GUATEMALENSIS*:
UN MODELO CON DATOS DE BIOLOGÍA REPRODUCTIVA

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Abstract

Background: The inclusion of information on the phenology of any given species can significantly improve the resulting of potential distribution models. Scientific literature does not provide up-to-date information on the abiotic and biotic factors that determine the distribution of *Croton guatemalensis*, a species native to communities in south Mexico. For the first time, the potential distribution of *C. guatemalensis* was determined using a model which includes reproductive biology data.

Questions: Which bioclimatic and climatic variables most contribute to the distribution of *C. guatemalensis*? Does reproductive biology data contribute significantly to the prediction of the species distribution?

Studied species/Mathematical model: *Croton guatemalensis*/Maximum Entropy Modeling.

Study area and dates: Chiapas, Mexico, January - December 2020.

Methods: The MaxEnt 4.4.4 algorithm was used, incorporating 16 variables, including bioclimatic, climatic and elevation. In addition, a habitat suitability layer was built.

Results: The model presented a precision of $AUC = 0.964 \pm 0.004$. Eight variables contributed to explain 86.5 % of the potential distribution of the species. According to their contribution to the model, the most important were the seasonality of precipitation, habitat suitability, elevation and April solar radiation. The species was found in the physiographic regions Central America South Mountain Range Subprovince, Central Depression of Chiapas Discontinuity, and Altos de Chiapas Subprovince.

Conclusions: The inclusion of reproductive biology data of *C. guatemalensis* contributed to improve the model. This information allows the development of more effective management and conservation plans by identifying the precise regions in which the species is found.

Keywords: Habitat suitability, MaxEnt 4.4.4, multipurpose species, phenology, physiology.

Resumen

Antecedentes: La inclusión de información sobre la fenología de las especies mejora significativamente el resultado de los modelos de distribución potencial. La literatura científica no brinda información actualizada sobre los factores abióticos y bióticos que determinan la distribución de *Croton guatemalensis*, especie nativa del sur de México. Por primera vez, se determina la distribución potencial de *C. guatemalensis* a partir de un modelo con datos de biología reproductiva.

Preguntas: ¿Cuáles son las variables bioclimáticas y climáticas que más contribuyen a la distribución de *C. guatemalensis*? ¿Los datos de biología reproductiva contribuyen significativamente a la predicción de la distribución de la especie?

Área de estudio y fechas: Chiapas, México, Agosto - Diciembre 2020.

Métodos: Se utilizó el algoritmo MaxEnt 4.4.4, incorporando 16 variables, incluyendo bioclimáticas, climáticas y de elevación. Además se construyó una capa de idoneidad de hábitat.

Resultados: El modelo presentó una precisión de $AUC = 0.964 \pm 0.005$. Ocho variables contribuyeron a explicar el 86.5 % de la distribución potencial de la especie. De acuerdo a su contribución al modelo las más importantes fueron la estacionalidad de la precipitación, idoneidad del hábitat, elevación y radiación solar en abril. La especie se encontró en las regiones fisiográficas de Subprovincia Sierras del Sur de Centroamérica, Discontinuidad Depresión Central de Chiapas y Subprovincias Altos de Chiapas.

Conclusiones: La inclusión de datos de biología reproductiva de *C. guatemalensis* contribuyó al modelo. Esta información permite desarrollar planes de manejo y conservación más efectivos al identificar las regiones en las que se encuentra la especie.

Palabras Clave: Especies multipropósito, fenología, fisiología, Idoneidad del hábitat, MaxEnt 4.4.4.

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Mexico is among the most biologically and culturally diverse countries in the world. It is ranked within the top five “megadiverse” countries, which house between 60 - 70 % of all known biodiversity in the planet (Mittermeier *et al.* 1998). It is the fourth richest country in terms of endemic and native plants (Orantes-García *et al.* 2015).

Biotic and abiotic factors play a fundamental role in the distribution of plant species, since their physiology and phenology require specific temperature, humidity, soil, and luminosity conditions for them to germinate, grow, bloom, and fructify (Martínez-Pastur *et al.* 2017, Quirós *et al.* 2017). Currently, natural and human-driven changes in ecosystems throughout the planet have contributed to the redistribution of species. This has in turn caused changes in their physiological and phenological processes, given the fact that each species has a different tolerance interval to shifts in environmental and anthropogenic phenomena (Arias-Aguilar *et al.* 2016, Martínez-Pastur *et al.* 2017). Due to the dramatic transformations that humans have produced on the environment, effects on natural ecosystems have been documented, as has the direct impact caused by the loss of species caused by changes in the use of soil and vegetation. These effects on ecosystems are expected to translate into alterations in the distribution and abundance of species, or in the disappearance of some species or populations (Godoy-Burki 2016).

Regarding this, several predictive models have been designed to help estimate the potential distribution of wild species as to inform management and preservation actions (Bañuelos-Revilla *et al.* 2019). The models help determine the locations where environmental conditions are most favorable for a species to prosper according to parameters obtained from prior data collections. These models have proven useful for studies evaluating distribution patterns, such as biogeography, ecology, or conservation analyses (Quirós *et al.* 2017, González-Hernández *et al.* 2018).

Most models predicting the likely presence of a species in an unexplored area generally correlate known sites in which the species prospers with a combination of environmental factors, particularly climate. Bioclimatic and climatic variables are significant factors affecting or determining the distribution of organisms. However, the inclusion of variables that incorporate the phenology or physiology of a given species, improves predictive models (Lira-Noriega *et al.* 2013), and helps heighten accuracy when determining the reasons for the presence or absence of a species at particular sites (Chuine 2010, Chuine & Beaubien 2001, Martinez *et al.* 2014, Visser & Both 2005). Each species has their own bioclimatic profile, so analyzing the variables affecting said profile can help quantify the differences between climatic dominions (that is, the niche or space in which the survival of a species is deemed likely in natural conditions) for different species (Godoy-Burki 2016). This knowledge is of particular relevance for species with a restricted distribution, or those with populations at risk of disappearing or under an endangered category.

Croton guatemalensis is a tree that measures 5-15 m high, it is a species native to southeast Mexico (Chiapas) and Central America (Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama), which is found within humid, dry, and mixed forests, commonly on rocky hillsides between 50 and 1,800 m asl. It is an evergreen tree with annual flowering (July-April) and fruiting (March-June) (Pozo-Gómez *et al.* 2020). Currently, it is under “Special protection” by Mexican law (SEMARNAT 2010) because there are no legal provisions for its use. Because it is a species used for multiple purposes, its availability is of great significance to diverse rural communities that count on it for construction, as firewood, as a live fence, or because of its medicinal properties (Pozo-Gómez *et al.* 2019).

Currently, no scientific literature exists on the potential distribution of *C. guatemalensis* so, for the first time, we determine this based on the use of climatic, bioclimatic variables and a layer of ideal habitat designed using variables of reproductive effort (number and size of seeds per fruit, seed health and viability) and reproductive success (germination rate). The inclusion of reproductive data in the model of potential distribution improves it providing precise information about the ideal habitats in which this species can thrive. Having precise data of the distribution of this multi-purpose protected species is of great relevance to establish management and conservation actions (Hernández-Ruiz *et al.* 2016).

Materials and methods

Study area. This study was carried out in the state of Chiapas, Mexico, which spans 75,634 km² at 17° 59', 14° 32' N and 90° 22', 94° 14' W (Figure 1). The study area includes nine local physiographic regions: I Coast Plain of Chiapas and Guatemala Discontinuity, II. South Chiapas Mountains Sub-Province, II. Central Depression of Chiapas Discontinuity, III. Central Depression of Chiapas Discontinuity, IV. Isthmus Plain Discontinuity, V. Central American Volcanoes Sub-Province, VI. Highlands of Chiapas Sub-Province, VII. Lacandon Mountain Range Sub-Province, VIII. Chiapas Northern Mountain Range Sub-Province, IX. Tabasco Plain and Swamp Sub-Province (El Colegio de la Frontera Sur, Ecosur 2005). *C. guatemalensis* may be located within tropical rain forests, medium strata tropical rainforest, tropical dry rainforests, and secondary vegetation, in soils with a pH ranging from 6.8 to 7.7 and which are rich in organic matter (3.01 - 4.20 %), have good porosity (40 - 55 %), and are clayey or highly clayey (Pozo-Gómez *et al.* 2019).

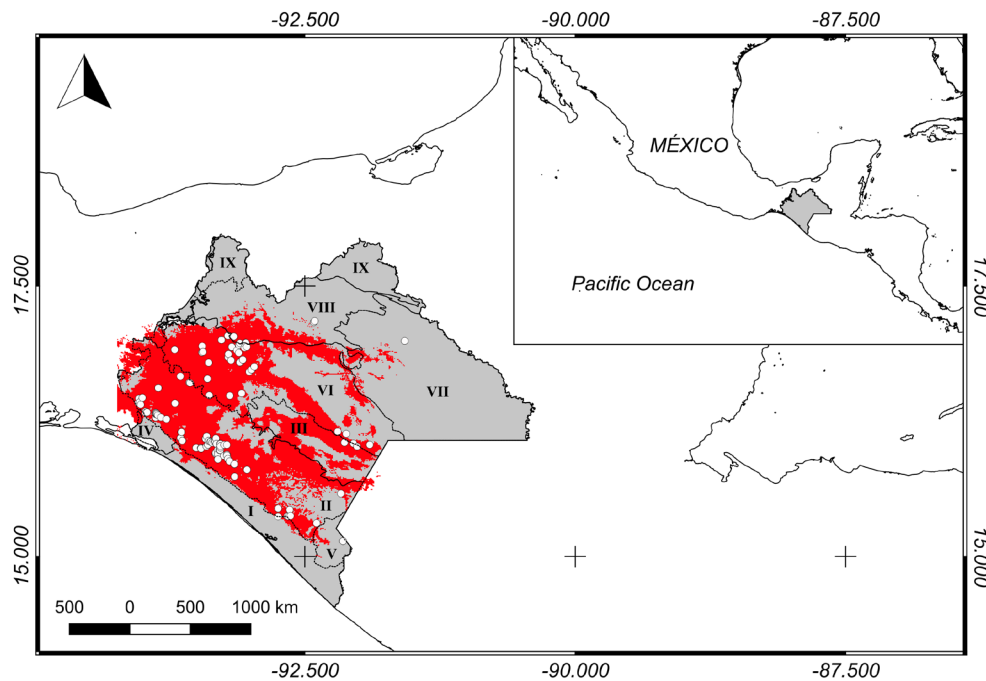


Figure 1. Potential distribution of *C. guatemalensis* at Chiapas, Mexico (red). The records used for the modeling of the species are showed (white dots). I. Coast Plain of Chiapas and Guatemala Discontinuity, II. South Chiapas Mountains Sub-Province, II. Central Depression of Chiapas Discontinuity, III. Central Depression of Chiapas Discontinuity, IV. Isthmus Plain Discontinuity, V. Central American Volcanoes Sub-Province, VI. Highlands of Chiapas Sub-Province, VII. Lacandon Mountain Range Sub-Province, VIII. Chiapas Northern Mountain Range Sub-Province, IX. Tabasco Plain and Swamp Sub-Province.

Database. A database containing field records of *C. guatemalensis* in Mexico from 1970 to 2020 was elaborated. The information was obtained from the following scientific databases: The Plant List (www.theplantlist.org/), Sistema Nacional de Información sobre Biodiversidad de México (www.snib.mx/), Comisión Nacional para el Conocimiento de la Biodiversidad (CONABIO 2019), COMPADRE and COMADRE (COMPADRE and COMADRE Matrix Databases 2019), Biodiversity Information Facility (www.gbif.org/es/), and Mesoamerican Flora (www.tropicos.org). The scientific collections from the Eizi Matuda, Instituto de Historia Natural y Ecología (CHIP), Herbario Nacional de México (MEXU), Facultad de Ciencias de la Universidad Nacional Autónoma de México (FCME), and El Co-

legio de la Frontera Sur (ECOSUR) in both its San Cristóbal de Las Casas and Tapachula units. Along with this, floristic listings and specialized journals (Lacandonia, Botanical Sciences, Polibotánica, Revista Mexicana de Biodiversidad, and Acta Botanica Mexicana) were consulted. Finally, a total of 350 records of *C. guatemalensis* were found for Chiapas.

Environmental Variables. We used 19 bio-climatic variables generated for the project version 1.4 WorldClim, as well as climatic and elevation layers (Hijmans *et al.* 2005), with a spatial resolution of 30° (~ 1 km²), which result from interpolating the monthly averages of worldwide meteorological stations from 1,950 to 2,000 (Hijmans *et al.* 2005). All environmental variables were clipped using the limits of the state of Chiapas as a mask. A selection of layers was carried out using a Pearson correlation coefficient test between all bioclimatic and climatic variables, choosing those with correlation values lower than 0.7 (Phillips & Dudík 2008, Gormley *et al.* 2011). Of the total correlated layers, 16 layers remained for analysis. Correlation analysis were developed using “base” package in R software (R Core Team 2018).

Additionally, a habitat suitability layer was created specifically for *C. guatemalensis*. To build this layer, information about the reproductive phenology and physiology of the species reported by Pozo-Gómez *et al.* (2019, 2020) was used. This included ideal conditions for reproductive effort (number and size of fruits), reproductive potential (number and size of seeds per fruit, health and viability of seeds), and reproductive success (germination rate). For the construction of the habitat suitability layer, we compile all the occurrences reported by Pozo-Gómez *et al.* (2019, 2020, pers. comm.), which were filtered, keeping only those where they reported the maximum values of reproductive effort, reproductive potential, and reproductive success. Only 20 occurrences that included these attributes were used. Later, these localities were projected geographically. Subsequently, for each occurrence the bioclimatic, climatic, and elevation information was obtained according to the layers of Hijmans *et al.* (2005). It was assumed that localities with the highest reproductive effort, potential and success represent the “ideal” habitat sites (appropriate for the species to establish and reproduce). Afterward, a new raster layer was created with each of the 16 environmental variables. Only the cells that contained the ideal values were kept. All these new raster layers were homogenized to a range of 0.00 to 1.00. Finally, the 16 raster layers were arithmetically added to obtain a single layer that had the combination of ideal conditions for the species. The final raster values were also homogenized to a range of 0.00 to 1.00 (considering the highest value as the maximum habitat suitability given that it meets all the optimal conditions for *C. guatemalensis*). A total of 17 layers were used for the final model (Table 1).

Potential Distribution. To create the model, we used the MaxEnt 4.4.4 algorithm (Palma-Ordaz & Delgadillo-Rodríguez 2014), which has been used for multiple purposes in biogeography, conservation biology, and ecology with good results (Phillips & Dudík 2008, Radosavljevic & Anderson 2014). MaxEnt 4.4.4 functions with presence data for a given species to predict its geographic distribution based on maximum entropy (closer to homogeneity), subject to restrictions and depending on both quantitative and qualitative environmental variables (Lira-Noriega *et al.* 2013), using a transformation of the relative occurrence rate (Phillips & Dudík 2008). As model calibration area, the Chiapas state was used. There are areas of the region in which the species has not been reported, and we wanted to know the probability of this species presence in such areas. Furthermore, the information on the ideal conditions for *C. guatemalensis* comes from localities within this same region. In order to reduce spatial correlation between species occurrence records a spatial thinning was applied (Aiello-Lammens *et al.* 2015). Also, Maxent option to remove duplicates was used. After those processes a total of 98 occurrence records remained. We used 75 % of the occurrence data for modeling, while the remaining 25 % were employed to evaluate errors of omission and commission. The configuration of the model was set to logistic function as the output format, creating response curves. A total of 10 replicates were developed using a crossed validation, consisting of re-sorting the data for modelling and for the evaluation of the obtained model under the new parameters, were used (Phillips *et al.* 2006). Random seed was selected, which prevents MaxEnt 4.4.4 from repeating the same sampling in every instance. Also, don't clamp, and no extrapolation were selected, which prevents MaxEnt 4.4.4 from taking a limit value from the calibration region and extending it, thus avoid-

ing undesirable extrapolations of the model. Regularization multiplier the default value of 1 was left. A maximum of 10,000 background points was selected. Through a Jackknife test, the variables used in the model were evaluated and the information they provide and percentage of the model they explain were obtained. Using the *Area Under the Curve* (AUC), we evaluated the predictive ability of the generated distribution models through a graph (Palma-Ordaz & Delgadillo-Rodríguez 2014). The AUC values can be interpreted as the probability that, when randomly choosing a presence and an absence spot, the presence spot will have a higher value of suitability or probability of presence on the model. According to graph (Palma-Ordaz & Delgadillo-Rodríguez 2014), a general classification guide for the precision of the model, considering the AUC, is: 0.50-0.60 = insufficient; 0.60-0.70 = poor; 0.70-0.80 = average; 0.80-0.90 = good; 0.90-1 = excellent. According to this criterion, the best model of the replicas was chosen as the final model (AUC = 0.964 ± 0.004). The distribution probability map was re-categorized into a binary map (0 = absence, 1 = presence), using the 10 percentile training presence value as a cut-off line (Liu *et al.* 2005).

The final potential distribution map was generated using QGIS 3.2. (qgis.org).

Table 1. Bioclimatic and climatic variables (from Hijmans *et al.* 2005), elevation, and habitat suitability variable (constructed from reproductive data of the species) used in the potential distribution model.

	Description
Bio_3	Isothermality (Bio_2/Bio_7) (×100)
Bio_5	Max Temperature of Warmest Month (°C)
Bio_7	Temperature Annual Range (Bio_5 - Bio_6) (°C)
Bio_14	Precipitation of Driest Month (mm)
Bio_15	Precipitation Seasonality (Coefficient of Variation)
	December Maximum Temperature
	April Solar Radiation
	May Solar Radiation
	September Solar Radiation
	September Precipitation
	October Precipitation
	November Precipitation
	June Solar Radiation
	October Monthly Minimum Temperature
	Elevation (m asl)
	Habitat suitability (0.00-1.00)

Results

The efficiency of prediction of our model showed that *C. guatemalensis* is at an interval of 0.964 ± 0.005 in its AUC value, that is, the precision of the model is excellent. The variables “seasonality of precipitation” (Bio 15), “habitat suitability”, “elevation”, “April sun radiation”, “June Solar Radiation”, “October Precipitation”, “November Precipitation” and “Temperature Annual Range” contribute 86.5 % to explain the potential distribution model (Table 2).

According to the potential distribution model, the presence of the species is continuous in the physiographic regions: Subprovince Central America South Mountain Range, Discontinuity Central Depression of Chiapas, and Subprovince Highlands of Chiapas (Figure 1).

Table 2. Contribution percentage from the most important variables according to the potential distribution model of *C. guatemalensis* in Chiapas, Mexico.

Variables	Contribution (%)
Precipitation Seasonality (Coefficient of Variation)	26.5
Habitat Suitability	17.8
Elevation	15.8
April Solar Radiation	7.7
June Solar Radiation	5.7
October Precipitation	4.4
November Precipitation	4.3
Temperature Annual Range	4.3

Discussion

The resulting model, with a prediction efficiency of 0.964 ± 0.005 , shows that the species is continuously distributed along three different regions: Subprovince Central America South Mountain Range, Discontinuity Central Depression of Chiapas, and Subprovince Highlands of Chiapas. These regions contain extensive areas with tropical dry rainforests, medium strata tropical rainforest, and tropical rain forests, with an average environmental temperature of 22 °C and an average annual rainfall of 1,000 mm, environmentally ideal conditions for the establishment and reproduction of *C. guatemalensis* (Pozo-Gómez *et al.* 2020). Regions with such environmental features allow an optimal development of trees year-round; the climate prevents hydric and thermal stress and plant communities are complex, providing appropriate microhabitats (Giraldo-Cañas 2000, Moles *et al.* 2004, Andreu *et al.* 2006).

Regardless of the results of the model, certain areas within these three regions, such as the Socoltenango and Venustiano Carranza municipalities in the Discontinuity Central Depression of Chiapas region, the Ángel Albino Corzo and Villa Flores localities in the Subprovince Central America South Mountain Range region, and Las Rosas in the Subprovince Highlands of Chiapas region do not have historic records of *C. guatemalensis*. It is highly likely that this is due to the fact that these areas lack exhaustive floristic studies.

The presence model discards the distribution of *C. guatemalensis* in all other physiographic regions of Chiapas, such as the Lacandon Mountain Range Subprovince, Northern Mountain Range Subprovince, and Tabasco Plain and Swamps Subprovince. This may be due to climatic factors (25 °C and 5,000 mm rainfall), the mountainous nature of the terrain with thin, rocky, limestone soils, and the presence of vegetable associations of oak-pine forests, which are inadequate for the establishment and reproduction of the species (Pozo-Gómez *et al.* 2020). The model also discards the presence of *C. guatemalensis* in the Chiapas and Guatemala Coast Plain Discontinuity, Isthmus Plain Discontinuity, and Central America Volcanoes Discontinuity, which are characterized by an average temperature of 24 °C and a rainfall of 3,000 mm. While these regions contain medium-stratum tropical rainforests, it has been almost completely substituted by livestock grazing fields and extensive crop lands, which, along with the presence of estuaries, mangroves and the aquatic vegetation characteristic of this littoral zone, provides inadequate conditions for *C. guatemalensis* (www.gob.mx/inafed).

According to our results, two bioclimatic variables (seasonality of precipitation and annual temperature range), five climatic variables (elevation, April solar radiation, June solar radiation, October precipitation and November precipitation), and a habitat suitability variable (habitat adequacy for the establishment and reproduction of the species), explain 86.5 % of the model. Pozo-Gómez *et al.* (2020) points out that all of these variables play relevant roles for the reproductive physiology of this species, from the production of flowers to seed germination. This species requires moderate rainfall and abundant sun radiation during its fruiting and fruit opening (for seeds success), as is the case for other tropical tree species (Vera 1995, Cortés-Flores *et al.* 2011). When light is scarce and rainfall abundant, the fruits of *C. guatemalensis* absorb humidity and tend to rot, causing the seed to become unviable (Pozo-Gómez *et al.*

2019, 2020). Fischer & Ordúz (2012) mention that tree growth and fruit production are closely related to light usage; the reduction of light intensity affects the induction of floral blooms, their differentiation, size, color, and the quality of fruit, more than it does tree growth. The flowering of *C. guatemalensis* happens from June through January, seasons with a radiation spanning 12 to 13 hours, and a temperature averaging at 22 °C, as well as a rainfall of 50 mm or absent (0 - 10 mm). On the other hand, Wright & Van Schaik (1994) state that certain arboreal species have a much larger flowering period in the driest time of the year, which is also the period with the most sun radiation; while Morellato *et al.* (2000) point out that the flowering and fruit bearing period in some arboreal species occurs shortly before the humid period, when days are longer and environmental temperature higher, as is the case for *C. guatemalensis* (Pozo-Gómez *et al.* 2019, 2020).

Including the variable of habitat suitability, based on previous knowledge of the reproductive phenology and physiology of the species (Pozo-Gómez *et al.* 2019, 2020) significantly contributed to predict the distribution of *C. guatemalensis*. Previous knowledge of the biotic and abiotic factors that a species requires for its physiologic and phenological processes in favorable environmental conditions, is essential to know and understand its distribution. Lira-Noriega *et al.* (2013), who analyzed how climate factors explain the distribution area of a parasite plant (*Phoradendron californicum*) in the Sonora and Mojave deserts, recommend the integration of different environmental and biological factors in geographic ranges to gain a fuller understanding of the distribution patterns of processes of different species. On the other hand, Bañuelos-Revilla *et al.* (2019) state that, for *Euphorbia antisyphilitica* (candelilla), knowing the habitat variables was relevant to obtain information about its potential distribution, abundance, and size, deducting that, naturally, the distribution of species depend on both environmental and anthropic factors.

These results provide updated information about the potential distribution of *C. guatemalensis* in Chiapas, which is indispensable not only to understand its biology or the reasons behind its presence or absence in a given site, but also to carry out management and preservation plans for this species and the environments where it is found.

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