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Characterizing environmental suitability of *Aedes albopictus* (Diptera: Culicidae) in Mexico based on regional and global niche models

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Abstract

The Asian tiger mosquito, *Aedes albopictus* (Skuse) (Diptera: Culicidae), is an invasive species and a vector of numerous human pathogens, including chikungunya, dengue, yellow fever, and Zika viruses. This mosquito had been reported from 36 geographic locations in Mexico by 2005, increasing to 101 locations by 2010 and 501 locations (spanning 16 states) by 2016. Here we modeled the occupied niche for *Ae. albopictus* in Mexico to characterize the environmental conditions related to its presence, and to generate updated environmental suitability maps. The predictors with the greatest contribution to characterizing the occupied niche for *Ae. albopictus* were NDVI and annual mean temperature. We also estimated the environmental suitability for *Ae. albopictus* in regions of the country where it has not been documented yet, by means of: 1) transferring its occupied niche model to these regions and 2) modeling its fundamental niche using global data. Our models will help vector control and public health institutions to identify areas where *Ae. albopictus* has not yet been recorded but where it may be present. We emphasize that most of Mexico has environmental conditions that potentially allow the survival of *Ae. albopictus*, which underscores the need for systematic mosquito monitoring in all states of the country.

Key words: *Aedes albopictus*, ecological niche modeling, Mexico, occupied niche, fundamental niche

The Asian tiger mosquito, *Aedes albopictus* (Skuse) (Diptera: Culicidae), is a vector of a large number of human, wild, and domestic animal pathogens (Paupy et al. 2009). It is also one of the most important invasive mosquito species worldwide (Lowe et al. 2000). More than 20 arboviruses are known to be transmitted by this species, some of which are of great public health importance such as

dengue, chikungunya, yellow fever, and Zika viruses (Paupy et al. 2009, Wong et al. 2013, Grard et al. 2014).

Ae. albopictus originated in the tropical and subtropical regions of south-east Asia (Ettinger and Feldman 2009) but has invaded other tropical and temperate areas in America, Europe, Africa, and Oceania (Benedict et al. 2007, Caminade et al. 2012, Gasperi et al.

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2012, Guillaumot et al. 2012). During the last three decades, international trade has triggered its still ongoing global expansion (Paupy et al. 2009). Numerous studies have documented recent invasions (e.g., Moore and Mitchell 1997, Toto et al. 2003, Aranda et al. 2006, Gasperi et al. 2012, Guillaumot et al. 2012), and identified a set of suitable environmental conditions that allow the establishment of this species (e.g., Benedict et al. 2007, Caminade et al. 2012, Campbell et al. 2015, Kraemer et al. 2015, Escobar et al. 2016).

In Mexico, *Ae. albopictus* was reported for the first time in Coahuila in 1993, close to the border with the United States (Ibáñez-Bernal and Martínez-Campos 1994). Currently, its known distribution follows a path from north-eastern to south-eastern Mexico, across the Sierra Madre Oriental, reaching the southern Pacific coast through the Tehuantepec isthmus, and reaching the border with Guatemala (Pech-May et al. 2016). In addition to locality-specific reporting (Rodríguez and Ortega 1994; Ibáñez Bernal et al. 1997; Orta-Pesina et al. 2001, 2005; Casas-Martínez and Torres-Estrada 2003; Villegas-Trejo et al. 2010; Salomón-Grajales et al. 2012; Farajollahi and Price 2013; Reyes-Villanueva et al. 2013; Torres-Avendaño et al. 2015; Ortega-Morales and Rodríguez 2016), its potential distribution in Mexico is also known through a series of global correlative niche modeling studies (Benedict et al. 2007, Campbell et al. 2015, Kraemer et al. 2015, Escobar et al. 2016) that have identified environmentally suitable areas for the mosquito through approximations to its fundamental niche (N_F) (Peterson et al. 2011).

Although these studies have allowed us to understand the limits of its physiological tolerance, there is still insufficient information to obtain detailed environmental suitability estimates and a geographical description of the area occupied by the mosquito in Mexico (an approximation to the occupied niche in this region, N_O) (Peterson et al. 2011). For instance, Pech-May et al. (2016) studied its population genetics and potential distribution in this country. However, their models have important limitations; they rely on transferring models calibrated in other countries to estimate the mosquito's N_F, but they did not use records representative of its entire geographic range. Moreover, their model for Mexico (approximation of N_O) only incorporated climatic and topographic variables.

In this study, we characterized the environmental conditions associated with the presence of *Ae. albopictus*, and modeled its occupied niche (N_O) in Mexico. In addition to climatic and topographic variables, we used the normalized difference vegetation index (NDVI), and its specific variability for three time periods of analysis: 2002–2006, 2002–2011, and 2002–2016. We hypothesized that the incorporation of this information could improve estimates of the N_O for *Ae. albopictus* because the NDVI provides information on vegetation condition that correlates to humidity and availability of larval development sites (Estallo et al. 2008, Nihei et al. 2014). We also estimated the global environmental suitability for *Ae. albopictus* based on a characterization of its N_F.

Matrials and Methods

Two environmental suitability maps for the mosquito were constructed. One based on a characterization of the species' occupied niche (N_O) in Mexico, and the other based on a characterization of its fundamental niche (N_F) through global modeling.

Models for Mexico
Presence Records
A database of presence records from 1993 to 2016 of *Ae. albopictus* in Mexico was compiled from the collection of medically important arthropods of the Instituto de Diagnóstico y Referencia Epidemiológicos (InDRE). A second database was then obtained by filtering the presence records with two distance thresholds, 10 and 30 km around each record, to reduce spatial autocorrelation and model overfitting (Veloz 2009, Boria et al. 2014). Both databases, the unfiltered and filtered, were used to calibrate the models.

Environmental Surfaces
To characterize the environmental conditions of Mexico, we obtained: 1) a set of climatic surfaces (spatial resolution = 30 arc-seconds; temporal resolution = 1910–2009) from the database 'Bioclimas Neotropicales' (http://www.bioclimasneotropicales.org/descarga-mexico.html) (Cuervo-Robayo et al. 2014) that represent temperature and precipitation conditions; 2) topographic variables (elevation, slope, and aspect) derived from the Shuttle radar topographic mission (SRTM; http://www2.jpl.nasa.gov/srtm/); and 3) the average, maximum, minimum, intervals, and standard deviation of the monthly NDVI between 2002 and 2016, obtained from the moderate resolution spectroradiometer (MODIS, https://modis.gsfc.nasa.gov/). We performed three principal components analysis (PCA) to reduce multicolinearity and the number of dimensions of the environmental surfaces with the PCARaster function of the ENMGadgets package (Barve and Barve 2013) in R (R Development Core Team 2017). The first of the PCAs was performed with the climatic and topographic surfaces ('varClim' hereafter), the second with the NDVI and topographic variables ('varNDVI' hereafter) and the third with all variables ('varALL'). From each PCA, we kept the leading components that collectively explained ≥95% of global variance (Yañez-Arenas et al. 2015).

Modeling the Occupied Niche in Mexico
We calibrated a preliminary set of models using only occurrences from 2002 to 2010 (this partition in our database was defined to have sufficient geographically and temporally independent evaluation data and to match occurrences and environmental predictors; the presence records from the most recent years were used to validate models), across a hypothesized historically accessible area (region M sensu, Soberón and Peterson 2005) to sample background data. Determining the M region is necessary because a lack of such a delimited region for the analysis could affect the calibration and validation of the models (VanDerWal et al. 2009, Barve et al. 2011). To create the M area, buffers with a 200 km radius (chosen to avoid truncating the species' response to variables) were merged around each presence record in the data used for these analyses. The rest of Mexico (beyond the buffer area) was used for model transference. The program Maxent 3.3.3k (Phillips et al. 2006) was used to estimate environmental suitability for *Ae. albopictus* in these analyses.

To establish the optimal parametrization of the suitability estimates in the calibration region, 81 different settings were tested: varying the occurrence data (unfiltered dataset – 'UF'; 10 km filtered dataset – 'F10km'; and 30 km filtered dataset – 'F30km'), the predictors ('varClim', 'varNDVI' and 'varALL'), the regularization multiplier of Maxent (value of 1 – 'RM1'; 2 – 'RM2'; and 4 – 'RM4'; the latter two are the optimal range to avoid overfitting according to Radosavljevic and Anderson 2014), and the type of features that Maxent is capable of fitting (default – 'Default', linear, and quadratic – 'LQ', and linear, quadratic, and hinge – 'LQH'). Output format (raw), number of replicates (10), percent used for testing (20%), type of validation (bootstrapping), maximum number of iterations (5000), convergence threshold (0.00001), and maximum number of background points (10,000) were fixed for each Maxent run.

The combination of settings that resulted in the model with the best predictive capacity (see statistical validation in the next section) was used to estimate environmental suitability for *Ae. albopictus* for the rest of Mexico (all areas beyond the 200 km buffer). Another series of models were also fitted with a subset of the original variables (used instead of the PCA components), after eliminating those that were highly correlated ($r_p > 0.7$). This step was employed to obtain the variables response curves.

Statistical Validation

The performance of each settings combination was assessed with the ratio of the area under curve (AUC) of the partial receiver-operator characteristic (ROC; Peterson et al. 2008). This technique is based on the traditional ROC, which contrasts the omission and commission errors across a gradient of thresholds of the model against a set of null expectations (Fielding and Bell 1997). The partial ROC is a niche modeling adaptation of the technique and differs in: 1) it graphs the proportion of the analysis area (M hypothesis) that the model predicts as suitable in the x-axis; and 2) the y-axis evaluates the presence points that have acceptable levels of omission error (e.g., taxonomic misidentifications, georeferencing errors, passerby occurrences, and records from sink populations). These analyses were performed with the 'Tool for Partial ROC' (Barve and Barve 2013) using the evaluation data (the presence records obtained after the year 2010) and allowing a 1% omission rate.

Model Comparison

To determine if the model's predictive capacity increased with the NDVI data, we performed one-way analyses of variance with the AUC mean ratio as dependent variable and predictors ('varCLIM', 'varNDVI', and 'varALL') as factors. A Tukey multiple comparison of means was also used to check for differences between factor pairs. Normality of data and homogeneity of variance were previously evaluated with the 'Shapiro-Wilk' and the 'Non-constant Variance Score' tests, respectively.

Global Models

Presence Records

We obtained *Ae. albopictus* presence records for its entire geographic range from the Kraemer et al. (2015) database, which is the most complete, up-to-date, and standardized collection of occurrences for this species. The data spans from 1960 to 2014 and is based on peer-reviewed literature and unpublished studies (e.g., entomologic samples from diverse countries and expert scientific networks around the world).

Environmental Surfaces

We used the global climatic variables of the CliMond database (Kriticos et al. 2012), which consists of 35 interpolated bioclimatic variables at 10′ (~17 km^2) resolution. The variables are the 19 bios from WorldClim, temperature and precipitation (Hijmans et al. 2005), and 16 that describe radiation and humidity (see Kriticos et al. 2012; Supplementary material [online only] for a detailed description). We also used the topographic variables derived from the SRTM resampled to the CliMond spatial resolution. Environmental data used here were not the same as in the modeling for Mexico due to the following reasons: 1) the climatic surfaces 'Bioclimas Neotropicales' are available only for Mexico and 2) it is generally accepted that different variables operate at certain corresponding 'scale domains.' For instance, climate and topography influence distributions at coarser scales, whereas vegetation features (e.g., NDVI) act at mesoscales (Pearson and Dawson 2003).

Modeling the Fundamental Niche

The program NicheA 3.0.1 (Qiao et al. 2016) was used to estimate the environmental suitability of *Ae. albopictus* with the variables described above. A multidimensional envelope was constructed based on a minimum-volume ellipsoid that described 99% of the worldwide presence records. The records for Mexico used for model validation were not included. The envelope was built with the first three components of the PCA of the CliMond variables. Then we
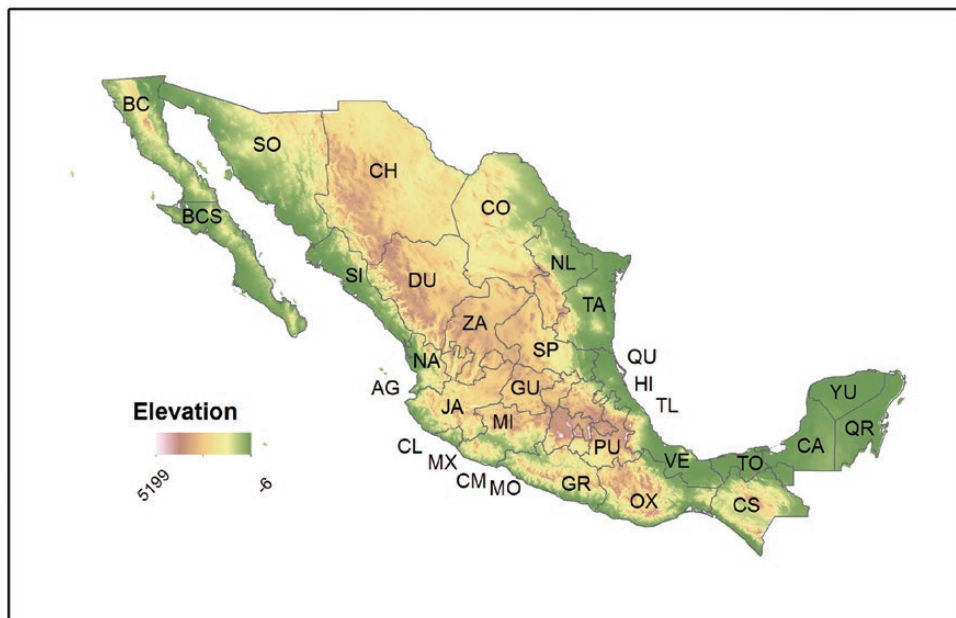

Fig. 1. Map of Mexico. State codes: BC (Baja California), BCS (Baja California Sur), SO (Sonora), CH (Chihuahua), CO (Coahuila), NL (Nuevo León), TA (Tamaulipas), SI (Sinaloa), DU (Durango), ZA (Zacatecas), SP (San Luis Potosí), NA (Nayarit), AG (Aguascalientes), JA (Jalisco), CL (Colima), MX (Estado de México), MI (Michoacán. GU (Guanajuato), CM (Ciudad de México), MO (Morelos), GR (Guerrero), PU (Puebla), QU (Querétaro), HI (Hidalgo), TL (Tlaxacala), VE (Veracruz), OX (Oaxaca), TO (Tabasco), CS (Chiapas), CA (Campeche), QR (Quintana Roo), and YU (Yucatán).
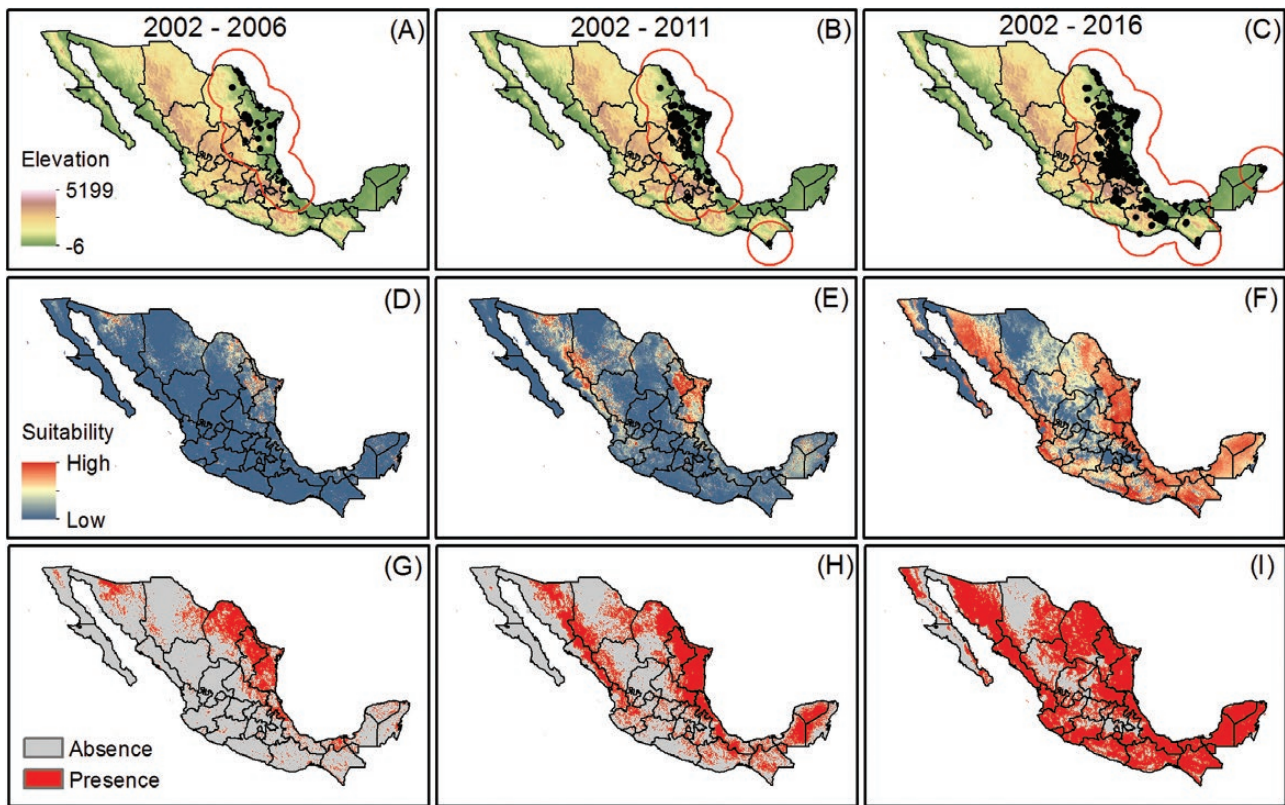
Fig. 2. Ecological niche models of *Ae. albopictus* in Mexico in three periods since its invasion. A, B, and C show the presence records documented up to that point in time overlaid on a digital elevation model. The buffers show the accessibility hypothesis (200 km radius). D, E, and F are the environmental suitability estimated with Maxent. G, H, and I show the presence and the absence of potential environmental conditions for the survival of this species.

projected the distance to the centroid (Yañez-Arenas et al. 2012, Martínez-Meyer et al. 2013) of the ellipsoidal envelope generated with the three components to Mexico and constructed two environmental suitability maps based on the distance to the ellipsoid centroid or a binary (suitable – unsuitable) threshold based on calibration data suitability values.

Model validation was performed with the partial ROC technique (Peterson et al. 2008) considering the presence records from Mexico, and allowing 1% of omission rate.

Final Models

We created a series of temporal subsets of occurrences beginning with year 2002 (initial year of MODIS data). The subsets were coded: 'base_06' (presence records from 2002 to 2006), 'base_11' (2002–2011), and 'base_16' (2002–2016). Maxent was used to estimate the N_O in Mexico, with the settings that improved predictive capacity as described above. Models were generated for the three time periods, matching the presence records, and NDVI predictors for each of the temporal subsets (we chose three periods of five years to have a better visual appreciation of the increase in presence reports and changes in the estimated distribution). The thresholds of the final models allowed 1% of omission rate, and the models were restricted to the suitable region estimated with the ellipsoid approach (N_F).

Results

Ae. albopictus was reported from 36 geographic locations in Mexico by 2005. The number of localities with mosquito records

Table 1. Contribution of the predictors towards model gain

Variable	Percent contribution
NDVI mean	40.8
Annual mean temperature (bio_1)	25.6
Precipitation seasonality (bio_15)	9.5
NDVI range	9.2
Isothermality (bio_3)	8.0
Mean diurnal range (bio_2)	6.3
Slope	0.5
Flow accumulation	0.1

then increased to 101 by 2010 and 501 by 2016 (unique spatial data). These records span 16 states of Mexico: Chiapas, Coahuila, Estado de Mexico, Guanajuato, Hidalgo, Jalisco, Morelos, Nuevo León, Oaxaca, Puebla, Querétaro, Quintana Roo, San Luis Potosí, Tabasco, Tamaulipas, and Veracruz (Figs. 1 and 2A–C).

For the N_O models in Mexico, all of Maxent's settings combinations had better performance than random expectations, according to the partial ROC tests (Supp Table S1 [online only]). However, we found differences in predictive performance between predictors ($F = 38.13$, $p < 0.001$). Specifically, predictive capacity improved significantly (pairwise comparisons: 'varCLIM' vs 'varALL' – $p < 0.001$, 'varNDVI' vs'varALL' – $p = 0.382$, 'varNDVI' vs 'varCLIM' – $p < 0.001$) with incorporation of NDVI data. The optimal parametrization to estimate the N_O was: occurrence data – 'UF', predictors – 'varALL', regularization multiplier – 'RM2', and features – 'Default' (Supp Table S1 [online only]).
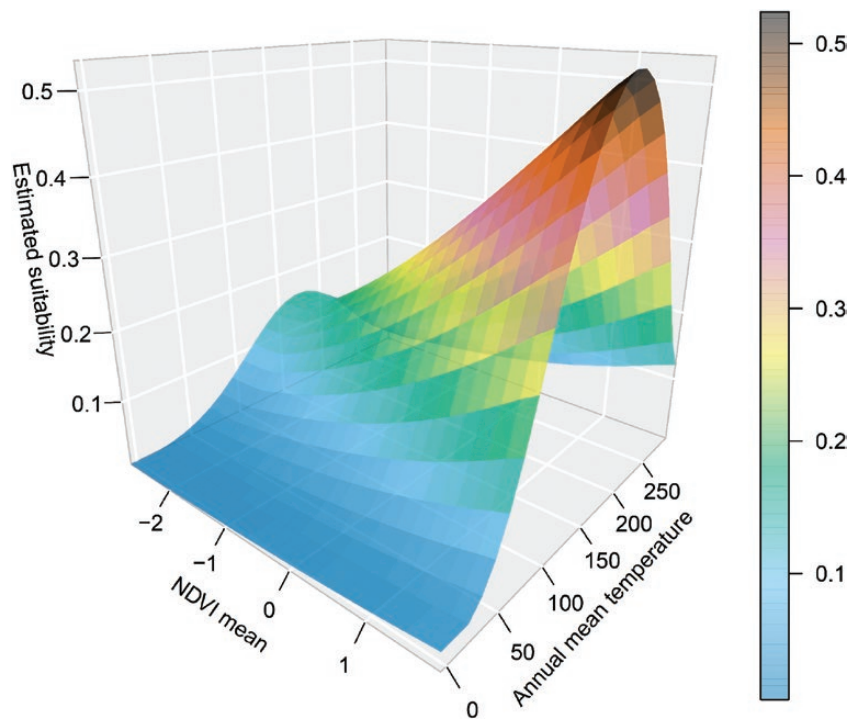
Fig. 3. Response curves to the predictors (NDVI mean and annual mean temperature) that had higher contributions towards gain in Maxent. The annual mean temperature is multiplied by 10.
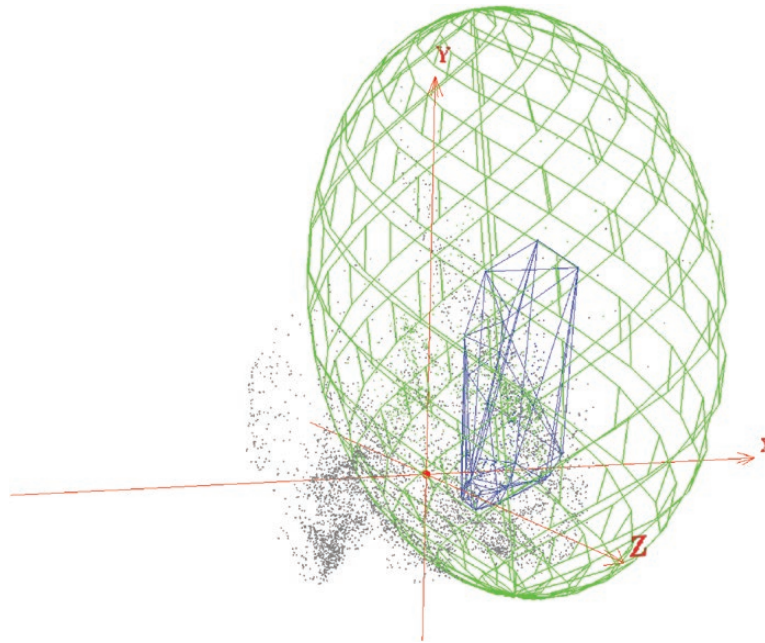

Fig. 4. Minimum-volume ellipsoid describing the fundamental niche of *Ae. albopictus*. Minimum-volume polyhedron representing the environments occupied by this species in Mexico. Points represent the environments of the world.

The increase in spatially unique occurrence records for *Ae. albopictus* through time allowed a better characterization of its N_O in Mexico. This resulted in a more extensive geographical estimation of the mosquito's environmental suitability (Fig. 2D, E and F) and potential distribution (Fig. 2G–I) for each time period. The environmental suitability surface increased from 15% of the Mexican territory in 2005, to >38% in 2010 and

almost 58% in 2016. In this updated model, every state has at least one pixel with adequate conditions for the mosquito's presence. However, it is important to mention that almost all the Baja California peninsula, a considerable portion of Chihuahua and northeastern Sonora had environmental conditions that were not present in the model calibration region. Consequently, any projection in these regions would result in strict model extrapolation

(Supp Fig. 2_1 [online only]) which increases uncertainty of our predictions.

The predictors with the greatest contribution to characterizing *Ae. albopictus* N_O were mean NDVI and the annual mean temperature, accounting for >66% of the gain in Maxent (Table 1). NDVI is positively associated with environmental suitability of the mosquito in Mexico, while annual mean temperature has an optimum maximum at 25°C and environmental suitability gradually decreases at warmer and cooler values (Fig. 3).

At a global scale, we obtained 22,137 presence records for *Ae. albopictus* (excluding Mexico, Supp Fig. S2_2 [online only]). The minimum-volume ellipsoid model (NicheA approximation of N_F) enclose many environments of the world (Fig. 4) depicting a very high invasive potential for this species in many countries (Fig. 5). In the specific case of Mexico, this model had a good capacity to estimate the environmental suitability of the mosquito (AUC ratio = 1.561). However, important differences were observed in the estimated suitability for some central and northwest states with respect to the N_O model (Fig. 6).
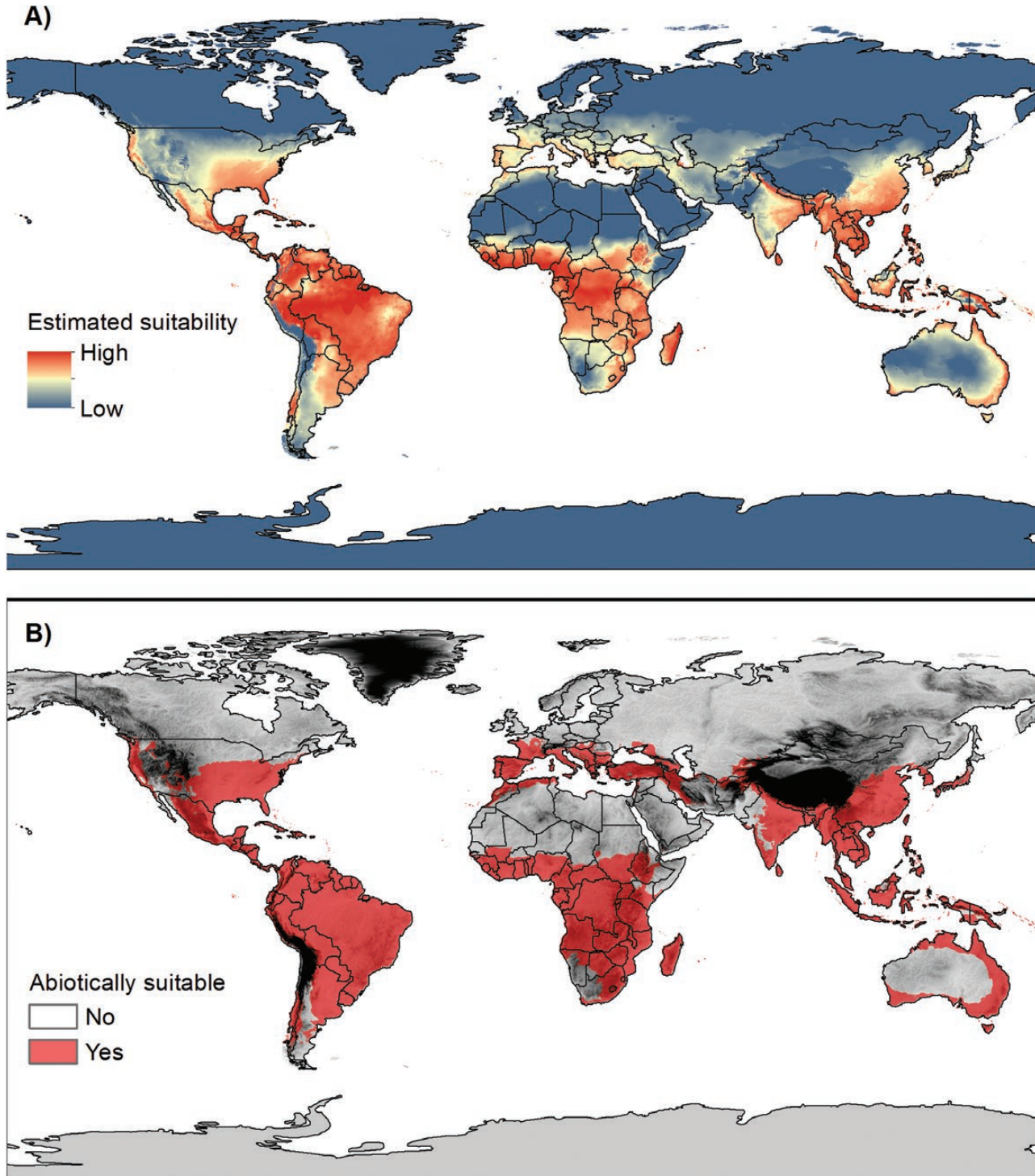

Fig. 5. Environmental suitability (A) and potential distribution (B) of *Ae. albopictus* in the world.
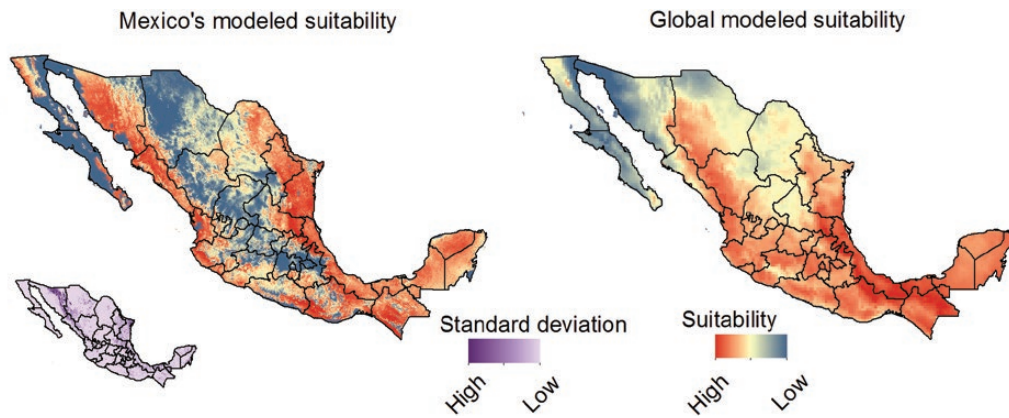
Fig. 6. Environmental suitability of *Ae. albopictus* in Mexico. Estimates from the occupied niche model (left); average and standard deviation of the 10 replicates generated with Maxent. Estimates from the fundamental niche model (right).

Discussion

This is the first time that correlative niche models have been used to investigate the environmental conditions associated with *Ae. albopictus* presence in Mexico. Previous studies (Pech-May et al. 2016) had focused on describing the geographical patterns, rather than characterizing the environmental conditions that define its distribution.

As expected, there was an increase in predictive performance with the addition of NDVI predictors in the occupied niche models. This index indirectly provides information about local characteristics that influence the life cycle of *Ae. albopictus*. High values are related to dense vegetation or crops at a maximum growth stage which indicate suitable habitat and water availability, characteristics that are important for the adult mosquitoes (Brown et al. 2008) and the development of the immature stages (Estallo et al. 2008, Nihei et al. 2014). Vegetation indices are important factors to explain the distributions of mosquito vectors and mosquito-borne diseases (Kerr and Ostrovsky 2003). Brown et al. (2008) used the disease water stress index to characterize larval habitats sites of the *Anopheles punctipennis* (Say 1823) mosquito, and recent studies (e.g., Noor et al. 2008, Cianci et al. 2015, Kraemer et al. 2015) have used the enhanced vegetation index (EVI), which tends to be more robust for areas with high chlorophyll concentrations (Huete 1988, Guerra et al. 2008).

In addition to vegetation, average annual temperature was important in explaining the distribution of *Ae. albopictus* in Mexico. According to our Maxent model the most suitable annual mean temperature for this species is 25°C. This coincides with experimental studies that found optimal temperatures between 20 and 30°C (Brady et al. 2013). However, its physiological thermal tolerance limits are much wider, ~11–40°C (Waldock et al. 2013). Certain lineages even can survive freezing above –10°C through diapause (Thomas et al. 2012).

The invasive potential of *Ae. albopictus* is very high, as shown in our binary maps (Figs. 2 and 5). Such invasive potential might be a product of its wide environmental tolerance, ecological plasticity, and competitiveness (Paupy et al. 2009). The potential distribution of *Ae. albopictus* in Mexico (Fig. 5), based on its N_F characterization, comprises almost the entire Mexican territory, except for regions of the Baja California peninsula and parts of the northwest. This contrasts with Benedict et al. (2007) and Campbell et al. (2015) who estimated that the potential distribution comprises only areas of the coastal plains in the Gulf of Mexico and the Yucatán peninsula. On

the other hand, our environmental suitability estimates based on the characterization of the N_O in Mexico partially coincides with Kramer et al. (2015) model, which identified large areas with high suitability in several states along the Pacific coast (Sonora, Sinaloa, Nayarit, Jalisco, Colima, Michoacán, and Guerrero) and in Tamaulipas in the Gulf of Mexico. Nonetheless, the same study found relatively few areas with high environmental suitability in the south and southeast, compared with our study (Oaxaca, Chiapas, Tabasco, Campeche, Yucatán, and Quitana Roo). We found more similarities with the models of Pech-May et al. (2016), although there seems to be some overfitting in their estimates towards the east coast of Mexico, which is where all their model training presences are located.

The differences between our study and the four published studies mentioned above (Benedict et al. 2007, Campbell et al. 2015, Kraemer et al. 2015, Pech-May et al. 2016) could be due to the following factors: 1) the scale of analysis (global in most of the other studies); 2) the presence record database (we used a more up-to-date database for *Ae. albopictus* presence records in Mexico); 3) the predictors used (we utilized NDVI data and specific climatic variables for Mexico to estimate the mosquito's N_O, and incorporated global surfaces of relative humidity and radiation to estimate its N_F; 4) the calibration area (the calibration region in some of the other studies was assumed to be the entire country, while ours was a polygon around presence localities representing the limits of an area that could have been colonized by the species); and 5) the algorithms and their settings (we tested a wide range of combinations of algorithm settings to identify the optimal fit). Regarding the last point, we consider varying the settings of Maxent to estimate N_O to result in a model with a better predictive capacity than a model with the default adjustments, as suggested by previous works (Shcheglovitova and Anderson 2013, Radosavljevic and Anderson 2014).

Some of the mentioned factors may also have caused the observed differences between our environmental suitability models. We understand this disagreement as complementary because each model is based on the characterization of different entities: the N_O and the N_F. The former may depict regional environmental preferences, and the latter could be related to the species' physiological tolerance limits.

This study allowed us to identify the environmental factors associated with the presence of *Ae. albopictus* in Mexico. Given the correlative nature of our analyses, it is not possible to establish if there is a causal relationship between the mosquito's presence and the identified factors. However, the response curves could serve as a basis for generating experimental hypotheses and the development of models based on physiological aspects

(e.g., Brady et al. 2014). Physiological models could provide a greater level of confidence by explicitly describing the mechanisms that allow the mosquito's survival by means of characterizing, at least for some dimensions, its fundamental niche (N_F) and its geographical representation (i.e., its potential distribution). In this sense, our NicheA model was used as an alternative with great predictive capacity to estimate the potential distribution of *Ae. albopictus* based on a characterization of its N_F.

Our models will help vector control and public health institutions to identify areas where *Ae. albopictus* has not yet been recorded but where it may be present. We emphasize that most of Mexico has environmental conditions that potentially allow the survival of *Ae. albopictus*, which underscores the need for systematic mosquito monitoring in all states of the country.

Acknowledgments

Supplementary Data

Supplementary data is available at *Journal of Medical Entomology* online.

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