Article

Potential Distribution of *Aedes* (*Ochlerotatus*) *scapularis* (Diptera: Culicidae): A Vector Mosquito New to the Florida Peninsula

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Simple Summary: *Aedes scapularis* is an important mosquito species capable of transmitting viruses and parasites to humans and animals. *Aedes scapularis* was previously known to occur throughout large portions of the Americas, from the lower Rio Grande Valley of southern Texas to Argentina and on several Caribbean Islands. Recently, this mosquito became established in southern Florida, marking the first time *Ae. scapularis* was found on the Florida Peninsula. Now that *Ae. scapularis* has reached the Florida Peninsula, it is expected to continue to expand its geographic distribution to fill contiguous areas with suitable environments. Here, we use a modeling approach that correlates environmental variables with known geographic collection locations of *Ae. scapularis* to predict the potential distribution of this species. The output of this model provides new information for mosquito control and public health agencies to help monitor the spread of this exotic vector mosquito and suggests a need for vigilance for the expansion of this mosquito in many of Florida's coastal counties.

Abstract: *Aedes scapularis* is a neotropical mosquito known to transmit pathogens of medical and veterinary importance. Its recent establishment in southeastern Florida has potential public health implications. We used an ecological niche modeling approach to predict the abiotic environmental suitability for *Ae. scapularis* across much of the Americas and Caribbean Islands. Georeferenced occurrence data obtained from the Global Biodiversity Inventory Facility and recent collection records of *Ae. scapularis* from southern Florida served as input for model calibration. Environmental layers included bioclimatic variables provided in 2000 to 2010 average Modern Era Retrospective-analysis for Research and Applications climatic (MERRAclim) data. Models were run in the software program Maxent. Isothermality values found often in costal environments contributed strongest to model performance. Model projections suggested areas predicted suitable for *Ae. scapularis* across portions of the Amazon Basin, the Yucatán Peninsula, the Florida Peninsula, and multiple Caribbean Islands. Additionally, model predictions suggested connectivity of highly suitable or relatively suitable environments spanning the United States Gulf Coast, which may facilitate geographic expansion of this species. At least sixteen Florida counties were predicted highly suitable for *Ae. scapularis*, suggesting vigilance is needed by vector control and public health agencies to recognize further spread of this vector.

Keywords: invasive species; ecological niche models; species distribution models; vector surveillance

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1. Introduction

Changes in the geographic distributions of medically important vector mosquitoes can result in broad-scale negative impacts on human and veterinary health [1,2]. Most notable, is the human-mediated dispersal and subsequent establishment of *Aedes aegypti* L. and *Aedes albopictus* Skuse in multiple regions of the world facilitating the spread of dengue, yellow fever, chikungunya, and Zika viruses into new geographic areas [1,3-7]. Although often overlooked, finer scale changes in the geographic distributions of mosquito vectors can also alter transmission risk, warranting close monitoring of local mosquito faunas for introductions of non-native mosquito species, and for the potential of introduced species to contribute to the transmission of mosquito-borne pathogens [8]. Further, anticipated changes in global climate may lead to shifts in the geographic, elevational, or seasonal occurrence of mosquito species, prompting concerns of increased uncertainty in potential transmission risks of mosquito-vectored pathogens [9].

Several factors facilitate or constrain geographic distributions of mosquito vector species [10,11]. Importantly, biotic variables including competition, predation, and resource availability in a specific area can influence species distributions at relatively fine scales, while abiotic climatic values can serve as broader scale constraints from which to characterize the potential distribution of a species [12-15]. Mosquitoes, as insects, are ectotherms, making them sensitive to temperature, while their small body size makes them vulnerable to low humidity. As such, abiotic climate variables have been used extensively to predict potential distributions and changes in distributions of medically important vector arthropod species and pathogens [16-22].

The geographic location of mainland Florida, USA, spanning multiple ecoregions and climatic gradients [23], along with its proximity to several Caribbean islands and high levels of trade and tourism, makes this area a prime candidate for the invasion and establishment of mosquito vector species from the Neotropics and elsewhere [24]. Importantly, of Florida's 16 non-native and suspected non-native mosquito species, 13 (81.3%) were first detected in the state since 1985, and 10 (62.5%) were first detected in the last 20 years.

The recent expansion in the geographic distribution of *Aedes scapularis* Rondoni onto peninsular Florida presents a new challenge to vector management and mosquito control programs [25]. *Aedes scapularis* is an important vector mosquito in the American Tropics [26]. A diverse assemblage of arboviruses and parasites have been detected in wild females, including flaviviruses (yellow fever, Rocio, and Ilhéus viruses [27-30]), an alphavirus (Venezuelan equine encephalitis virus [31-34]), an orbivirus (Yunnan orbivirus [35]) and filarial nematodes (*Dirofilaria immitis* [36] and *Wuchereria bancrofti* [37]). Prior to its recent range expansion into the Florida Peninsula, the known geographic distribution of *Ae. scapularis* comprised large portions of South and Central America, southern and eastern Mexico, and several Caribbean islands, outlined in a map produced by Arnell [26] plotting the approximate collection locations of examined *Ae. scapularis* specimens. Because the recent observations of *Ae. scapularis* indicate a northward expansion in the geographic distribution of this species onto the contiguous US mainland, a need exists to update and to characterize its potential distribution to help inform future veterinary and public health surveillance and control efforts.

In Florida, *Ae. scapularis* is currently established in Miami-Dade and Broward Counties [25]. Mark-recapture studies indicate that adult female *Ae. scapularis* can disperse relatively large distances, up to 4.1 km [38], making it likely that the geographic distribution of *Ae. scapularis* on the Florida Peninsula will expand to fill adjacent suitable environments over time. Ecological niche modeling, or species distribution modeling, is a correlative modeling approach that utilizes environmental data collected at georeferenced locations where a species has been observed to predict where similar combinations of environments occur across a broader geographic area [39]. Predicting the potential distribution of vector species provides a useful tool to help target monitoring and surveillance efforts, contributing to more efficient vector control and public health management strategies [40]. Here, we use ecological niche modeling to predict the potential distribution of *Ae. scapularis* incorporating recently published georeferenced records from the southern Florida Peninsula.

2. Materials and Methods

Georeferenced *Ae. scapularis* occurrence data were downloaded from the Global Biodiversity Inventory Facility (GBIF) (https://www.gbif.org/) and combined with *Ae. scapularis* records collected in southern Florida [25]. Data without geographic coordinates and occurrence records for which the precision of the decimal degree was less than three decimal places were removed from the data set. Georeferenced occurrence data were then mapped and thinned spatially at a 0.25 decimal degree distance to help prevent overrepresentation of environmental combinations owing to sampling bias and to help reduce potential impacts from spatial autocorrelation on model calibration [41].

Calibration Area

A major component in ecological niche modeling is delineation of the model calibration region (**M**-calibration region) [42]. The **M**-calibration region included the geographic region available to *Ae. scapularis* with a limiting boundary in the north based on a general transition to colder environments; transitions to colder environments also served as the limiting boundary at the southern end of the calibration region in South America. The resulting **M**-calibration region encompassed a large portion of South America, all of Central America, multiple Caribbean islands, Mexico, and a portion of the southern United States in North America (Figure 1).

Environmental Data

Combinations of bioclimatic variables derived from average temperature and specific humidity variables were acquired at a 2.5’ spatial resolution (~ 5 km) for the years 2000 to 2010 from the Modern Era Retrospective-analysis for Research and Applications climatic data set (MERRAclim) [43]. The MERRAclim data consists of bioclimatic variables derived from satellite-based temperature and specific humidity data collections at an hourly time interval from 1981 to 2010 [43]. The MERRAclim bioclimatic variables served as environmental variables in model calibration. Bioclimatic layers were masked to the **M**-calibration region using the ‘raster’ package in R v3.6 [44].

Correlation between environmental variables is common when using bioclimatic layers, which can result in redundancy and highly complex models that produce interpretation challenges [45]. We calculated a Pearson’s correlation matrix using environmental values obtained within the **M**-calibration region to identify pairwise correlations between each environmental variable and generated five candidate sets that included variables that were not highly correlated (Figure S1 & Table S1, Table1).

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Table 1. Bioclimatic variables included in candidate environmental data sets used to develop a model predicting the potential geographic distribution of *Ae. scapularis* in North and South America.

Bio1	Average Annual Temperature
Bio3	Average Isothermality (mean diurnal range/temperature annual range)
Bio5	Average Maximum Temperature of the Warmest Month
Bio6	Average Minimum Temperature of the Coldest Month
Bio12	Average Annual Specific Humidity
Bio16	Average Specific Humidity of the Wettest Quarter
Bio17	Average Specific Humidity of the Driest Quarter

Model Calibration

Ecological niche models were generated using a maximum entropy algorithm in the Maxent 3.41 software package [46], executed within the 'kuenm' package in R [47]. The Maxent software package discriminates the range of environments at georeferenced occurrence locations (i.e. presence locations) with the range of environments found at a set of 'background' locations, distributed randomly across the calibration area [48,49]. A regularization multiplier helps to control for overfitting, which can reduce predictive performance, and contributes to the variable selection process [50]. Models were run using a random subset of 70% of the occurrence data with the remaining 30% of the data withheld for model evaluation. Candidate models were generated for each of the five environmental data sets, using a combination of feature classes (i.e., linear [l], quadratic [q], product [p], linear+quadratic [lq], linear+product [lp], quadratic+product [qp], linear+quadratic+product [lqp]) and regularization multipliers ranging between 0.1 and 10. Initial model runs included an internal 50% random subset for training and testing with 10 bootstrap replicates at 500 iterations each, and 10,000 background points.

Model Evaluation

Model evaluation followed a three-step process outlined in Cobos et al. [47]. Calibration results were filtered first to identify models with statistically significant partial area under the curve of the receiver operating characteristic values (pROC) [51], and only models with omission rates $< 5\%$ were retained. Filtered calibration results were ranked from lowest to highest using Akaike's information criterion scores corrected for small sample sizes (AICc) to identify a final candidate set of models [52]. Model projections were then generated from the best performing model identified in the model evaluation process using the joint occurrence data, and the median of 100 bootstrap replicates served as the final model projection using Maxent's 'cloglog' output [53]. Visual inspection of model predictions from the best performing model were compared to the relative locations described in Arnell [26] to identify outstanding distribution questions, gaps in model predictions, and to target future priority sampling areas.

 doi:10.20944/preprints202012.0502.v1

3. Results

A total of 781 georeferenced occurrence points were acquired for ecological niche models. After removing duplicates and spatially thinning the data, 97 occurrence points remained (Fig 1). Of these 97 occurrence points, 61 were used for model training and 36 were used for model evaluation. A total of 595 candidate models were generated across the five environmental data sets (Table S2). Model evaluation indicated that two models met the criteria of statistical significance (Table S3), with omission rates <5%, and the model with the lowest AICc score was chosen as the final model. The best performing model included four bioclimatic data layers, included quadratic and product features, and a regularization multiplier of 0.3 (Figure 2), and an AUC value of 0.80 (Figure S2).

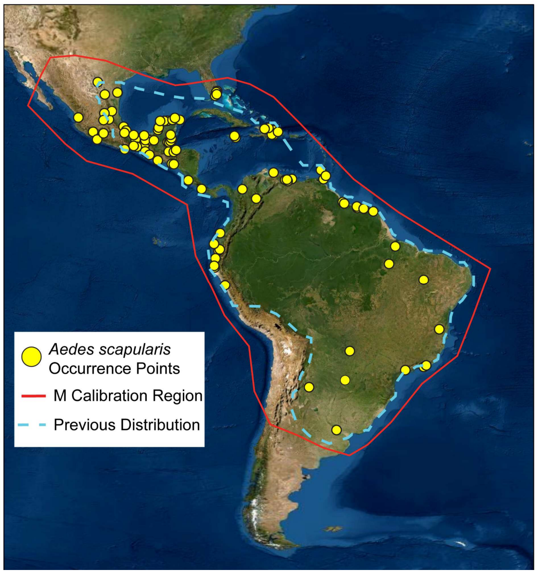

Fig 1. Distribution of *Aedes scapularis* georeferenced occurrence points used in model calibration and evaluation (yellow points); red polygon represents the M calibration region. Blue, hashed-line polygon indicates previously recognized distribution of *Ae. scapularis*, redrawn from Arnell (1976). Base map provided by ESRI.

Environmental variables in the final model included Bio1 (mean annual temperature), Bio3 (average isothermality (mean diurnal range/temperature annual range)), Bio5 (mean maximum temperature of the warmest month), and Bio17 (average specific humidity of the driest quarter). Of these variables, Bio3 contributed the greatest to model performance with 48.6% contribution, followed by Bio17 (22.3% contribution), Bio1 (15.6% contribution), and Bio5 (13.5% contribution).

Marginal response curves for Bio3 indicated that environmental suitability decreased as average isothermality increased. For Bio17, results indicated that predicted environmental suitability was optimal at a value of approximately 1,000 for average specific humidity of the driest quarter, and results suggested an increase in suitability with increases of Bio1 (average annual temperatures). Response curves for Bio5 indicated a slight decrease in predicted suitability when mean maximum temperature of the warmest month reach approximately 35° C.

 doi:10.20944/preprints202012.0502.v1

The model projection predicted several regions to be highly suitable for *Ae. scapularis* across the study region (Figures 3A & 4A). Regions where predicted environmental suitability for *Ae. scapularis* were highest included the Pacific coastline of the Americas, from northern Chile to southern Sonora, Mexico, a broad longitudinal belt across much of South America, along the southern side of the Amazon River, from coastal Brazil west to northern Peru, the llanos of Venezuela around the Orinoco River, the Yucatán Peninsula, southern and Central Nicaragua and the Nicoya Peninsula of Costa Rica, most Caribbean Islands with the exception of the interior of Hispaniola, the Florida Peninsula, and along the Gulf Coast of the United States between Texas and the Florida Panhandle.

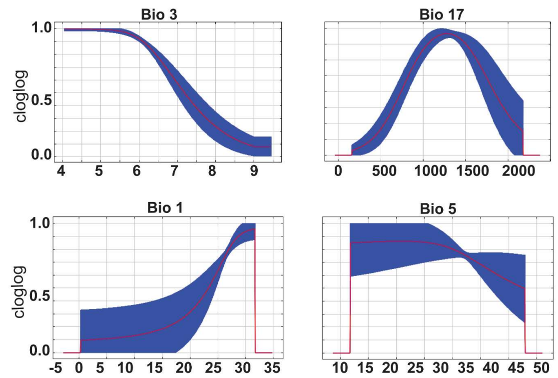

Figure 2. Response curves of bioclimatic variables included in the final model. Bio3, Bio1, and Bio5 values are in units of degrees Celsius; Bio17 specific humidity values are units of 100,000 * kg of water/kg of air.

Plots of the standard deviation of the 100 replicates indicated relatively low variation across the model outputs for the majority of the study area. Areas with higher standard deviation values included the southwestern tip of Chile in South America, a portion of the Amazon Rainforest in Pará and Amazonas States in Brazil, in Colombia, where elevation values increase at Pico Cristóbal Colón,

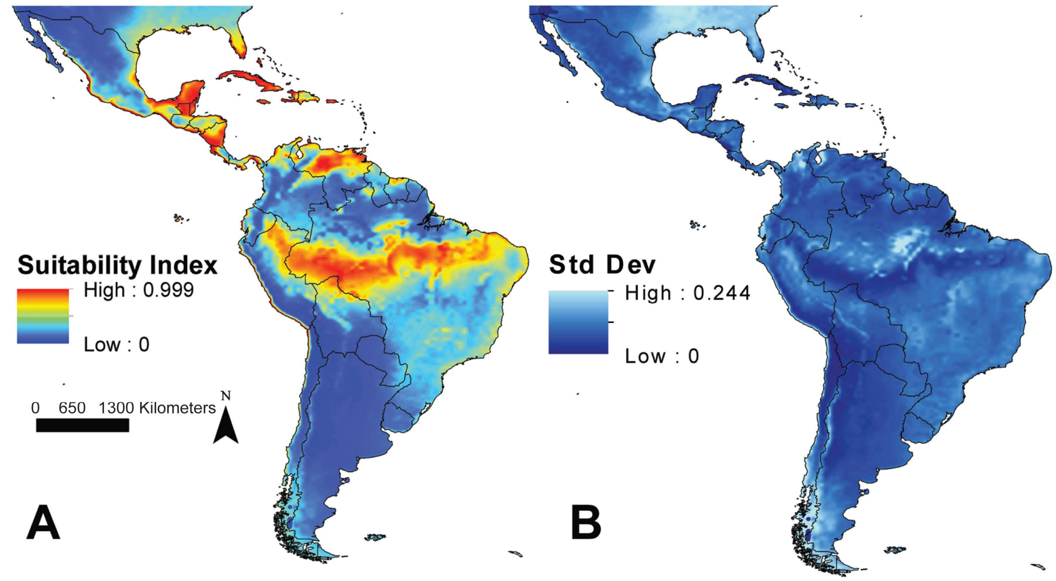

Figure 3. A) Model prediction; red areas indicate high predicted suitability and blue areas indicate low predicted suitability; B) standard deviation of predicted suitability values across 100 bootstrap replicates; light blue areas indicate higher standard deviation values and dark blue areas indicate low standard deviation values.

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and then more generally, in the southeastern United States, beginning in central Florida and moving north- and westward (Figure 3B).

Other than the southern Florida Peninsula, and areas predicted highly suitable along the coast of the Gulf of Mexico from Florida to Texas and Mexico's Pacific coast, areas predicted highly suitable

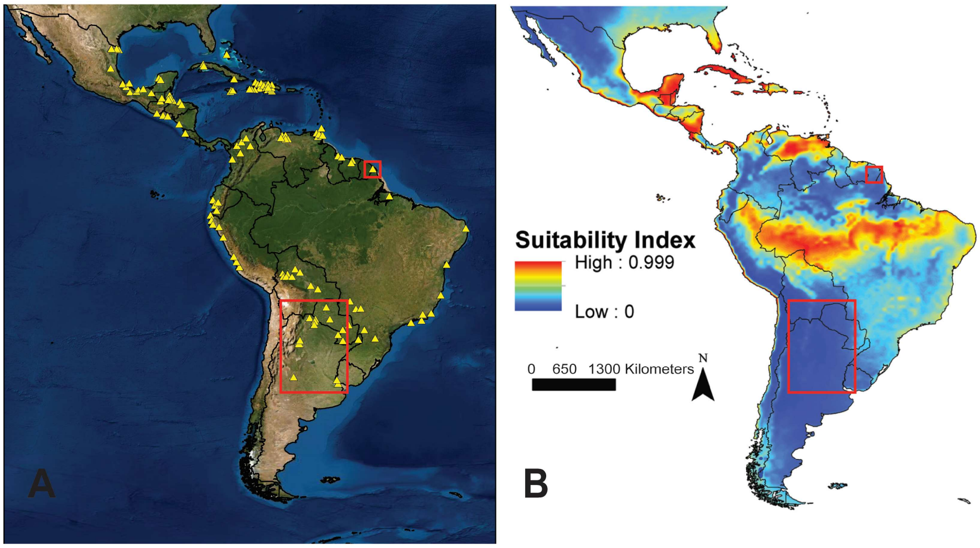

Figure 4. A) *Aedes scapularis* collection records (yellow triangles) reported in and adapted from Arnell 1976. B) *Aedes scapularis* model output. Red squares indicate areas of discrepancy where *Ae. scapularis* collections were reported and examined by Arnell (1976) and where model outputs did not predict suitable environments for *Ae. scapularis*.

were within the previously reported distribution of *Ae. scapularis* (see Figure 1 & Figure 4A) [26]. Comparison of *Ae. scapularis* collection records described in Arnell 1976 (Figure 4A) with model predictions (Figure 4B) indicated a discrepancy in southern South America, where georeferenced occurrence data were not available for our model calibration. Model outputs suggested unsuitable environments for *Ae. scapularis* in this region, but observations were described in Arnell [26]. Additionally, model outputs predicted unsuitable environments in French Guiana, even though Arnell [26] described *Ae. scapularis* in this area and a georeferenced occurrence point was available for model calibration.

Observations of predicted values in North America, beginning in the Yucatán Peninsula and moving northward around the Gulf Coast into the states of Texas, Louisiana, Mississippi, Alabama, and Florida indicated relative connectivity of suitable environments across this region, with areas predicted highly suitable in the Yucatán Peninsula, through Tabasco and Veracruz to Tamaulipas (Figure 5A). Additional areas predicted highly suitable were located along the Gulf Coast of the

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United States at the southern tip of Texas, across the southern coastal edge of Louisiana including the City of New Orleans, in Gulf County in the Panhandle of Florida, and then along the Gulf Coast of the Florida Peninsula. Areas predicted to be moderately suitable for *Ae. scapularis* are located throughout portions of eastern Texas, Louisiana, inland in Mississippi, southern Georgia, South Carolina, and nearly the entirety of Florida; although, standard deviation values across these areas suggest, in general, relatively high variability in model outputs in these areas (Figure 5B).

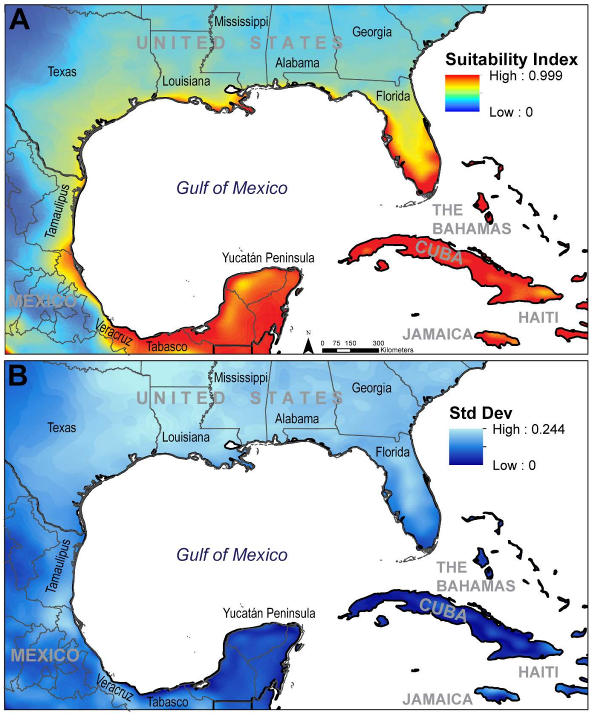

Figure 5. Southeastern United States, Caribbean Islands, and Mexico; A) predicted suitability, B) standard deviation.

Model outputs predicted that much of the Florida Peninsula and Florida Panhandle were relatively suitable for *Ae. scapularis*, with suitability decreasing northward onto the Atlantic Coastal Plain of the United States, with a narrow band of high suitability along much of the United States' Gulf of Mexico coastline (Figure 6A). Specifically, several Florida counties contained areas predicted highly suitable for *Ae. scapularis*, including Miami-Dade, Broward, Palm Beach, and Martin Counties along the Atlantic Coast, with predicted values decreasing, moving northward into St. Lucie, Indian River, and Brevard Counties. Counties containing areas predicted highly suitable on the Gulf Coast of Florida included Monroe, Collier, Lee, Charlotte,

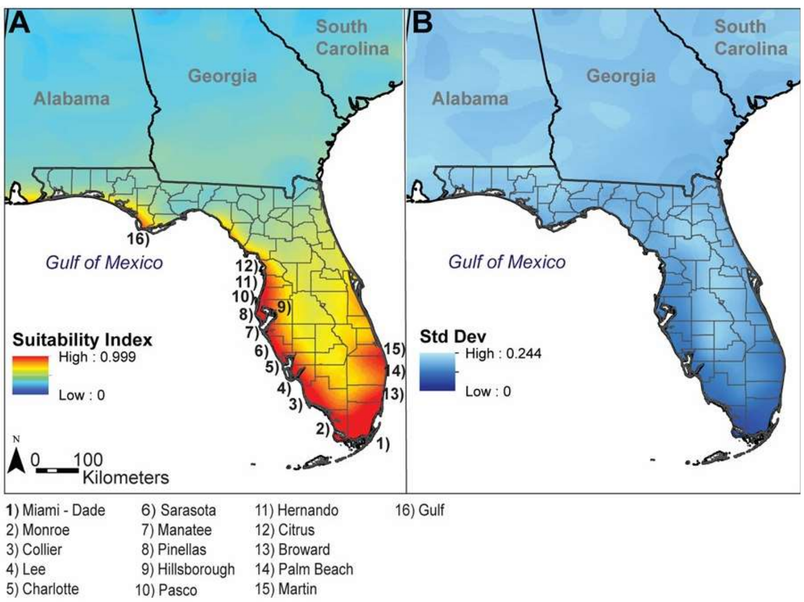

Figure 6. A) Predicted suitability for *Ae. scapularis* in Florida and surrounding states; B) Standard deviation values in Florida and surrounding states.

Sarasota, Manatee, Pinellas, and portions of Hillsborough, Pasco, Hernando, and Citrus Counties, with predicted values decreasing continuing northward along the coast of the Big Bend region and onto the Florida Panhandle, before increasing again in Gulf County. Standard deviation values within Florida indicated higher variability beginning in central Florida and moving northward, with greater values in model predictions in the southeastern United States, beginning in central Florida and moving northward and across portions of the Florida Panhandle (Figure 6B).

4. Discussion

The objective of this study was to predict the potential geographic distribution of *Ae. scapularis*, an important vector of multiple arboviral and parasitic diseases. The recent identification of established *Ae. scapularis* populations on the Florida Peninsula indicated a recent expansion in the known geographic range of this species and highlights the need to monitor further geographic expansion by characterizing environments that may be suitable for this species.

Here, we used an ecological niche modeling approach to predict the potential geographic distribution of *Ae. scapularis* across much of the Americas and the Caribbean Islands, with emphasis on environments that may be suitable for this species along coastal areas of North America, and more specifically, in the State of Florida in the United States. The best performing model included four environmental variables summarizing temperature and specific humidity values. Model results indicated that locations that did not have extreme ratio values between average diurnal temperature values and overall temperature values, that generally had warmer average annual temperatures, but not extreme maximum temperatures, and relatively average specific humidity values were predicted suitable for *Ae. scapularis*.

Model outputs predicted suitable environments for *Ae. scapularis* matching closely to historical collection localities outlined by Arnell [26] and adapted in Figure 4A, as did the majority of the occurrence records used here for model calibration, with the exception of a few regions for which precise georeferenced occurrence points were not available, and in Florida, where the recent geographic expansion occurred. Arnell's records and the georeferenced occurrence points used here generally tracked along or near coastal regions with fewer observations present in inland regions, and this phenomenon was evident in the model results, with average isothermality (mean diurnal range/temperature annual range) contributing the greatest to model performance. Model outputs predicted highly suitable environments along several coastal areas where maritime climates with ocean waters that mediate large temperature fluctuations between daylight and nighttime hours are present [54] and in additional regions exhibiting similar isothermality values. These results may highlight the importance of average isothermality values to the survival and reproduction of *Ae. scapularis*, but the possibility also exists that these results may be an indicator of greater sampling effort and accessible sampling opportunities across coastal regions, where higher densities of people were present, and the terrain does not present an obstacle to sampling.

While coastal regions appear to be highly suitable for *Ae. scapularis*, an important and outstanding question remains regarding the extent to which *Ae. scapularis* utilizes inland environments, given the less frequent but described inland observations. Of particular interest is the extent to which *Ae. scapularis* may inhabit heavily forested environments such as the Amazon Basin. There, our model outputs suggested highly suitable environments south of the Amazon River, where mid-range average isothermality values were present, while predicting low suitability north of the

Amazon River, where average isothermality values rise. Additionally, many of Arnell's observations in Paraguay and northern Argentina that were not predicted suitable in our model fall within the "dry chaco" ecoregion, a hot and semiarid lowland natural region of the Río de la Plata Basin that has a long (6-month) dry season. Predicted suitability was also low further south in the Province of Río Negro, Argentina [55], where the climate is likely at the extreme limits of minimum temperature tolerance for this species. A lack of precise georeferenced occurrence records representing the combination of environments at these inland locations in model calibration likely contributed to this outcome, highlighting the benefit of continued and updated georeferenced data to inform model outputs. Considering that *Ae. scapularis* occurs across a broad temperate area in the southern portion of its range, cool winters on the central and northern Florida Peninsula may not inhibit northward expansion of this species' geographic distribution. As *Ae. scapularis* continues to expand its geographic range, and additional georeferenced occurrence points become available, we anticipate the potential for an increase in inland occurrence data and that these additional data points may alter the contribution of environmental variables to model performance and predictions.

Model predictions suggested highly suitable or relatively suitable environments for *Ae. scapularis* along much of the Gulf Coast of the United States. Importantly, no major gaps in highly suitable or relatively suitable values occurred across this area, suggesting that the environments in this region could serve as an environmental corridor for continued range expansion throughout the region. Although we emphasize the introduction of *Ae. scapularis* in southern Florida, connectivity of suitable environments along the Gulf Coast could also facilitate movement of this species between northern Mexico and the Florida Panhandle. Since 1916 *Ae. scapularis* has been known from southernmost Texas (Cameron and Hidalgo Counties) [26], but to our knowledge, no additional published records from elsewhere in Texas exist to indicate its distribution has expanded there beyond the lower Rio Grande Valley. Interestingly, *Culex coronator*, *Culex declarator* and *Culex interrogator*, all now established non-native species in Florida, likely arrived to Florida via a recent north- and eastward expansion from southern Texas along the Gulf Coast [8,56,57], suggesting that environmental and climatic trends may facilitate geographic expansions across a Gulf Coast route. Additionally, major port cities along the Gulf Coast (Houston, New Orleans, Gulf Port, and Mobile) provide entry points that could further facilitate the geographic expansion of *Ae. scapularis*.

Until recently, *Ae. scapularis* was formerly known to occur across much of the Neotropics, including some Caribbean islands, but was not known from the Florida mainland. The recent collections of *Ae. scapularis* in Miami-Dade and Broward Counties [25], Florida suggests that *Ae. scapularis* could expand its mainland distribution northward and westward, and possibly into the southeastern United States, as no substantial geographic barriers limit its expansion except environmental unsuitability. While human-mediated transport is a likely culprit in the establishment of *Ae. scapularis* in mainland Florida, continued changes in abiotic environmental conditions and human-mediated habitats will be important to monitor, when considering further distributional expansions.

Our model predictions suggested that mosquito surveillance programs in Florida, particularly those along both coasts, should be vigilant for this species. Many Florida counties have robust mosquito control programs which actively trap mosquitoes in these areas [58]. Close inspection of *Aedes* Ochlerotatus Group specimens is warranted as *Ae. scapularis* could be misidentified as morphologically similar species known from Florida: *Aedes infirmatus* and *Aedes condolescens*. *Aedes*

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condolescens is limited to coastal areas of the southern peninsula, while *Ae. infirmatus* occurs statewide. The three species share a conspicuous patch of silvery or light-colored scales on the anterior scutum, but only *Ae. scapularis* has a stripe of pale scales on the hindtibia. (see [59] and for details on morphological identification of *Ae. scapularis*). Mosquito surveillance programs in Florida, particularly those situated in counties predicted high suitability for *Ae. scapularis* (Fig. 6) should be aware of the potential for this mosquito to be present within their jurisdictions.

Our finding that we could calibrate a robust *Ae. scapularis* distribution model using abiotic climatic variables is in agreement with the notion that this species is considered a generalist in its use of habitats, occurring in both sylvatic and human-dominated areas at low and middle elevations. The larvae develop in temporary pools filled by rainfall or overflowing waterways [26]. Adult females are considered opportunistic in their host use, though they feed frequently from endothermic hosts, especially mammals [60-67]. Humans are frequent hosts for female *Ae. scapularis*, and in some human dominated areas, the species shows synanthropic adaptations such as readily entering buildings, and host-seeking and blood-feeding indoors [68,69]. The wide host breadth and frequent use of human hosts coupled with synanthropic adaptions suggests that *Ae. scapularis* may be well positioned, ecologically, to serve as a bridge vector for human and animal pathogens, highlighting further the need to utilize robust tools to monitor the expansion of this species in the Florida Peninsula.

Further investigation using next generation sequencing and population genomics analyses may reveal dispersal patterns of *Ae. scapularis*, the general time scale of when it arrived in the Florida mainland, and how this species is utilizing its environment. Identifying the pathway or pathways through which *Ae. scapularis* arrived will be critical to understanding the potential for future introductions of medically important mosquito species, particularly as anticipated global climate changes stimulate changes in the occurrence of mosquito species. Documenting continued changes in *Ae. scapularis* distributions in mainland Florida will provide valuable information toward understanding how future synanthropic species introductions may spread and utilize the environment.

Aedes scapularis is a neotropical vector mosquito that transmits arboviruses and parasites of medical and veterinary importance. Its recent establishment in the southeastern peninsular Florida has potential public health implications, requiring vigilant surveillance and utilization of modeling approaches to predict where the environment may be suitable for this species. The ecological niche model presented here provides a valuable tool to help inform vector control and public health surveillance efforts, characterizing areas that may be suitable for the geographic expansion of this species, while providing more detailed information about environmental suitability throughout its previously known distribution. As global connectivity continues to increase and environmental conditions continue to change, combining quantitative modeling approaches with field collected data will be critical to maximizing surveillance tools to monitor medically important mosquito vectors.

5. Conclusions

Aedes scapularis is a neotropical vector mosquito that transmits arboviruses and parasites of medical and veterinary importance. Its recent establishment in the southeastern peninsular Florida has potential public health implications, requiring vigilant surveillance and utilization of modeling approaches to predict where the environment may be suitable for this species. The ecological niche model presented here provides a valuable tool to help inform vector control and public health

surveillance efforts, characterizing areas that may be suitable for the geographic expansion of this species, while providing more detailed information about environmental suitability throughout its previously known distribution. As global connectivity continues to increase and environmental conditions continue to change, combining quantitative modeling approaches with field collected data will be critical to maximizing surveillance tools to monitor medically important mosquito vectors.

Supplementary Materials: Figure S1: Correlation plot of environmental variables, Table S1: Pearson's correlation matrix of environmental variables, Table S2: Best candidate models, Table S3: Results of the full 595 candidate models sets, Figure S2: Area under the curve of the receiver operating characteristic (AUC) for best performing model.

Author Contributions: Conceptualization, Lindsay P. Campbell, Nathan Burkett-Cadena and Lawrence Reeves; Data curation, Lindsay P. Campbell, Evaristo Miqueli, Isik Unlu, Kristin Sloyer, Johana Medina, Chalmers Vasquez, William Petrie and Lawrence Reeves; Formal analysis, Lindsay P. Campbell; Methodology, Lindsay P. Campbell; Project administration, Lindsay P. Campbell and Lawrence Reeves; Writing – original draft, Lindsay P. Campbell, Nathan Burkett-Cadena and Lawrence Reeves; Writing – review & editing, Lindsay P. Campbell, Evaristo Miqueli, Isik Unlu, Kristin Sloyer, Johana Medina, Chalmers Vasquez, William Petrie and Lawrence Reeves.

Funding: This research received no external funding.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Gubler, D.J. Dengue, Urbanization and Globalization: The unholy trinity of the 21(st) Century. *Trop Med Health* **2011**, *39*, 3-11, doi:10.2149/tmh.2011-S05.
2. Reisen, W.K. Landscape epidemiology of vector-borne diseases. *Annu Rev Entomol* **2010**, *55*, 461-483, doi:10.1146/annurev-ento-112408-085419.
3. Brady, O.J.; Hay, S.I. The global expansion of dengue: How *Aedes aegypti* mosquitoes enabled the first pandemic arbovirus. *Annu Rev Entomol* **2020**, *65*, 191-208, doi:10.1146/annurev-ento-011019-024918.
4. Wahid, B.; Ali, A.; Rafique, S.; Idrees, M. Global expansion of chikungunya virus: Mapping the 64-year history. *Int J Infect Dis* **2017**, *58*, 69-76, doi:10.1016/j.ijid.2017.03.006.
5. Christofferson, R.C. Zika virus emergence and expansion: Lessons learned from dengue and chikungunya may not provide all the answers. *Am J Trop Med Hyg* **2016**, *95*, 15-18, doi:10.4269/ajtmh.15-0866.
6. Reiter, P. *Aedes albopictus* and the world trade in used tires, 1988-1995: The shape of things to come? *J Am Mosq Control Assoc* **1998**, *14*, 83-94.
7. Rochlin; I.; Gaugler, R.; Williges, E.; Farajollahi, A. The rise of the invasives and decline of the natives: insights revealed from adult populations of container-inhabiting A*edes m*osquitoes (Diptera: Culicidae) in temperate North America. *Biological Invasions* **2013**, *15*, 991-1003.
8. Connelly, C.R.; Alto, B.W.; O'Meara, G.F. The spread of *Culex coronator* (Diptera: Culicidae) throughout Florida. *J Vector Ecol* **2016**, *41*, 195-199, doi:10.1111/jvec.12213.
9. Franklinos, L.H.V.; Jones, K.E.; Redding, D.W.; Abubakar, I. The effect of global change on mosquito-borne disease. *Lancet Infect Dis* **2019**, *19*, e302-e312, doi:10.1016/S1473-3099(19)30161-6.
10. Lounibos, L.P.; Juliano, S.A. Where Vectors Collide: The importance of mechanisms shaping the realized niche for modeling ranges of invasive *Aedes* mosquiotes. *Biol Invasions* **2018**, *20*, 1913-1929, doi:10.1007/s10530-018-1674-7.

 doi:10.20944/preprints202012.0502.v1

11. Juliano, S.A.; Lounibos, L.P. Ecology of invasive mosquitoes: effects on resident species and on human health. *Ecol Lett* **2005**, *8*, 558-574, doi:10.1111/j.1461-0248.2005.00755.
12. Soberón, J.; Nakamura, M. Niches and distributional areas: concepts, methods, and assumptions. *Proc Natl Acad Sci U S A* **2009**, *106 Suppl 2*, 19644-19650, doi:10.1073/pnas.0901637106.
13. Chase, J.M.; Leibold, M.A. *Ecological niches : linking classical and contemporary approaches*; University of Chicago Press: Chicago, 2003; pp. ix, 212 p.
14. Soberon, J.; Peterson, A.T. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodivers. Informatics* **2005**, *2*, 1 - 10.
15. Soberón, J. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol Lett* **2007**, *10*, 1115-1123, doi:10.1111/j.1461-0248.2007.01107.x.
16. Kraemer, M.U.; Sinka, M.E.; Duda, K.A.; Mylne, A.Q.; Shearer, F.M.; Barker, C.M.; Moore, C.G.; Carvalho, R.G.; Coelho, G.E.; Van Bortel, W., et al. The global distribution of the arbovirus vectors *Aedes aegypti* and *Ae. albopictus*. *Elife* **2015**, *4*, e08347, doi:10.7554/eLife.08347.
17. Campbell, L.P.; Luther, C.; Moo-Llanes, D.; Ramsey, J.M.; Danis-Lozano, R.; Peterson, A.T. Climate change influences on global distributions of dengue and chikungunya virus vectors. *Philos Trans R Soc Lond B Biol Sci* **2015**, *370*, doi:10.1098/rstb.2014.0135.
18. Peterson, A.T.; Campbell, L.P.; Moo-Llanes, D.A.; Travi, B.; González, C.; Ferro, M.C.; Ferreira, G.E.M.; Brandão-Filho, S.P.; Cupolillo, E.; Ramsey, J., et al. Influences of climate change on the potential distribution of Lutzomyia longipalpis sensu lato (Psychodidae: Phlebotominae). *Int J Parasitol* **2017**, *47*, 667-674, doi:10.1016/j.ijpara.2017.04.007.
19. Mordecai, E.A.; Ryan, S.J.; Caldwell, J.M.; Shah, M.M.; LaBeaud, A.D. Climate change could shift disease burden from malaria to arboviruses in Africa. *Lancet Planet Health* **2020**, *4*, e416-e423, doi:10.1016/S2542-5196(20)30178-9.
20. Ryan, S.J.; Carlson, C.J.; Mordecai, E.A.; Johnson, L.R. Global expansion and redistribution of *Aedes*-borne virus transmission risk with climate change. *PLoS Negl Trop Dis* **2019**, *13*, e0007213, doi:10.1371/journal.pntd.0007213.
21. Peach, D.A.H.; Almond, M.; Pol, J.C. Modeled distributions of *Aedes japonicus japonicus* and *Aedes togoi* (Diptera: Culicidae) in the United States, Canada, and northern Latin America. *J Vector Ecol* **2019**, *44*, 119-129, doi:10.1111/jvec.12336.
22. Escobar, L.E.; Romero-Alvarez, D.; Leon, R.; Lepe-Lopez, M.A.; Craft, M.E.; Borbor-Cordova, M.J.; Svenning, J.C. Declining Prevalence of Disease Vectors Under Climate Change. *Sci Rep* **2016**, *6*, 39150, doi:10.1038/srep39150.
23. Griffith, G.; Omernik, J. *Ecoregions of Florida (EPA)*; Environmental Information Coalition, National Council for Science and the Environment: Washington DC, 2008.
24. Wilke, A.B.B.; Benelli, G.; Beier, J.C. Beyond frontiers: On invasive alien mosquito species in America and Europe. *PLoS Negl Trop Dis* **2020**, *14*, e0007864, doi:10.1371/journal.pntd.0007864.
25. Reeves, L.; Medina J; Miqueli, E.; Sloyer, K.; Petrie, W.; Vasquez, C.; Burkett-Cadena, N. Establishment of *Aedes* (Ochlerotatus*) scapularis* (Diptera: Culicidae) in Mainland Florida, with Notes on the Ochlerotatus Group in the United States. *Journal Medical Entomology* **2020**, *2020 Nov 23:tjaa250. doi: 10.1093/jme/tjaa250.*
26. Arnell, J. Mosquito studies (Diptera, Culicidae) XXXIII. A revision of the scapularis group of A*edes*. *Contrib. Am. Entomol. Inst* **1976**, *13* 1–144.

27. Shannon, R.C.; Whitman, L.; Franca, M. Yellow fever virus in jungle mosquitoes. *Science* **1938**, *88*, 110-111, doi:10.1126/science.88.2274.110.
28. Mitchell, C.J.; Forattini, O.P.; Miller, B.R. Vector competence experiments with Rocio virus and three mosquito species from the epidemic zone in Brazil. *Rev Saude Publica* **1986**, *20*, 171-177, doi:10.1590/s0034-89101986000300001.
29. Aitken; Anderson, C. Virus transmission studies with Trinidadian mosquitoes II. Further observations. *Am J Trop Med Hyg* **1959**, *8*, 41-45, doi:10.4269/ajtmh.1959.8.41.
30. Pauvolid-Corrêa, A.; Kenney, J.L.; Couto-Lima, D.; Campos, Z.M.; Schatzmayr, H.G.; Nogueira, R.M.; Brault, A.C.; Komar, N. Ilheus virus isolation in the Pantanal, west-central Brazil. *PLoS Negl Trop Dis* **2013**, *7*, e2318, doi:10.1371/journal.pntd.0002318.
31. Causey, O.; Causey, C.; Maroja, O.; Macedo, D. The isolation of arthropod-borne viruses, including members of two hitherto undescribed serological groups, in the Amazon region of Brazil. *Am J Trop Med Hyg* **1961**, *10*, 227-249, doi:10.4269/ajtmh.1961.10.227.
32. Sellers, R.; Bergold, G.; Suarez, O.; Morales, A. Investigations during Venezuelan equine encephalitis outbreaks in Venezuela - 1962-1964. *Am J Trop Med Hyg* **1965**, *14*, 460-469, doi:10.4269/ajtmh.1965.14.460.
33. Scherer, W.F.; Dickerman, R.W.; Diaz-Najera, A.; Ward, B.A.; Miller, M.H.; Schaffer, P.A. Ecologic studies of Venezuelan encephalitis virus in southeastern México III. Infection of mosquitoes. *Am J Trop Med Hyg* **1971**, *20*, 969-979, doi:10.4269/ajtmh.1971.20.969.
34. Sudia, W.D.; Newhouse, V.F. Epidemic Venezuelan equine encephalitis in North America: a summary of virus-vector-host relationships. *Am J Epidemiol* **1975**, *101*, 1-13, doi:10.1093/oxfordjournals.aje.a112066.
35. Méndez-López, M.R.; Attoui, H.; Florin, D.; Calisher, C.H.; Florian-Carrillo, J.C.; Montero, S. Association of vectors and environmental conditions during the emergence of Peruvian horse sickness orbivirus and Yunnan orbivirus in northern Peru. *J Vector Ecol* **2015**, *40*, 355-363, doi:10.1111/jvec.12174.
36. Lourenço-de-Oliveira; R; Deane, L. Presumed D*irofilaria immitis* infections in wild-caught A*edes taeniorhynchus* and A*edes scapularis* in Rio de Janeiro, Brazil. *Memórias do Instituto Oswaldo Cruz* **1995**, *90*, 387–388.
37. Rachou, E.; Lima, M.; Neto, J.; Martins, C. A*ëdes scapularis*, a new proved vector of W. *bancroftii* in southern Brazil. *Revista Brasileira de Malariologia e Doenças Tropicais* **1954**, *6*, 145.
38. Causey, O.; Kumm, H. Dispersion of forest mosquitoes in Brazil; preliminary studies. *Am J Trop Med Hyg* **1948**, *28*, 469-480, doi:10.4269/ajtmh.1948.s1-28.469.
39. Peterson, A.T. *Ecological niches and geographic distributions*; Princeton University Press: Princeton, N.J., 2011; pp. x, 314 p.
40. Peterson, A.T. *Mapping disease transmission risk : enriching models using biogeography and ecology*; Johns Hopkins University Press: Baltimore, 2014; pp. xiv, 210 pages.
41. Boria, R.; Olson, L.; Goodman, S.; Anderson, R. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling* **2014**, 73-77.
42. Barve, N.; Barve, V.; Jímenez-Valverde, A.; Lira-Noriega, A.; Maher, S.P.; Peterson, A.T.; Soberon, J.; Villalobos, F. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol. Modell* **2011**, *222*, 1810 - 1819.
43. Vega, C.G.; Pertierra, L.R.; Olalla-Tarraga, M.A. MERRAclim, a high-resolution global dataset of remotely sensed bioclimatic variables for ecological modelling. *Sci Data* **2017**, *4*, 170078, doi:10.1038/sdata.2017.78.

44. Hijmans, R. raster: Geographic Data Analysis and Modeling. *R package version 2.5-2* **2015**, *https://CRAN.R-project.org/package=raster*.
45. Merow, C.; Smith, M.J.; Silander, J.A. A practical guide to Maxent for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography (Cop.)* **2013**, *36*, 1058-1069.
46. Phillips, S.; Dudík, S.; Shapire, R. [Internet] Maxent software for modeling species niches and distributions. Version 3.4.1. Available from: url: http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed 2020-10-6.
47. Cobos, M.; Peterson, A.; Barve, N.; Osorio-Olvera, L. kuenm: an R package for detailed development of ecological niche models using Maxent. *Peerj* **2019**, *7*, doi:10.7717/peerj.6281.
48. Phillips, S.J.; Anderson, R.P.; Schapire, R.E. Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **2006**, *190*, 231-259.
49. Syfert, M.M.; Smith, M.J.; Coomes, D.A. The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS One* **2013**, *8*, e55158, doi:10.1371/journal.pone.0055158.
50. Phillips, S.; Dudík, M. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **2008**, *31*, 161-175, doi:10.1111/j.2007.0906-7590.05203.x.
51. Peterson, A.T.; Papeş, M.; Soberón, J. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol. Modell.* **2008**, *213*, 63-72.
52. Warren, D.L.; Seifert, S.N. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecol Appl* **2011**, *21*, 335-342.
53. Phillips SJ; Anderson RP; Dudík M; Schapire RE; ME, B. Opening the black box: An open-source release of Maxent. *Ecography* **2017**, *40*, 887-893, doi:doi: 10.1111/ecog.03049.
54. Arbogast, A.F. *Discovering physical geography*, Second edition. ed.; John Wiley & Sons: Hoboken, NJ, 2011; pp. xxxiii, 639 pages.
55. Mitchell, C.; Darsie, R. Mosquitoes of Argentina Part II: Geographic distribution and bibliography. *Mosquito Systematics* **1985**, *17*, 279-360.
56. Darsie, R.F.; Shroyer, D.A. *Culex* (Culex) *declarator*, a mosquito species new to Florida. *J Am Mosq Control Assoc* **2004**, *20*, 224-227.
57. Shin, D.; O'Meara, G.F.; Civana, A.; Shroyer, D.A.; Miqueli, E. *Culex interrogator* (Diptera: Culicidae), a mosquito species new to Florida. *J Vector Ecol* **2016**, *41*, 316-319, doi:10.1111/jvec.12230.
58. Lloyd, A.; Connelly, C.; Carlson, D. Florida Mosquito Control: The state of the mission as defined by mosquito controllers, regulators, and environmental managers. Florida Coordinating Council on Mosquito Control: Vero Beach, FL, 2018.
59. Darsie, R.; Morris, C. Keys to the adult females and fourth instar larvae of the mosquitoes of Florida (Diptera, Culicidae). *Florida Mosquito Control Association, Fort Myers, FL.* **2003**.
60. Forattini, O.; de Castro Gomes, A.; Natal, D.; Kakitani, I.; Marucci, D. Preferências alimentares de mosquitos Culicidae no Vale do Ribeira, São Paulo, Brasil. *Revista de Saúde Pública* **1987**, *21*, 171–187.
61. Forattini, O.; de; Castro Gomes, A.; Natal, D.; Kakitani, I.; Marucci, D. Preferências alimentares e domiciliação de mosquitos Culicidae no Vale do Ribeira, São Paulo, Brasil, com especial referência a *Aedes scapularis* e a *Culex* (M*elanoconion)*. *Revista de Saúde Pública* **1989**, *23*, 9-19.
62. Gomes, A.; Silva, N.; Marques, G.; Brito, M. Host-feeding patterns of potential human disease vectors in the Paraíba Valley Region, State of São Paulo, Brazil. *J. Vector Ecol* **2003**, *28*, 74–78.

63. Loroso, E.; Faria, M.; De Oliveira, L.; Alencar, J.; Marcondes, C. Blood meal identification of selected mosquitoes in Rio de Janeiro, Brazil. *J. Am. Mosquito Contr* **2010**, *26*, 18–23.

64. de Carvalho, G.C.; Malafronte, R.o.S.; Miti Izumisawa, C.; Souza Teixeira, R.; Natal, L.; Marrelli, M.T. Blood meal sources of mosquitoes captured in municipal parks in São Paulo, Brazil. *J Vector Ecol* **2014**, *39*, 146-152, doi:10.1111/j.1948-7134.2014.12081.x.

65. Alencar, J.; Mello, C.F.; Gil-Santana, H.R.; Giupponi, A.P.; Araújo, A.N.; Lorosa, E.S.; Guimarães, A.; Silva, J.o.S. Feeding Patterns of Mosquitoes (Diptera: Culicidae) in the Atlantic Forest, Rio de Janeiro, Brazil. *J Med Entomol* **2015**, *52*, 783-788, doi:10.1093/jme/tjv098.

66. Mucci, L.F.; Júnior, R.P.; de Paula, M.B.; Scandar, S.A.; Pacchioni, M.L.; Fernandes, A.; Consales, C.A. Feeding habits of mosquitoes (Diptera: Culicidae) in an area of sylvatic transmission of yellow fever in the state of São Paulo, Brazil. *J Venom Anim Toxins Incl Trop Dis* **2015**, *21*, 6, doi:10.1186/s40409-015-0005-z.

67. Santos, C.S.; Pie, M.R.; da Rocha, T.C.; Navarro-Silva, M.A. Molecular identification of blood meals in mosquitoes (Diptera, Culicidae) in urban and forested habitats in southern Brazil. *PLoS One* **2019**, *14*, e0212517, doi:10.1371/journal.pone.0212517.

68. Klein, T.; Lima, J.; Tang, A. Seasonal distribution and diel biting patterns of Culicine mosquitoes in Costa Marques, Rondônia, Brazil. *Memórias do Instituto Oswaldo Cruz* **1992**, *87*, 141–148.

69. Forattini, O.P.; Kakitani, I.; Massad, E.; Marucci, D. Studies on mosquitoes (Diptera: Culicidae) and anthropic environment. 9-Synanthropy and epidemiological vector role of *Aedes scapularis* in south-eastern Brazil. *Rev Saude Publica* **1995**, *29*, 199-207, doi:10.1590/s0034-89101995000300007.