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Ecological niche modeling for predicting the potential geographical distribution of *Aedes* species (Diptera: Culicidae): A case study of Enugu State, Nigeria

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ABSTRACT

Arbovirus transmission by *Aedes* mosquitoes has long been a significant problem in Africa. In West Africa, *Aedes* vector management faces significant challenges; lack of recent *Aedes* distributional data and potential distributional modeling hinder effective vector control and pose serious public health issues. In this study, larval and adult mosquitoes were collected from four study sites in Enugu State, Nigeria every other month between November 2017 and September 2018. A total number of 2997 *Aedes* mosquitoes were collected and identified, and 59 positive field occurrence points for both *Aedes* adult and larvae were recorded. A total of 18 positive occurrence points were used for modeling. Ecological Niche Models (ENMs) were used to estimate the current geographic distribution of *Aedes* species (*spp.*) in Enugu State, south-east Nigeria, and mosquito presence was used as a proxy for predicting risk of disease transmission. Maximum Entropy distribution modeling or “MaxEnt” was used for predicting the potential suitable habitats, using a portion of the occurrence records. A total of 23 environmental variables (19 bioclimatic and four topographic) were used to model the potential geographical distribution area under current climatic conditions. The most suitable habitat for *Aedes* spp. was predicted in the northern, central, and southeastern parts of Enugu State with some extensions in Anambra, Delta, and Edo States in the west, and Ebonyi State in the east. Seasonal temperature, precipitation of the wettest month, mean monthly temperature range, elevation, and precipitation of the driest months were the highest estimated main variable contributions associated with the distribution of *Aedes* spp. We found that *Aedes* spp. prefer to be situated in environmental conditions where precipitation of wettest month ranged from 265 to 330 mm, precipitation of driest quarter ranged from 25 to 75 mm while precipitation of wettest quarter ranged from 650 to 950 mm. *Aedes* mosquitoes, such as *Ae. aegypti* and *Ae. albopictus*, pose a significant threat to human health, hence, the results of this study will help decision makers to monitor the distribution of these species and establish a management plan for future national mosquito surveillance and control programs in Nigeria.

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1. Introduction

Arboviral infections are a public health concern that is receiving increased attention globally (Wilder-Smith et al., 2017) and particularly in Africa due to the wide distribution of *Aedes* (*Ae.*) *spp.* Mosquitoes and the escalating burden and risk of *Aedes*-borne acute febrile diseases (Weetman et al., 2018). Two major mosquito vectors, *Ae. aegypti* (Linnaeus) and *Ae. albopictus* (Skuse), are responsible for the transmission of viruses such as dengue, Zika, yellow fever (YF) and chikungunya in West Africa, and have shown tremendous global expansion (Kraemer et al., 2015). These viruses have also been isolated from *Ae. vittatus* (Bigot), which is thought to play an important role in the maintenance and transmission of these diseases based on experimental evidence of transmission (Sudeep and Shil, 2017). In East Africa, epidemics of YF may be vectored by *Ae. bromeliae* (Theobald), the only anthropophilic member of the *Ae. simpsoni* (Theobald) species complex which contains 10 subspecies (Huang, 1986). Additionally, the distribution and frequencies of Zika virus (ZIKV) infected mosquitoes suggest that *Ae. africanus* and *Ae. lutocephalus* are involved in sylvatic ZIKV transmission cycles, however, ZIKV detection in field-collected mosquitoes does not prove its role as vector (Kraemer et al., 2015).

The emergence or re-emergence of arboviruses involved in human epidemics is associated with the coincidence of several factors including: the presence of sufficient numbers of susceptible hosts, the presence of the vectors, and the ecological conditions allowing for the establishment of a transmission cycle (Sall et al., 2010; Pfeffer and Dobler, 2010; Weaver and Reisen, 2010; Vasilakis et al., 2011). Lack of recent *Aedes* distributional data and potential distributional modeling hinders effective vector control and poses a serious public health issue Nigeria. Therefore, applying techniques such as Ecological Niche Modeling (ENM) are important in bridging knowledge gaps in the distribution of organisms and hence the risk of disease transmission (Peterson et al., 2005; Escobar et al., 2016).

The ecological niche can be characterized as the set of natural conditions (abiotic variables) in which a species is able to preserve reasonable population sizes without migration (Grinnell, 1917 and 1924; Fath, 2018). ENM provides a prediction of the suitable habitats for mosquito species in an explicit spatial manner derived from extracting and comparing environmental factors that are similar to the areas where the species occurs, thus filling the gaps resulting from surveillance data shortages (Jiménez-Valverde et al., 2011). It is not only used to analyze species distributions, but also to predict the presence or absence of species or their habitats in unrecorded areas (Guisan and Hofer, 2003; Araújo et al., 2005; Wintle et al., 2005; Elith et al., 2006; Elith and Leathwick, 2009).

An accurate and thorough understanding of the roles that geographical distribution of vectors and ecological effects play on arboviral transmission dynamics may allow the prediction, and potential prevention, of epidemics and reduce the disease impact on humans. The goal of this study is to model the potential geographical distribution of *Aedes* spp. in Enugu, south-east Nigeria and develop an ecological niche model that will address information gaps and provide accurate data for public health decision makers for future national surveillance and control programs. Vector surveillance data that couples climatological and mapping data offers robust tools for predict population dynamics of vectors (Foley et al., 2011).

2. Material and methods

2.1. The study area

Enugu State is one of five states within the south-east geopolitical zone of Nigeria and lies inside the tropical rainforest zone. Enugu State is at approximately 223 m (732 ft) above sea level; the soil is well depleted amid its rainy seasons. The mean temperature in Enugu State within the hottest month of February is around 87.16 °F (30.64 °C), and the lowest temperatures typically occur within the month of November, at 60.54 °F (15.86 °C). Precipitation is highest in July (35.7 cu cm [2.18 cu in]), and lowest in February (0.16 cu cm [0.0098 cu in]).

Study sites: Four sites (Ugbawka, Agbalenyi, Gmelina Forest and Opi) were selected for collecting adult *Aedes* spp. according to the three senatorial zones of the state (Fig. 1).

Enugu East Senatorial Zone: Ugbawka, in Nkanu West local government area (LGA), is located on Latitude 6.2761 and Longitude 7.5936. It is approximately 25 km (16 miles) away from Enugu metropolis. Gmelina Forest, in Enugu North LGA, is located on Latitude 6.4660 and Longitude 7.4872.

Enugu West Senatorial Zone: Agbalenyi, in Oji River LGA, is located on the coordinates within plus/minus 10Km from Latitude 6.2677 and Longitude 7.2828.

Enugu North Senatorial Zone: Opi, in Nsukka LGA, has coordinates of Latitude 6.7777 and Longitude 7.4210.

The four communities selected (Ugbawka, Agbalenyi, Gmelina Forest and Opi) were largely agrarian, growing varieties of both food and cash crops, and determined to be favourable mosquito breeding habitats. Five houses in each community were randomly selected for trap placement. This was done to adequately cover the community, ensuring that the mosquito population was fairly represented.

2.2. Mosquito sampling and identification

Adult mosquitoes were collected during the period between November 2017 and September 2018 for seven consecutive days every other month. The same set of houses were used for the two periods of sampling (0600–1800 and 1800–0600) in each site. The Bio-gents® Sentinel Traps (BGS) baited with a lure were used from 0600 to 1800, after which they were removed and replaced with the Centers for Disease Control and Prevention (CDC) Ultra Violet (UV) traps baited with lure and CO₂ which lasted from 1800 to 0600. In each period of sampling, one trap was set around one house. The trapped mosquitoes were retrieved and transported to National

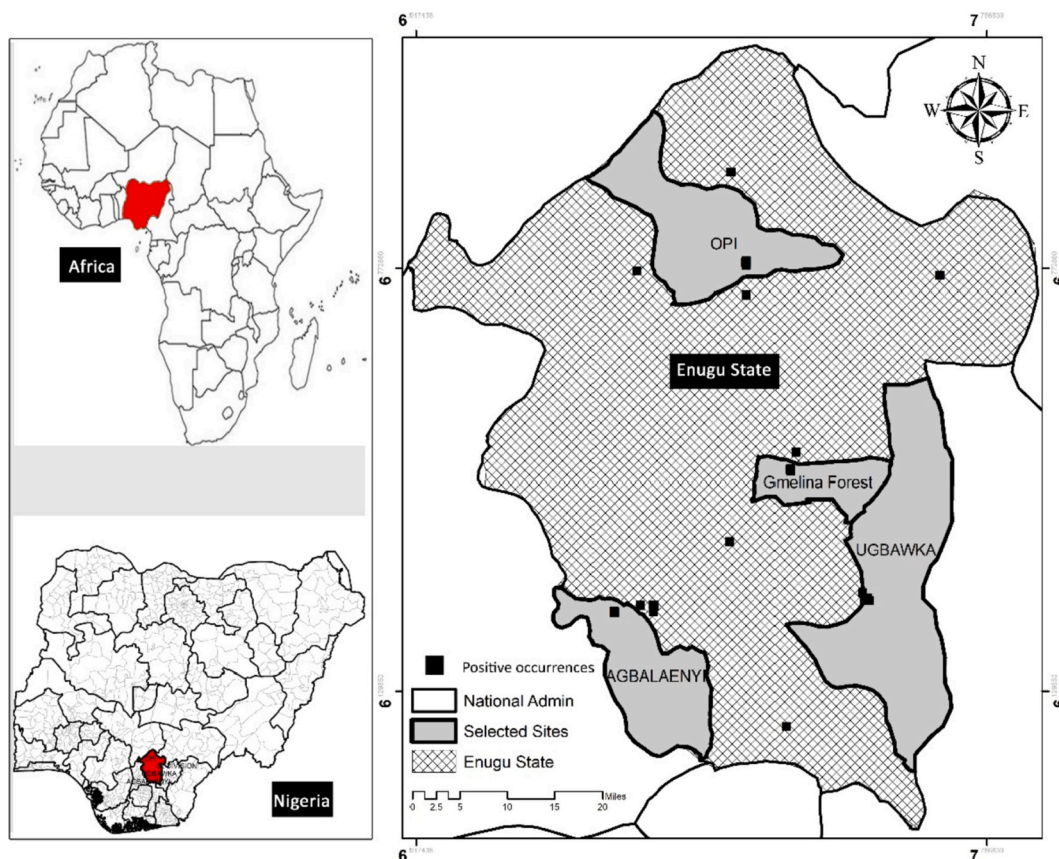


Fig. 1. Enugu State map presenting the selected adult mosquito surveillance sites and the positive occurrences of *Aedes* spp.

Arbovirus and Vectors Research Centre (NAVRC), Enugu Laboratory for identification and processing. All collected *Aedes* adult mosquitoes were identified to species level using the morphological keys of Rueda (2004). *Aedes* mosquito larvae were also collected from potential breeding sites in Enugu State, on-site identification of *Aedes* larvae was made and the corresponding geographical coordinate was recorded as positive or negative for *Aedes* larvae.

2.3. Ecological Niche Modeling (ENM)

2.3.1. Environmental variables

To determine the possible distribution of *Aedes* spp. in Enugu State using the prediction model, a total of 59 positive occurrences for *Aedes* spp. were recorded from the field study (including *Aedes* adult and larvae). The autocorrelation problems were addressed by eliminating redundant presences on the scale of the bioclimatic variables used in each 1×1 km grid (de Luis et al., 2018). In addition, records for spatial autocorrelation were screened in ArcGIS 10.4.1 using average nearest neighbor analyses to remove spatially correlated data points (Bosso et al., 2016; Smeraldo et al., 2018). After this selection, a total of 18 *Aedes* positive occurrence points were used to create a prediction model. We considered twenty-three environmental variables (19 bioclimatic and 4 topographic) as potential predictors of the target species habitat distribution (Khafagi et al., 2011, 2013). These variables were chosen based on their biological relevance to the target species distributions and other habitat modeling studies (Kumar et al., 2006; Guisan et al., 2007; Pearson et al., 2007). Nineteen bioclimatic variables, biologically more meaningful to define eco-physiological tolerances of a species (Graham and Hijmans, 2006; Muriienne et al., 2009), with a 30 arc-second spatial resolution (about. 1 km^2) were downloaded from the WorldClim database (<http://www.worldclim.org/>) (Hijmans et al., 2005). Elevation data 1 km^2 -resolution was obtained from the Shuttle Radar Topography Mission (SRTM). The elevation data was used to generate slope, aspect, and hillshade (all in degrees) using the Spatial Analyst tool/surface in using ArcGIS 10.4.1 software. Then we utilized the standard geographic coordinates in decimal degrees (to five decimal places) in WGS 84. Then we spatialized and checked the geographic coordinates on Google Earth. After

Table 1
Environmental variables used for modeling the potential distribution of *Aedes* spp. in the present study.

No	Variable	Code/Unit	Source
1	Elevation	Elev (m)	WorldClim
2	Slope	SL (%)	Derived from DEM
3	Aspect	AS (degrees)	Derived from DEM
4	Hill Shad	Degrees	Derived from DEM
5	Mean diurnal range (max. temp – min. temp)	Bio2 (°C)	WorldClim
6	Temperature seasonality (SD × 100)	Bio4 (°C)	WorldClim
7	Max temperature of warmest month	Bio5 (°C)	WorldClim
8	Min temperature of coldest month	Bio6 (°C)	WorldClim
9	Mean temperature of wettest quarter	Bio8 (°C)	WorldClim
10	Precipitation of wettest month	Bio13 (mm)	WorldClim
11	Precipitation seasonality (Coefficient of variation)	Bio15	WorldClim
12	Precipitation of driest quarter	Bio17 (mm)	WorldClim
13	Precipitation of coldest quarter	Bio19 (mm)	WorldClim

downloading the climatic files (covering the period 1950–2000), the Nigeria layer was extracted by using a boundary mask. After that, extracted files were converted to ASCII format via using ArcGIS 10.4.1 software to be use later with Maxent software.

All combinations of the 23 environmental variables have been tested for multi-collinearity through the calculation of R-squared in linear regression analysis in SPSS ver. 25. In this study, because topographic, and bioclimatic variables were strongly correlated ($R^2 \geq 0.7$), only those variables that showed little correlation with other predictors were retained; following Kalle et al. (2013), and Omar and Elgamal (2021). A total of 13 environmental variables were selected in this study ($R^2 < 0.7$); elevation, slope, aspect, hillshade, mean diurnal range (max. temp – min. temp) (bio2), temperature seasonality (SD × 100) (bio 4), max temperature of warmest month (bio5), min temperature of coldest month (bio 6), mean temperature of wettest quarter (bio 8), precipitation of wettest month (bio13), Precipitation seasonality (Coefficient of variation) (bio 15), precipitation of driest quarter (bio17), and precipitation of coldest quarter (bio19) (Table 1).

2.3.2. Modeling procedure

The modeling technique maximum entropy distribution or Maxent were used in this study; which has been found to be the most effective among several different modeling methods (Elith et al., 2006; Ortega-Huerta and Peterson, 2008; Khafagi et al., 2013), and may continue to be effective even with small sample sizes (Hernandez et al., 2006; Papes and Gaubert, 2007; Pearson et al., 2007; Wisz et al., 2008; Khafagi et al., 2011). For the study area, it only requires species presence data (not absence) and environmental variable (continuous or categorical) layers. We used the freely available Maxent software, version 3.3.3, which generates an estimate of the probability of the presence of the species that varies from 0 “unsuitable” to 0.99 “best habitat suitability”. ASCII files of the 13 selected environmental variables and a CSV file of species presence coordinates in decimal degrees were used to create the module. Maxent’s performance was assessed using a threshold independent Receiver-Operating Characteristic (ROC) analysis and Area Under Receiver-Operating Characteristic Curve (AUC) values (0.5 = random to 1 = perfect discrimination). The algorithm either runs 1000 iterations of these processes or continues until convergence is reached (threshold 0.00001).

For the model, the relative importance of each environmental predictor was evaluated using the percentage contribution of the Jackknife test, which is the best index for small sample sizes according to Pearson et al. (2007). The default logistic output format was chosen, i.e. related to the probability of suitable conditions, ranging from 0 to 1. A total of 75% of the location point data were used for training, and the remaining 25% to test the predictive ability of the model, in addition 10 replicates were considered. Average and Standard deviation values for training and test AUC for the 10 models were extracted from the Maxent text result output. The ASCII output map for the average model for the target species was loaded in ArcGIS 10.4.1 where the prediction models of habitat suitability were divided based on Choudhury et al. (2016) into 4 classes; ≤ 0.10 very low to unsuitable, 0.11–0.30 Low Probability, 0.31–0.70 Moderate Probability, and ≥ 0.71 High Probability for the presence of the species.

3. Results

3.1. Mosquito sampling and identification

Between November 2017 and September 2018, a total number of 2997 *Aedes* adult mosquitoes were collected and identified from the four sites in Enugu State, south-east Nigeria. Also, potential mosquito breeding sites were checked for the presence or absence of *Aedes* larvae. Out of 92 sites checked, 59 coordinates were positive for *Aedes* adults and larvae. *Aedes* larvae were found mainly in used tyres, plastic containers and earthen pots for cooking.

Eight *Aedes* spp. were recorded; *Ae. albopictus* (51.6%), *Ae. aegypti* (22.3%), *Ae. africanus* (15.8%), *Ae. luteocephalus* (7.7%), *Ae. simpsoni* (1.6%), *Ae. vittatus* (0.5%), *Ae. circumluteolus* (0.5%) and *Ae. longipalpis* (0.03%) (Table 2, Fig. 2). Three of the eight *Aedes*

Table 2
Aedes spp. distributed within the four communities in Enugu State, Nigeria.

Species/Study area	Gmelina	Ugbawka	Agbalenyi	Opi	Total
<i>Ae. albopictus</i>	759	216	425	147	1547
<i>Ae. aegypti</i>	205	122	189	152	668
<i>Ae. africanus</i>	0	2	71	400	473
<i>Ae. simpsoni</i>	7	18	12	10	47
<i>Ae. luteocephalus</i>	0	13	13	205	231
<i>Ae. vittatus</i>	0	1	0	15	16
<i>Ae. circumluteolus</i>	0	10	2	2	14
<i>Ae. longipalpis</i>	0	0	0	1	1

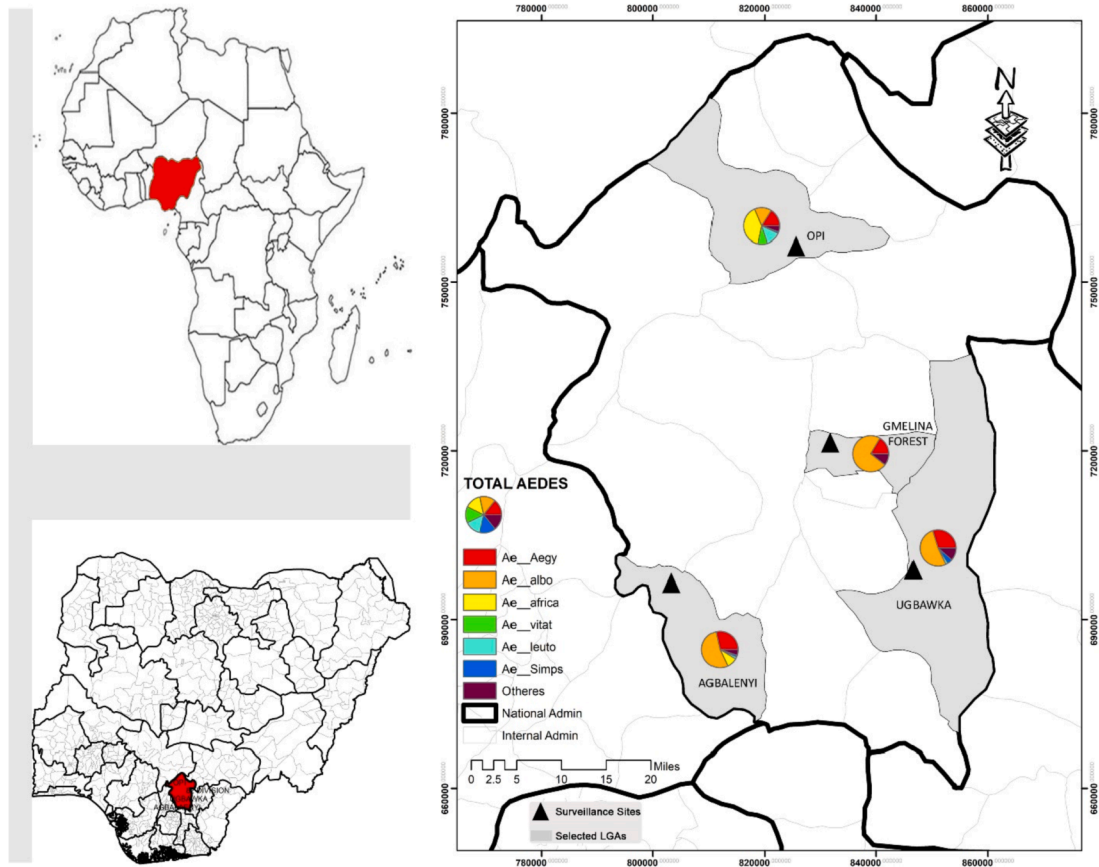


Fig. 2. Spatial distribution of adult *Aedes* spp. collected from 4 sites in Enugu State during November 2017 to September 2018.

species recorded (*Ae. aegypti*, *Ae. albopictus* and *Ae. simpsoni*) were found in all surveyed sites in both dry and rainy seasons, while *Ae. africanus* was collected from Agbalenyi and Opi only (Table 2).

Fig. 3 shows the total number of *Aedes* mosquitoes collected across the four sites. Gmelina forest recorded the highest number which represented 32.4% ($n = 971$) of the overall *Aedes* collected followed by Opi 31.1% ($n = 932$), and then Agbalenyi 23.8% ($n = 712$) and lastly Ugbakwa 12.7% ($n = 382$).

In the area investigated by the current study, *Aedes* species were present year-round. However, seasonal variation markedly affected the number of collected *Aedes* mosquitoes with the highest number collected in May 33.1% ($n = 992$) and July 26.6% ($n = 798$) (rainy season starts April through July 2018). However, during September, November, January and March, *Aedes* mosquitoes were collected in low numbers 17.2% ($n = 514$), 6.3% ($n = 190$), 0.9% ($n = 27$) and 15.9% ($n = 476$), respectively (Fig. 4).

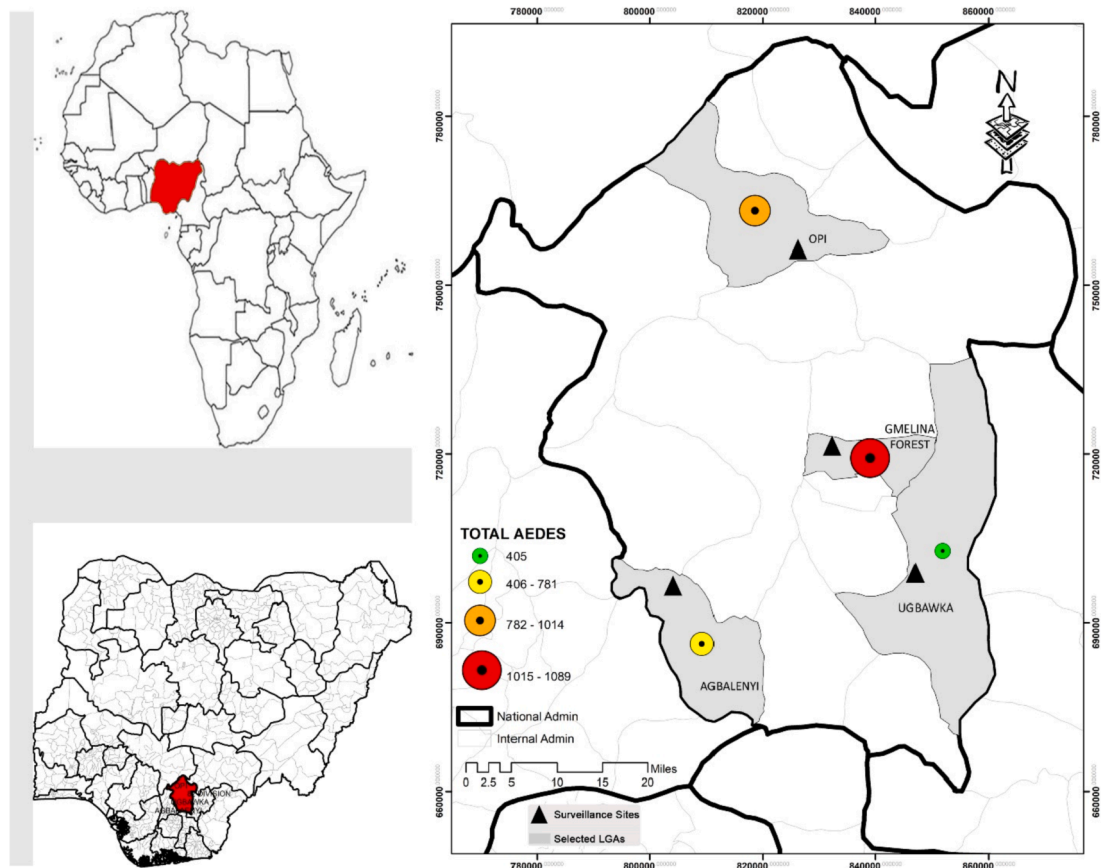


Fig. 3. Comparison of the total number of *Aedes* mosquitoes collected from the 4 study areas.

3.2. Potential habitat distribution

The MaxEnt model predicted potential suitable habitat with high success rates, where training AUC 0.98 ± 0.001 and test AUC 0.98 ± 0.007 at Lowest Presence Threshold (LPT). The most suitable habitat for *Aedes* spp. was predicted in the northern, central, southwestern parts of the Enugu State with some extensions in Anambra, Delta, and Edo States from the west and Ebonyi State from the east (Fig. 5), and its distribution is quite fragmented.

The MaxEnt model's internal jackknife test of variables' contribution showed that temperature seasonality (STD * 100) (Bio4) (24.5%), precipitation of wettest month (Bio13) (20.1%), mean monthly temperature range (Bio2) (18.7%), Elevation (16.7%), and precipitation of driest quarter (Bio17) (8.8%) are the highest mean contributions that determine the distribution of *Aedes* spp. in Enugu state (Table 3).

Variables with the highest importance gain (>0.85) were: Precipitation of the wettest month (Bio13), precipitation of the driest quarter (Bio17), and precipitation of coldest quarter (Bio19) (Table 3). Table 3 provides an indicative estimate of the relative contributions and training acquisition of environmental variables in the MaxEnt model. To determine and quantify that estimate to the contribution of the corresponding variable, the increment of uniform gain is added to each iteration of the training algorithm.

Fig. 6 shows the main highest estimated environmental variables (contributions) that affect the distribution of *Aedes* spp. in Enugu State and area around it. Spatial distribution analysis was done to determine the geographical variability in the mentioned variables among Enugu State.

The response curves of eight variables to *Aedes* spp. habitat suitability are shown in (Fig. 7). From our model we find that precipitation is one of the most important environmental variables controlling the distribution of *Aedes* spp. in Enugu State. We found that precipitation of wettest month (Bio13) ranged from 265 to 330 mm, precipitation of driest quarter (Bio17) ranged from 25 to 75 mm while precipitation of wettest quarter (Bio16) ranged from 650 to 950 mm. Annual precipitation (Bio12) ranged from 1250 to 2300 mm, and elevation ranged from 100 to 1800 m.

The prediction model of habitat suitability was divided into 4 classes; ≥ 0.71 High Suitability, 0.70–0.31 Moderate Suitability, and 0.30–0.11 Low Suitability, and ≤ 0.10 very low to unsuitable for the presence of the species (Fig. 8). It was recorded that *Aedes* spp. potential distribution cover an area of 16,420 km². This area divided as; 1011 km² high probability (≥ 0.71), 6119 km² moderate probability (0.70–0.31), and 9289 km² low probability (0.30–0.11); and 890,495 km² recorded as unsuitable.

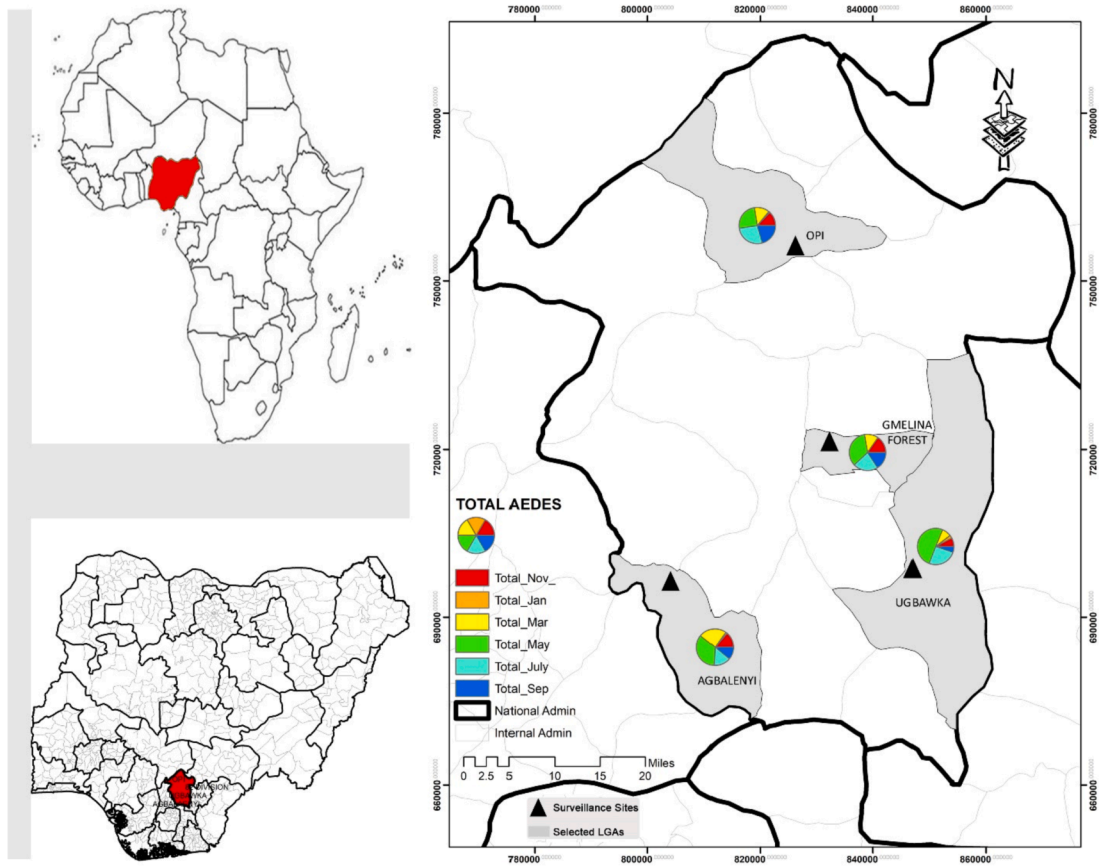


Fig. 4. Comparison of the number of *Aedes* spp. collected in different months.

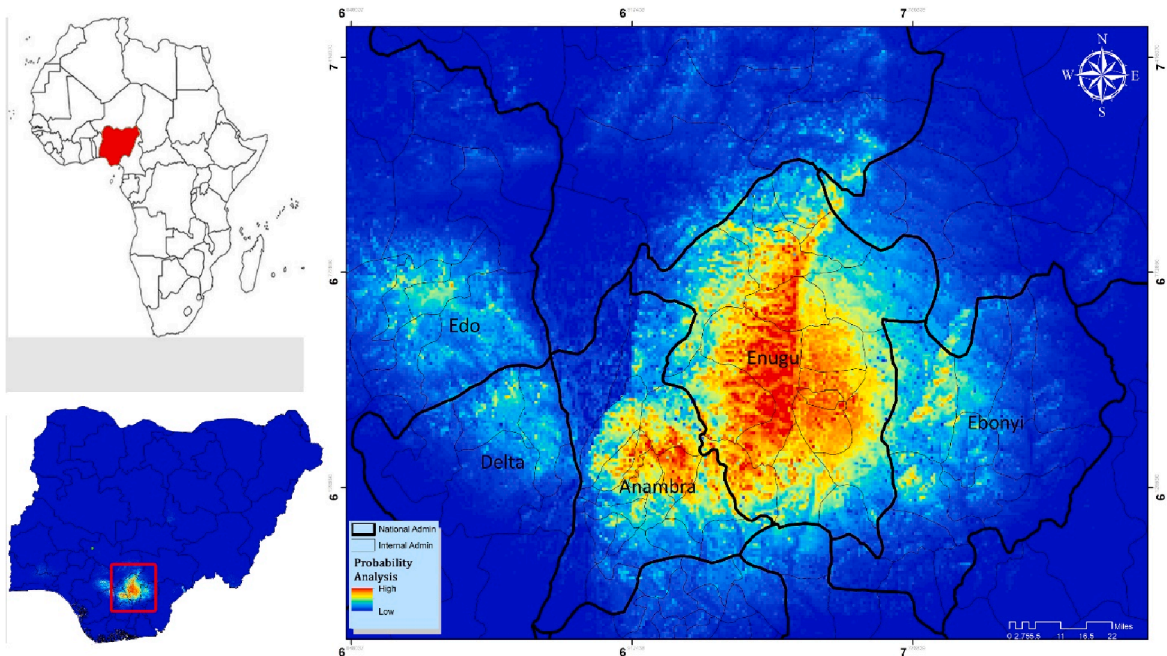


Fig. 5. Potential geographical distribution of *Aedes* spp. in Enugu state using MaxEnt. Warmer colors show areas with better habitat suitability.

Table 3
Contributions, importance gain of the environmental variables used in MaxEnt modeling of *Aedes* spp. in Enugu state.

Variables	Contribution	Training gain (Importance)
bio2	18.799	0.543
bio4	24.530	0.591
bio5	0.120	0.119
bio6	3.529	0.004
bio8	0.834	0.128
bio13	20.172	1.139
bio15	1.163	0.587
bio17	8.887	0.962
bio19	1.202	0.948
Elevation	16.718	0.226
aspect	0.811	0.041
hill_shad	2.433	0.047
slope	0.779	0.208

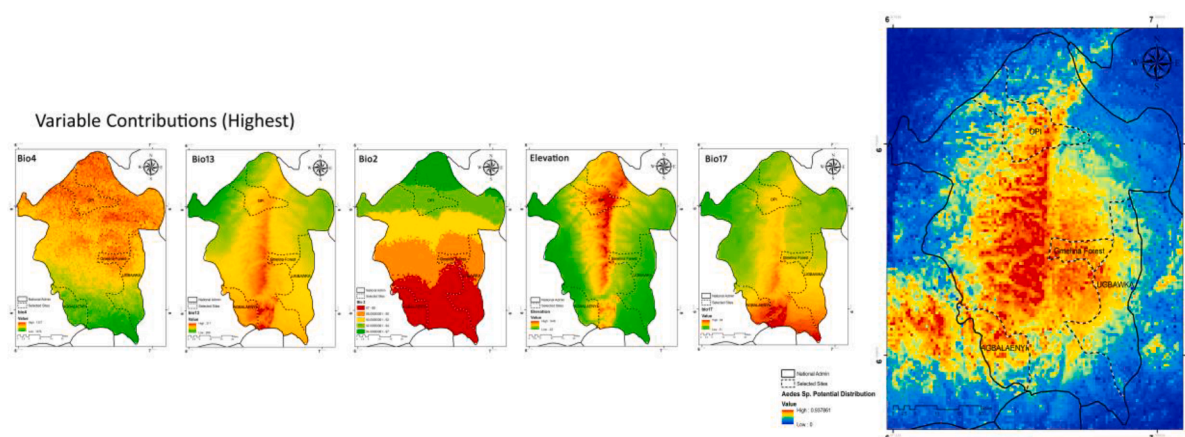


Fig. 6. The Highest environmental variables that estimate to control the geographical distribution of *Aedes* spp. in Enugu State. Variable contributions (Bio4, 13, 2, Elevation, and Bio17).

4. Discussion

In West Africa, lack of recent *Aedes* potential distributional modeling hinders effective vector control interventions and poses a serious public health issue. This kind of information is incredibly important to public health. To support these efforts, this study was conducted in Enugu State, Nigeria. During the current study, *Aedes* mosquitoes (adults and larvae) were collected in close proximity to human habitation, and they were found to breed in transient water collections, including tree holes, rock pools, vehicle tires, and water storage containers.

Three of the eight *Aedes* species recorded (*Ae. aegypti*, *Ae. albopictus* and *Ae. simpsoni*) were found in all surveyed sites in both dry and rainy seasons, while *Ae. africanus* was collected from Agbalenyi and Opi only. All recorded *Aedes* spp. with the exception of the *Ae. circumluteolus* and *Ae. longipalpis* are known to transmit viruses of public health concerns.

Aedes. albopictus was the most abundant *Aedes* spp. collected throughout the study. This agrees with the findings of [Chukwuekezie et al., 2018](#) who reported that *Ae. albopictus* was the dominant species from their collections. This result was predicted since it had been described as one of the most invasive species based on their global spread ([Bonizzoni et al., 2013](#)).

A. aegypti was the second most abundant *Aedes* species in all collections. During the study, it was demonstrated that *Ae. aegypti* and *Ae. albopictus* shared many of the same biological and behavioral characteristics; both were found to compete with each other for surrounding resources, which supports the findings of [Richards et al. \(2012\)](#). This study, consistent with the findings of [Fatima et al. \(2016\)](#), demonstrated that the distribution of *Ae. aegypti* is highly correlated with the presence and proximity of urban infrastructure and proximity to humans.

The discovery of *Ae. bromeliae*, which is part of *Ae. simpsoni* complex, as a vector for the largest outbreak YF virus registered in Ethiopia in 1961–1962 ([Sérié et al., 1964](#)), and in laboratory studies, is a major vector for the newly emergent East or Central African viral genotype ([Ellis et al., 2012](#)).

The low capture numbers of *Aedes africanus* in this study was anticipated as this species is expected to be more prominent in tropical rain forest zones as Delta and Abia states than in Enugu state.

Aedes vittatus has been found only in Opi, and mainly in rainy season. This agrees with the findings of [Diallo et al. \(2011\)](#) who

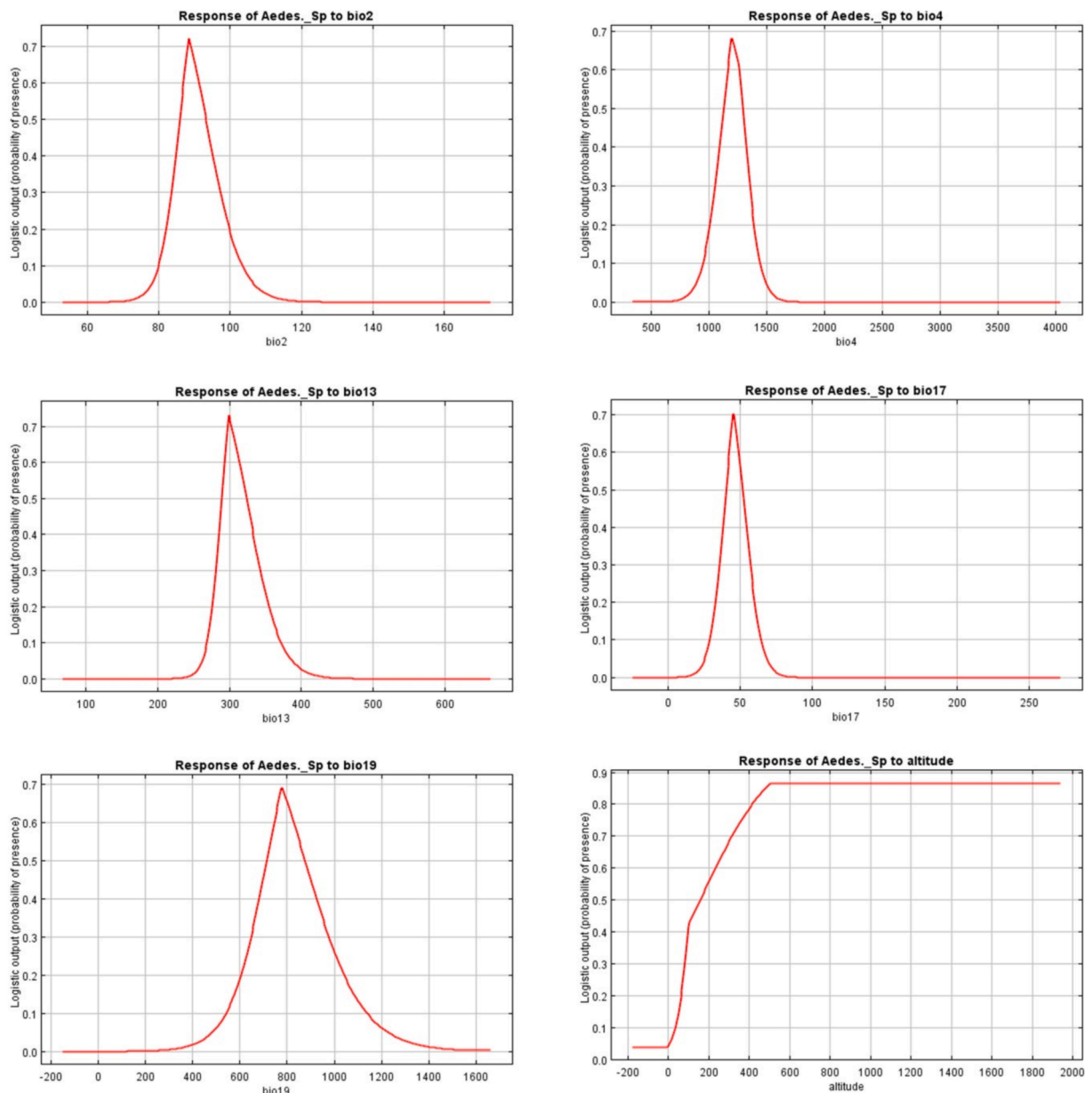


Fig. 7. Response curves of eight environmental predictors used in MaxEnt model for *Aedes* spp.

recorded *Ae. vittatus* in rural areas in Africa and Diallo et al. (2012) who reported its presence mainly from June to October in village land covers. Little importance has been given to mosquitoes as vectors, despite the retention of bio-retroviruses, specifically dengue, chikungunya, YF and Zika infections (Sudeep and Shil, 2017).

The MaxEnt-created model for *Aedes* spp. highlighted the northern, central, southwestern parts of the Enugu state as the most suitable habitats for *Aedes* spp. Also noteworthy was the eastern zone (Agbalenyi) that was not predicted to be suitable. This is in agreement with the low numbers of *Aedes* spp. collected in this area during the current study compared to the rest of the state.

As predicted, *Aedes* mosquito occurrence showed a positive association with variables reflecting precipitation. This finding was also supported by Richman et al. (2018) who reported similar findings while mapping *Aedes* mosquito vectors of chikungunya virus in south-east Senegal. Relative humidity is always high if rainfall is high. The current study supports previous studies reporting a positive correlation of *Aedes* larval population with the amount of rainfall and relative humidity (Goncalves Neto and Rebelo, 2004; Ratho et al., 2005; Zeidler et al., 2008). Mouchet et al. (1996) reported that rainfall can promote transmission by creating breeding sites therefore, adults *Aedes* can lay eggs and increase their population size. Also, survival and growth of mosquito is facilitated when the relative humidity is high (Nakhapakorn and Tripathi, 2005).

Elevation showed a great effect on the distribution of *Aedes* spp. as the response curve showed that the probability of finding *Aedes*

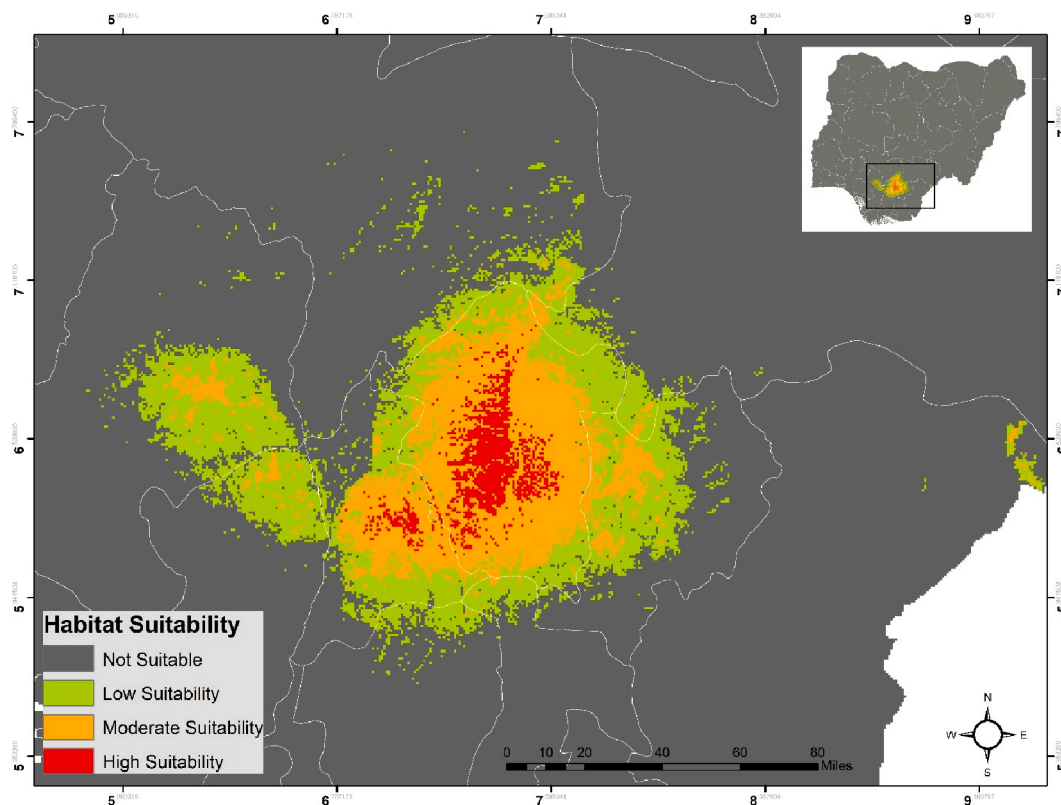


Fig. 8. Map for potential current habitat suitability of *Aedes* spp. according to occurrence records in Enugu State, Nigeria. Habitat suitability classes include: not suitable (0–0.1), low suitability (0.11–0.30), moderate suitability (0.31–0.70) and high suitability (0.71–1.0).

spp. increases with increased elevation (Fig. 7). Many studies have acknowledged the effect of elevation on the distribution of *Aedes* species. Brady et al. (2014) concluded that elevation is a potential intermediary for *Ae. aegypti* extent as it could be more promptly comprehended and operationalized than time-subordinate meteorological elements. Elevation is a possible alternative to interpretation of *Ae. aegypti* range because it can be understood, interpreted and measured more easily than time-dependent meteorological factors. Elevation is an alternative clear environmental factor to elucidating the *Ae. aegypti* range because it is associated with a variety of other essential dynamic environmental factors critical to mosquito development such as temperature. Coblentz and Riitters (2004), and Stein et al. (2014) concluded that the major environmental predictor of species wealth is topographical heterogeneity, including elevation, aspect, and slope. As the topography and complexity are increased, the environmental heterogeneity is expected to increase. The high complexity of topography probably leads to a high diversity of habitats and therefore to a great local niche (Scherrer and Körner, 2011).

Although the prediction model showed high success rates, there are some limitations, where the situation was evaluated based on presence data only in addition to relying exclusively on climatic and topographic data only, while Hamlet et al. (2021) mentioned that there are other factors that may be responsible for the YF virus spread, including the presence of agricultural areas and other variables.

Currently, the World Health Organization utilizes elevation as a factor in advising travelers on the risks of acquiring YF virus, pardoning the prescribed immunization for explorers whose agendas are constrained to territories above 2300 m in some African and South American areas (Shlim et al., 2010; Jentes et al., 2011).

5. Conclusions

In this study we demonstrated predictive models for habitat distribution patterns for *Aedes* spp. using a limited number of records and natural factors using Maxent. This study provides the first predictive habitat distribution map for these species in Enugu State. Pearson (2007) and Muriene et al. (2009) previously concluded that Maxent map can predict base niche (different from the actual occupied niche) of species by using appropriate climate and topographic variables of *Aedes* spp. Our distribution map of potential habitats for arboviral vectors benefits health protection planning and land-use management around Enugu State's current populations. It also supports discovering new potential disease clusters, prioritizing vector survey sites, habitat restoration efforts, and effectively utilize vector control resources. Our results support Enugu State's public health efforts by providing data that will aid in developing mitigation strategies to contain and prevent vector borne disease outbreaks before they spread. Further research is needed to determine whether the existing study area adequately covers all suitable habitats for these species. Area-wide, species-focused studies will

provide granularity to data and help reveal additional geographical variation among species based on topography, ecology, climate, and social aspects.

Declaration of Competing Interest

All authors declare that there is no conflict of interest.

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References

- Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species-climate impact models under climate change. *Glob. Chang. Biol.* 11, 1504–1513.
- Bonizzoni, M., Gasperi, G., Chen, X.G., James, A.A., 2013. The invasive mosquito species *Aedes albopictus*: current knowledge and future perspectives. *Trends Parasitol.* 29 (9), 460–468.
- Bosso, L., Di Febraro, M., Cristinzio, G., Zoina, A., Russo, D., 2016. Shedding light on the effects of climate change on the potential distribution of *Xylella fastidiosa* in the Mediterranean basin. *Biol. Invasions* 18, 1759–1768.
- Brady, O.J., Golding, N., Pigott, D.M., Kraemer, M.U.G., Messina, J.P., Reiner, R.C., et al., 2014. Global temperature constraints on *Aedes aegypti* and *Ae. albopictus* persistence and competence for dengue virus transmission. *Parasit. Vectors* 7, 338. <https://doi.org/10.1186/1756-3305-7-338>.
- Choudhury, M.R., Deb, P., Singha, H., Chakdar, B., Medhi, M., 2016. Predicting the probable distribution and threat of invasive *Mimosa diplotricha* Suavalle and *Mikania micrantha* Kunth in a protected tropical grassland. *Ecol. Eng.* 97, 23–31. <https://doi.org/10.1016/j.ecoleng.2016.07.018>.
- Chukwuekezie, O.C., Nwankwo, A.C., Nwosu, E.O., 2018. Diversity and distribution of *Aedes* mosquitoes in Nigeria. *New York Sci. J.* 11 (2), 50–57. <https://doi.org/10.7537/marsnys110218.07>.
- Coblentz, D.D., Riitters, K.H., 2004. Topographic controls on the regional-scale biodiversity of the South-Western USA. *J. Biogeogr.* 31 (7), 1125–1138.
- Diallo, D., Sall, A.A., Diagne, C.T., Faye, O., Faye, O., Hanley, K.A., Buenemann, M., Weaver, S.C., Diallo, M., 2011. Zika virus emergence in mosquitoes in southeastern Senegal. *PLoS One* 9 (10), e109442.
- Diallo, D., Diagne, C., Hanley, K.A., Sall, A.A., Buenemann, M., Ba, Y., Dia, I., Weaver, S.C., Diallo, M., 2012. Larval ecology of mosquitoes in sylvatic arbovirus foci in southeastern Senegal. *Parasit. Vectors* 5, 286.
- Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. *Evol. Syst.* 40, 677–697.
- Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S.E., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Ellis, B.R., Sang, R.C., Horne, K.M., Higgs, S., Wesson, D.M., 2012. Yellow fever virus susceptibility of two mosquito vectors from Kenya, East Africa. *Trans. R. Soc. Trop. Med. Hyg.* 106, 387–389.
- Escobar, L.E., Romero-Alvarez, D., Leon, R., Lepe-Lopez, M.A., Craft, M.E., Borbor-Cordova, M.J., Svenning, J.C., 2016. Declining prevalence of disease vectors under climate change. *Sci. Rep.* 6, 39150.
- Fath, B.D., 2018. *Encyclopedia of Ecology*. Elsevier.
- Fatima, S.H., Atif, S., Rasheed, S.B., Zaidi, F., Hussain, E., 2016. Species distribution modelling of *Aedes aegypti* in two dengue-endemic regions of Pakistan. *Tropical Med. Int. Health* 21, 427–436.
- Foley, D., Maloney, F.A., Harrison, F.J., Wilkerson, R.C., Rueda, L.M., 2011. Online spatial database of US Army public health command region-west mosquito surveillance records: 1947–2009. *Army Med. Depart. J.* July–September 2011, 29–36. <http://www.cs.amedd.army.mil/dasqaDocuments.aspx?type=l>.
- Goncalves Neto, V.S., Rebelo, J.M., 2004. Epidemiological characteristics of dengue in the Municipality of Sao Luis, Maranhao, Brazil, 1997–2002. *Cad Saude Publica* 20, 1424–1431.
- Graham, C.H., Hijmans, R.J., 2006. A comparison of methods for mapping species ranges and species richness. *Glob. Ecol. Biogeogr.* 15 (6), 578–587.
- Grinnell, J., 1917. Field tests of theories concerning distributional control. *Am. Nat.* 51, 115–128.
- Grinnell, J., 1924. Geography and evolution. *Ecology* 5, 225–229.
- Guisan, A., Hofer, U., 2003. Predicting reptile distributions at the mesoscale: relation to climate and topography. *J. Biogeogr.* 30, 1233–1243.
- Guisan, A., Graham, C.H., Elith, J., Huettmann, F., The NCEAS Species Distribution Modelling Group, 2007. Sensitivity of predictive species distribution models to change in grain size. *Divers. Distrib.* 13, 332–340.
- Hamlet, A., Ramos, D.G., Gaythorpe, K.A., Romano, A.P.M., Garske, T., Ferguson, N.M., 2021. Seasonality of agricultural exposure as an important predictor of seasonal yellow fever spillover in Brazil. *Nat. Commun.* 12 (1), 1–11.
- Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29, 773–785.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Huang, Y.M., 1986. *Aedes (Stegomyia) bromeliae* (Diptera: Culicidae), the yellow fever virus vector in East Africa. *J. Med. Entomol.* 23, 196–200.
- Jentes, E.S., Pomeroy, G., Gershman, M.D., Hill, D.R., Lemarchand, J., Lewis, R.F., Staples, J.E., Tomori, O., Wilder-Smith, A., T.P., 2011. Monath; informal WHO working group on geographic risk for yellow fever. 2011. The revised global yellow fever risk map and recommendations for vaccination: consensus of the informal WHO working group on geographic risk for yellow fever. *Lancet Infect. Dis.* 11, 622–632. [https://doi.org/10.1016/S1473-3099\(11\)70147-5](https://doi.org/10.1016/S1473-3099(11)70147-5).
- Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragón, P., Lobo, J.M., 2011. Use of niche models in invasive species risk assessments. *Biol. Invasions* 13, 2785–2797.
- Kalle, R., Ramesh, T., Qureshi, Q., Sankar, K., 2013. Predicting the distribution pattern of small carnivores in response to environmental factors in the Western Ghats. *PLoS One* 8 (11), e79295.

- Khafagi, O., Hatab, E.E., Omar, K., 2011. Predicting the potential geographical distribution of *Nepeta septemcrenata* in Saint Katherine Protectorate, South Sinai, Egypt using Maxent. *Academia Arena* 3 (7), 45–50.
- Khafagi, O., Hatab, E.E., Omar, K., 2013. Ecological niche modeling as a tool for conservation planning: suitable habitat for *Hypericum sinaicum* in South Sinai, Egypt. *Univers J Environ Res Technol* 2 (6), 515–524.
- Kraemer, M.U.G., 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., Hendrickx, G., Schaffner, F., Elyazar, I.R., Teng, H.J., Brady, O.J., Messina, J.P., Pigott, D.M., Scott, T.W., Smith, D.L., Wint, G.R., Golding, N., Hay, S.I., 2015. The global distribution of the arbovirus vectors *Aedes aegypti* and *Ae. albopictus*. *eLife* 4, e08347.
- Kumar, S., Stohlgren, T.J., Chong, G.W., 2006. Spatial heterogeneity influences native and nonnative plant species richness. *Ecol.* 87, 3186–3199.
- de Luis, M., Bartolomé, C., Cardo, Ó.G., Álvarez-Jiménez, J., 2018. *Gypsophila bermejoi* G. López: a possible case of speciation repressed by bioclimatic factors. *PLoS One* 13, e0190536.
- Mouchet, J., Faye, O., Juivez, J., Manguin, S., 1996. Drought and malaria retreat in the Sahel, West Africa. *Lancet* 348, 1735–1736.
- Murienne, J., Guilbert, E., Grandcolas, P., 2009. Species' diversity in the new Caledonian endemic genera *Cephalidiosus* and *Nobarnus* Insecta: Heteroptera: Tingidae, an approach using phylogeny and species' distribution modelling. *Bot. J. Linn. Soc.* 97, 177–184.
- Nakhapakorn, K., Tripathi, N.K., 2005. An information value based analysis of physical and climatic factors affecting dengue fever and dengue haemorrhagic fever incidence. *Int. J. Health Geogr.* 4 (13), 1–11.
- Omar, K., Elgamal, I., 2021. Can we save critically endangered relict endemic plant species? A case study of *Primula boveana* Decne ex Duby in Egypt. *J. Nat. Conserv.* 61, 126005.
- Ortega-Huerta, M.A., Peterson, A.T., 2008. Modeling ecological niches and predicting geographic distributions: a test of six presence-only methods. *Revista Mexicana De Biodiversidad* 79, 205–216.
- Papes, M., Gaubert, P., 2007. Modelling ecological niches from low numbers of occurrences: assessment of the conservation status of poorly known viverrids (Mammalia, Carnivora) across two continents. *Divers. Distrib.* 13, 890–902.
- Pearson, R.G., 2007. *Species' Distribution Modeling for Conservation Educators and Practitioners. Synthesis*, American Museum of Natural History. Available at: <http://ncep.amnh.org>.
- Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, A.T., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.* 34, 102–117.
- Peterson, A.T., Martínez-Campos, C., Nakazawa, Y., Martínez-Meyer, E., 2005. Time-specific ecological niche modeling predicts spatial dynamics of vector insects and human dengue cases. *Trans. R. Soc. Trop. Med. Hyg.* 99 (9), 647–655.
- Pfeffer, M., Dobler, G., 2010. Emergence of zoonotic arboviruses by animal trade and migration. *Parasit. Vectors* 3 (1), 35.
- Ratho, R.K., Mishra, B., Kaur, J., Kakkar, N., Sharma, K., 2005. An outbreak of dengue fever in peri urban slums of Chandigarh, India with social reference to entomological and climatic factors. *Indian J. Med. Sci.* 59 (12), 519–527.
- Richards, S.L., Anderson, S.L., Alto, B.W., 2012. Vector competence of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) for dengue virus in Florida Keys. *J. Med. Entomol.* 48, 942–946.
- Richman, R., Diallo, D., Diallo, M., Sall, A.A., Faye, O., Diagne, C.T., Dia, I., Weaver, S.C., Hanley, K.A., Buenemann, M., 2018. Ecological niche modeling of *Aedes* mosquito vectors of chikungunya virus in southeastern Senegal. *Parasit. Vectors* 1 (1), 255.
- Rueda, Leopoldo, 2004. Pictorial keys for the identification of mosquitoes (Diptera: Culicidae) associated with Dengue Virus Transmission. *Zootaxa* 589. <https://doi.org/10.11646/zootaxa.589.1.1>.
- Sall, A.A., Faye, O., Diallo, M., Firth, C., Kitchen, A., Holmes, E.C., 2010. Yellow fever virus exhibits slower evolutionary dynamics than dengue virus. *J. Virol.* 84 (2), 765–772.
- Scherrer, D., Körner, C., 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *J. Biogeogr.* 38 (2), 406–416. <https://doi.org/10.1111/j.1365-2699.2010.02407.x>.
- Sérié, C., Andral, L., Lindrec, A., Neri, P., 1964. Epidémie de fièvre jaune en Ethiopie (1960–1962): observations préliminaires. *Bull. World Health Organ.* 30 (3), 299.
- Shlim, D.R., Freedman, D.O., Keystone, J.S., Tan, K.R., Kozarsky, P.E., Borwein, S.T., 2010. CDC health information for international travel 2010. In: Brunette Gary, W. (Ed.), *CDC Health Information for International Travel*, vol. 2009. Oxford University Press, New York, pp. 242–269.
- Smeraldo, S., Di Febbraro, M., Bosso, L., Flaquer, C., Guixé, D., Lisón, F., Meschede, A., Juste, J., Prüger, J., Puig-Montserrat, X., Russo, D., 2018. Ignoring seasonal changes in the ecological niche of non-migratory species may lead to biases in potential distribution models: lessons from bats. *Biodivers. Conserv.* 27, 2425–2441.
- Stein, A., Gerstner, K., Krefth, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* 17 (7), 866–880. <https://doi.org/10.1111/ele.12277>.
- Sudeep, A.B., Shil, P., 2017. *Aedes vittatus* (Bigot) mosquito: an emerging threat to public health. *J. Vector Borne Dis.* 54 (4), 295–300.
- Vasilakis, N., Cardoso, J., Hanley, K.A., Holmes, E.C., Weaver, S.C., 2011. Fever from the forest: prospects for the continued emergence of sylvatic dengue virus and its impact on public health. *Nat. Rev. Microbiol.* 9 (7), 532–541.
- Weaver, S.C., Reisen, W.K., 2010. Present future arboviral threats. *Antivir. Res.* 85, 328–345.
- Weetman, D., Kamgang, B., Badolo, A., Moyes, C.L., Shearer, F.M., Coulibaly, M., Pinto, J., Lambrechts, L., McCall, P.J., 2018. *Aedes* mosquitoes and *Aedes*-borne arboviruses in Africa: current and future threats. *Int. J. Environ. Res. Public Health* 15 (2), 220.
- Wilder-Smith, A., Gubler, D.J., Weaver, S.C., Monath, T.P., Heymann, D.L., Scott, T.W., 2017. Epidemic arboviral diseases: priorities for research and public health. *Lancet Infect. Dis.* 17, e101–e106.
- Wintle, B.A., Elith, J., Potts, J.M., 2005. Fauna habitat modelling and mapping: a review and case study in the Lower Hunter Central Coast region of NSW. *Aust. Ecol.* 30, 719–738.
- Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., NCEAS Predicting Species Distributions Working Group, 2008. Effects of sample size on the performance of species distribution models. *Divers. Distrib.* 14, 763–773.
- Zeidler, J.D., Acosta, P.O.A., Barreto, P.P., Cordeiro, J.D.S., 2008. Dengue virus in *Aedes aegypti* larvae and infestation dynamics in Roraima, Brazil. *Rev. Saude Publica* 42 (6), 9–14.