Modelling the potential distribution of arbovirus vector *Aedes aegypti* under current and future climate scenarios in Taiwan, China

Running title: *Aedes aegypti* distribution modelling

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Abstract

BACKGROUND: *Aedes aegypti* is one of the most important mosquito species which is a common disease-transmitting pest in tropical areas. Various infectious arbovirus diseases can be transmitted by *Ae. aegypti*. As the ongoing global climate change, we are facing an increasing public health threat from the rapid spread of disease vectors into wider geographical areas. To better understand the current ecological niche range and possible future expansion of *Ae. aegypti*, an ecological niche modelling approach was adopted to predict its current and future potential habitat in Taiwan, China.

RESULTS: Based on observed occurrence records and environmental layers reflecting climate and land-use conditions, predictions with high-resolution of 30 arcsec (approx. 1km × 1km) were made by our model. *Ae. aegypti* was predicted to expand its habitat in varying degrees out of its current niche range under different climate scenarios for the future 21st century. Winter temperature and dry season precipitation were considered as important predictors among climate variables. And croplands, pasture, forested lands and urban lands were important land-use
variables.

CONCLUSION: *Ae. aegypti* are expected to establish new habitats out of its current niche range under the trend of global climate change. The extent of habitat expansion varies under different climate scenarios. Measures should be taken to control its expansion to broader scale. Our study has important strategic implications for mosquito surveillance and the prevention and control of mosquito-borne diseases.

**Key words:** *Aedes aegypti*, climate change, disease-transmitting pest, ecological niche model, mosquito-borne diseases

**Introduction**

Mosquitoes are common pests which can transmit a variety of infectious human and animal diseases. Due to the wide geographical distribution of mosquitoes, mosquito-borne diseases pose a great threat to the global public health. Dengue fever (DF) is an acute infectious disease, and is one of the most prevalent arbovirus diseases. Human morbidity and mortality caused by DF is higher than any other mosquito-borne diseases. It is estimated that there are 390 million global infections of DF per year. More than 125 countries are affected by dengue virus all over the world. The spread of dengue is considered to be caused mainly by international trade and travel, urbanization, insufficient vector monitoring and global climate change.
The history of DF in Taiwan area can be traced back to 1902 in Penghu Islet. The first documented outbreak of DF in Taiwan Island was in 1924. After the 1942-1943 epidemic, DF was silenced in Taiwan area for nearly 37 years until the re-emerging in 1981 in Liu-Chiu Island. And DF outbroke again in southern Taiwan Island in 1987-1988, mainly in Kaohsiung and Pingtung. Until now, dengue cases continue to occur in Taiwan. The major concern is that there is neither no vaccine against DF nor specific antiviral therapy to treat DF. Currently, the available method to prevent and control DF effectively is to control its vectors. To develop prevention and control strategies for DF, it is essential to study the distributions of DF vectors in Taiwan.

*Aedes aegypti* is the primary vector in the transmission of dengue fever. *Ae. aegypti* originated in Africa but is currently distributed in tropical and sub-tropical regions all over the world. More than 90% of female *Ae. aegypti* bloodmeals are taken from humans. Infectious females are able to transmit virus repeatedly to multiple hosts. In addition to dengue fever, *Ae. aegypti* is also competent vector of many other arbovirus diseases, such as chikungunya fever, yellow fever and Rift Valley fever. Adequate management of *Ae. aegypti* is indispensable for the prevention and control of mosquito-borne diseases.

Ecological niche modelling is a widely accepted approach to predict the potential
distribution of various species, microorganisms and even epidemic diseases 19-22. Based on detailed species presence records and environmental variables which are considered to have an impact on the target species, the relationship between them can be estimated by using statistical algorithms. Risk assessments of vector-borne diseases by ecological niche modelling the vectors have been highlighted in many previous studies, such as the modelling of *Culex tritaeniorhynchus* for Japanese Encephalitis, *Phlebotomus chinensis* for Leishmaniasis, and snails for Schistosomiasis 23-25. Species distribution models can help improve the targeted monitoring of vectors and guide the development of controlling programs.

Nowadays, high-resolution geographic layer datasets reflecting the global environment can be conveniently accessed and applied. And the well-developed surveillance system in Taiwan provides accurate presence locations of mosquitoes 26. A comprehensive understanding of the potential niche range of *Ae. aegypti* and its future diffusion trend are able to carried out by ecological niche modelling. Our model was established under several assumptions for future climate conditions to account for the uncertainty of global climate change in the future 21st century.

**Materials and Methods**

**Mosquito occurrence data**

The collections of *Ae. aegypti* were obtained from the Global Biodiversity
Information Facility (GBIF) (https://www.gbif.org/) and the database established by Kraemer et al. Both databases contain comprehensive global occurrence records of *Ae. aegypti*. Owing to the well-developed mosquito monitoring program in Taiwan Island, 9101 occurrences within the period from 1990 to date were obtained. To avoid the possible confounding caused by spatial stratified heterogeneity (SSH), we calculated Wang’s q-Statistic by GeoDetector to test the presence of SSH in our sample. Town level occurrences were paired with integer codes representing the county level administrative district which they belong to. The q-Statistic test indicates no significant stratified spatial heterogeneity exists ($q = 0.124; p = 0.728$). By removing duplicate records and spatially autocorrelated records, 415 unique occurrences were used to form the final *Ae. aegypti* database (Fig 1).

**Environmental variables and data processing**

Nineteen bioclimate variables and twelve land-use variables were used to establish the model (Table 1 and 2). Data for current climate conditions were accessed and downloaded from WorldClim dataset (http://worldclim.org/version1). Variables in this dataset, representing temperature and precipitation conditions, were provided as the baseline for future climate scenarios. Data for future climate conditions were provided by the Consultative Group for International Agricultural Research (CGIAR) Research Program on Climate Change, Agriculture and Food Security (CCAFS).
We used the latest assumptions for future climate conditions, which were derived from the fifth Intergovernmental Panel on Climate Change (IPCC) assessment report (AR5). The “Representative Concentration Pathways” (RCPs) describes assumptions about the possible future emission of greenhouse gases. RCPs under the Climate System Model of the Beijing Climate Center (BCC-CSM1-1) model were used in our study. The BCC-CSM1-1 climate model is one of the most commonly used models for simulating the climate change in China. We chose RCP 2.6 as the minimum emission scenario, RCP 6.0 as the medium, and RCP 8.5 as the maximum.

Land-use variables were downloaded from the Land-Use Harmonization (LUH2) database (http://luh.umd.edu/index.shtml). A dataset of land-use scenarios from 850 to 2100 were provided as part of the World Climate Research Program Coupled Model Intercomparison Project (CMIP6).

We extracted future bioclimate and land-use variables with the same RCPs (RCP 2.6, RCP 6.0 and RCP 8.5) and time periods (2030s, 2050s and 2070s). All environmental layers were resampled to 30 arcsec (approx. 1km × 1km) resolution using bilinear interpolation and cropped to the geographical area of Taiwan island. All operations were accomplished in ArcGIS 10.2 (ESRI Inc., Redlands, CA, USA).

Multicollinearity test of these variables was performed by calculating the variance...
inflation factor (VIF), using the car package in R \(^{32,33}\). Variables with VIF > 10 were considered to have collinearity problem \(^{34}\). Finally, variables with significant collinearity were removed out of the model.

**Establishing the Maxent models**

Maxent 3.4.1 (http://biodiversityinformatics.amnh.org/open_source/maxent/), which is one of the most widely used niche modelling methods, was used to establish the model \(^{35}\). Among various presence-only modelling methods, Maxent has shown outstanding predictive performance in modelling niches of species, and scores well in comparative studies \(^{36-38}\). Maxent gives prediction of probability distribution with the maximum entropy based on known environmental and species presence data \(^{39}\). In ecological niche modelling, sampling bias is a common problem. To counter the sampling bias of occurrences, a background selection process was implemented by using SDMtoolbox v2.2 (http://sdmtoolbox.org/), a python-based plugin for ArcGIS \(^{40}\). Ten thousand pseudo-absences with the same spatial bias as the occurrences were generated and then introduced into the model \(^{41,42}\). The average of 20 replicates for each model were taken as the final predictions.

**Suitable habitat shifts**

The possible shift of suitable habitat under future climate scenarios was simulated by our model. Binary models are widely used to convert suitability for species into
presence/absence in species distribution modelling. To estimate the area that is suitable for mosquito survival, sensitivity equals specificity threshold was applied to generate binary models \(^{42-44}\). By comparing the future models with the current model, we separately estimated the area of maintain suitable, become suitable and no longer suitable for *Ae. aegypti*.

**Model evaluation and interpretation**

The receiver operating characteristic curve (ROC) was used to evaluate the model performance. A greater area under the curve (AUC) value (0 ~ 1) indicates a better predictive performance. Jackknife test was adopted to assess the importance of each variable in the modelling \(^{45}\). Whether the training gain increases when a variable is used in isolation, or decreases when it is discarded, the variable is considered important for the modelling.

**Results**

**Potential distribution under current and future climate conditions**

The probability of *Ae. aegypti* presence predicted by Maxent is shown in Fig 2. The current model performed well in representing the distribution of occurrence records. In Taiwan, the suitable habitat for *Ae. aegypti* is currently limited in the southwestern part of the island. And the future models showed the possible range changes for *Ae. aegypti* under future climate scenarios. The shifts of areas with high habitat
suitability can be observed in future models.

*Ae. aegypti* shows the tendency to expand its habitat under all climate assumptions. In the future 21st century, the suitable habitat of *Ae. aegypti* is likely to expand to the central island. There is also a certain possibility that some parts of the eastern coastal areas will become suitable for the survival of *Ae. aegypti*. The AUC value of our model is 0.927.

**Change in suitable habitat**

Binary models were reclassified from the continuous models (as shown in Fig 2) based on the sensitivity equals specificity threshold, which is 0.3357 output by Maxent. Modelled current suitable habitat for *Ae. aegypti* covers the central and southwestern Tainan, southwestern Kaohsiung, western and southern Pingtung (Fig 3). Predictions under three future climate scenarios show different degrees of expansion and partial contraction of habitat. *Ae. aegypti* shows the tendency of spreading northward and eastward. Under all three scenarios for the 2030s, the eastern Tainan, central Kaohsiung and eastern Pingtung is predicted to become suitable for the survival of *Ae. aegypti*. Under RCP 6.0 and 8.5 for the 2050s and 2070s, the habitat is predicted to expand continuously to central Chiayi and southern Taitung. The prediction under RCP 2.6 is expected to cover northwestern Tainan and western Chiayi in the 2050s and 2070s. The contraction of suitable habitat is
predicted to occur in the southernmost area of the island under all scenarios. The greatest contraction will occur in the midwestern Tainan under RCP 8.5.

Under RCP 2.6 and 8.5, the area of suitable habitat is expected to continue growing until the 2070s (Fig 4). In the 2030s and 2050s, RCP 6.0 provides the largest suitable area among RCPs, and RCP 2.6 for the 2070s.

The RCP 2.6 scenario provides the smallest contraction area of suitable habitat in the 2050s and 2070s but the largest in the 2030s. RCP 6.0 provides the largest gained area in the 2030s and 2050s but the smallest in the 2070s. RCP 8.5 provides both the largest gained area and the largest contraction area in the 2070s. The largest total suitable habitat is predicted to be caused by RCP 6.0 in the 2030s and 2050s, and RCP 2.6 in the 2070s.

**Variable importance**

The relative importance of variables was assessed by the Jackknife test (Fig 5). Among bioclimate variables, Bio 11 (Mean temperature of the coldest quarter) and Bio 17 (Precipitation of the driest quarter) show great importance in the modelling. Among land-use variables, the presence of *Ae. aegypti* is indicated to be significantly associated with cropland, pasture, forested primary land and urban land.

**Discussion**

The monitoring of arbovirus vector is of great help for the prevention and control of
vector-borne infectious diseases. In our current study, an approach of ecological
niche modelling based on presence-only records was used to predict the potential
distribution of Ae. aegypti in Taiwan, China. Combined with the epidemic situation of
mosquito-borne diseases, adequate management of Ae. aegypti can be carried out
according to the habitat suitability map, such as targeted surveillance and eradication,
pathogen detection among mosquitoes and model verification.
The current model well represents the observed occurrences of Ae. aegypti. And the
future models demonstrate the possible ecological range changes of Ae. aegypti
under future climate conditions. Suitable habitat under RCP 2.6 is predicted to be
more likely to expand northward. However, the prediction under RCP 6.0 and 8.5
indicates the possibility of establishing new habitats in the northeast. This shows the
different diffusion trends of Ae. aegypti under different future climate assumptions.
In addition, in areas of Hualien and Taitung, in the east of the island, there is a
certain possibility that it will become suitable for the survival of Ae. aegypti in the
future (Fig 2). In general, under all assumptions, a significant northward shift is
expected to occur in the northern boundary of the suitable habitat. Based on
experience, Ae. aegypti is currently considered to be only distributed in areas south
of about 23.5°N \(^{46}\). The current distribution predicted by our model is located south
of 23.3°N. And in the future predictions, the northernmost boundary can reach

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23.8°N (under RCP 6.0). This indicates that, according to the current trend of climate change, the suitable habitat for *Ae. aegypti* will inevitably expand northward, which may pose a growing threat to public health. However, the predicted contraction of suitable habitats in the southern island can be explained by the inability of *Ae. aegypti* to adapt to higher temperatures. Although the size of the habitat changes varies with different climate change scenarios, we can notice that the RCP 6.0 scenario is predicted to result in the most serious situation in the nearer future (until the 2050s) and RCP 2.6 would result in the most serious situation in the further future (in the 2070s). Moreover, the RCP 8.5 scenario provides the most dramatic prediction with both the largest contraction and the largest expansion in the 2070s.

We considered using climate and land-use variables as predictors for the mosquito distribution and found variables which may have significant impact on the survival of *Ae. aegypti*. According to the Jackknife test, Bio 11 (Mean temperature of the coldest quarter) was given the greatest importance in the modelling. A previous study on the influence of temperature on the survival of *Ae. aegypti* showed that 13.8°C in winter was considered to be the critical low temperature for *Ae. aegypti* in Taiwan. Another study determined the minimum temperature threshold for the development of *Ae. aegypti* as 8.3 ± 3.6°C. Cold winter limits the occurrence of *Ae. aegypti*. As the continuously warming of climate in Taiwan due to global climate change, the
habitat is expected to expand its extent to higher latitudes in the north and higher altitudes in the east. Bio 17 (Precipitation of the driest quarter) also showed great importance among climate variables. Drought is unfavorable for mosquito survival because water is necessary for the hatching of eggs and the development of mosquitoes. Among land-use variables, cropland, pasture, forested land and urban land showed significant impact on the distribution of mosquitoes. Human water supply is considered to have great impact on the reproduction of mosquitoes. Agricultural irrigation in croplands and artificial water containers in urban area can both provide stable and abundant water for mosquito breeding. The preference for *Ae. aegypti* to rest indoors makes them more suitable for living in urban areas. In addition to bloodmeals on human, the sugar feeding activities of mosquitoes depends on plants in pasture and forested lands.

Our study is novel in our purpose on modelling not only the current distribution but also the future distribution of the important arbovirus vector *Ae. aegypti* in Taiwan, China. Based on the available datasets of high-resolution predictions for future climate and land-use conditions, we established the model to estimate the extent of mosquito expansion. The relative importance of predictors was also assessed by our model. For the first time, an exhaustive understanding of the current and future status of *Ae. aegypti* in Taiwan was carried out. Our findings can serve as a reference.
for current and future mosquito surveillance and will contribute not only to the prevention and control of DF, but other mosquito-borne diseases as well.

There are still some limitations in our study. Firstly, the suitable habitats under future climate conditions are modelled based on the assumption that there is no disperse limitation for *Ae. aegypti* into the modelled new habitats. Therefore, our prediction is an ideal state, can only serve as a reference for future mosquito surveillance and needs to be verified by field investigations. Secondly, although our model considered precipitation as a relative important predictor in the modelling by a Jackknife test. The correlation between precipitation and habitat suitability should be interpreted with caution. The lifecycle of *Aedes* mosquitoes is characterized by a process of dehydration of the eggs (several days to months) after spawning, and then rehydration to hatch once precipitation occurs. This shows that precipitation is not a sufficient condition for the hatching of *Aedes* eggs. A complete and successful hatching process of *Aedes* eggs requires the alternation of rainfall and desiccation. Further ecological research in Taiwan is required to explore the specific relationship between environmental variables and the reproduction of mosquitoes.

According to the ongoing global warming trends, continuous surveillance of *Ae. aegypti* in the future is recommended in areas with higher habitat suitability predicted by our model. Further monitoring data can be used to verify and improve
the model. Based on our study, a seasonal dynamic model can be carried out to investigate the seasonal distribution change pattern of mosquitoes under the premise of the introduction of long time series of environmental data.

**Conclusion**

Our study on modelling the current and future distribution of *Ae. aegypti* in Taiwan, China shows the possible habitat shifts under future climate scenarios. *Ae. aegypti* is assumed to be able to establish vast new habitats out of its current range in the future 21st century. The extent of habitat expansion varies under different climate scenarios. Certain climate and land-use variables are considered important for the survival of *Ae. aegypti*. Our model can serve as a reference in management of disease-transmitting pest and risk assessments of mosquito-borne diseases.

**Acknowledgments**

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Heilongjiang, China (GA18B203).

Supporting Information

Table S1. Mosquito occurrences database.

Table S2. Estimated gain, stable and lost area of suitable habitat.

Figure S1. Receiver operating characteristic (ROC) curve.

References


40. Brown JL, SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and


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<th>Variable</th>
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Table 1. Bioclimate variables used in the model.

1^ Data for current climate conditions were accessed from WorldClim (http://worldclim.com/version1)
2^ Data for future climate projections were accessed from CCAFS (http://ccafs-climate.org/)

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Table 2. Land-use variables used in the model.

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¹Data for current land-use conditions and future land-use projections were accessed from LUH2 (http://luh.umd.edu/index.shtml)
Figure titles

Fig 1. Occurrence records of *Aedes aegypti* in Taiwan Island.

Fig 2. Modelled habitat suitability of *Aedes aegypti* under current and future climate scenarios.

Fig 3. Suitable habitat change under future climate scenarios.

Fig 4. Estimated gain, stable and lost area of suitable habitat compared to current.

Fig 5. The result of Jackknife test. Variables with longer blue bar or shorter green bar are considered to have greater relative importance in the modelling.