# Estimations of Fine-Scale Species Distributions of *Aedes*aegypti and *Aedes albopictus* (Diptera: Culicidae) in Eastern Florida Kristen A. Hopperstad, Mohamed F. Sallam, and Michael H. Reiskind Department of Entomology and Plant Pathology, North Carolina State University, Campus Box 7613, Raleigh, NC 27696, Department of Biology, University of Nevada, Reno - Reno, NV, and Corresponding author, e-mail: kahopper@ncsu.edu

Subject Editor: Gabriel Hamer

Received 13 April 2020; Editorial decision 27 August 2020

# **Abstract**

Many species distribution maps indicate the ranges of *Aedes aegypti* (Linnaeus) and *Aedes albopictus* (Skuse) overlap in Florida despite the well-documented range reduction of *Ae. aegypti*. Within the last 30 yr, competitive displacement of *Ae. aegypti* by *Ae. albopictus* has resulted in partial spatial segregation of the two species, with *Ae. aegypti* persisting primarily in urban refugia. We modeled fine-scale distributions of both species, with the goal of capturing the outcome of interspecific competition across space by building habitat suitability maps. We empirically parameterized models by sampling 59 sites in south and central Florida over time and incorporated climatic, landscape, and human population data to identify predictors of habitat suitability for both species. Our results show human density, precipitation, and urban land cover drive *Ae. aegypti* habitat suitability, compared with exclusively climatic variables driving *Ae. albopictus* habitat suitability. Remotely sensed variables (macrohabitat) were more predictive than locally collected metrics (microhabitat), although recorded minimum daily temperature showed significant, inverse relationships with both species. We detected minor *Aedes* habitat segregation; some periurban areas that were highly suitable for *Ae. albopictus* were unsuitable for *Ae. aegypti*. Fine-scale empirical models like those presented here have the potential for precise risk assessment and the improvement of operational applications to control container-breeding *Aedes* mosquitoes.

Key words: habitat suitability model, maximum entropy model, MaxEnt, Aedes aegypti, Aedes albopictus

Patterns of insect-borne disease depend on the spatial distribution of disease vectors across heterogeneous landscapes, including pathogens transmitted by container Aedes spp. (Diptera: Culicidae) (Pavlovsky 1966, Kitron 1998). Aedes aegypti (L.) was found throughout the southeastern United States in recent history, but its range was drastically reduced upon the introduction of Aedes albopictus (Skuse) in the 1980s (O'Meara et al. 1995, Lounibos and Juliano 2018). Competitive displacement of Ae. aegypti by Ae. albopictus resulted in Ae. aegypti range reduction and partial spatial segregation of the two species, with Ae. aegypti persisting primarily in urban refugia. The distributions of Ae. aegypti and Ae. albopictus in the United States demonstrate an interplay between fundamental and realized niches. Although Ae. aegypti could potentially persist broadly in the southeastern United States based on physiological tolerances and its historical range, its realized distribution is restricted, in part, by exclusion after the invasion of Ae. albopictus (Hutchinson 1957, Soberon 2007, Reisen 2010).

Scenopoetic models have described the coarse geographical range of *Ae. aegypti* on a global scale (Benedict et al. 2007, Kraemer et al. 2015, Hahn et al. 2016, Ding et al. 2018), but at a finer scale (tens of meters), biotic interactions may determine the presence of this species (Juliano et al. 2002, Rey et al. 2006, Bargielowski et al. 2013, Obenauer et al. 2017). Multiple models predict widespread habitat suitability for *Ae. aegypti* across the southern United States, but empirical data indicate that fine-scale distributions of *Ae. aegypti* are restricted and patchy (Benedict et al. 2007, Bargielowski et al. 2013, Hopperstad and Reiskind 2016). This suggests the Eltonian Noise Hypothesis, which posits biotic factors, such as competition, may determine the presence of species at high resolutions, but such 'noise' is undetectable at coarse, broad extents (Soberon and Nakamura 2009).

Biotic and abiotic habitat characteristics both contribute to the suitability of an area for either species. Suitable habitat for these anthropophilic mosquitoes is determined by the presence, density,

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and behavior of humans, their primary host (Burkett-Cadena et al. 2013, Rochlin et al. 2016, Obenauer et al. 2017). Human population density is known to have significant interactions with patterns of Ae. aegypti in the dynamics of dengue transmission (Padmanabha et al. 2012), and human-mediated dispersal is the primary mode of long-distance dispersal for both species (Damal et al. 2013, Medley et al. 2015, Ding et al. 2018). Fine-scale land cover heterogeneity and microclimate also affect species presence (Rey et al. 2006, Landau and Leeuwen 2012, Reiskind and Lounibos 2013, Hopperstad and Reiskind 2016, Lounibos et al. 2016). Aedes aegypti are more desiccation-tolerant at both the egg and adult stage than Ae. albopictus (Juliano et al. 2002, Costanzo et al. 2005, Reiskind and Lounibos 2009), and although Ae. albopictus is typically the superior larval competitor, warm, dry climates favor Ae. aegypti by alleviating the effects of competition via differential mortality of Ae. albopictus eggs (Juliano et al. 2002). Differing environmental requirements influence interspecies interactions that result in partial spatial segregation on the landscape, with Ae. aegypti generally occurring in warm, drier, heavily urbanized environments and Ae. albopictus prevailing in broader, wet, peri-urban, and rural environments (Braks et al. 2003, Rey et al. 2006, Leisnham et al. 2008, Reiskind and Lounibos 2013, Hopperstad and Reiskind 2016). We are interested in the combination of environmental conditions that favor one species or the other and the potential to map context-dependent competition.

The selection of training datasets used to parameterize predictive models is a critical step in determining a model's purpose and performance (Merow et al. 2013). Compiled occurrence records that do not differentiate between ephemeral and established populations are commonly used to parameterize habitat suitability models (Monaghan et al. 2016, Johnson et al. 2017), which typically results in broad, encompassing suitability maps that represent where the species may be found. The distinction between ephemeral and established samples is especially relevant for Ae. aegypti and Ae. albopictus because ephemeral occurrences via long distances by vehicular traffic are likely (Guagliardo et al. 2015, Medley et al. 2015). Although the use of occurrence records is appropriate for global and regional models, fine-scale models should be matched with input data of a similar spatiotemporal scale (Merow et al. 2013). Further, the area of investigation should be restricted to an extent that is representative of the environmental conditions under which training data were collected (Merow et al. 2013).

Fine-scale suitability modeling has the potential for improving risk assessment of mosquito-borne disease and informing surveillance efforts of mosquito control districts (Sallam et al. 2016, Sallam et al. 2017b). The ability to identify high-risk areas would allow for prioritization of surveillance efforts. Further, future climate scenarios and anticipated urbanization will likely increase contact between humans and *Aedes* spp. disease vectors, as well as change local conditions that may favor one species (Vora 2008, Terando et al. 2014). A thorough understanding of predictors for species presence can be used to estimate future mosquito distributions in risk models at a scale appropriate to the biology of the species (Liu et al. 2019).

Many current distribution models are too broad to provide information relevant to mosquito control districts (Sallam et al. 2017a). To address this issue, we modeled the distribution of *Ae. aegypti* and *Ae. albopictus* using locally collected mosquito occurrence data across five counties in eastern Florida. We combined collection data from 59 sites with climatic, landscape, and human population data to select the most influential macrohabitat factors that predict the presence of each species. We also modeled the impact of microhabitat variables, including ambient temperature, relative humidity, presence of vegetation, and other container-breeding insects in predicting the

presence of each *Aedes* species. We then used the most predictive factors in a maximum entropy model to produce estimations of fine-scale habitat suitability and similarity (Phillips et al. 2006, Elith et al. 2011, Merow et al. 2013).

## **Materials and Methods**

## Model Inputs and Covariates

Study area. The study area encompassed approximately 7,214 km<sup>2</sup> across five counties in southeastern Florida (Fig. 1). Aedes aegypti has been present in the area since the colonial period (Madden 1945), and O'Meara et al. (1995) documented the spread of Ae. albopictus throughout Florida in the 1990s. We collected samples at 59 sites arranged on twelve, 15-km-long transects. A subset of data from this study was previously reported in a publication that examined temporal changes in species distributions in Palm Beach County, FL (Hopperstad and Reiskind 2016). Transects spanned urbanization gradients longitudinally or latitudinally. On longitudinal (East to West) transects, we selected sites at 0, 1, 3, 8, and 15 km from the coastline, and on latitudinal (North to South) transects, we selected sites within 0.5-3 km of the coastline at 0, 3, 7, 11, and 15 km. Site selection characteristics are outlined in Reiskind et al. 2013. The sampling strategy included latitudinal transects to: 1) verify concordance with previously observed Aedes distribution patterns (Reiskind and Lounibos 2013, Hopperstad and Reiskind 2016), and 2) assess species distributions on exclusively coastal transects to assess the potential for an effect of distance to the coast (Yee et al. 2014). Distance to the coast, latitude, and longitude were assessed as potential predictors of mosquito presence in standard least-squares effect leverage models and a binomial regression analysis using a logit probability model and an AICc validation method.

Mosquito sample collection and microhabitat characteristics. We collected eggs and larvae using three oviposition traps per site on a weekly basis from 28 May to 11 July and reared eggs to the pupal stage for identification. This collection window was selected because it encompassed high numbers of both species based on previous data from Reiskind et al. 2013. We recorded temperature and relative humidity at 10-min intervals for a minimum of three weeks per site using iButton data loggers (Maxim Corp., Dallas, TX) and noted the presence of vegetation and other container-breeding insects in the aquatic fraction of the traps. Ovitrap construction and placement followed previously published protocols, as did the handling of trap contents and mosquito identification (Hopperstad and Reiskind 2016). We buffered trap locations to relate collection data to the composite surrounding habitat, rather than treat traps as single points within a landscape. We selected a 100-m buffer distance because the typical flight distance of Ae. aegypti and Ae. albopictus is limited to tens of meters (Reiter et al. 1995, Marini et al. 2010, Landau and Van Leeuwen 2012, Sallam et al. 2017a). To grasp the relative abundance of either species, we calculated the mean egg index (MEI), which has been used to reflect seasonal activity for both species in previous studies (Carvalho de Resende et al. 2013, Žitko and Merdić 2014). We estimated MEI for each site by multiplying site-level species proportions by total egg count and dividing by the total number of ovitraps recovered over the sampling period.

Land cover variables. To characterize the habitat of these highly focal mosquitoes, we approximated land cover using two methods and compared the relationships between each method and *Aedes* 

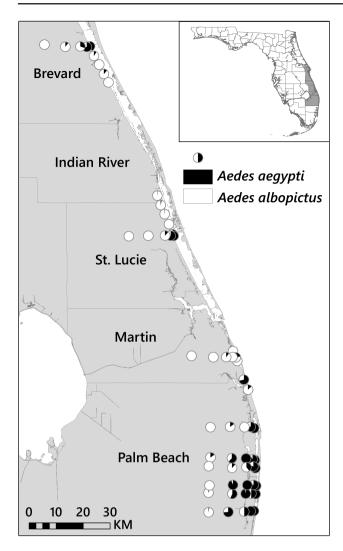


Fig. 1. Study area and species proportions by site. The left panel shows collections within the overall study area: Pie charts show the proportion of *Aedes aegypti* (black) to *Aedes albopictus* (white) collected at each site. The upper right panel shows the locations of counties in Florida in dark gray. County and shoreline boundaries are reprinted with permission from the University of Florida GeoPlan Center (fgdl.org), public domain 2015.

presence. We did this to determine whether a classification of the full study extent at a microscale would add value to our study, or if publicly available, 30-m<sup>2</sup> resolution land cover data are sufficient. First, we hand-digitized land cover within a 100-m buffer of each site using high-resolution orthoimagery in Esri ArcMap ver. 10.4.1 software (Esri, Redlands, CA; 0.3-m2 pixel resolution, Palm Beach County Information System Services, 2013). The classification system we used was modified from the Anderson Land Cover Classification System (Anderson et al. 1976) and included six land cover types: building/structure, pavement, bare ground, fine vegetation, coarse vegetation, and water. Second, we downloaded publicly available 30-m<sup>2</sup> National Land Cover Database (NLCD) classifications merged into nine composite classes (Supp Table 1 [online only]. The NLCD class 'open water' was only present at one site and was replaced with high-resolution data from the National Hydrography Dataset Plus. To verify that sampling sites were representative of the study extent, we compared summary statistics for the average composition of a 100-m<sup>2</sup> site and the entire study area. We found that 1-m<sup>2</sup> resolution data performed similarly

to 30-m<sup>2</sup> NLCD land cover classifications in model selection and determined that an intensive classification of the full study extent at 1 m<sup>2</sup> was unnecessary; NLCD classifications were used in our final model selection and in MaxEnt projections.

Bioclimate data variables. To approximate climate, we utilized downscaled bioclimatic data layers from 2000 to 2020. We obtained nineteen continuous bioclimatic data layers from General Circulation Models for the IPCC Special Range of Emission Scenarios (SRES B1), global circulation model CSIRO-Mk3.0. This scenario was imported from the database at Centro Internacional de Agricultura Tropical (http://www.ccafs-climate.org/data/). We downloaded data at a spatial resolution of 30 arc sec (~1 km<sup>2</sup>) and resampled to ~30-m<sup>2</sup> cell size using ModelBuilder in ArcMap ver. 10.4.1. Resampling did not provide finer resolution information of data values, but allowed us to combine bioclimatic raster layers with others in maximum entropy modeling. We elected to use the B1 scenario because it is the most optimistic and thus the most conservative. Eight of the nineteen available bioclimatic data layers available were omitted due to artifacts related to sampling bias. Average values of climate data within 100-m buffer radii around each trap location were extracted in preparation for the regression analysis and model selection. We calculated pairwise Pearson coefficients and generated four sets of noncollinear bioclimatic variables that we tested independently during model selection.

Human density and human movement. We downloaded human dasymetric population data from the EPA EnviroAtlas Toolbox. Census data assumes human populations are even across each census block, while EnviroAtlas uses dasymetric mapping to spatially distribute census data based on land cover classifications in the National Land Cover Database. This is an improved estimation of where people live because uninhabitable areas like open water and slopes greater than 25% are removed. We saved the raster in an ASCII grid format in Esri ArcMap. Since long-distance mosquito dispersal has been shown to be human-mediated, we also considered traffic intensity as a possible predictor (Guagliardo et al. 2015, Eritja et al. 2017). We buffered annual average daily traffic (AADT) polyline data by 15 m and created an AADT raster layer sampled to ~30-m² cell size.

#### Model Covariate Selection and Collinearity Analysis

First, we examined the statistical distribution patterns and data normality of both species and covariates using normal quantile plots and goodness of fit tests using the Shapiro-Wilk W statistic. Second, we used a logit probability model in a generalized regression analysis and corrected Akaike Information Criterion values (AICc) to select significant predictors of Aedes presence. Model selection was conducted for two purposes: to overcome redundancy by excluding collinear variables prior to maximum entropy modeling and to identify influential factors within the typical Aedes flight range around sampling sites (Sallam et al. 2016, 2017a). The selected significant predicting variables of Aedes presence were later used in building the distribution models of Aedes presence in MaxEnt (Fig. 2). We conducted two series of model selection using either remotely sensed variables to represent macrohabitat characteristics, or locally recorded variables at the site level to reflect the microhabitat factors. Local variables were recorded at the site level and included minimum, mean, and maximum daily temperature and relative humidity, the presence of vegetation in ovitraps, and the presence of

other arthropods in ovitraps. Remotely sensed predictors included land cover, bioclimate data variables, human density, and average annual daily traffic (Table 1). We selected the most influential factors from remote-sensed (macrohabitat) and locally recorded variables (microhabitat) to include in maximum entropy models based on the significant minimum AICc and maximum  $r^2$  values (P < 0.05), and evaluated the validity of regression models by using root mean square standardized errors (RMSSE); a value close to 1 indicated an appropriate model. A regression analysis was used to estimate the response of *Aedes* presence to their constraints within the 100-m buffer radius in JMP Pro 14.0.0.

## Habitat Suitability Modeling

The maximum likelihood of habitat suitability for *Ae. aegypti* and *Ae. albopictus* was modeled using MaxEnt software v. 3.3. In this analysis, we used *Aedes* presence records and selected significant influential variables from the generalized regression analyses to generate suitability maps (Fig. 2). Accordingly, we used jackknife tests to evaluate the percent contribution of the variables in habitat suitability models. We used a combined 58 presence records to generate *Aedes* mosquito distributions. Records were randomly partitioned for model evaluation into two subsamples: 75% of the records were used for training and model construction, and 25% of the records were used for testing model accuracy. Habitat suitability maps were created for sampled and un-sampled areas

based on the habitat similarity between sampled and unsampled regions in model projections produced in MaxEnt. To ensure that the spatial models created by MaxEnt were valid, we performed cross-validation tests during the analysis. MaxEnt systematically removed each data point and predicted the removed point by using the remaining training data. To increase the precision of the model, we had MaxEnt generate 100,000 background points and utilized five regularization multipliers.

Because the selection of training and testing points is random, five replicated runs were used to estimate the average, maximum, minimum, and median distributions of suitability for Aedes presence. Forty-four Ae. aegypti-positive sampling sites were used to build Ae. aegypti MaxEnt models. Across five replicates, an average of 33.6 training points and 8.4 testing sampling points were used. Aedes albopictus was present at 51 sampling sites, which were used to build Ae. albopictus MaxEnt models. Across five replicates, an average of 36 training points and 9 testing sampling points were used. We used two thresholds to examine the specificity of the fractional predicted area in the models: 1) the logistic threshold at 10 percentile training presence to delineate between suitable and unsuitable habitats, and 2) the area under the curve (AUC) of the receiver operating characteristics (Sallam et al. 2017b). The similarity between habitat suitability maps was calculated by finding the overlap in the total suitable area above the 10% logistic threshold for both species in ArcGIS.

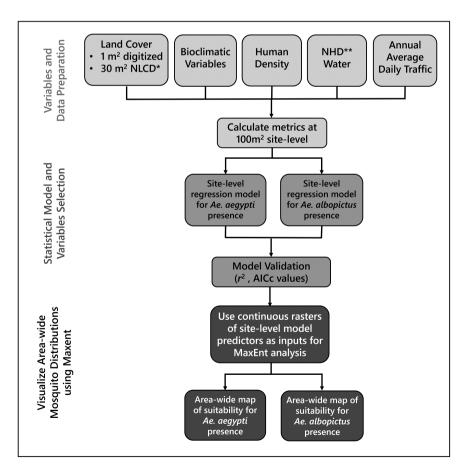


Fig. 2. Statistical pipeline to produce habitat suitability maps for the presence of *Aedes aegypti* and *Aedes albopictus*. Independent variables were estimated at the site-level (within 100 m of study sites) and regression models determined which variables were the most influential for either species. Significant predictors from regression models were used to parameterize MaxEnt projections and produce habitat suitability maps. \*National Land Cover Database, \*\*National Hydrography Dataset.

Table 1. Candidate variables for habitat suitability predictions of Aedes aegypti and Aedes albopictus

Variable	Type	Units	Resolution
Landscape factors			
Bareground $^a$	Categorical	Square meter	$1 \text{ m}^2$
Buildings <sup>a</sup>	Categorical	Square meter	$1 \text{ m}^2$
Coarse vegetation <sup>a</sup>	Categorical	Square meter	$1 \text{ m}^2$
Fine vegetation <sup>a</sup>	Categorical	Square meter	$1 \text{ m}^2$
Pavement <sup>a</sup>	Categorical	Square meter	$1 \text{ m}^2$
Water <sup>a</sup>	Categorical	Square meter	$1 \text{ m}^2$
Forest/grassland <sup>b</sup>	Categorical	Square meter	$30 \text{ m}^2$
Open development <sup>b</sup>	Categorical	Square meter	$30 \text{ m}^2$
Low development <sup>b</sup>	Categorical	Square meter	$30 \text{ m}^2$
Medium development <sup>b</sup>	Categorical	Square meter	$30 \text{ m}^2$
High development <sup>b</sup>	Categorical	Square meter	$30 \text{ m}^2$
Cultivated <sup>b</sup>	Categorical	Square meter	$30 \text{ m}^2$
Wetland $^b$	Categorical	Square meter	$30 \text{ m}^2$
Hydrography <sup>c</sup>	Categorical	Square meter	1:24,000
Climatic factors			
Annual mean temperature $(1)^d$	Continuous	Degree Celsius	$1 \text{ km}^2$
Mean diurnal range (2) <sup>d</sup>	Continuous	Degree Celsius	$1 \text{ km}^2$
Isothermality (3) <sup>d</sup>	Continuous	Percent	$1 \text{ km}^2$
Temperature seasonality (4) <sup>d</sup>	Continuous	Percent	$1 \text{ km}^2$
Max temp of warmest month $(5)^d$	Continuous	Degree Celsius	$1 \text{ km}^2$
Min temp of coldest month (6) <sup>d</sup>	Continuous	Degree Celsius	$1 \text{ km}^2$
Temperature annual range (7) <sup>d</sup>	Continuous	Degree Celsius	$1 \text{ km}^2$
Annual precipitation (12) <sup>d</sup>	Continuous	Millimeter	$1 \text{ km}^2$
Precipitation of wettest month (13) <sup>d</sup>	Continuous	Millimeter	$1 \text{ km}^2$
Precipitation of driest month (14) <sup>d</sup>	Continuous	Millimeter	$1 \text{ km}^2$
Precipitation seasonality (15) <sup>d</sup>	Continuous	Percent	$1 \text{ km}^2$
Human and behavioral factors			
Annual average daily traffic (AADT) <sup>e</sup>	Continuous	Cars/day	Polyline
Human density <sup>f</sup>	Continuous	Count/30 m <sup>2</sup>	$30 \text{ m}^2$
Site-level factors			
Temperature	Continuous	Degree Celsius	>1 m <sup>2</sup>
Relative humidity	Continuous	Percent	>1 m <sup>2</sup>
Presence of vegetation in ovitrap	Categorical	0 or 1	>1 m <sup>2</sup>
Presence of arthropods in ovitrap	Categorical	0 or 1	>1 m <sup>2</sup>

Landscape, climatic, human density, and human behavior data layers used in model selection and generation of species distribution models were gridded to 30 m² spatial resolution and projected into the NAD 1983 (2011) Contiguous U.S. Albers projection. Site-level factors refer to data recorded by data loggers and human observers at ovitrap locations.

- <sup>a</sup>Hand-digitized using 2013 NAIP imagery (earthexplorer.usgs.gov).
- <sup>b</sup>National Land Cover Database 2011 (mrlc.gov/data/nlcd-2013-land-cover-conus).
- Florida National Hydrography Database (geodata.dep.state.fl.us).
- <sup>d</sup>WorldClim Global Climate database v1.4 (ccafs-climate.org).
- <sup>e</sup>2013 Florida Department of Transportation Information (fdot.gov/statistics/trafficdata)
- 'EPA EnviroAtlas Dasymetric Toolbox (19january2017snapshot.epa.gov/enviroatlas/dasymetric-toolbox\_.html)

## **Results**

#### Summary Statistics and Model Inputs

Aedes aegypti eggs were present at 44 of the 59 sample sites over the 6-wk period (Fig. 1), with a mean egg index (MEI  $\pm$  SE) of 6.492  $\pm$  1.113 for positive traps. Aedes albopictus was present at more sites than Ae. aegypti (51 of the 59 sample sites) and was more abundant (Fig. 1), with a mean of  $16.605 \pm 2.574$  MEI for positive traps. Species co-occurred at 38 out of 59 sites, as well as in 127 out of 783 ovitraps. The standard least-squares effect leverage models demonstrated that distance to coast, latitude, and longitude had no effect alone or when combined with land cover variables, suggesting distance from the coast does not intrinsically drive local species distributions. The presence of foreign biotic material was variable, with vegetation found in  $66.6 \pm 18.5\%$  of ovitraps, and nonculicine, container-inhabiting arthropods in  $24.7 \pm 16.3\%$  of containers.

With regard to microclimate, mean daily temperatures across sites averaged  $26.8 \pm 0.8$ °C, and the mean daily minimum to maximum temperature ranged from  $23.7 \pm 1.2$ °C to  $30.4 \pm 1.7$ °C. Relative humidity was high, at an average of  $85.1 \pm 4.0$ %, and the mean daily minimum to maximum ranged from  $67.6 \pm 6.5$ % to  $94.4 \pm 3.1$ %.

# Model Covariate Selection and Collinearity Analysis

Responses to explanatory variables differed between species. *Aedes aegypti* presence had a significant positive association with high-intensity urban development, examples of which include apartment complexes, row houses, and commercial/industrial areas. *Aedes aegypti* also had a significant negative association with open development, which most commonly includes large-lot single-family housing units, parks, and golf courses (Table 2, AICc = 39.829,  $r^2 = 0.719$ ). *Aedes albopictus* presence had a significant positive association with

 Table 2.
 Species presence using remotely sensed and locally collected, site-level explanatory variables

Model	Explanatory variables	Coefficient	95% CI	SE	Wald $\chi^2$	Ь	AICC	$\mathbb{R}^2$
Remotely sensed variables Aedes aegypti	High development	63.15	33.98 to 92.32	14.88	18.0	<0.0001*	39.829	0.719
;	Precipitation of driest month	11.89	-4.53 to 28.31	8.38	2.01	0.1558		
	Human density	10.51	-2.65 to 23.68	6.72	2.45	0.1175		
	Open development	-8.16	-15.27 to $-1.06$	3.63	5.07	0.0243*		
	Precipitation seasonality	-8.72	-21.89 to 4.46	6.72	1.68	0.1947		
Aedes albopictus	Isothermality	69.57	7.28 to 131.86	31.78	4.79	0.0286*	31.899	0.603
	Min temp of coldest month	-34.92	-56.87 to $-12.97$	11.20	9.72	0.0018*		
	Precipitation seasonality	-52.70	-107.52 to 2.11	27.968	3.55	0.0595		
Site-level variables								
Aedes aegypti	Ovitrap arthropod presence	10.28	8.26 to 12.31	1.03	99.12	< 0.0001*	116.325	0.194
	Minimum daily temp	1.75	0.55 to 2.95	0.61	8.12	0.0044*		
Aedes albopictus	Ovitrap arthropod presence	0.91	-0.52 to 2.33	0.73	1.56	0.2166	122.047	0.406
	Minimum daily temp	-0.15	-0.25 to $-0.04$	0.05	7.49	0.0062*		

Predictors of Aedes presence were selected using logit probability models in a generalized regression analysis and corrected AICc values. Parameter estimates are for centered and scaled predictors.

isothermality and a significant negative association with the minimum temperature of the coldest month (Table 2, AICc = 31.899,  $r^2 = 0.603$ ).

Models built with remotely-sensed variables (macrohabitat) considerably outperformed models built with locally collected variables (microhabitat). For example, the *Ae. aegypti* locally collected variable model showed significant positive associations with the presence of arthropods in ovitraps and minimum daily temperature, but the model AICc was equal to 116.325, a comparatively poor fit (Table 2,  $r^2 = 0.194$ ). Like *Ae. aegypti*, *Ae. albopictus* presence showed a positive association with the presence of arthropods in ovitraps, but a significant negative association with minimum daily temperature (Table 2, AICc = 122.047,  $r^2 = 0.406$ ).

# Habitat Suitability Models

The average predictive performance of the resulting model for Ae. aegypti presence was high with an AUC value of 0.919 for training and 0.897 for test occurrence records with a standard deviation of 0.032. The fractional predicted area at 10-percentile training presence was 0.400 and equal test sensitivity and specificity logistic threshold was 0.421. These points were classified as significantly better than random (P < 0.001). Human density, precipitation seasonality, and precipitation of the driest month considerably improved the model, followed by a negligible gain with open development (Table 3, Supp Fig. 1 [online only]). The average predictive performance of the resulting model for Ae. albopictus presence was high with an AUC value of 0.873 for training and 0.871 for test occurrence records with a standard deviation of 0.035. The fractional predicted area at 10-percentile training presence was 0.321 and equal test sensitivity and specificity logistic threshold was 0.426. These points were classified as significantly better than random (P < 0.001). Minimum temperature of the coldest month substantially improved the model, followed by precipitation seasonality (Table 3, Supp Fig. 1 [online only]).

Habitat suitability similarity. Considerable overlap in suitable habitat existed for *Ae. aegypti* and *Ae. albopictus*, with *Ae. albopictus* having a larger area considered suitable. For the presence of both species, in nearly all areas that *Ae. aegypti* could exist spatially, so could *Ae. Albopictus* (Fig. 3). Habitat was suitable for both species in 1,888 km² out of 7,214 km² total study area, approximately 26.2% of the total area. The total suitable range for *Ae. aegypti* was 2,324 km² (32.2% total area) and 3,576 km² (49.5% total area) for *Ae. albopictus*.

## **Discussion**

We identified habitats highly suitable for Aedes aegypti and Aedes albopictus presence at a fine-scale in five Florida counties using a combination of publicly available landscape and climatic data and our own mosquito data. Nearly all areas that were classified as suitable for Ae. aegypti were also suitable for Ae. albopictus; however, some semirural areas were suitable for Ae. albopictus but not Ae. aegypti. This may be partially due to Ae. albopictus having a lower minimum threshold for human host density. Aedes albopictus is a more generalist feeder than the strictly anthropophilic Ae. aegypti, and thus may be able to occupy more human-sparse areas (Richards et al. 2006, Harrington et al. 2014). Alternatively, Ae. aegypti presumably occupied low human density areas prior to Ae. albopictus invasion and may have been outcompeted; however, historical data

Table 3. MaxEnt percent contribution and permutation importance of predictors of habitat suitability

Model	AUC	Predictive variables (+/-)	Percent contribution	Permutation importance
Aedes aegypti	0.897	Human density (+)	37.9	4.2
		Precipitation seasonality (-)	33	59.8
		Precipitation of driest month (+)	28.4	35.3
		Open development (-)	0.8	0.7
Aedes albopictus	0.879	Min temp of coldest month (+)	50.2	47
		Precipitation seasonality (-)	49.8	53

to support this hypothesis is lacking (Morlan and Tinker 1965). In addition to detecting some spatial segregation, we found considerable overlap in suitable habitat. Species co-occurred at 38 out of 59 sites, which resulted in high similarity between suitability maps. This overlap may accurately reflect natural conditions as we collected both species at most sites, with just 7 *Ae. aegypti*-only sites and 14 *Ae. albopictus*-only sites. Alternatively, the nuanced conditions that determine the outcome of competition may not be represented by the predictors we tested in our approach; competition may be influenced by subtle differences in desiccation regimes, which may vary widely at a finer scale and were undetected here (Costanzo et al. 2005).

Global suitability maps have shown that the entire state of Florida is suitable habitat for both species to varying degrees (Benedict et al. 2007, Medley 2010, Kraemer et al. 2015, Ding et al. 2018). This may be because environmental conditions physiologically extreme to Aedes are included in such models; the resolving power for more 'mild' habitats like Florida may be reduced. We were able to identify unsuitable habitat within Florida for both species, and remotely sensed variables in our study extent were more predictive than locally recorded variables and ultra-fine scale (<1 m<sup>2</sup>) land cover. This emphasizes the importance of screening environmental variables at multiple scales and careful selection of a study extent. For example, other studies have found 10 m<sup>2</sup> to be an optimal resolution for predicting Ae. aegypti and Ae. albopictus distributions in Texas (Sallam et al. 2017a), and 30 m<sup>2</sup> as an ideal buffer distance to represent habitat composition (Landau and Leeuwen 2012). Of the local meteorological variables tested, minimum daily temperature recorded at the site level showed significant, opposite relationships with both species. As minimum daily temperatures increased, Ae. aegypti presence increased, while Ae. albopictus presence decreased. This is consistent with Wijayanti et al. (2016); the average minimum daily temperature was reported to be the only significant meteorological factor that predicts the presence of Ae. aegypti with an increasing minimum daily temperature.

Maximum entropy models were generally congruent with regression models in identifying important variables, but the relative importance of variables varied between the two approaches. For example, isothermality had a significant positive effect in the Ae. albopictus regression model, but virtually no contribution in the maximum entropy model (Tables 2 and 3). This may be because regression models evaluated explanatory variables at the site level (within 100 m of sampling sites), while maximum entropy models accounted for the entire study extent. When we consider the specific components of maximum entropy models, human density emerges as a major contributor to habitat suitability for Ae. aegypti. This re-emphasizes the importance of vector host distributions in determining the spatial distribution of vectors (Pavlovsky 1966, Burkett-Cadena et al. 2013). Obenauer et al. (2017) demonstrated the importance of including human host distributions by using population density and poverty variables in multiple models of Ae. aegypti habitat suitability. Similar distribution modeling studies have employed human

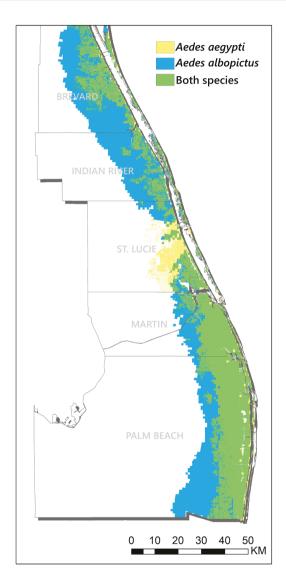


Fig. 3. Aedes aegypti and Aedes albopictus habitat suitability. Suitable habitat for Ae. aegypti, Ae. albopictus, and areas suitable for both species are indicated. County and shoreline boundaries are reprinted with permission from the University of Florida GeoPlan Center (fgdl.org), public domain 2015.

density in the creation of distribution maps with high model performance (Sallam et al. 2017b). *Aedes albopictus* habitat suitability was primarily driven by climatic variables. Notably, both species had negative relationships with precipitation seasonality, indicating that areas with more variable precipitation patterns were associated with lower *Aedes* habitat suitability.

Errors and uncertainties related to maximum entropy modeling include bias in sampling data, selection of predictor variables, and

selection of background points (Elith et al. 2011). We addressed these issues by: 1) using mosquito collection data of known, standardized sampling methods, 2) limiting the study extent to an area representative of mosquito sampling sites, 3) testing for collinearity, and 4), reducing the number of variables used in models to avoid overfitting. By using systematically collected mosquito data, we had the benefit of making multiple visits over time to a single site to confirm 'true' presences or absences, although we were limited in our total sampling window. Resampling this area annually and adding stratified random validation points in unsuitable, suitable, and highly suitable areas would greatly improve model accuracy. We were also limited to the use of census data—highly populated areas are typically split into many small blocks (1s of km<sup>2</sup>), and areas that are sparsely populated can cover great expanses (100s of km<sup>2</sup>). Thus, highly populated areas more accurately reflect human density, while the geographic accuracy of predicted anthropophilic mosquito distributions is limited in rural areas.

In regression and MaxEnt models, the remote sensing data variables (macrohabitat) demonstrated high contribution in predicting both Aedes species compared to the site-level factors (microhabitat). This was indicated by the highest  $r^2$ , AUC, and lowest AICc values from these models. Varying combinations of urban land cover variables, human density, and climatic variables relating to temperature and rainfall play an important part in habitat suitability for Ae. aegypti and Ae. albopictus in eastern Florida. We were able to detect some Aedes habitat segregation on the landscape: some semirural inland areas were suitable for Ae. albopictus but not Ae. aegypti. This may indicate a stronger reliance of Ae. aegypti on human density, as a macrohabitat predictor, or competitive exclusion by Ae. albopictus, as a microhabitat predictor on the site level. Suitability maps for Ae. aegypti were also more heterogeneous than those for Ae. albopictus, indicating a more sensitive association with landscape variables. These predictions provide guidance on areas of high-risk for mosquito presence and potential mosquito-borne disease transmission, helping us to better understand species interactions on the landscape and target high-risk areas for vector surveillance and control.

# **Supplementary Data**

Supplementary data are available at Journal of Medical Entomology online.

# Acknowledgments

We would like to thank Dr. L. Phil Lounibos and Dr. Walter Tabachnick of the Florida Medical Entomology laboratory in Vero Beach, FL for sharing their facility and expertise and Kyle Jones for his field assistance. We also thank Thomas Pleasant and Cole Keenan for digitizing site-level land cover. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. (DGE-1252376), USDA Multistate Project NE-1943, and the Triangle Center for Evolutionary Medicine.

#### **Author Contributions**

KAH, MFS, and MHR conceived the study. KAH collected the data. KAH and MFS analyzed the data. KAH, MFS, and MHR wrote the manuscript.

#### Conflict of interest

The authors declare no competing interests.

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