

Estimating the Geographic Distribution of Host-Seeking Adult *Amblyomma americanum* (Acari: Ixodidae) in Florida

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Abstract

The lone star tick, *Amblyomma americanum* (Linnaeus) (Acari:Ixodidae), is the most commonly reported human-biting tick in the southeastern United States and is a vector for several human and livestock pathogens. Although it is endemic to Florida, little is known about the ecological preferences and current spatial distribution within the state. Using occurrence records of adult *A. americanum* collected between August 2015 and September 2016, a logistic regression model was used to estimate environmental associations, as well as to predict the distribution of the tick at a one hectare resolution. Occurrence of adult lone star ticks was associated with land cover and bioclimatic variables, namely the presence of forested areas and precipitation seasonality. The estimated spatial distribution indicated that central and northern regions show greater suitability than the southern half of the state. Furthermore, areas predicted to be suitable for the species decreases from north to south with very little area deemed suitable in the far southern reaches of the state. High heterogeneity in the distribution of suitable habitat has implications for the distribution of tick-borne disease cases in the state. The subcounty resolution of the estimated distribution is an improvement over distributions currently published and may better inform the public and state or federal agencies of potential risk of exposure to *A. americanum* and its associated pathogens.

Key Words: *Amblyomma americanum*, Florida, species distribution model, logistic regression

In the United States, tick-borne diseases are the most commonly reported vector-borne diseases, outpacing reports of mosquito-borne illness by a factor of 9:1 during the decade from 2004 to 2013 (Beard et al. 2016). The species of ticks that transmit these pathogens are not homogeneously distributed which results, nationwide, in disparate areas of both exposure risk and disease incidence. The lone star tick, *Amblyomma americanum*, is the most abundant nuisance tick in many areas of the southeastern United States, and is the most frequently encountered by humans (Felz et al. 1996, Armstrong et al. 2001, Childs and Paddock 2003). This species is of major public health concern due to its voracious, nonspecific biting habits, and its competence for transmitting a number of human pathogens (Childs and Paddock 2003). While the lone star tick is not a competent vector of *Borrelia burgdorferi*, it can transmit *Ehrlichia chaffeensis* and *E. ewingii*, *Francisella tularensis*, and is suspected in the transmission of the presently uncharacterized agent of Southern Tick Associated Rash Illness (STARI) (Hopla 1953, 1955; Anderson et al. 1992; Anderson et al. 1993; Ledin et al. 2005; Masters et al. 2008; Goddard and Varela-Stokes 2009).

Several dozen cases of locally acquired tick-borne illness are reported every year in Florida (Table 1), however, little is known about the statewide distributions of the vector species beyond regional distribution maps and localized sampling efforts (Bishopp and Trembley 1945, Taylor 1951, Rogers 1953, Smith Jr. 1981, Greiner et al. 1984, Forrester et al. 1996, Cilek and Olson 2000, Allan et al. 2001, Springer et al. 2014). The seminal work by Bishopp and Trembley (1945) provided the basis for The Centers for Disease Control and Prevention (CDC) published map of the regional distribution of the lone star tick and indicates all of Florida falls within the species' potential range (CDC 2017). However, increased understanding of vector distributions and ecological preferences provide insights into areas at-risk for vector-borne pathogens suggesting spatial heterogeneity is an important aspect to evaluate (Glass et al. 1995, Ostfeld et al. 2005, Eisen et al. 2006).

There are several statistical and pattern matching approaches to estimate the distribution of organisms in the environment. These techniques can range from purely theoretical to mechanistic or empirical (Guisan and Zimmermann 2000). Predictive species distribution

Table 1. Yearly incidence of suspected and confirmed locally acquired reportable tick-borne diseases in Florida from 2010 to 2016 (Florida DoH 2017)

Diseases	Year	2010	2011	2012	2013	2014	2015	2016
	Total	Counts	Counts	Counts	Counts	Counts	Counts	Counts
	433	41	50	80	53	79	63	67
Anaplasmosis	11	3	6	1	0	0	0	1
Ehrlichiosis	120	8	13	20	17	23	16	23
Lyme Disease	210	22	22	39	21	35	35	36
Spotted Fever Rickettsiosis (including Rocky Mountain Spotted Fever)	92	8	9	20	15	21	12	7

models, are intended to detect nonrandom associations between location-specific occurrence observations and environmental conditions (often as raster-based predictors) to estimate a response at unobserved locations (Guisan and Zimmermann 2000, Blackburn 2010). Here, we apply a general linear model (GLM) framework to estimate the distribution of *A. americanum* in Florida. This study is our first effort to estimate the distribution of the species at high resolution for the state. Previously published distribution maps for Florida have been limited to broad regional maps or have limited spatial predictions to the county level (Springer et al. 2015, CDC 2017).

Materials and Methods

Study Area

The surveyed area included mainland Florida and excluded the Florida Keys. The state encompasses a range of environmental conditions with high climatic variability from north to south, which supports numerous habitats. The National Oceanic and Atmospheric Administration (NOAA) divides the state into seven distinct regions considered climatically homogeneous (Keim et al. 2005). Both the El Niño Southern Oscillation (ENSO), and the Atlantic Multidecadal Oscillation (AMO) impact long-term climate trends in Florida, however, the dominant drivers include latitude (as reflected in the NOAA climate divisions), prevailing winds and pressure systems, as well as ocean currents (Tsai et al. 2014). Northerly regions of Florida experience greater seasonal variability and receive a larger proportion of rainfall during the winter months than southern regions. The seasonal precipitation patterns are reflected in patterns of changing greenness (using the Normalized Difference Vegetation Index [NDVI]), wherein greenness tends to increase in the fall and winter and decline in the spring (Tsai et al. 2014).

Site Selection

Selected sampling sites were chosen to ensure broad geographic coverage of mainland Florida and to incorporate variability in local environmental and climatic conditions. A total of 33 sites were selected including Florida State Parks, county extension service locations, and University of Florida affiliated Institute of Food and Agricultural Science research and education centers (IFAS-REC) (Fig. 1). Each site was composed of one or more biotopes with sampled habitats ranging from monoculture agricultural crop fields, pastures, seasonal wetlands, hardwood forests, and pine scrub. Central and southern regions of the state contained a high percentage of seasonal fields and orchards, primarily citrus crops.

Tick Collection Data

We used field-collected data of observed presence or absence of adult *A. americanum* in Florida between August 2015 and September 2016 as the basis for modeling the geographic distribution. The majority

of our collection effort occurred between April and August to coincide with reported peak seasonal activity of adult *A. americanum* in the southeastern United States (Semtner and Hair 1973, Cilek and Olson 2000, Kollars Jr et al. 2000, Allan et al. 2001). A second collection period from October 2016 through May 2017 was used as a validation dataset. All tick collections were performed in accordance with the Florida Department of Environmental Protection under Research and Collection Permits #03111610 and 02211710. Each site was visited at least twice during the collection period, with most sites being repeatedly sampled approximately once per month between April and September.

Collections were performed via flagging along 100–200 m transects; flags were checked for ticks approximately every 10 m. Transects were geotagged by latitude and longitude with the World Geodetic System 1984 (WGS84) using a GPS-enabled Nexus 7 tablet (Google LLC, Mountain View, CA) at the start, middle, and end points of the transects using the DoForms application for Android to input data (DoForms 2017). Each GPS-tagged location was time stamped and accompanied by a photograph of the surrounding land cover including canopy and understory for ground-truthing of land cover characterization. A minimum of one set of paired transects were run at any given site although sites with multiple biotopes included upwards of five pairs of transects (10 total transects at the site). Each transect was given a unique identifier by county, site name, date, and transect number. Ticks were removed from flags and placed into vials containing 100% ethanol. Ticks were identified morphologically by species and life stage based on standard taxonomic keys (Strickland et al. 1976, Keirans and Litwick 1989) and adults and nymphs were stored at -80°C . The midpoint of each transect was used to demarcate the geographic location.

Predictive Variables

The initial choices of habitat and climatic variables were based on reported associations with tick presence/absence in the literature (Brownstein et al. 2003, Brown et al. 2011, Fryxell et al. 2015, James et al. 2015, Springer et al. 2015). Variables describing habitat parameters were land cover, NDVI measures for the study period (2015–2016), elevation, and distance to waterbodies. These datasets were retrieved from the Florida Geographic Data Library (FGDL) and derived from the Florida Cooperative Land Cover Database (CLC), MODIS NDVI 16-d composites (2015–2016), the ASTER Global DEM, and the national hydrography dataset, respectively. Variables describing climate parameters were the 19 ‘bioclimatic variables’ (BioClim) calculated by Hijmans et al. (2005) from the WorldClim Version1.4 climate database and used the same naming schema. The native resolution for the MODIS imagery, ASTER DEM, and BioClim variables were 250 m, 30 m, and 1 km, respectively.

The CLC database included statewide classifications of all major land cover types at a native resolution of 10 m. Using the existing

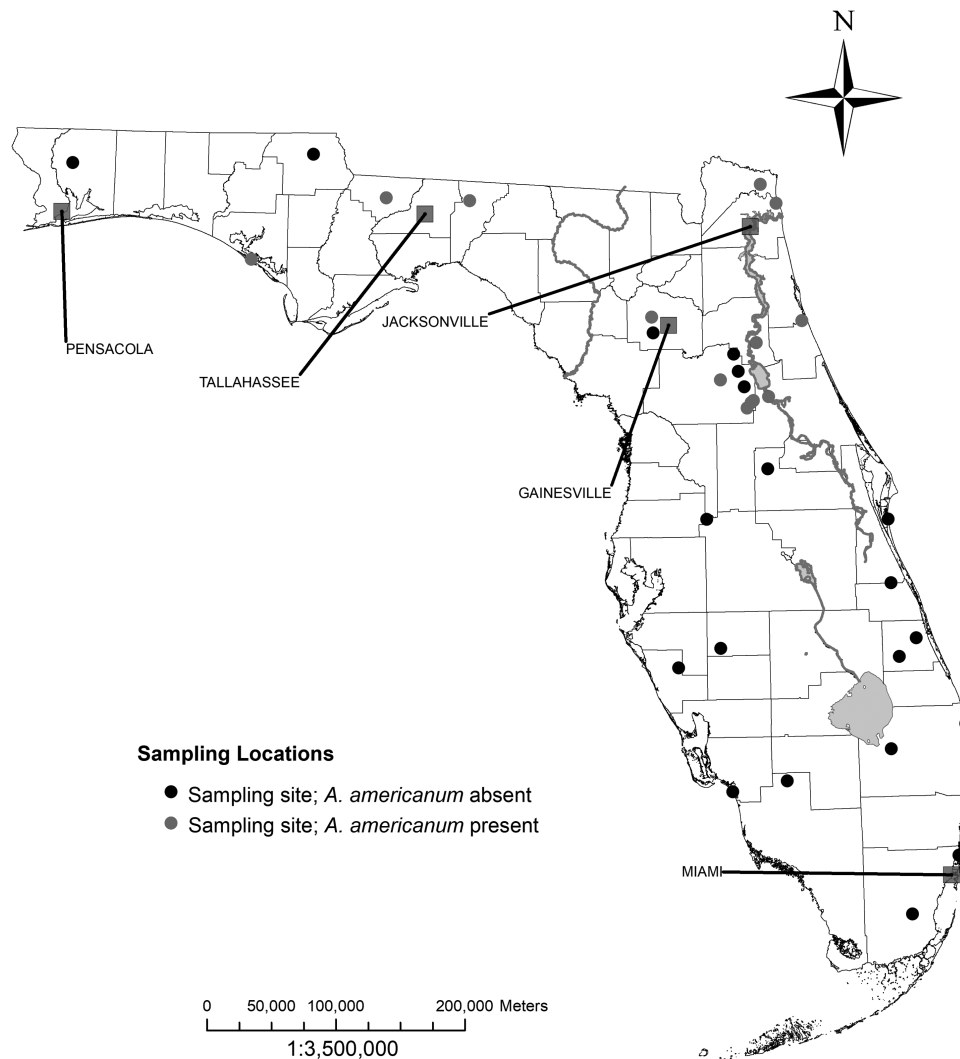


Fig. 1. Distribution of sample collection sites from August 2015 to August 2016 indicating where adult *Amblyomma americanum* were collected (gray circle), and locations that returned no adult *A. americanum* (black circle).

hierarchical classification scheme, major state-level land cover types were reclassified as one of five primary types: Forest, which included pine and hardwoods; Shrub, encompassed shrub and brush lands; Grasses; Wetlands; and a final, general category including all other land types such as water bodies, urban areas, and seasonal agriculture.

Distribution Model

Preprocessing of tick occurrence data was performed to ensure major assumptions of the GLM framework were met. The procedure of repeatedly sampling at sites, over time, resulted in multiple, proximal points with similar counts of adult *A. americanum* producing a high degree of spatial autocorrelation of tick presence or absence between transects. To evaluate the impact of this sampling scheme, and spatial autocorrelation, semivariogram analysis of *A. americanum* abundance was performed to establish the distance at which the number of collected adult specimens was independent of findings at ‘nearby’ transects (the range of the semivariogram) (Legendre 1993). The average nearest-neighbor distance was calculated between all points and used to set the bin width in the semivariogram. The resulting range of the semivariogram indicated independence of observations from neighboring observations; i.e., where the semivariance between observations stopped increasing (Karl and Maurer 2010). All points

located closer than the calculated range were collapsed to a single central point in ArcGIS. The resulting point was designated as having presence or absence (1 or 0) of *A. americanum* if adult specimens were collected from one or more transects represented by that point. Points separated by greater than the range distance were retained as individual points. This procedure reduced the sample size of presence/absence points used to develop the GLM. All environmental and climatic data layers were resampled to 100×100 m to match the spatial scale of the aggregated point data. The discrete values of the land cover data set were resampled using a nearest-neighbor method in ArcGIS. All other data were resampled to the extent and resolution of the land cover layer using bilinear interpolation in R (Richards 2013). All layers and data were projected to an Albers Conic Equal Area projected coordinate system to minimize linear scale and areal distortion (Snyder 1987). Unless otherwise noted, ArcGIS version 10.3.1 and R were used for all statistical and spatial analyses.

The distribution of habitat suitable for *A. americanum* was estimated using a multivariate logistic regression. As part of an initial exploratory data analysis, univariate relationships were evaluated to identify covariates with significant ($P < 0.05$) associations with the dependent variable (presence/absence of *A. americanum*) (Springer et al. 2015). Those with insignificant associations were excluded from further consideration. Many of the remaining

variables considered in this analysis were derived from precipitation and temperature measurements. As a result, many of those spatial patterns were highly correlated (Springer et al. 2015). To reduce the likelihood of introducing collinearity into the model, a stepwise procedure was implemented in R using the ‘usdm’ package to calculate the variance inflation factor (VIF) for the remaining predictors and exclude those with the greatest collinearity (VIF > 10) (Naimi et al. 2014). The remaining uncorrelated variables were evaluated with an exhaustive logistic regression model search to select a ‘best’ model from first-order variable interactions, which minimizes the small sample size corrected Aikake information criterion (AICc) (Buckland et al. 1997, Calcagno and de Mazancourt 2010).

The selected best model was evaluated for fit and predictive accuracy using several metrics. The regression residuals of the selected best model were evaluated for spatial autocorrelation using Global Moran’s I (Moran 1950) and goodness of fit of the model was evaluated using the Hosmer-Lemeshow test (Hosmer and Lemeshow 1989). Predictive performance was evaluated using repeated k-fold cross validation ($k = 10$ -folds, 100 repetitions) due to the relatively small number of positive points in the dataset (Arlot and Celisse 2010). The predictions from each fold were compared to the known values and results were assessed using a measure of sensitivity/specificity and the Kappa statistic (Landis and Koch 1977, Fielding and Bell 1997, Allouche et al. 2006). The model was further evaluated using an external dataset to which the model was naïve. The testing dataset consisted of 316 transects performed during a subsequent field season (October 2016 and May 2017) using the same collection procedures and sites (with an additional 4 sites). The model was used to generate probability estimates for locations of this testing dataset and estimate model accuracy metrics (sensitivity, specificity, accuracy), and Kappa values.

Spatial Prediction

Estimated habitat suitability for *A. americanum* was determined by generating a map of output probabilities from the logistic regression model. The raster layers for each variable included in the final model were stacked in R. The values of each pixel at a given location provided the inputs for the logistic regression and output a probability value for that location. The potential distribution of *A. americanum* in Florida was estimated by reclassifying the map of suitability probabilities based on a selected cutoff criterion. The chosen cutoff value was the probability where the sensitivity and specificity of the model were equivalent indicating an equal tradeoff between false predictions of both presence and absence (Fielding and Bell 1997, Freeman and Moisen 2008, Springer et al. 2015). All probability values greater than the sensitivity/specificity cutoff are deemed suitable for presence of adult *A. americanum*, and all values less than the cutoff are deemed unsuitable for adults of the species.

Results

A total of 328 transects were run during the initial study period, 33 transects returned adult *A. americanum* (10%). After aggregating proximal transects based on a 100 m neighborhood, 130 presence/absence points were used to develop the logistic regression model ($n = 23$ presence points). An additional 316 transects were available for model validation.

Model Selection

Initial analysis of univariate relationships with tick occurrence found 16 predictors were significantly associated ($P < 0.05$). Notably, of

the five land cover variables, only forest was retained as significant. Further reduction of variables was achieved by eliminating highly collinear variables. The final set of variables used in model selection consisted of one land cover variable (forest), a suite of bioclimatic measures pertaining primarily to precipitation, and two measures of NDVI (Table 2).

A set of potential ‘best’ models generated from an exhaustive model search differed in AICc values by less than 2.0 units, indicating they were of essentially equal quality (Symonds and Moussalli 2011). Ultimately, the model with the lowest AICc was selected. The variables included in the final model were forest cover, maximum NDVI, Bio3 (temperature stability or isothermality), Bio8 (mean temperature of wettest quarter), Bio13 (precipitation of wettest month), and Bio15 (precipitation seasonality) (Table 3).

Both forested land cover (which included predominantly coniferous forest, deciduous forest, and mixed forests) and maximum NDVI (a proxy for vegetation health) were positively associated with tick presence. Three of the four bioclimatic variables: Bio3, Bio8, and Bio13 were all negatively associated with *A. americanum* presence. Thus, as isothermality increased (Bio3) occurrence of *A. americanum* was likely to decrease. Similarly, areas that received the highest amounts of rainfall during the wettest months (Bio13) or were the warmest during the wettest quarter (Bio8) were associated with a lower probability of occurrence for *A. americanum*. The final bioclimatic variable included in the model, precipitation seasonality (Bio15) was positively associated with tick presence indicating that as intra-annual variation in precipitation increased the probability of occurrence for *A. americanum* increased.

The model performance assessed via the Hosmer-Lemeshow goodness of fit test and cross validation (Table 4) showed the model performed well on both training and testing data. Validation via k-fold CV indicated that the model performed well in identifying true positive points (sensitivity), but did a poorer job of discerning true negative points (specificity) in the training data. The calculated Kappa statistic (0.43) indicated a solid improvement in model performance over chance, alone (Fielding and Bell 1997). Model accuracy was reduced against the testing dataset with a reduction in sensitivity and Kappa also indicated reduced performance (Table 4).

Spatial Prediction

The spatial prediction based on the model (Fig. 2) classified large portions of northern and central Florida as moderate to high predicted habitat suitability for *A. americanum*. The areas with the highest predicted suitability occur in the far western panhandle,

Table 2. Environmental and climatic variables with low collinearity determined by VIF; highly collinear variables not shown

Variable	VIF
Forest	1.104511
Bio3_fl	4.587343
Bio7_fl	4.507246
Bio8_fl	2.272024
Bio9_fl	4.087867
Bio13_fl	6.758279
Bio15_fl	7.523549
Bio18_fl	8.014768
NDVI_max	1.982174
NDVI_mean	2.06272

Variables listed constitute final variable set considered in logistic regression model selection.

Table 3. Coefficients and variables included in the best logistic regression model to predict presence of *Amblyomma americanum* across Florida

	Coefficients:				
	Beta	Std. Error	Z-Value	Pr(> z)	
Intercept	-3.1486	0.5878	-5.356	8.49E-08	***
Forest	1.3328	0.6366	2.094	0.034006	*
Bio3	-1.1053	0.5214	-2.12	0.034006	*
Bio8	-1.0896	0.4937	-2.207	0.027313	*
Bio13	-1.4302	0.6082	-2.352	0.018692	*
Bio15	1.6852	0.6718	2.508	0.012126	**
Max NDVI	1.4121	0.387	3.648	0.000264	***
Sign. Codes	0 '***'	0.001 '**'	0.01 '*'	0.05 '.'	0.1 ' '

Table 4. Model validation metrics indicating model fit against training and testing datasets indicating a reduction in overall accuracy and sensitivity.

	Hosmer-Lemeshow Goodness of Fit (P-value)	Sensitivity	Specificity	Accuracy	Kappa
Training	0.087	0.94	0.48	0.86	0.43
Testing	-	0.63	0.83	0.81	0.278

gulf coast, and the far northeastern corner extending south along the Atlantic coast to the Melbourne (28.7°N) area and inland to the Ocala National Forest (29°N). The spatial prediction indicated that most of southern Florida is not suitable for questing adult *A. americanum*.

The cutoff value to delineate presence (suitable) from absence (unsuitable) was 0.186, which was where the model correctly predicted approximately 78% of presence and absence values. This lowest presence threshold (LPT) cutoff value was similar to other values in the literature (James et al. 2015). The average probability value of suitable areas based on the LPT in the present study was 0.42. The spatial prediction was reclassified based on this cutoff to produce a map of the estimated spatial distribution of adult *A. americanum* (Fig. 3) in Florida.

Suitable habitat for adult *A. americanum* comprised 30–50% of all areas from the 'Big Bend' area (29.6°N) northwards. Less than 10% of land in southern Florida was predicted to be suitable for the species. Highly suitability areas, defined as areas with probability values greater than the mean value of suitable areas (areas with probability values greater than the LPT), roughly mirrored suitable areas in general. However, there was a distinct reduction in the suitability of areas within the estimated distribution in southern areas of the state. The far southern regions of the state were not highly suitable for the species at all.

Discussion

The lone star tick is increasingly recognized as a species of public health importance; however, in many areas the distribution of the species is unknown at resolutions below the county level (Brown et al. 2011, Raghavan et al. 2016). The estimated distribution map of adult *A. americanum* presented here is an effort to produce a spatial distribution of suitable habitat for Florida. Large numbers of nymphal *A. americanum* were also collected during this study but not included in this analysis as they co-occurred with adults with few exceptions ($n = 3$ sites with nymphs but no adults). The results

predict that a large portion of the state is environmentally favorable to this tick species; however, the favorable areas are not uniformly distributed. The estimated distribution indicates far greater heterogeneity in habitat suitability across the state than suggested by previous regional or county level continental-scale distributions (see Springer et al. 2015, CDC 2017). Grain size has been shown to affect the accuracy of distribution models and can obscure important distributional patterns and resulting conclusions (Guisan et al. 2007, Seo et al. 2009, Gottschalk et al. 2011). This can impact estimates of pathogen distributions and human exposure risk (Diuk-Wasser et al. 2010).

Areas of suitable habitat decrease significantly south of Lake Okeechobee (27°N). During the study period adult *A. americanum* were not collected from any sites south of Ocala National Forest, which supports the prediction of limited habitat suitability farther south. However, subsequent collections have returned adult *A. americanum* as far south as Lake Okeechobee in areas predicted to be suitable (data not shown).

Previous distribution models have not captured the same meridional gradient in habitat suitability although it was suggested (Springer et al. 2015). Our results reflect reports in the literature that adult lone star ticks in southern Florida are scarce; it is still unclear if this is due solely to lower sampling intensity in the southern portion of the state or because of lower habitat suitability in these areas (Diuk-Wasser et al. 2006, Springer et al. 2014). Allan et al. (2001) indicated regional proportions of *A. americanum* from ticks collected from deer and swine in Florida dropped markedly across northern, central, and southern regions (deer: 56.9, 47.9, and 0%; swine: 27.3, 0.6, and 1.5%, respectively). While collections by flagging more closely resemble what could be expected of casual human exposure, estimates of tick presence or density derived from free-ranging wildlife potentially provide a more sensitive representation of the tick occurrence in the landscape (Ginsberg and Ewing 1989). It is therefore assumed that the significant reduction in *A. americanum* prevalence found by Allan et al. (2001) across the three ecoregions is associated with ecological conditions, and not simply local variability between sampling locations.

One region in the 'Big Bend' area (29.6°N) of Florida, along the gulf coast was predicted to be especially favorable to *A. americanum*. This region was not sampled and it is unknown if the high probability estimates will be substantiated by additional sampling or if the results are erroneous. Springer et al. (2015) do not note particularly suitable habitat in this region. Collections by Sayler et al. (2014) returned large numbers of adult *A. americanum* from several Florida state parks bordering this area. However, visualization of the BioClim climate coverages used in this study reveal sharp transitions in temperature and precipitation trends at this location indicative of

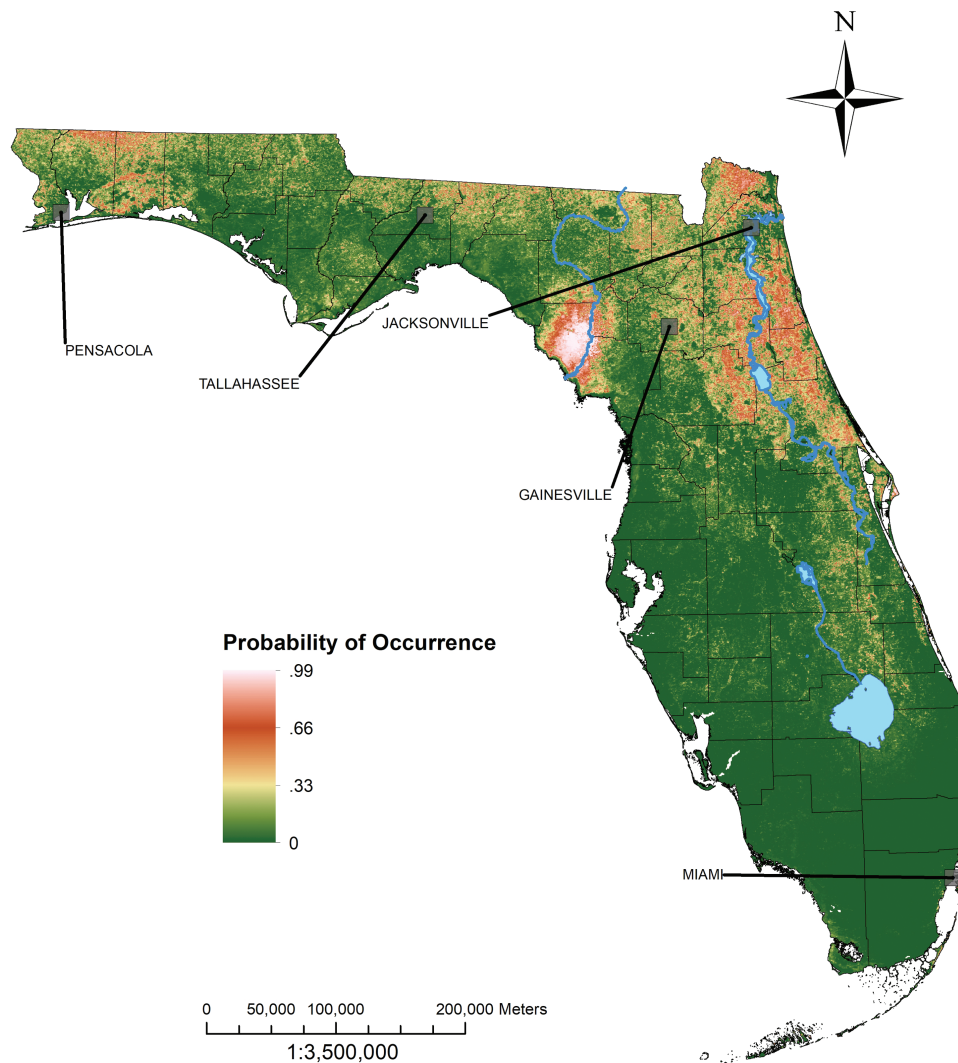


Fig. 2. Probabilities of occurrence of *Amblyomma americanum* in Florida. Green shading and red shading indicates low and high probability of occurrence, respectively.

possible interpolation challenges, which would indicate that there is no biological basis for the high predicted suitability in this area (Supplementary Material).

The variables included in the final model; forest cover, maximum NDVI, Bio3 (temperature stability or isothermality), Bio8 (mean temperature of wettest quarter), Bio13 (precipitation of wettest month), and Bio15 (precipitation seasonality), can be interpreted as biologically relevant to the ecological preferences of *A. americanum* (Table 3) and may be associated with some underlying, intervening variables that drive tick occurrence, or they may directly act on *A. americanum*.

Both forested land cover and maximum NDVI (a proxy for vegetation health) were positively associated with tick presence, and is indicative of *A. americanum* in areas with higher vegetation health (greenness) and in forested areas. Previous studies indicated ticks utilize the microclimate provided by dense leaf litter and brushy understory to lay eggs or to prevent desiccation; the highest numbers of adult *A. americanum* were found on brushy vegetation due to the relatively high humidity (Oliver Jr 1989, Anderson and Magnarelli 2008). NDVI is a proxy for vegetation health and productivity. Healthy vegetation produces high humidity microclimates utilized by questing ticks (Vail and Smith 2002, Anderson and

Magnarelli 2008). Vegetation growth is generally the greatest during summer months resulting in maximum NDVI values during a time of the year when temperatures are highest and ticks are most prone to desiccation. Whether high NDVI also reflects soil moisture, the abundance of vertebrate host populations using the local microhabitats or aspects of the vegetation itself cannot be ascertained by this study.

Three of the four included bioclimatic variables: Bio3, Bio8, and Bio13 were negatively associated with *A. americanum* presence. Thus, as isothermality (Bio3) increased occurrence of *A. americanum* was likely to decrease. Isothermality quantifies how day–night temperature variation ranges relate to summer–winter oscillations. High isothermality is indicative of temperature evenness over the course of the year (as occurs in southern Florida), whereas a low isothermality indicates that the size of temperature swings vary between summer and winter (as occurs in more temperate regions of the state). James et al. (2015) posits that isothermality impacts immature development for *D. variabilis* and Oliver (1989) states that lone star tick development rates is accelerated under laboratory conditions by increasing ambient temperature. The negative relationship between *A. americanum* presence and isothermality ($\beta = -1.10$, $\alpha < 0.05$), suggest that uniform temperatures reduce the

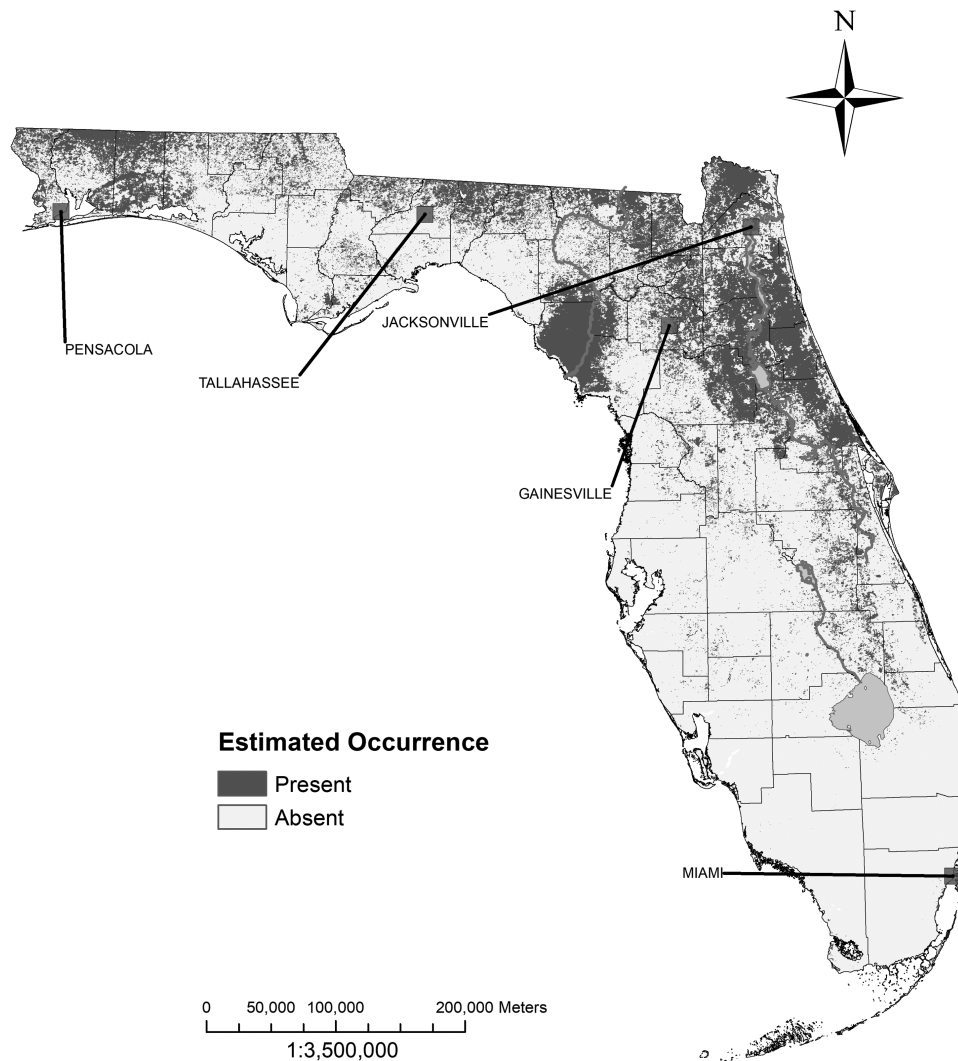


Fig. 3. Estimated distribution of *Amblyomma americanum* based on an LPT indicating substantial areas of suitable habitat in northern Florida and increased unsuitable areas in southern Florida.

probability of *A. americanum* occurrence, appears to contradict the general biology of the species. Previous studies of the environmental preferences of ticks at various spatial scales have considered isothermality but found it to be nonsignificant (James et al. 2015, Springer et al. 2015). It may be that isothermality has an indirect effect not related to the biology of the species, but should be evaluated further.

Areas that receive the highest amounts of rainfall during the wettest month (Bio13) or are the warmest during the wettest quarter (Bio8) are similarly associated with a lower probability of occurrence for *A. americanum*. The mean temperature of the wettest quarter (Bio8) was negatively associated with tick presence ($\beta = -1.08$, $\alpha < 0.05$). High temperatures can decrease survivorship in ticks through desiccation during host seeking activities (Knulle and Rudolph 1981, Vail and Smith 2002, Anderson and Magnarelli 2008). While moisture can reduce this risk by increasing relative humidity, laboratory studies on survivorship among multiple larval *Rhipicephalus* (*Boophilus*) species show that even at high relative humidity (97%) survival is negatively impacted by temperature increases from 20 to 25°C (Davey et al. 1991). In the current study, no ticks were found in southern Florida, which coincidentally experiences the highest average temperatures in the state during the wettest months (>25°C). Springer et al. (2015) found that mean temperature

of the wettest quarter was not consistently a significant predictor of *A. americanum* presence (not a predictor of presence using GLM, Boosted Regression Trees, or Multivariate Adaptive Regression Splines models, and had differing response curves for Random Forest and Maxent).

Precipitation during the wettest month (Bio13) could impact egg development and larval survivability (James et al. 2015). In our analysis greater precipitation during the wettest month was negatively associated with adult tick presence ($\beta = -1.43$, $\alpha < 0.05$). The combination of high annual precipitation and extensive low-lying areas makes many areas in Florida prone to flooding or standing water. During the peak of Florida's monsoon season, large precipitation events may result in standing water long enough (>1 mo) to reduce survivability of eggs or larvae and ultimately impacting adult tick populations. Weiler et al. (2017) showed that major flood events reduce the abundance of questing ticks. Adejinni (2011) also found that prolonged submersion decreased hatchability of *Rhipicephalus sanguineus* and *Haemaphysalis leachi* eggs. Similarly, precipitation seasonality (Bio15) was positively associated with tick presence indicating that areas with more pronounced wet and dry seasons had increased probability of occurrence for *A. americanum*. Koch (1986) showed in the laboratory *A. americanum* could survive submersion

for several weeks so periodic flooding had little long-term effect on the species. Springer et al. (2015) and James et al. (2015) found precipitation seasonality to be a significant predictor of *A. americanum* (negative relationship) and *Dermacentor variabilis* distributions (unspecified relationship), respectively. The apparent differences in species-environment relationship can be explained by a number of factors related to model specification (variables, geographic extent or scale, or included data), species biology, or other factors (El-Gabbas and Dormann 2017).

The preliminary examination of significant relationships (via univariate logistic regression during the variable selection process) between the considered environmental variables and the presence of *A. americanum* revealed that only a fraction of the habitat and vegetation characteristics (Forest cover, and two measures of NDVI) had any association. Distance to water bodies, all other land cover types, and a third measure of NDVI had nonsignificant associations with tick presence. Of the climate variables, six of 19 considered variables were not significant predictors. Tick physiology is notably modulated by abiotic conditions so the dominance of climate measures may be not surprising. Survivorship of all life stages, reproductive success, and development are affected by temperature and moisture availability (Randolph et al. 2002, Yoder and Benoit 2003, Yoder and Tank 2006, Anderson and Magnarelli 2008). For this reason, many attempts to estimate the geographic distributions of ticks have focused on associating presence or abundance with temperature and moisture measurements (Estrada-Pena 1998, Porretta et al. 2013, Atkinson et al. 2014, James et al. 2015, Springer et al. 2015, Raghavan et al. 2016). Furthermore, limited findings (76 sample sites across 74.5 km²) have indicated that habitat and vegetation characteristics including land cover type, NDVI, and distance to water, are not adequate predictors of tick presence or abundance in the southeastern United States (Fryxell et al. 2015). The observed relationships between *A. americanum* and the variables in this study appear to support the notion that measured climatic conditions (temperature and moisture) are important determinants of the distribution of the species in Florida.

Distributional estimates for pathogen vectors can be an important step in targeting at-risk areas for vector-borne disease. At least three limitations could contribute to the spatial distribution presented here. First, the extensive size of the study area (ca. 170,000 sq km) was a major challenge in determining the locations, number of sites that could be practically sampled, as well as the frequency and intensity of sampling at each site. The sites were selected to broadly sample the geographic distribution and variability of local environmental and climatic conditions. Another limitation stems from differences in unmeasurable variables such as host availability and active management practices. Differences in active management strategies occur at many sites for conservation or other purposes. This active management may influence subtle land cover, understory, or other habitat characteristics that are not captured by current classifiers. For example, controlled burning or canopy thinning results in significantly reduced long-term tick counts for *A. americanum* and other species (Stafford et al. 1998, Gleim et al. 2014). However, recent burning may increase tick abundance due to reintroduction by large herbivores grazing on re-emergent understory vegetation (Cilek and Olson 2000). However, the tradeoff is that many of these variables are not captured at broader geographic scales, nor are they updated in timely fashions.

Historically, tick collections efforts have under-sampled many counties in Florida potentially resulting in underestimates of the species distribution and the human risk of exposure to this species and its pathogens. The spatial prediction of questing *A. americanum*'s

distribution in Florida produced by this research contributes to the current understanding of exposure risk to ticks and their pathogens by providing an initial indication of potentially risky landscapes and may inform control measures by county, state, and federal agencies.

The major role of the lone star tick as a vector of multiple human pathogens should guide future work on evaluating human exposure risk to this vector and its pathogens. In this study, we found a number of temperature and precipitation variables predicted the distribution of adult *A. americanum* in Florida. Further consideration of other aspects of tick ecology, such as host distribution or density, and additional climate variables or variable interactions should be incorporated to determine if they improve estimated distribution maps. Models based upon tick densities, pathogen prevalence, or tick-borne disease incidence may improve estimates of exposure risk to ticks and tick-borne diseases as these approaches address important aspects of transmission not addressed by habitat suitability (Diuk-Wasser et al. 2010, Diuk-Wasser et al. 2012). Future efforts to produce better-resolved distribution maps of *A. americanum* in Florida should attempt to reduce the limitations of a GLM modeling approach. In future studies, we will use ensemble predictions to reduce the bias of any single model by leveraging agreement between models allowing us to corroborate the validity of existing distribution estimates.

Supplementary Material

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

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