ENVIRONMENTAL DRIVERS OF GULF COAST TICK RANGE EXPANSION IN THE UNITED STATES

BY

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THESIS

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ABSTRACT

In the United States, the Gulf Coast tick (*Amblyomma maculatum*) is a species of growing medical and veterinary significance, serving as the primary vector of the pathogenic bacterium, *Rickettsia parkeri*, in humans and the apicomplexan parasite, *Hepatozoon americanum*, in canines. Ongoing reports of *A. maculatum* from areas outside its core distribution in the southeastern United States suggest the possibility of current and continuing range expansion. Using an ecological niche modeling approach, I combined new occurrence records with high-resolution climate and land cover data to investigate environmental drivers of the current distribution of *A. maculatum* in the United States. I found that environmental suitability for *A. maculatum* varied regionally and was primarily driven by climatic factors such as annual temperature variation and seasonality of precipitation. I also found that presence of *A. maculatum* was associated with open habitat with minimal canopy cover. My model predicts large areas beyond the current distribution of *A. maculatum* to be environmentally suitable, suggesting the possibility of future northward and westward range expansion. These predictions of environmental suitability may be used to identify areas at potential risk for establishment and to guide future surveillance of *A. maculatum* in the United States.

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CHAPTER 1: INTRODUCTION

Emerging infectious diseases pose an imminent threat to the health and prosperity of communities around the world. More than 60% of emerging infectious diseases are zoonotic in origin, meaning they are transmitted to humans from wildlife (Jones et al. 2008). Among zoonotic diseases, those transmitted to humans via the bite of a blood-feeding arthropod (vector-borne zoonotic diseases) are emerging at a faster rate than directly transmitted human diseases despite making up a smaller fraction of total infectious diseases (Swei et al. 2020). Tick-borne diseases represent an especially significant threat to human health. Compared to other blood-feeding arthropods like mosquitoes and fleas, ticks transmit the widest variety of disease-causing microorganisms to humans (Sonenshine and Roe 2013). Included among these are the causative agents of Lyme disease (*Borrelia burgdorferi, B. mayonii*), Rocky Mountain spotted fever (*Rickettsia rickettsii*), and Crimean-Congo hemorrhagic fever (Crimean-Congo hemorrhagic fever virus).

In North America, the Gulf Coast tick (*Amblyomma maculatum*) has emerged as a species of considerable importance to human and animal health. *Amblyomma maculatum* is the primary vector of *Rickettsia parkeri* (Paddock et al. 2004), a pathogenic bacterium responsible for an emerging spotted fever group rickettsiosis whose clinical presentation in humans closely resembles that of Rocky Mountain spotted fever (Paddock et al. 2008). Infection with *R. parkeri* is likely to result in persistent fever and fatigue and may be increasing in prevalence in the United States (Paddock and Goddard 2015). *Amblyomma maculatum* is also a vector of *Hepatozoon americanum* (the causative agent of American canine hepatozoonosis), making it a species of significant veterinary importance (Mathew et al. 1998).

Amblyomma maculatum is native to the western hemisphere and is currently distributed throughout broad portions of the Americas. Historically, the distribution of *A. maculatum* in the United States has been described as restricted to the southeastern and south-central states, particularly those along the Gulf Coast (Hooker 1912). However, increasing reports over the last 50 years of *A. maculatum* from areas outside this range have highlighted the need for a reassessment of the distribution of this species in the United States (Teel et al. 2010). Recently, established populations of *A. maculatum* have been identified in Arizona (Allerdice et al. 2017), Illinois (Phillips et al. 2020), and Connecticut (Molaei et al. 2021), suggesting northward and westward range expansion. Range expansion of *A. maculatum* is of particular concern to public health due to the resulting increase in distributional overlap with the more common and widespread lone star tick (*A. americanum*). While *A. maculatum* currently serves as the primary vector of *R. parkeri*, spill-over into *A. americanum* individuals via co-feeding could amplify transmission of *R. parkeri* to humans (Wright et al. 2015). Range expansion of *A. maculatum* and *R. parkeri* may also result in increased misdiagnosis of different spotted fever group rickettsioses owing to a lack of taxonomic specificity in tests for human infection.

Range expansion of *A. maculatum* in North America is likely facilitated by long-distance dispersal of juvenile ticks by migratory birds as well as by inter-state transport of cattle (Teel et al. 2010, Florin et al. 2014, Paddock and Goddard 2015). Juvenile ticks typically parasitize ground-foraging birds and small mammals – often rodents – while adults are more commonly found on large mammals such as white-tailed deer, cattle, and swine (Teel et al. 2010). Given the diversity of common hosts used by *A. maculatum*, it is unlikely that its distribution in North America is limited by host availability (Sonenshine 2018). Conversely, availability of suitable habitat appears to be an important factor in predicting the presence of *A. maculatum* (Nadolny and Gaff 2018). In Virginia, Nadolny and Gaff (2018) found that open, xeric habitats dominated by grasses and shrubs were most strongly associated with the presence of established *A. maculatum* populations. In Texas and neighboring states, habitat associations include coastal upland and tallgrass prairies (Scifres et al. 1988, Teel et al. 2010). High rainfall, temperature, and humidity have also been cited as important environmental factors for supporting *A. maculatum* populations (Paddock and Goddard 2015). However, apart from these regional descriptions, a critical analysis of *A. maculatum* habitat associations is lacking.

As tick species distributions continue to expand or otherwise shift in response to anthropogenic climate and land-use change (Ogden 2006, Dergousoff et al. 2013, Swei et al. 2020), there is an increasing need to understand the biotic and abiotic associations underpinning current distributions. With the advent of modern remote sensing technologies and the increasing availability of species occurrence data, ecological niche modeling has emerged as a powerful tool for understanding the environmental drivers of species distributions. Ecological niche modeling refers to a statistical approach by which species occurrence records are compared against relevant environmental covariates to identify associations and make predictions about environmental suitability for the species being modeled (Merow et al. 2013). Here, I use the popular ecological niche modeling software, MaxEnt, to investigate habitat associations for *A. maculatum* and provide an assessment of its potential distribution in the United States.

CHAPTER 2: METHODS

2.1 Occurrence data

Occurrence data for *A. maculatum* were derived from three sources: (1) field collections, (2) scientific literature, and (3) the Global Biodiversity Information Facility (GBIF).

2.1.1 Field collections

Ticks were sampled from 53 sites in Illinois during the summer of 2020 using standard drag sampling techniques. Sites were selected for sampling based on previously documented habitat and host associations identified by Teel et al. (2010) and Nadolny and Gaff (2018), as well as previously recorded sites of *A. maculatum* occurrence from Phillips et al. (2020). In accordance with US Centers for Disease Control and Prevention standards for tick collections (Centers for Disease Control and Prevention 2020), a minimum of five 150-meter transects were drag-sampled at each site, and up to ten transects were drag-sampled at sites where *A. maculatum* was collected. In total, 350 total transects were sampled at the 53 sites. Drag cloths were checked at 10-meter intervals along each transect and any ticks present were immediately removed with forceps and placed in 85% ethanol for later identification using taxonomic keys (Keirans and Litwak 1989) and morphological descriptions (Mertins et al. 2010, Lado et al. 2018). Transect locations were selected to represent the heterogeneity of each site (i.e., edge/core habitat, upland/lowland features, etc.). GPS coordinates were obtained at the beginning of each transect and any transect that yielded *A. maculatum* was recorded as a presence (uncertainty = 150 m).

2.1.2 Literature search

A search of the Web of Science Core Collection using key words "*Amblyomma maculatum*" or "Gulf Coast tick" returned 405 results. Of these, 35 studies reported collection of *A. maculatum* from the environment (i.e., not attached to a host) and provided information on the sampling location. These collection records were georeferenced according to Chapman and Wieczorek (2020) and records with a final coordinate uncertainty of less than 1,000 meters were retained as presence records. A maximum uncertainty threshold of 1,000 meters was applied to all occurrence data to ensure that the uncertainty associated with occurrence data did not exceed the uncertainty associated with any environmental covariates used in model development.

2.1.3 Global Biodiversity Information Facility (GBIF)

Occurrence records and associated metadata for *A. maculatum* were downloaded from gbif.org on July 8, 2021. Using the CoordinateCleaner (v2.0-18; Zizka et al. 2019) package in R 4.0.5 (R Core Team 2020), records without numeric coordinates or coordinate uncertainty values were removed. To avoid including occurrence records of dubious origin, records meeting the following criteria were also removed: identical latitude and longitude; within 10,000 meters of country capitals; within 1,000 meters of country or province centroids; within 100 meters of zoos, botanical gardens, herbaria, universities, or museums; non-terrestrial; outside reported country or province; or having coordinate uncertainty greater than 1,000 meters. The remaining occurrences were retained as presence records.

2.2 Environmental data

2.2.1 Climate

Global historical climate data (1970-2000) in the form of WorldClim's 19 bioclimatic variables (Fick and Hijmans 2017) were downloaded from worldclim.org on July 8, 2021, at a resolution of 30 seconds. The variables BIO8, BIO9, BIO18, and BIO19 were excluded *a priori* from any analyses due to known spatial artifacts identified by Escobar et al. (2014).

2.2.2 Landscape

Data describing the biophysical landscape were obtained from the US Geological Survey's National Land Cover Database (Yang et al. 2018). Two distinct data layers from this database were used: (1) a categorical classification of land cover, and (2) a continuous measurement of percent tree canopy cover. Both data layers were downloaded at a resolution of

30 meters by 30 meters. To accommodate the constraints of the chosen modeling technique, the layers were resampled to a coarser resolution of 30 seconds to match the climate data. The categorical land cover data layer was resampled according to the most frequent value within each grid cell, while the percent tree canopy cover data layer was resampled according to the mean value within each grid cell. Using the proximity algorithm in QGIS 3.16.7 (QGIS Development Team 2021), the minimum distance from each grid cell to each land cover class was calculated, resulting in a continuous measurement of distance to each of 10 land cover classes. Elevation data were also downloaded from worldclim.org at a resolution of 30 seconds (Fick and Hijmans 2017). Elevation and land cover data were included to represent habitat features of potential importance to *A. maculatum* and other tick species and have been included in several similar analyses of environmental suitability for ticks (Soucy et al. 2018, Pascoe et al. 2019).

2.3 Model development

2.3.1 Spatial bias

To reduce spatial autocorrelation and remove dubious presence records, occurrence points were first manually filtered in QGIS to remove points located at residential or commercial properties and on roads, highways, or parking lots. The remaining occurrence points were spatially rarefied using the spThin (v0.2.0; Aiello-Lammens et al. 2015) package in R – occurrence points within 10,000 meters of another occurrence point were removed in random order. A 500 km circular buffer was constructed in R around the final set of occurrence points to define the geographic extent to be used for model calibration and to serve as a conservative estimate of accessible dispersal area for *A. maculatum*. Finally, a bias file representing the spatial clustering of occurrence points was created using the Two-Dimensional Kernel Density Estimation (kde2d) function in the MASS (v7.3-54; Venables and Ripley 2002) package in R. The bias file instructs MaxEnt to select background points according to the spatial clustering of occurrence points, thus aligning and thereby ‘canceling out’ their spatial biases (Merow et al. 2013).

2.3.2 Model evaluation

To determine which combination of environmental covariates was most appropriate for predicting environmental suitability for *A. maculatum*, an initial evaluation was performed using the ENMeval (v2.0.1; Kass et al. 2021) package in R. This evaluation compared measures of model performance for 98 unique combinations of feature class and regularization multiplier values using all environmental covariates under consideration (15 bioclimatic variables, distance to 10 land cover classes, percent tree canopy cover, and elevation). From the results of this evaluation, the model with the lowest corrected Akaike Information Criterion (AICc) value was selected (Warren and Seifert 2011). The selected model – using linear, quadratic, and threshold feature classes and a regularization multiplier value of 3 – was subsequently run in MaxEnt 3.4.1 (Phillips et al. 2019) to explore relationships between environmental covariates and to assess their relative contributions to model performance.

Multicollinearity of the environmental covariates was assessed by calculating Pearson's correlation coefficient (r) using the raster (v3.4-10; Hijmans and van Etten 2015) package in R. Covariates with $r \geq 0.7$ were removed from consideration with respect to their permutation importance as calculated by MaxEnt's jackknife analysis such that high-contributing variables were retained and lower-contributing, collinear variables were removed. Subsequently, any covariates that resulted in negative test gain in isolation or that caused an increase in average test gain when excluded were removed. Using the remaining environmental covariates, the same 98 models were again evaluated using the ENMeval package in R and the model with the lowest AICc value was again selected. The results of the evaluation were constrained to only include models with average test AUC ≥ 0.7, average AUC standard deviation < 0.05, and average test omission rate < 0.10 (Warren and Seifert 2011, Radosavljevic and Anderson 2014). The selected model – using linear, quadratic, and hinge feature classes and a regularization multiplier value of 4 – was subsequently run in MaxEnt using the crossvalidate run type with 10 replicates. Using the results of MaxEnt's multivariate environmental similarity surface (MESS) analysis as a guide, model outputs were spatially restricted to exclude areas that were highly dissimilar with respect to the values of environmental covariates between the training sample and the prediction region (Elith et al. 2010). Areas with this degree of environmental dissimilarity have little predictive value and thus should not be included in any interpretation of environmental suitability.

CHAPTER 3: RESULTS

3.1 Occurrence data

During field collection of ticks in Illinois, 42 out of 350 transects (16 out of 53 sites sampled) yielded at least one *A. maculatum* individual and were recorded as presences to be used for modeling. The literature search resulted in 35 publications containing relevant geographic information about *A. maculatum* collected from the environment. Georeferencing produced 62 occurrence records to be used for modeling. GBIF provided a list of 625 georeferenced records of *A. maculatum*; 125 were retained to be used for modeling following the filtering methods described above. The combined 229 occurrence records were then spatially rarefied to reduce sampling bias and to remove dubious records according to the methods described above. In total, 144 occurrence records were used in model development (Fig. 1).

3.2 Model development

The preliminary MaxEnt model including all environmental covariates under consideration (15 bioclimatic variables, distance to 10 land cover classes, percent tree canopy cover, and elevation) yielded a ranked list of permutation importance for each environmental covariate. Permutation importance provides an estimate of each covariate's individual contribution to the overall predictive performance of the model by measuring the change in AUC when each covariate is, in turn, randomly permuted (Phillips 2017). Using the ranked list of permutation importance as a guide, highly collinear ($r \geq 0.7$) covariates were sequentially removed such that highly ranked covariates were retained. Covariates resulting in negative test gain in isolation or an increase in average test gain when excluded were removed. In total, 6 environmental covariates were retained (Table 1). Using the final set of 6 covariates to evaluate model performance as described above, the model with the lowest AICc value used linear, quadratic, and hinge feature classes and a regularization multiplier value of 4 and was subsequently run in MaxEnt using the crossvalidate run type with 10 replicates.

3.3 Final model results

The final MaxEnt model had an average test AUC of 0.8235, average AUC standard deviation of 0.0436, average test gain of 0.7234, and average 10 percentile training omission rate of 0.0932. The covariates with the highest permutation importance were minimum temperature of the coldest month (32.7), mean diurnal temperature range (31.8), and precipitation seasonality (25.3), with percent tree canopy cover, distance to cultivated crops, and distance to grassland making up the remaining permutation importance (10.2; Table 1).

Areas with suitable environmental conditions for *A. maculatum* were predicted throughout the United States, but the pattern was spatially heterogeneous. Here, environmental suitability is interpreted as the goodness of fit of the model predictions with respect to the training sample. Higher suitability was predicted in coastal regions while the arid, high-elevation regions of the intermountain west were largely predicted to be environmentally unsuitable (Fig. 2a). Minimum temperature of the coldest month was positively associated with predicted environmental suitability for *A. maculatum* (Fig. 3a), while mean diurnal temperature range (calculated as the average difference between monthly maximum and minimum temperatures) was negatively associated with predicted environmental suitability (Fig. 3b). Precipitation seasonality above 50% was associated with an increase in predicted environmental suitability, while no relationship was observed below 50% (Fig. 3c). Environmental suitability was generally predicted to decrease with increasing percent tree canopy cover (Fig. 3d), as well as with increasing distance to cultivated crops (Fig. 3e) and to grassland/herbaceous land cover (Fig. 3f).

CHAPTER 4: DISCUSSION

The ongoing reports of new occurrence records of the medically important Gulf Coast tick indicate a non-static geographic distribution in the United States and highlight the value of environmental niche modeling approaches for predicting the possible future distribution of this species. This study combined occurrence records from three distinct sources with high-resolution climate and land cover data to explore the environmental drivers of the current distribution of *A. maculatum* in the United States. Of the broad spectrum of environmental covariates initially considered, six were selected to be used in modeling environmental suitability for *A. maculatum*. Based on their permutation importance and individual contributions to model test gain, the climate variables included in this modeling exercise proved to be more important in explaining the current distribution of *A. maculatum* compared to the landscape factors considered. While habitat features are still important to understanding the current and potential future distribution of this species, this result highlights the instrumental role of climate in determining the distribution of *A. maculatum* in the United States.

The important role of climate in explaining the distribution of *A. maculatum* is not surprising considering known environmental constraints of ticks. Ticks spend a significant portion of their lives detached from their hosts and are thus geographically constrained in large part by the abiotic conditions of their local environment. Important among these abiotic factors are temperature and relative humidity (Sonenshine and Roe 2013). Of the many environmental covariates considered in this study, three climate variables were retained to model environmental suitability for *A. maculatum*: (1) minimum temperature of the coldest month (Fig. 2b), (2) mean diurnal temperature range (Fig. 2c), and (3) precipitation seasonality (Fig. 2d). Minimum temperature of the coldest month showed a positive association with predicted environmental suitability for *A. maculatum*, indicating that warmer temperature minima contributed to greater environmental suitability. High predicted suitability (> 0.8) was associated with minimum temperatures above 5°C (Fig. 3a). Conversely, mean diurnal temperature range showed a negative association with predicted environmental suitability for *A. maculatum*, indicating that predicted environmental suitability decreased with increasingly broad daytime temperature ranges (Fig. 3b). Here, mean diurnal temperature range is calculated as the average difference between monthly maximum and minimum temperatures. Finally, precipitation seasonality showed a positive association with predicted environmental suitability for *A. maculatum* (> 50%; Fig. 3c) indicating that greater variation in precipitation throughout the year, beyond a threshold of approximately 50% seasonality, contributed to greater environmental suitability.

In addition to the three climate variables used to model environmental suitability for *A. maculatum*, three variables describing the biophysical landscape were retained: (1) percent tree canopy cover, (2) distance to cultivated crops, and (3) distance to grassland/herbaceous land cover. Percent tree canopy cover was negatively associated with predicted environmental suitability for *A. maculatum*, suggesting a preference for open habitat with relatively little canopy closure. Environmental suitability was maximized (~0.7) at approximately 15% canopy cover and gradually declined as percent canopy cover increased (Fig. 3d). Distance to cultivated crops (Fig. 3e) and distance to grassland/herbaceous land cover (Fig. 3f) also showed a negative association with predicted habitat suitability for *A. maculatum*. Suitability was maximized (~0.7) within 1 km and declined steadily with increasing distance, suggesting that areas near cultivated crops and grasslands were most favorable. These variables are likely linked in that agricultural fields and grassland ecosystems tend to have a low degree of canopy cover. Despite their relatively low contribution to model predictive performance compared to the climate variables, the three landscape variables provide valuable insight into the habitat associations of *A. maculatum*. Here, open habitat with minimal tree canopy cover was shown to be favorable, which is supported by observations of *A. maculatum* from field surveys (Scifres et al. 1988, Teel et al. 2010, Nadolny and Gaff 2018).

Based on the results of the model built with the six environmental covariates described above, predicted environmental suitability for *A. maculatum* was spatially heterogeneous (Fig. 2a). Coastal regions were predicted to be highly environmentally suitable, while the inter-mountain region further inland was predicted to be very unsuitable. High environmental suitability was predicted for many areas outside the current distribution of *A. maculatum* in the United States, suggesting that range expansion for this species could continue provided that biotic conditions are favorable (e.g., effective dispersal, suitable host communities). In the eastern United States, highly suitable areas appeared to be restricted to the coast at higher latitudes. For example, parts of coastal New England (Maine, Massachusetts, Rhode Island, and Connecticut) were predicted to have high environmental suitability, while further inland areas were predicted to be unsuitable. The same pattern can be observed in Wisconsin, with coastal suitability along Lake Michigan predicted to be much higher than areas further inland. This pattern may be due, in part, to the temperature-buffering effects of large bodies of water on adjacent coastal lands. In these regions, temperature minima tended to be higher (Fig. 2b) and average temperature range tended to be lower (Fig. 2c). Large swaths of western Washington, Oregon, and California were predicted to be highly environmentally suitable for *A. maculatum*. While the western United States is geographically disconnected from *A. maculatum*'s core distribution in the eastern United States, the recent detection of numerous high-density populations in Arizona, New Mexico, and western Texas suggests that dispersal to other parts of the western United States is possible (Hecht et al. 2020, Paddock et al. 2020).

The taxonomic relationships between *A. maculatum* and closely related taxa have been contested since their initial description by Koch in 1844 (Koch 1844, 1847, Kohls 1956). In North America, the taxonomic relationship between *A. maculatum* and *A. triste* is especially contentious, and misidentifications are common owing to subtle and often unreliable morphological distinctions (Estrada-Peña et al. 2005). *Amblyomma triste* has been reported in the United States (Mertins et al. 2010), however, the most recent molecular phylogenetic analysis supports the conspecificity of *A. triste* and *A. maculatum* (Lado et al. 2018). Following the detection of *A. maculatum* populations in Arizona, morphological ambiguities among the collected specimens called their taxonomic identity into question (Allerdice et al. 2017, Hecht et al. 2020). Recent work has indicated some degree of reproductive incompatibility between *A. maculatum* specimens collected in Arizona and those collected in the eastern United States, indicating that some individuals collected from southwestern populations may constitute a distinct species, but further investigation is required to confirm their taxonomic status (Allerdice et al. 2020). A recent analysis by Cuervo et al. showed that the southwestern morphotype exhibits significant niche divergence from *A. maculatum* populations in the eastern United States, suggesting local adaptation to novel environmental conditions (Cuervo et al. 2021).

Alkishe et al. (2021) used a similar approach to model environmental suitability for *A. maculatum* in the United States as part of a broader study of tick distributional shifts under future climate change scenarios. Occurrence records were compiled from a variety of sources including GBIF, VectorMap, BISON, and published literature. Climate variables using average data from WorldClim were used to model current climate conditions and multiple general circulation models (GCMs) were used to model future climate conditions. The results of their analysis indicated that much of the southeastern United States was predicted to be environmentally suitable for *A. maculatum* under current climate conditions. Under future climate conditions, suitable area was predicted to extend northward to include much of the midwestern and north Atlantic regions. Even under future climate conditions, predicted suitability waned in the higher latitudes of New England with suitable areas confined to the coast. Areas of environmental suitability under current climate conditions were also predicted in the western Unites States throughout Washington, Oregon, and California. Sections of southeastern Arizona were also predicted to be environmentally suitable, corresponding to the recently discovered populations mentioned above. In general, the results from Alkishe et al. align with those of the study presented here. In the eastern United States, my results predicted areas of environmental suitability occurring further north than predicted by Alkishe et al. based on current climate conditions. This is likely due, in part, to my inclusion of a large number of occurrence records from southern Illinois which had not yet been collected at the time of Alkishe et al.'s analysis. These occurrence records corresponded to climate conditions that were underrepresented in the rest of the occurrence set and thus likely contributed to a northward shift in predicted environmental suitability under current climate conditions. Additionally, my results predicted a larger area of environmental suitability in the southwestern United States compared to Alkishe et al. This could similarly be due to my inclusion of a large number of occurrence records from recently published literature describing *A. maculatum* populations in Arizona, New Mexico, and Texas (Hecht et al. 2020, Paddock et al. 2020) that may not have been available to Alkishe et al. at the time of their analysis.

Pascoe et al. (2019) modeled potential habitat for *A. maculatum* and other *Amblyomma* spp. ticks in California using a combination of climate and landscape variables. Occurrence data were sourced from relevant literature and online databases including GBIF, VectorMap, and BISON. Climate data consisted of WorldClim's 19 bioclimatic variables, and landscape variables included elevation, slope, and average and standard deviation of normalized difference vegetation indices (NDVI). In their final model of environmental suitability for *A. maculatum*, Pascoe et al. included the following four environmental covariates: (1) minimum temperature of the coldest month, (2) precipitation of the wettest month, (3) elevation, and (4) NDVI average. Minimum temperature of the coldest month was associated with an increase in environmental suitability (peaking at ~0.75) from -10 to 7 °C, followed by a subsequent decrease in suitability above 7°C. Average NDVI (which is likely linked to percent tree canopy cover) was associated with a general decrease in environmental suitability for *A. maculatum*. Based on the results of their analysis, much of western California was predicted to be environmentally suitable for *A. maculatum*, which is largely in agreement with my findings. Significant portions of coastal California were excluded from my model predictions due to a high degree of environmental dissimilarity compared to the training sample as revealed by the results of MaxEnt's MESS analysis. It is likely that Pascoe et al. did not observe this degree of dissimilarity as a result of using a different set of environmental covariates in their final model.

A major limitation of this approach to modeling tick distributions is the lack of information regarding biotic interactions, most notably, interactions with host communities. While understanding the range of abiotic conditions tolerated by a species is certainly informative, host availability can significantly impact population density and dispersal capabilities of ticks. Furthermore, as many tick-borne pathogens are host-acquired, information on host communities is essential for linking ecology and epidemiology. Another limitation of this approach is related to the way in which occurrence data are often collected. In this study and many others, the observation of a single tick, either from the environment or collected from a host, is interpreted as a presence record despite the possibility that it is not representative of a reproducing population. In this way, an observation of an adventive tick from far outside its established range is treated the same as a tick collected from within a reproducing population. For some more widely researched species, it may well be possible to model environmental suitability using only occurrence records collected from reproducing populations. Such an approach was not employed here due to the resultant reduction in sample size and increase in sampling bias. Nonetheless, every effort was made to ensure that the majority of occurrence records used in the present study were representative of potentially reproducing populations and that sampling bias was reduced to the greatest extent possible.

Based on the results of this and other recent studies of environmental suitability for *A. maculatum*, some broad inferences can be made regarding the status of *A. maculatum* in the United States. In the eastern United States, *A. maculatum* is predicted to occur at higher latitudes than formerly noted. Recent field collections of *A. maculatum* from this region in this study and others (Florin et al. 2013, 2014, Phillips et al. 2020) lend support to this prediction. Large swaths of the western United States are also predicted to be environmentally suitable for *A. maculatum,* namely in Washington, Oregon, California, and Arizona. These predictions are largely based on recent reports of established populations in Arizona, New Mexico, and western Texas (Hecht et al. 2020, Paddock et al. 2020). Regardless of their current taxonomic ambiguity, rates of *R. parkeri* infection among ticks from these populations create concern regarding consequences for human health resulting from range expansion throughout potentially suitable areas of the western United States (Allerdice et al. 2017). Further studies of *A. maculatum* in North America should seek to incorporate information on host identity and availability throughout the species' potential range. Some work has been done to date investigating *A. maculatum* host associations in a variety of settings (Semtner and Hair 1973, Moraru et al. 2012, Nadolny and Gaff 2018, Cumbie et al. 2020), but such information has yet to be considered in estimates of current and potential future distribution. As tick species distributions continue to change, effective surveillance remains an essential component in preventing and preparing for increases in tick-borne disease incidence at local scales. With increasing awareness of *A. maculatum* as a species of considerable significance to public health, the habitat associations and distributional predictions provided in this study can help guide continued surveillance of this species in the United States.

TABLE AND FIGURES

Table 1. Environmental covariates used in final model iteration listed in order of average permutation importance across 10 replicate models as calculated by MaxEnt's jackknife analysis.

Environmental Covariate	**Average Permutation Importance**
Minimum temperature of coldest month	32.7226
Mean diurnal temperature range (mean of monthly (maximum temperature – minimum temperature))	31.7504
Precipitation seasonality (coefficient of variation)	25.2627
Percent tree canopy cover	5.9673
Distance to cultivated crops	3.9097
Distance to grassland/herbaceous land cover	1.0709

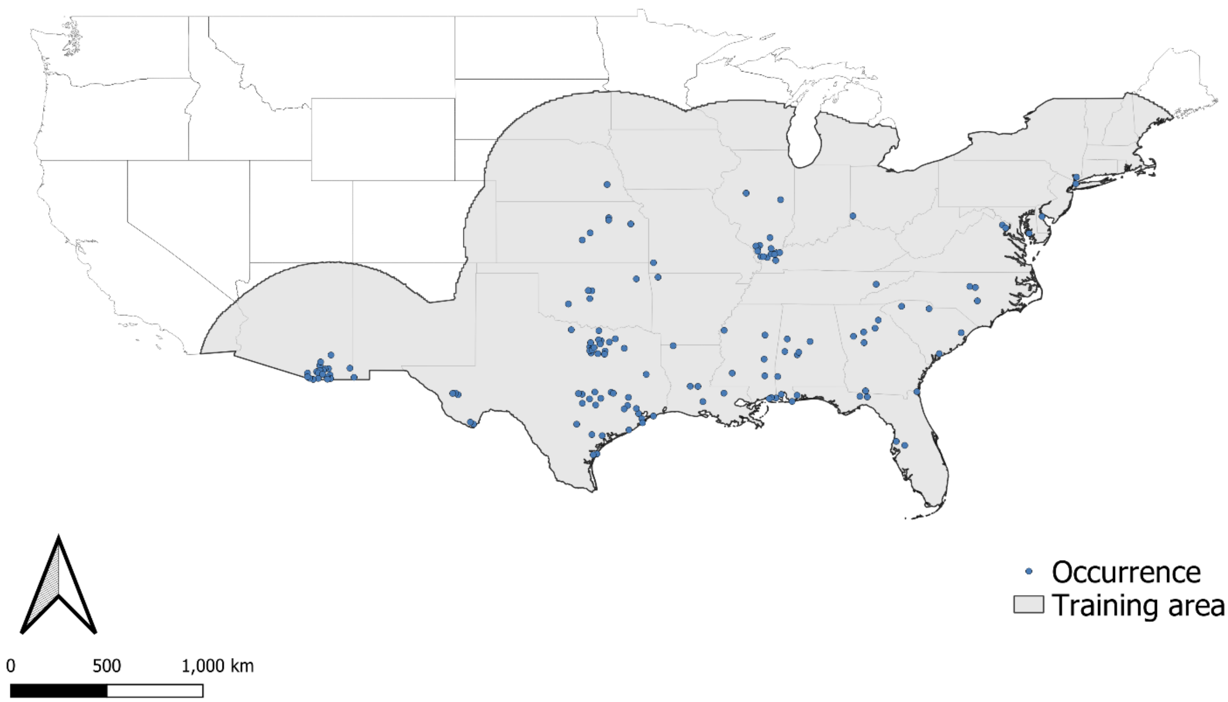

Figure 1. *Amblyomma maculatum* occurrence records (post-filtering) in the continental United States taken from field collections, published scientific literature, and GBIF. Occurrence records were manually filtered to remove dubious records and were spatially rarified to a minimum distance of 10,000 meters to reduce sampling bias. The shaded region was constructed by applying a 500-kilometer circular buffer around occurrence points and represents the spatial extent used for model training.

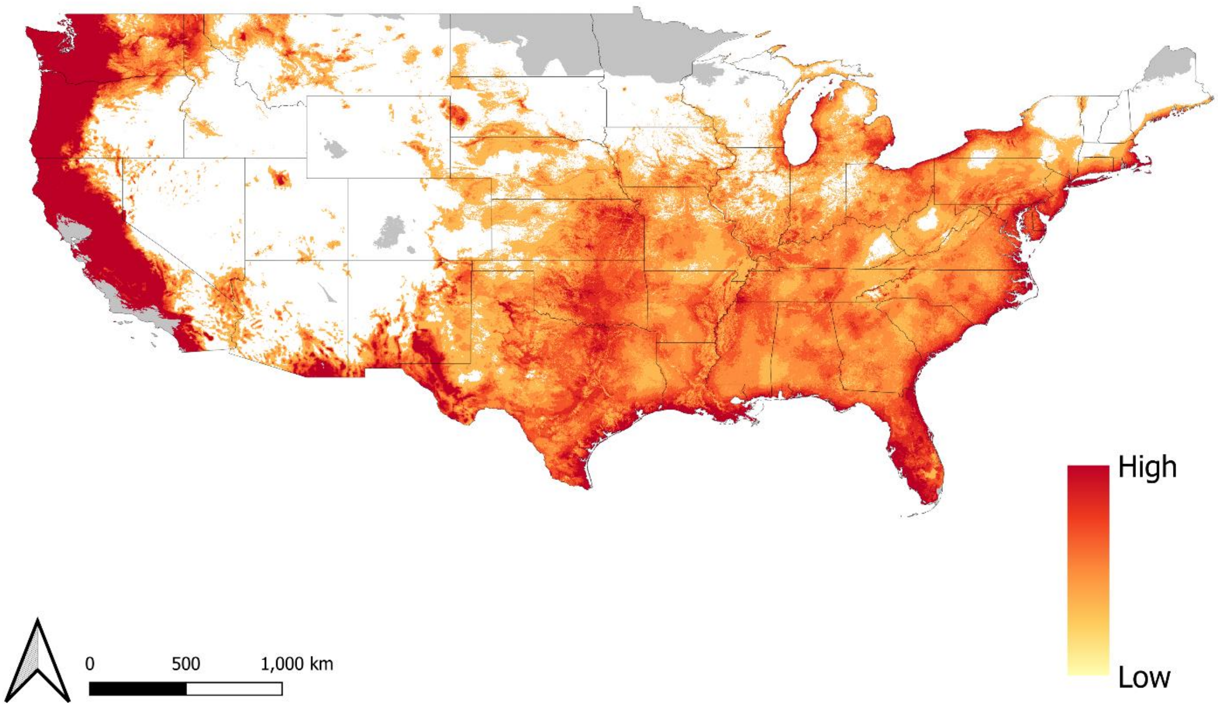

Figure 2a. Predicted environmental suitability for *A. maculatum* based on the median output of the final model iteration produced in MaxEnt. Red shades indicate higher predicted environmental suitability, while lighter orange shades indicate lower predicted environmental suitability. White areas indicate still lower predicted environmental suitability, below a threshold of 0.17. Grayed-out areas exhibited highly dissimilar environmental conditions compared to the training sample according to MaxEnt's MESS analysis and should be interpreted as having unknown environmental suitability for *A. maculatum*.

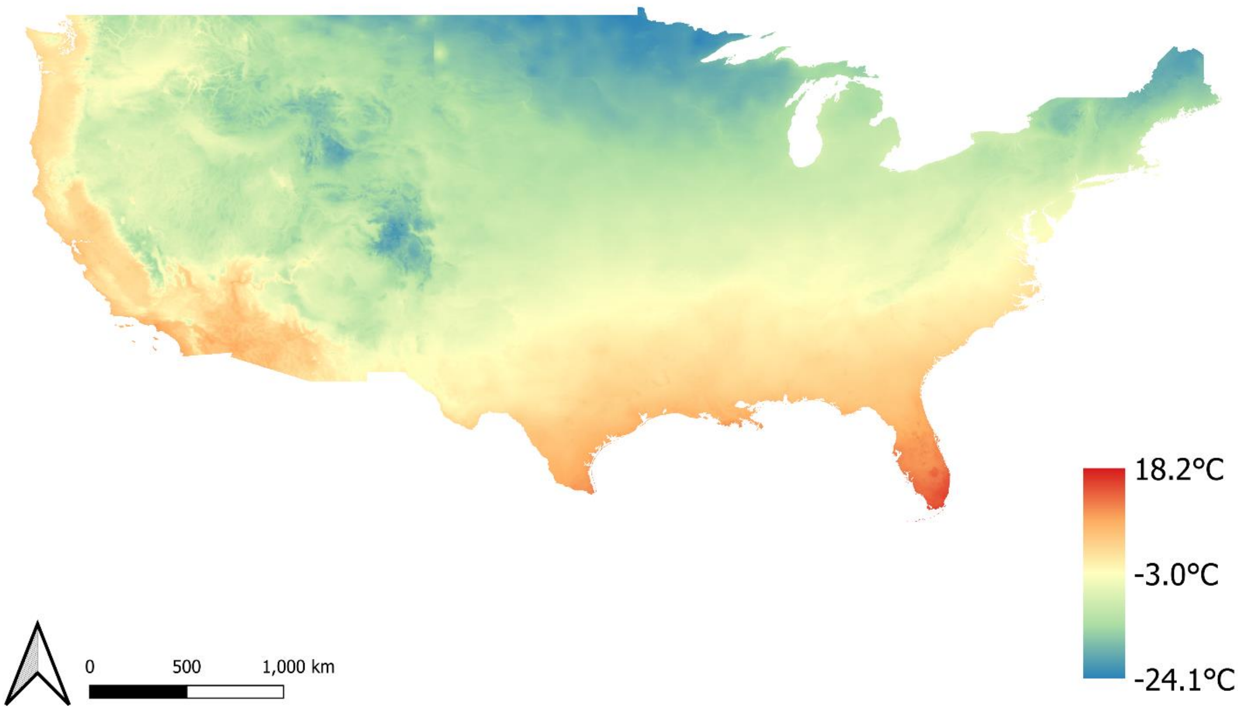

Figure 2b. Minimum temperature of the coldest month in the United States based on global historical climate data (1970-2000) from WorldClim. Warm colors correspond to higher temperature minima, while cold colors correspond to lower temperature minima.

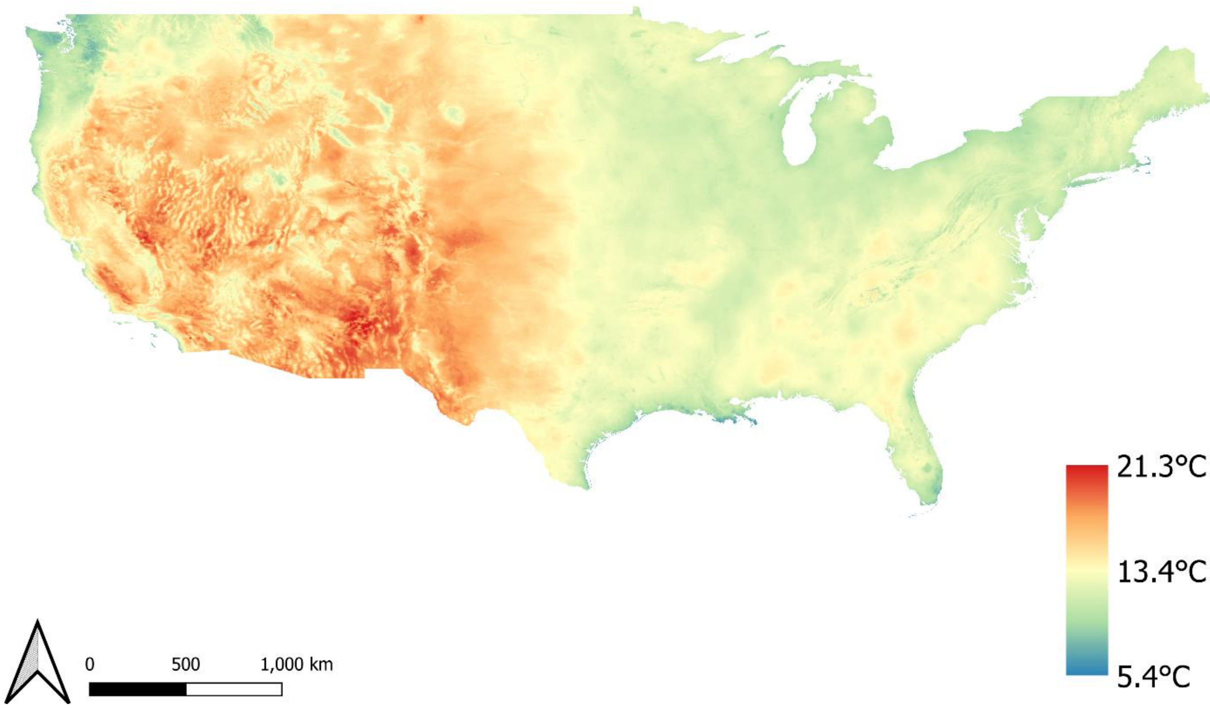

Figure 2c. Mean diurnal temperature range in the United States based on global historical climate data (1970-2000) from WorldClim. Mean diurnal temperature range is calculated as the average difference between monthly maximum and minimum temperatures. Warm colors correspond to areas with a larger average temperature range, while cold colors correspond to areas with a smaller average temperature range.

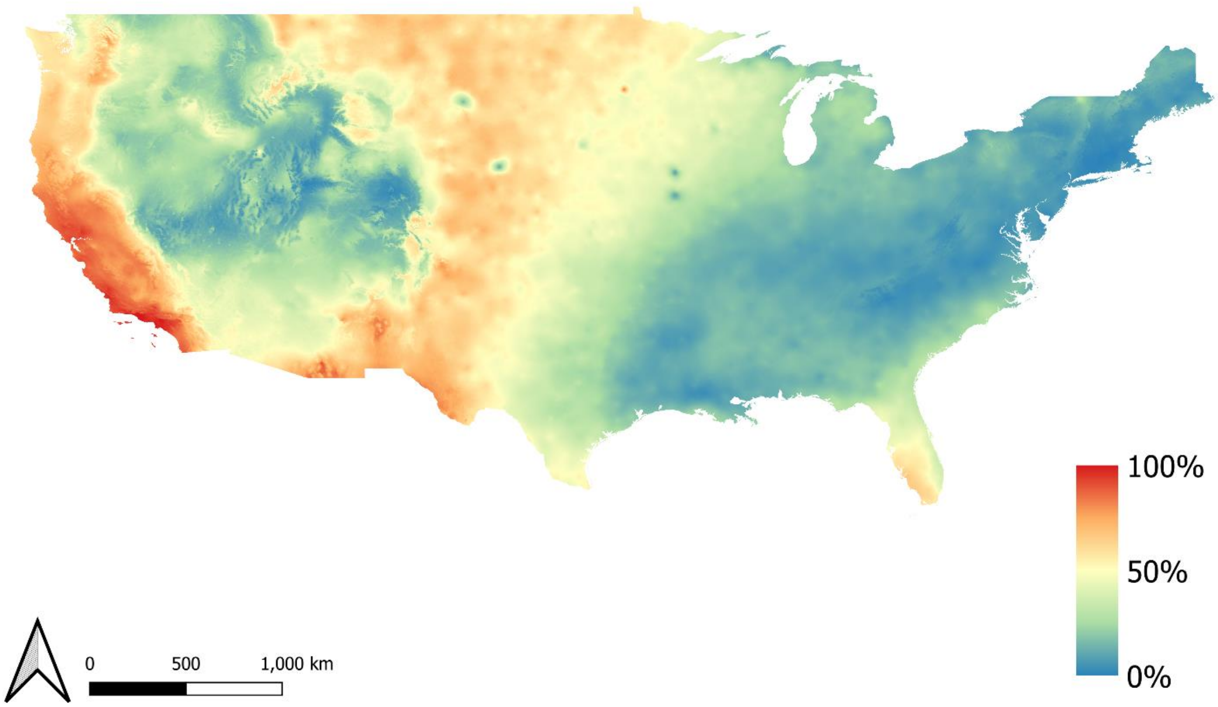

Figure 2d. Precipitation seasonality in the United States based on global historical climate data (1970-2000) from WorldClim. Warm colors correspond to areas with highly seasonal precipitation, indicating greater variation in precipitation throughout the year. Cold colors correspond to areas with lower precipitation seasonality, indicating less variation in precipitation throughout the year.

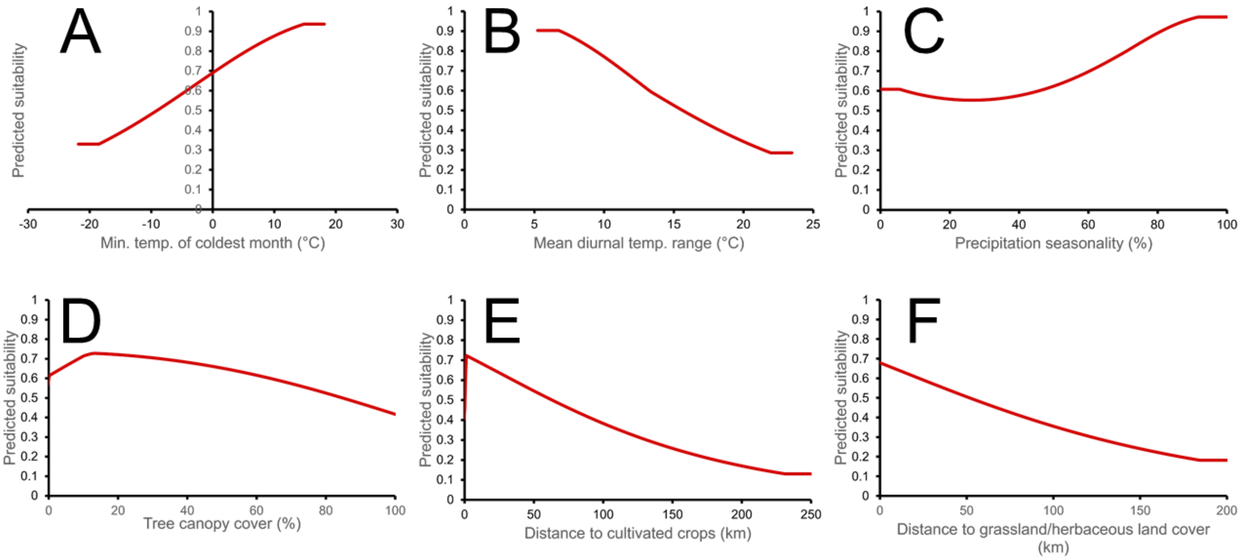

Figure 3. Response curves showing the relationship between predicted environmental suitability for *A. maculatum* and the six environmental covariates used in the final model iteration when all other variables were held constant. (A) Minimum temperature of the coldest month, (B) mean diurnal temperature range (mean of monthly (maximum temperature – minimum temperature)), (C) precipitation seasonality (coefficient of variation), (D) percent tree canopy cover, (E) distance to cultivated crops, and (F) distance to grassland/herbaceous land cover.

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