

CLIMATE CHANGE AND DISEASE-VECTORS: THE RANGE EXPANSION OF *A.*
AMERICANUM

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Abstract:

Climate change has been observed to be affecting the patterns of infectious diseases around the world (Tokarevich et al, 2011; Scharlemann et al. 2008). One of the primary climate-associated mechanisms of change for disease vectors is the expansion or contraction of their geographical ranges. The goal of this thesis was to investigate the relationship between climate change and the distribution of insect vectors by modeling the distribution of the Lone Star tick (*Amblyomma americanum*). The Lone Star tick is endemic to the eastern United States and has been expanding its range from the southeastern United States to more northern latitudes (Cooley and Kohls, 1944; Good, 1972, Mixson et al, 2006). The tick transmits several pathogens that can cause diseases in humans including human monocytotropic ehrlichiosis, and is a public health concern. The methods for this research were to take the current distribution of the tick (based on distribution information compiled from published scientific literature, Veterinary Services laboratories of the USDA, and the US National tick collection), and build a statistical niche model with 18 climate datasets using Maximum Entropy (MaxEnt) statistical software. The climate data were obtained from WorldClim database, who acquired their data from Global Historical Climatology Network, the FAO, the WMO, the International Center for Tropical Agriculture (CIAT). Once the tick's current niche model (based on climate) had been constructed it was projected into the future using eight different future climate scenarios. The results and future distribution maps suggest a high probability for range expansion of the tick to higher latitudes

and to western United States. In addition, the models with the most extreme warming scenarios predicted relatively lower probability for range expansion of the tick in comparison to models that had more moderate global warming scenarios. The climate variables that were most significant in determining the niche of the tick were extreme temperature and precipitation parameters, possibly showing that tick distribution is limited by temperature and precipitation maximum and minimums.

Introduction

Climate change has been observed to be affecting the distribution of infectious agents globally (Tokarevich et al, 2011; Scharlemann et al. 2008; Gilbert, 2009; Cumming and Vuuren, 2006; Ogden et al 2006). The climate-disease relationship is hard to define, yet critical to understand in order to mitigate the effects disease expansion may have on human health. There has been an increasing amount of research studying the relationship between projected changes in climatic conditions (e.g., mean temperature, variance in annual precipitation) and the responses of pathogens and the organisms that transmit them. Vector-borne diseases are caused by pathogens transmitted to humans by organisms such as mosquitoes, ticks, and fleas—usually defined as a “blood-sucking arthropod” (CDC, 2011). These diseases are important to study in relation to climate change because their transmission is controlled by organisms that are sensitive to climate, and thus their range and distributions could be altered by climate change. The goal of this thesis was to determine how climate change may potentially affect the range of

disease vectors by considering a particular tick species and how its niche might change in response to changes in climate.

The methods for this research project involved statistically analyzing historical climatic patterns in relation to the historical distribution of the Lone Star tick, *Amblyomma americanum*. The goal was to create a model of the relationship between current distribution and climatic factors that could be used to predict future range changes based on projected climate trends. This would provide insights into ways that vector-borne diseases might respond to climate change. Before investigating the specific relationship between range of the Lone Star tick and climate, general effects of climate change on pathogens and their insect vectors were reviewed and are summarized below.

There are several general classes of proposed effects that climate change could have on vectors, which will have cascading effects on the pathogens they transmit and the epidemiology of associated diseases. One general effect of climate change on disease vectors involves physiological changes of the organisms themselves. Increased temperatures and climate change could cause an increase in reproductive rates, an increase in metabolism, and changes in immune system responses of disease vectors, affecting the risk for human infection by disease-vector organisms. A study of 38 insect species across a range of latitudes investigated the fitness consequences of climate warming. The results suggested that warming temperatures will increase the fitness of species at higher latitudes (Deutsch et al, 2008). High latitude-species are currently living at environmental temperatures cooler than optimal such that temperature increase may enhance

fitness (Deutsch et al, 2008; Kingslover, 2011). Enhanced fitness of disease vectors (which tend to be insects) could cause an increase in abundance, reproductive output, and longevity and thereby affect disease transmission. In addition, climate change will likely cause more extreme weather patterns and therefore increase environmental stressors to organisms (Harvell et al, 2002). Environmental stressors can affect hormone regulation, reproduction, and immune system function (Demas and Nelson, 2011). These physiological changes may affect interactions of disease-carrying organisms with human populations, and thus associated physiological changes of disease vectors are relevant for assessing potential health risks. The insect stress response involves an increase of octopamine and adipokinetic hormones (“flight or fight behavior”), and can result in a decline in disease resistance (Adamo and Parsons, 2006). Because of this, environmental stressors may cause a decline in immune function and an increase of infection rate in insect populations with cascading effects for humans. Understanding potential physiological changes in pathogenic species may help predict potential risk factors for disease spreading to human populations. The effects of changes in climate on the physiology of insects is likely to be complex and could have a variety of outcomes that both promote or suppress pathogen transmission.

Another potential effect of climate change on host/pathogen interactions is the changing of phenologies. Phenology is the timing of life cycle events and it is influenced by seasonal and inter-annual variations in climate. The interaction between climate and phenology varies among organisms and will affect the overall interaction of pathogens and hosts. For example, a meta-analysis of 203 different

species predicted that with increasing temperatures, amphibians will shift toward earlier breeding, and butterflies are expected to migrate three times earlier than the first flowering plants (Both & Visser, 2001). Changes in the phenology of insect vectors could influence their exposure to pathogens and humans. In general, the average timing of Organismal phenological schedules in the Northern Hemisphere is expected to advance 2.8 days per decade (Both & Visser, 2001; Memmott et al., 2007). These two examples show that interactions between organisms could be altered by their changing life cycle—which could have a huge effect on host-pathogen interactions and infection rates for vectors. Shifts in the seasonal timing of breeding and feeding of disease vectors could alter the probability of exposure to pathogens and the likelihood of transmission of pathogenic agents to humans. For example, studies show that increased temperature changes the timing of questing in ticks and can prolong tick development (Suss and Klaus, 2008). In addition, reproductive schedules of disease vectors could be altered by climate change. Many organisms time their reproductive schedules based on energy limitations and seasonal controls through hormone regulation. Reproductive schedule refers to the time of year or lifetime organisms reproduce, as well as how often. The reproductive schedule of many organisms is strongly influenced by diurnal variation in temperature (Ashley and Wingfield 2005). It has been found that in insects, immune activity and reproduction are often inversely related (Seva-Jothy et al, 2005). Climate change could thus cause an increase in reproduction and a decrease in immune function in insect vectors.

Life history characteristics also play important roles in the response of organisms to climate change. Although this is not a “response” to climate change, it is still important to take into consideration when mapping disease vector changes with climate change because it effects the interactions between organisms, and thus the transmission of disease. Many vector species (e.g., mosquitoes) have relatively “fast” life histories: they tend to be associated with higher metabolic rates, quicker development times, faster breeding rates, and shorter life spans (O’Neal and Ketterson, 2005). These attributes may afford vector species a high capacity to respond to changing environmental conditions, and some of these traits may have consequences for host/pathogen interactions and pathogen transmission. Fast-paced species with short life spans tend to allocate resources to current reproduction over future survival because they have less opportunity for future breeding (O’Neal and Ketterson, 2005). Environmental and immunological stressors may cause more earlier death in reproduction for fast-paced species (Walther et al. 2002). Organisms with low adaptability and dispersal capacities are more likely to become endangered or extinct (Walther et al. 2002). Smaller organisms (e.g., R-generalists and insects) that have fast life histories could adapt more quickly, whereas specialist species with longer lifespans (K-specialists) may not adapt as rapidly.. Because of this, disease vectors may potentially adapt more rapidly to climate change and thus become relatively more abundant, increasing disease risk.

Another potential effect of climate change on the transmission of vector-borne disease could come through climate-mediated changes in insect behavior. As

an example, it has been found that mosquitoes capable of transmitting malaria feed more frequently in warmer climates, apparently due to higher metabolic rates under those conditions, and this could increase rates of disease transmission to humans (Githeko et al, 2000). Similarly, because tick questing behavior is usually observed at temperatures above 7°C (Suss, 2008) a rise in global temperature could broaden the temporal window during which this host-seeking behavior is expressed. -The rate and host preference of biting insects could also be sensitive to climate-related phenomena (Githeko et al 2000). It has also been found that temperature affects the reproductive rate of pathogens in mosquitoes, which in turn, affects the rate at which salivary secretions are infected (Reiter, 2011). Understanding potential behavioral responses of organisms to environmental changes will also help add to the greater picture of mapping disease vectors with climate change.

Perhaps one of the most frequently considered responses of disease vectors to climate change involves shifts in the geographic distribution of vector species, particularly via range expansions. Many studies have shown an increase in the range of pathogen-carrying species correlated with increasing average global temperatures (Tokarevich et al, 2011; Scharlemann et al. 2008; Gilbert, 2009; Cumming and Vuuren, 2006; Ogden et al 2006). Expanding ranges of mosquito-borne pathogen like malaria have been associated with rising annual temperatures, and many other species are expected to respond to the shifting climate by extending their distributions into higher latitudes (Walther, 2002). It is estimated that by 2100, average global temperatures will have risen by 1-3.5°C, and it has been shown

that the effect of climate change on pathogen transmission is likely to be observed at the extremes of the possible temperature range that pathogens can be transmitted (Githeko et al, 2000). When considering range expansions of organisms, temperature changes, precipitation, and seasonality factors all have to be considered. Global warming is not a linear trend throughout the world, and some areas are experiencing greater warming, and more or less precipitation, than others. Below is a summary table of observed climatic changes throughout the globe, that is relevant to disease transmission (Githeko et al, 2000):

Africa	Vector-borne diseases: Malaria, schistosomiasis, onchocerciasis, trypanosomiasis, filariasis, leishmaniasis, plague, Rift Valley Fever, yellow fever, tick-born haemorrhagic fever	• Estimated warming of 1.4-1.6 deg C by 2050 • Precipitation increase in East Africa • General increase of 300 mm precipitation per century
Europe	Prominent Vector-borne diseases: Lyme disease, Malaria, Sindbis Virus, tick-born encephalitis, Leishmaniasis	• Warmed .8 degrees C the past 100 years • Likely to become wetter in the north, and drier in the east • Milder winters, drier summers
S. America	Prominent Vector-borne diseases: Malaria, leishmaniasis, dengue fever, Chagas disease, schistosomiasis, yellow fever, Venezuelan equine encephalitis	• Increased heavy rains due to more severe El Nino-Southern oscillation • Increases in water run-off over north-west S. America • Projected increase of 2 degrees C in the next century
N. America	Prominent Vector-borne diseases: Malaria, dengue fever, West Nile virus, Lyme disease, Rocky Mountain spotted fever and ehrlichiosis, pulmonary hantavirus	• Observed rise of .4 degrees C in the last century • Increases in cloud cover and precipitation (increases in extremes of precipitation—drought and rain) • Warm wet winters, hot, dry

		summers Increased flooding and extreme weather
Asia, Australia, Islands of Western Pacific	Prominent Vector-borne diseases: Malaria, dengue fever, dengue hemorrhagic fever, schistosomiasis, Murray Valley virus	- Mean surface temperatures have increased .3-.8 degrees Celsius in the past century - Temp projected to rise .4-4.5 degrees by 2070 - Increase in rainfall and humidity in many regions - Increased flooding

This table can provide useful information for the potential range expansion of vector-borne diseases. For example, the tick *Ixodes ricinus* likely expanded into higher latitudes due to a milder climate experienced in 1990. The Hadley Center's coupled atmosphere-ocean general circulation model predicts that an additional 25 million people will be exposed to malaria in South America due to climate change and increases in precipitation (Githeko et al, 2000).

Background

Ticks as the Ideal Candidate

This work focused on ticks to model the relationships between vector distribution and climatic conditions. Ticks are an ideal focus for studies of this type for at least two reasons. First, ticks are sensitive to climate and are capable of inhabiting broad niches when considering biotic factors necessary for survival. The distribution of ticks is probably a good reflection of the limiting influences of abiotic environmental and climate conditions since constraints associated with biological resource availability or dispersal potential are relatively less important for ticks.

Ticks prefer a relative humidity of 85%, and air temperatures of greater than 6-7°C and these climate conditions are likely to become more common in many parts of Europe (Suss, 2008). In contrast to these rather specific limitations of the physical environment, ticks are generalist species in the sense that they can feed on a variety of different hosts (Süss and Klaus, 2008; Kock and Burg, 2006). As a result, when colonizing a new location, finding a new food source would not be difficult for some ticks. Additionally, by virtue of their frequent association with highly mobile hosts (e.g., birds) ticks are highly mobile and capable of long distance movements. Many ticks feed on birds during the larval and nymphal stages, and this can facilitate dispersal over large geographical areas with little if any limitation by barriers such as mountain ranges or bodies of water (Kordick, et al, 1999). A particular study in Canada in the spring of 2005 and 2006 captured birds at 12 different bird observatories to investigate their role in the range expansion of *Borrelia burgdorferi*, carried by the *Ixodes scapularis* tick. The authors found that the prevalence of *I. scapularis* on birds was .35%, but also did another study concluding the more appropriate statistic to be 2.2% (Ogden et al, 2008). As a result, the distribution of ticks and tick-borne pathogens may be more strongly influenced by climate than dispersal or aspects of the biological environment (i.e., host availability).

Second, ticks are carriers of many infectious diseases that are of concern to humans. Ticks are known to spread *Borrelia. burgdorferi* (etiologic agent of Lyme disease), human monocytic ehrlichiosis, human granulocytic ehrlichiosis, Rocky Mountain spotted fever, and Tularemia—all of which can cause very serious sickness in humans (Ringdahl, 2001). In the past two decades, the incidence of

various tick-borne encephalitids has increased 3-fold in Sweden, doubled in the Czech Republic, and increased substantially in Lithuania and Poland (Randolph, 2004). In the US alone, there were 29,959 cases of Lyme disease in 2009, and its only known mode of transmission to humans other than blood transfusions is via tick bites (CDC, 2012). In addition, the number of cases of Rocky Mountain spotted fever (transmitted by the Rocky Mountain wood tick, *Dermacentor andersoni*) has increased in the last decade from less than 2 cases per million people to 6 cases per million people (CDC, 2012).

Tick Expansion and Climate Change in the Literature

Many previous studies have established relationships between climate change and tick range expansion. Research has demonstrated a relationship between increasing temperatures and the expansion of ticks to higher latitudes (Cumming and Vuuren, 2006, Tokarevich et al, 2011). A compelling tick expansion model for Canada was published by Ogden and Maarof in 2006 showing range expansion of *I. scapularis* in relation to climate change projections. Their study modeled *I. scapularis* populations in correlation with temperature projections from IPCC Global Climate Models. They found that the theoretical range for *I. scapularis* moved 200km northwards by 2020, and 1000 km by 2080. Essentially the same results were generated for each of two Global Climate Models based on different greenhouse gas emission scenarios. Another study by Tokarevich and colleagues investigated temperature increases and tick migration. This study showed a northward expansion of the *Ixodes persulcatus* in northern Europe due to a

considerable predicted increase of both mean annual air temperatures and the number of days with temperatures exceeding 10°C (Tokarevich et al, 2011). The authors argued that the 62nd parallel had historically been used as a geographic threshold beyond which the distribution of the tick was limited by cold temperatures, but after warming global temperatures the tick was able to expand northward beyond this boundary. A predictive model developed by Cumming and Van Vuuren (2006) demonstrated that African tick species are expected to experience an average increase in global habitat suitability between 1 million and 9 million square kilometers by 2100. The results of this study also show that 73 tick species in Africa will likely experience increases in the geographic extent of suitable habitat (Cumming and Vuuren, 2006).

Apart from tick distribution modeling, field research has also been conducted to study the relationship between changing climate and tick range. Long term field studies of *D. andersoni* were conducted in Colorado and show that there were very fast and measureable changes in the spatial distribution and abundance of the tick in direct correlation with warming climate (Eisen, 2005). This evidence makes it clear that there is a relationship between global warming and changes in tick populations and distribution.

In addition to predictions about tick range expansion in the literature, there has also been research showing an increase in abundance and survival of ticks due to more favorable climatic conditions. A survey of trends in tick abundance in the UK showed that 73% of the locations considered were characterized by an increase in tick abundance over the past 5-10 years (Scharlemann et al. 2008). Other recent

studies linked the increase in tick abundance to increasing temperatures and host abundance. A population model for the tick *I. ricinus* in Europe in 2011 showed that more consistent warmer temperatures throughout the year decreased tick mortality and allowed populations to build up (Dobson and Randolph, 2011). Work by Ogden and Maarof (2006) showed that with projected increasing temperatures, the threshold amount of immigrating ticks necessary to establish new populations would likely decrease in the coming centuries. This is a significant finding considering the concern that it will be even easier for ticks to expand and colonize new locations. Ogden and Maarof also found that tick abundance at the northern limits of the species will double in the coming decades. This is caused by increased tick survival due to more ideal temperatures (Ogden et. al, 2006). Another study done in Germany observed that climate change was causing an increase of winter activity in ticks, acceleration of life cycle and an increase in population density, and an occurrence of ticks at higher altitudes in mountainous areas, northward movement of ticks in Europe, and a higher incidence of Tick-borne diseases (Süss and Klaus, 2008). In Scotland, a research project examined *I. ricinus* tick abundance in relation to climate change by using altitudinal gradients as a proxy, and also considering the effects of host abundance, and vegetation. This study found that tick abundance decreased with altitude due to the unfavorable climatic conditions seen at higher altitudes (colder temperatures, less moisture) (Gilbert, 2009). This research shows that ticks are sensitive to climatic conditions and with the observed warming, conditions for ticks may be favorable at higher latitudes.

Aspects of the tick life cycle have also been shown to be affected by climate change. For example, it has been demonstrated that the duration and developmental cycle of ticks from egg to the adult stage is dependant on temperature conditions. The tick life cycle can range from 2-6 years depending on weather conditions, and increased temperatures have been correlated to an acceleration *and* extension of the tick's developmental cycle (Suss and Klaus, 2008). There has also been an observed trend of increasing population density, and an increase in egg production. The studies cited above all reported changes in abundance and survival of ticks due to more favorable climactic conditions.

Ticks and Climate Tolerances

In general ticks prefer a relative humidity range of greater than 85% with air temperatures between 6-7°C (Suss, 2008). Because they require environments with high relative humidity, regions that are predicted to have an increase in precipitation rate may be more favorable for tick colonization. Very dry conditions will increase mortality in ticks (Jongejan, 2007). Increased temperatures can shorten tick lifecycle, but increase reproductive rate, and extremely high temperatures can cause mortality. There has also been research published demonstrating a relationship between temperature and nymphal questing behavior (questing is the act of seeking out a host). The actual risk of tick-borne disease transmission within an area is directly related to the number of questing nymphs. A study done by Schulze and Jordan showed that nymphal ticks typically seek out microhabitats within the soil that have the smallest temperature fluctuations and the highest relative humidity. Saturation deficit of the soil was the best questing

predictor, with much less questing ticks when saturation deficit was higher (Schulze and Jordan, 2003). If the temperature is too cold for ticks to seek out hosts, mortality and a failure to colonize a new location may occur.

The Lone Star tick: *A. americanum*

Life Cycle and Feeding Habits

The Lone Star tick, *A. americanum*, is endemic to the United States and currently distributed from Texas to the lower Midwest, and north along the eastern seaboard into Maine (Childs and Paddock, 2003). It is recognized as the first tick to be described in the United States—named in 1758 (Jackson et al., 1996). The Lone Star tick inhabits woodland areas including forests and meadows, and resides in leaf litter between bouts of host feeding. A study by Bishopp and Trembley (1945) showed that the tick is found in much greater populations in heavily wooded areas than in areas with less vegetation. The tick is active from early spring to fall, with populations peaking in June, and although the tick is known to take on all stages throughout the year, it is less abundant in the winter due to relatively harsh conditions (Bishopp, Trembley, 1944).

The life cycle of *A. americanum* last for 2-3 year and consists of three different life stages: larvae, nymphs, and adults (Koch, 1984). The species is a three-host parasite with a very broad range of feeding habits, parasitizing a variety of mammalian and avian hosts including white-tailed deer, the domestic dog, turkeys, small rodents, humans, and various other available vertebrates, which are abundant food sources throughout North America (Cooley and Kohls 1944 and Bishopp and

Trembley 1945). Because of the wide range of potential hosts, the Lone Star tick is very adaptable to finding nutrition in range of locations. All three life stages can feed on humans and the species is known for its aggressive behavior (Cooley and Kohls 1944 and Bishopp and Trembley 1945). These characteristics of aggressiveness and non-specific feeding habits make *A. americanum* an important economic pest of animals and a public health concern for humans (Cooley and Kohls, 1944). Larvae typically feed for four days and then drop into leaf litter. Nymphs spend 5-6 days feeding on a mammal host after which they fall into the leaf litter where they molt into adults (Süss and Klaus, 2008).

Pathogens of the Lone Star Tick

Range expansion of the Lone Star tick is a public health concern due to various parasites and pathogens the species is known to transmit including *Francisella tularensis*, *Ehrlichia chaffeensis*, *E. ewingii*, and *Theileria cervi* (Childs and Paddock 2003, Chalaire et al, 2010). Transmission of pathogens occurs via the tick's salivary glands by a pump mechanism (Süss and Klaus, 2008). In particular, human monocytotropic ehrlichiosis can be transmitted by this tick, which can cause morbidity and severe illness without treatment in humans (Goddard and Varela-Stokes, 2009).

F. tularensis, the causative agent of tularemia in humans, was isolated from the Lone Star tick in the early 1950s and since then, there have been multiple experimental studies demonstrating that Lone Star ticks are strongly correlated with tularemia in the United States. In fact, one study showed that among 1026

tularemia cases 63% of affected individuals reported an attached tick (Childs and Paddock, 2003).

The association of *A. americanum* with the transmission of *Rickettsia rickettsii* is less clear, and studies have been done both supporting and opposing evidence that the Lone Star tick as a transmission vector of this pathogen. Although physiologically capable of transmitting the pathogen, recent research has failed to identify natural infection of *A. americanum* with *R. rickettsii*. In 1983 and 1984, 3067 adult *A. americanum* were sampled from the mid Southwest, and none were infected with *R. rickettsii* (Goddard and Norment, 1986).

Human ehrlichiosis is one disease that is strongly correlated with *A. americanum*, and is a serious concern for public health. There was a study identifying attachment to humans of Lone Star ticks as far North as Michigan, and as far West as Nebraska and New Mexico (Merten, 2000). Many studies have been done sampling Lone Star ticks in areas where *E. chaffeensis* is endemic, and the research shows about 5% to 15% of the tick populations are infected with this pathogen (Childs and Paddock, 2003)

Climate Tolerances of *A. americanum*

Most research that has considered the relationship between ticks and climate has been conducted on species other than the *A. americanum*, so for the purposes of this study, I will assume climate tolerances of this species are similar to other tick species. Results of studies focused specifically on *A. americanum* should be noted. A field study done by Schulze and Jordan showed that *A. americanum*

nymphs were collected in greater numbers in locations with higher temperatures and lower humidity in comparison to *I. scapularis*. This could mean that *A. americanum* is more tolerant to drying conditions. *A. americanum* has also been shown to have more a compatible metabolic response to lower ambient relative humidity than other tick species (Clark 1995; Schulze and Jordan, 2003). This ability to tolerate higher drying conditions may make *A. americanum* more tolerant to future changes in climate.

Another study showed that *A. americanum* can maintain unfed conditions at greater than 95% relative humidity. Ticks preferred to be in shaded areas because the cooler, more humid conditions increased the amount of time they could spend searching for hosts until water loss was detrimental to survival (Koch and Burg, 2006). The Critical Equilibrium Humidity for adult ticks is estimated at approximately 85%, which means that at below 85% relative humidity, ticks start giving up water to the environment (Semter et al 1971). Temperature is also a very important factor, and additional studies have shown that water loss at particular relative humidity levels is correlated with temperature. Higher temperatures could cause an increase in metabolic activity in Lone Star ticks, which would cause more significant water losses when exposed to environments below the Critical Equilibrium Humidity. This increase in temperature may induce behavioral changes causing the tick to migrate downward in the soil (Semtner et al 1971).

Observed Range Expansion of *A. americanum*

After considering the potential for *A. americanum* to transmit pathogens of both humans and animals, it is important to understand the geographical areas currently inhabited by this species and those into which the tick may expand in the future. The range expansion of *A. americanum* is a pattern observed throughout the eastern United States. This tick was considered only a southern species well into the latter half of the 20th century, so the current range of the Lone Star tick northwards into Maine represents a significant recent range expansion (Cooley and Kohls, 1944; Good, 1972). In the last 20 years specifically, Lone Star tick populations have increased their density and expanded their range in the northeastern and midwestern United States (Mixson et al, 2006). The Lone Star tick was found to have spread to New York in the 1970s, and has since become well established there (Means, 1997). Reasons for the range expansion have been studied in relation to host abundance, adaptability of the tick, and climate change. Host abundance may be playing a role in the expansion of the tick. One conservation program dedicated to the recovery of white-tailed deer, has led to an increase of 17 million more deer, making the range of suitable habitat for the tick increase as well (Childs and Paddock, 2003). The other important factor is the ability of the Lone Star tick to adapt to its newly colonized habitats. *A. americanum* nymphs can maximize the utility of their habitat by being able to move independently and regulate their microclimate temperature and humidity conditions through movement. In addition to being capable of adapting to new environments climate change has potentially caused a greater range of habitat that is suitable for Lone Star tick colonization and survival. The range expansion has

been attributed to climatic conditions becoming more favorable at larger geographical areas, as well as expansion of vertebrate hosts that the tick will follow (Kock and Burg, 2006).

Intro to the study:

The purpose of this study is to model the niche of *A. americanum* in relation to climatic variables to see how climate change may affect the future distribution of the species. I attempted to model the fundamental niche of this tick using climate data. The fundamental niche is the range a species can occupy without considering biotic factors such as predation and competition (Molles, 2010). An assumption of this project was that the limitation of tick expansion is not greatly affected by biotic interaction, but more dependent on climate factors. Biotic limitations should be considered when drawing extensive conclusions from this research, however.

The study can be broken down into two principle components:

1. Create an ecological niche model by statistically analyzing the relationship between the observed current range of *A. americanum* and historical to present climate conditions. An updated and comprehensive map of the distribution of *A. americanum* that included historical to present tick data was recently generated and obtained from a collaborator (Y. Springer, in prep). This map was used to model the Lone Star tick's fundamental niche.
2. Use the ecological niche model to forecast future range changes of the Lone Star tick based on predictions about future climate conditions.

Methods:

Distribution Data

The first step was to obtain a comprehensive distribution map of *A. americanum*, which was recently generated by collaborators, (Y. Springer, pers com). This map was created using collection records gathered from published literature, from submission to the Veterinary Services laboratories of the USDA and to the US National Tick collection (Figure 1). The distribution map for the tick only included the continental United States, and identified areas where the species is established at the county level. The tick was considered established in a particular county if at least 6 individual ticks, or two life stages, were collected during a discrete sampling bout. The distribution map contains counties that have both established and reported records, however only established records were used in the modeling process. The tick records started as early as 1898, continuing on to the most recent record in 2013. Most of the records were collected in the 1990s and 2000s.

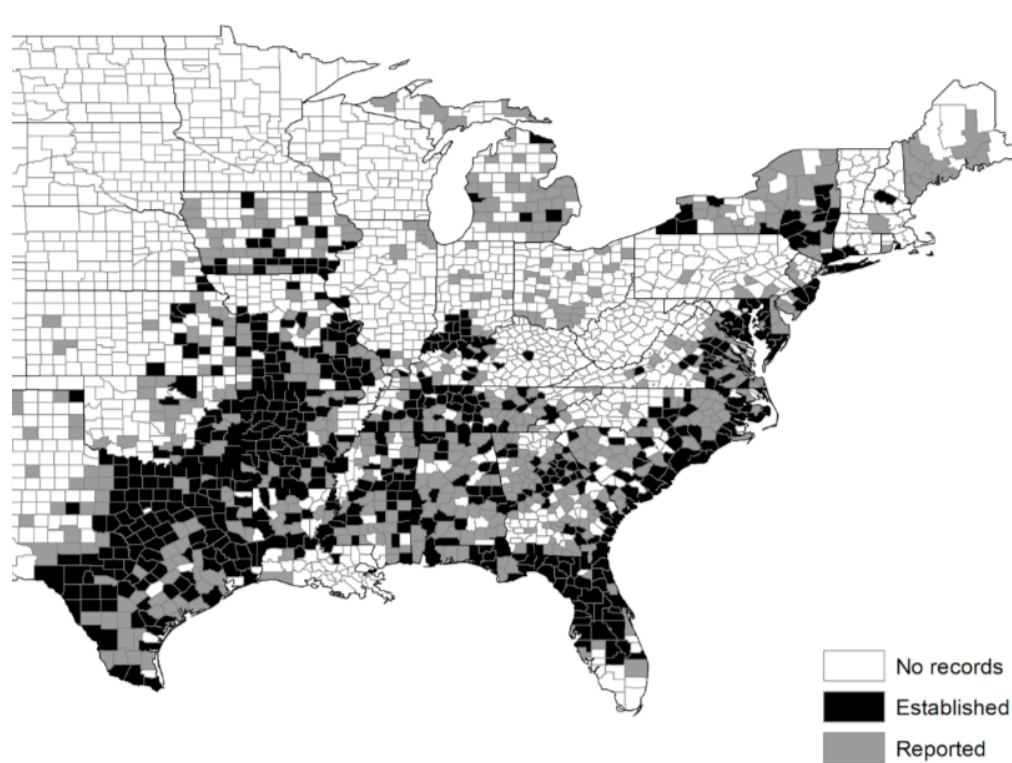


Figure 1: Distribution map for occurrence records of the *A. americanum* (Springer, 2012). Black pixels show counties where established tick colonies were documented, white pixels are counties with no records, and grey pixels are areas with reported tick but not established.

Present day ecological niche modeling

The next step in the modeling process was to find historical climate data for the time period over which the records for tick collections were made. Climate data were obtained from the WorldClim database, and the climate data provided were generated for the time period from 1950-2000. These data were compiled by the Global Historical Climatology Network, the FAO, the WMO, the International Center for Tropical Agriculture (CIAT), R-HYdronet, and additional other minor databases from Australia, New Zealand, the Nordic European Countries, Ecuador, Peru, Bolivia, and additional others (Hijmans, et al, 2005). Eighteen different climate parameters were considered including: annual mean temperature, mean diurnal range (Mean of

monthly (max temp - min temp), isothermality, temperature seasonality, max temperature of warmest month, min temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter.

The climate variables were generated by WORLDCLIM by interpolation of average monthly climate data from climate stations. Interpolation of climate surfaces is the method of taking point data (such as measured from a weather/climate station) and smoothing them over a geographical range. Interpolation can be accomplished with various different techniques, including the PRISM method, which involves spatial knowledge of meteorological trends (eg orographic rain with altitude), Inverse Distance Weighting and Kriging, and ANUSPLIN (Hijmans, 2005). The interpolation used in this model was ANUSPLIN, which puts smoothing splines to average meteorological station readings over geographical areas. Climatic data averages were calculated for 1960-1990 (only records where there were at least 10 years of data were used) (Figure 2).

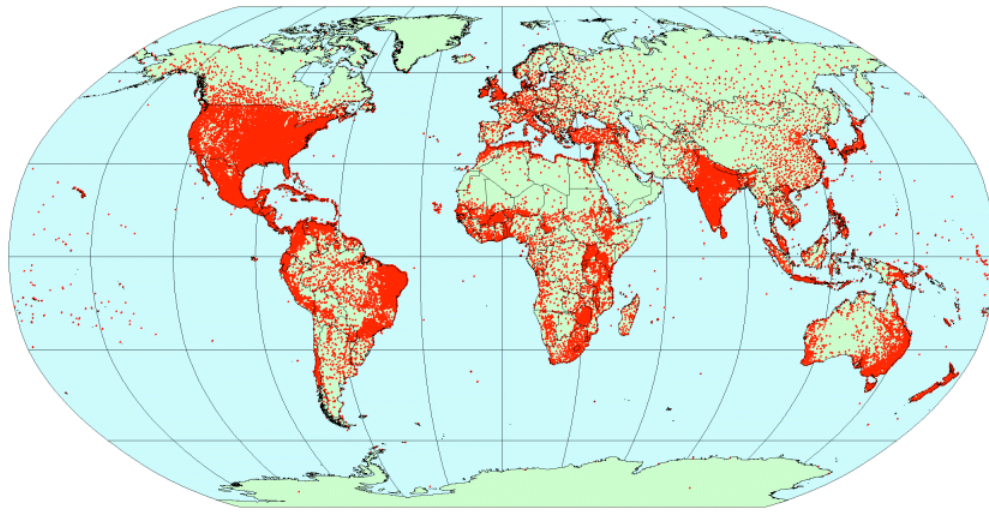


Figure 2: Global Climate station models collected to quantify historical climate conditions. Source: (hijmans, R.J, S.E. Cameron, J.L. Parra, P.F. Jones and A. Jarvis, 2005. Very high resolution interpolated climate surfaces for global land areas.

The climate data were downloaded with a 2.5 arcmin ($\sim 2\text{km}$) resolution. They were then put into ArcGIS with the tick occurrence data using bilinear interpolation. Points of latitude and longitude that marked the center of each county where *A. americanum* is currently established were generated using ArcGIS. There were a total of 610 such points. The climate “layers” were put in the form of a number of ascii raster grids—each of which described an environmental variable that could be overlaid onto the species distribution (Medley, 2010). The climate data were clipped to the same spatial extent as the tick distribution data.

Modeling

After layering and aligning the tick occurrence and climate data in ArcGIS the modeling process could begin. I used the MaxEnt software to develop a statistical model that related Lone Star tick distribution to the climate variables corresponding to its realized niche. MaxEnt, short for maximum entropy, is a

statistical program that uses machine-learning and can predict species distributions based on ecological and/or climate data when paired with distribution data for a species. MaxEnt bases its modeling on having infinite possible factors that could affect species distribution (covariables) but maximizes statistical probability for the variables given. It is more robust to spatial errors in occurrence data than other algorithms (Elith, et al, 2006, Phillips et al, 2006, Ortega-Huerta and Peterson, 2008, Medley, 2010). One key aspect of MaxEnt is that it uses presence only data for species distribution. This is arguably more reliable as it eliminates problems of unreliable or inaccurate absence records (Jimenes-Valverde et al, 2008). It is likely to acquire data that include inaccurate records of absences, which will have a strong biasing effect on the results of the model. However, presence-only datasets are prone to sampling bias. The entropy term simply refers to a measure of “dispersedness,” of the organism, and it uses probability density functions to determine niche models for a species with the given variables (in this case, all of the climate variables). Probability density functions describe the relative likelihood of random variables over their range (Elith, 2011). MaxEnt generates a probability distribution for each pixel on the map. It does this by measuring the amount of statistical “gain” the probability of a presence value for the focal species will change by including and excluding certain climate variables. For example, if the statistical probability of an occurrence point for a tick at a certain location significantly decreases if you take “mean annual rainfall” out of the algorithm, that climate variable is given a certain amount of statistical weight. The goal is to average the logarithm of the probability of the presence for the species for each pixel, and then

repeating until the best fit model is generated. The “gain” measure is the likelihood that there is a “presence” data point for the grid point being tested depending on the “covariates” which are the climate variables in this model (Princeton Maxent tutorial, 2005). One feature of the maximum entropy model is the ability to split datasets in training data and testing data. Training data are used to construct the model and then test data are used to evaluate the fit of the model to actual data. This can be helpful in determining how robust the model is. The area under the receiver operator curve (ROC) value (AUC) is a measure of how good the model is. The AUC value is the probability that a randomly chosen presence site on the map will be ranked at a higher probability than a randomly chosen absence site’s probability (or if the distribution data does not include absences, a “pseudoabsence” or background point will be used). A completely random model will have an AUC of .5, and a perfect fit is 1 (Phillips, 2008).

The Lone Star Model

To model the fundamental niche of the Lone Star tick using climate variables I used a variety of methods to find the best statistical settings to achieve the most robust model. To do this, I ran 10 model-building replicates in MaxEnt. The purpose for running replicates was to test model performance while taking advantage of all available data without having an independent dataset. The approach allows for the use of smaller data sets (Phillips, 2008). I also used the “bootstrap” sampling method for the model. The bootstrap sampling method refers to sampling with replacement. This means that for each run the model does, the test

data are sampled with replacement more than once. In addition, I used a random test percentage of 30 such that 70 percent of the data (425 of 610 tick occurrence datapoints) were used to train (build) models and 30 percent of the data (181 of 610 tick occurrence datapoints) were used to test the performance of the models. The “Jackknife” feature to measure variable importance was also used. This feature allows the model to run multiple times, each time excluding one climate variable, and measuring the change of the model in the absence of that variable. This feature also helps to assess the importance, of particular climate variables on species distribution.

I also took into consideration, the “regularization multiplier,” which is a MaxEnt setting that affects the focus, or tightness of fit of the model and output distribution range of the species (Phillips, Maxent Tutorial, 2005). The larger the regularization multiplier, the less localized the output distribution will be, and the more spread out the model will be. The smaller the regularization multiplier, the tighter the output fit will be. Regularization is important for smoothing the model and making it more regular (Elith, 2008). The regularization multiplier should be adjusted to maximize the AUC value, which is a measure of the model’s fit (Phillips, 2005). I used a regularization multiplier of 1.

The model used to represent niche distribution of the Lone Star tick with climate had a bootstrap setting with all climate variables included. In addition to this, the auto features were used which included regularization values of linear,

quadratic, product (.05), categorical (.250), threshold (1), and hinge (.5). I ran ten replicates of each model.

Modeling niche distribution into the Future

Future Climate Data:

Data on predicted future climatic conditions were obtained from WORLDCLIM data resource and based on various IPCC climate change scenarios.

(All information is based on: <http://www.ipcc.ch/pdf/special-reports/spm/sres-en.pdf>)

- The A1 storyline scenarios for IPCC future climate projections include (IPCC, 2007):
 - Very rapid economic growth
 - Global population peaking mid-century and then declining after
 - Rapid introduction of new and efficient technologies
 - Global convergence, and increased social and cultural interaction
 - Substantial reduction in regional differences in per capita income
 - A1FI Fossil energy sources
 - A1T Non-fossil energy sources
 - A1B balance of energy sources

- The A2 scenario for climate projections has the following assumptions about future global functions:
 - Heterogeneous world with fertility patterns converging slowly
 - Continuous increasing global population
 - Economic development is regionally oriented (globally segregated)
 - Technological change is slower
- The B1 scenario has the following future global assumptions:
 - Global population peaking mid-century and declining after
 - Economic shift toward information economy and reduction in material economy
 - Introduction of clean, resource-efficient, and renewable resources
 - Global emphasis on social, economic, and environmental sustainability and improved equity
- The B2 scenario assumes the following future conditions:
 - Emphasis on local solutions to economic, social, and environmental sustainability

- Continuous, and lesser increase in global population
- Intermediate economic development,
- Less rapid technological development
- Focused on local and regional social equity

In terms of future CO₂ emission projections, the most extreme emission scenario is the A1/A2 scenarios, and the most optimistic is the B1 scenario (Figures 3, 4). The A2 scenario is arguably more realistic, basing future conditions on not much social and economic change, whereas the B1 and B2 scenarios involve more limited impacts. The B1 scenario bases the global future on a more integrated world, and the B2 scenario is a more divided world. The climate data resource I used for the future modeling of the tick niche, is WorldClim bioclimatics, and they have A2A and B2A scenarios that I used for the model. More specifically, for the A2A Worldclim scenario, this is known as the “extreme” situation with a predicted warming of 5.8 degrees Celsius (1.8 degree standard deviation) (Domisch et al 2013). The B2A scenario is the “moderate” scenario, which predicts a warming of 4.4 degrees Celsius (1 degree standard deviation). These models are based on the 4th Assessment Report of the Intergovernmental Panel of Climate Change (Nakicenovic, et al, 2000). The future climate projections used for the Lone Star niche model, are the A2a and the B2a scenario because of their contrasting situations for climate projections. The A2a assumes future high-energy

requirements, and the B2a assumes lower energy requirements, so using both future projections would provide valuable results that account for different future energy scenarios.

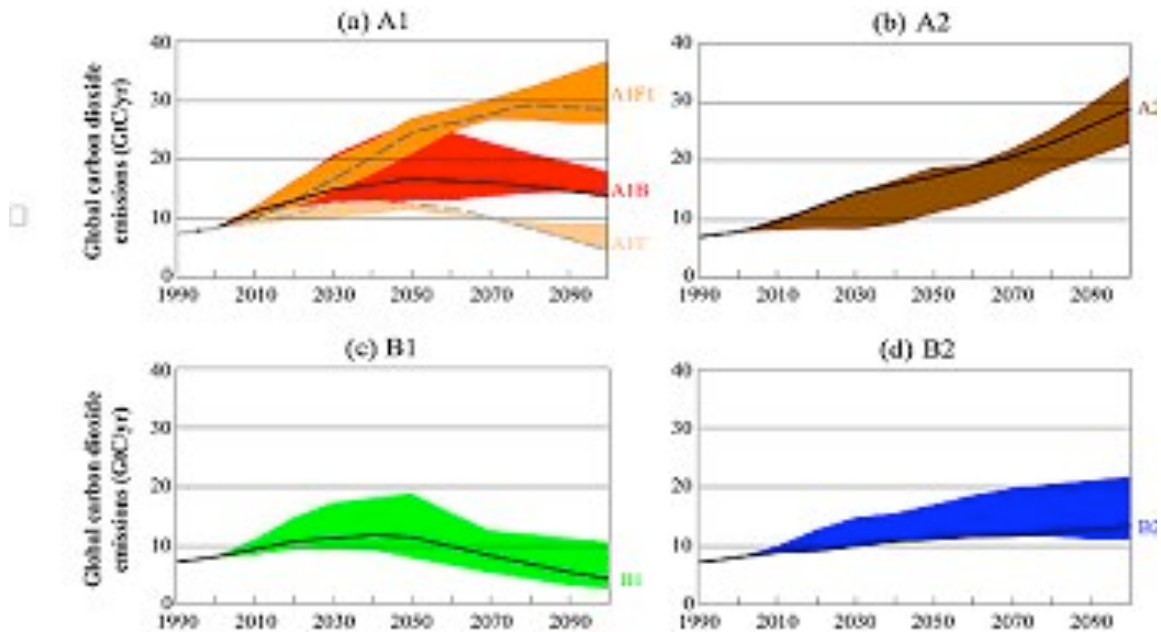


Figure 1: IPCC carbon dioxide emission storylines for the next century: A1, A2, B1, B2. Source: IPCC Emission Scenarios: A Special Report of IPCC Working Group III, 2000

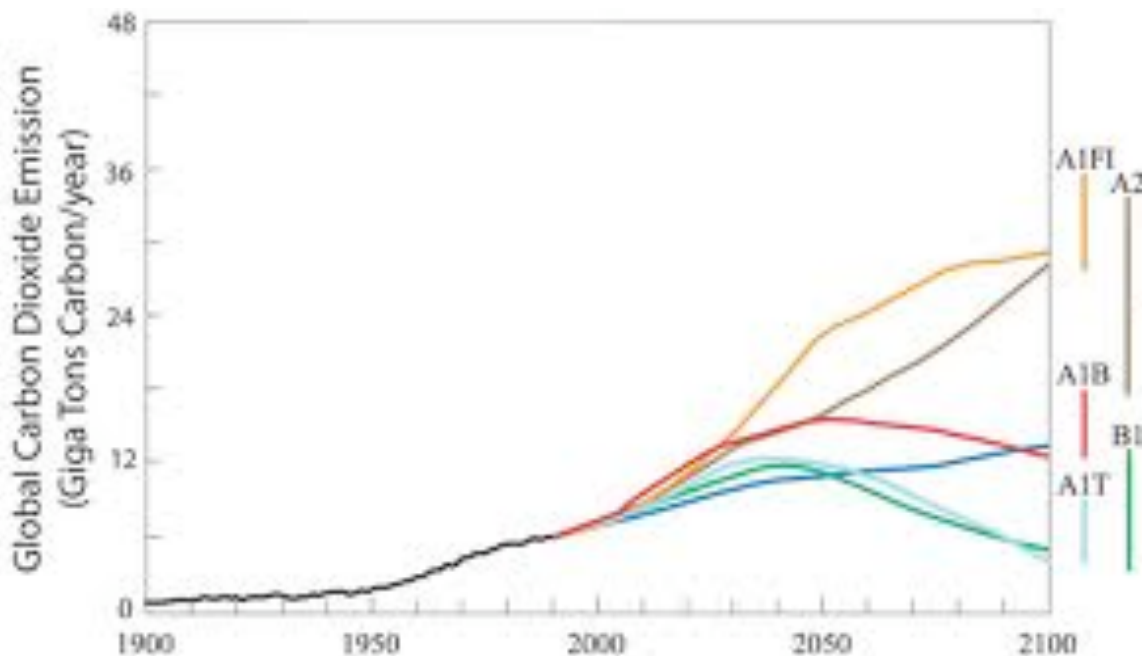


Figure 2: Global Carbon dioxide emission projections in Giga Tons/Year for the A1, A2, B1, B2 emission story lines. Source: IPCC Climate Scenarios: A Special Report of IPCC Working Group III, 2000

IPCC Climate Scenarios: A Special Report of IPCC Working Group III

In addition to using certain IPCC emission scenarios, two different Global Climate Models were chosen for the future climate data: the CSIRO-mk2 Global climate model and the Hadley Center HCCPR-hadcm3 coupled model. The CSIRO Global Climate Model is from Commonwealth Scientific and Industrial Research Organization Modeling and Analysis (Hirst et al., 1996, 1999), and the HCCPR-hadcm3 model was developed at the Hadley center in the UK (Johns, T. C. et al, 2003). These models were chosen based on their prevalence in the literature, as well as their robustness. All future projections were also done for two different time periods—2040 and 2080. Essentially, there were 8 different models run combining all different scenarios, models, and time periods. The following are the different scenarios run in the format: “*Climate Model, IPCC Scenario, Year:*”

1. CSIRO, A2A, 2050
2. CSIRO, B2A, 2050
3. CSIRO, A2A, 2080
4. CSIRO, B2A, 2080
5. HCCPR, A2A, 2050
6. HCCPR, B2A, 2050
7. HCCPR, A2A, 2080
8. HCCPR B2A, 2080

Modeling the future distribution of *A. americanum*

After choosing the future climate scenarios to be used in modeling the future distribution of *A. americanum*, I overlaid the current climate-based fundamental niche model onto future climate projection layers. I used the same methodological approach as outlined above but substituted future predicted climate data for the historical climate data used to model the present-day fundamental niche of *A. americanum*.

Results

Present Day Niche Model

The model with the best fit for niche modeling of the Lone Star tick had a smaller projected niche range than all of the lesser fit models. The model an AUC (area under the receiver operator curve) value of 0.836, which means the model was a good fit for predicting tick occurrence (Figure 3).

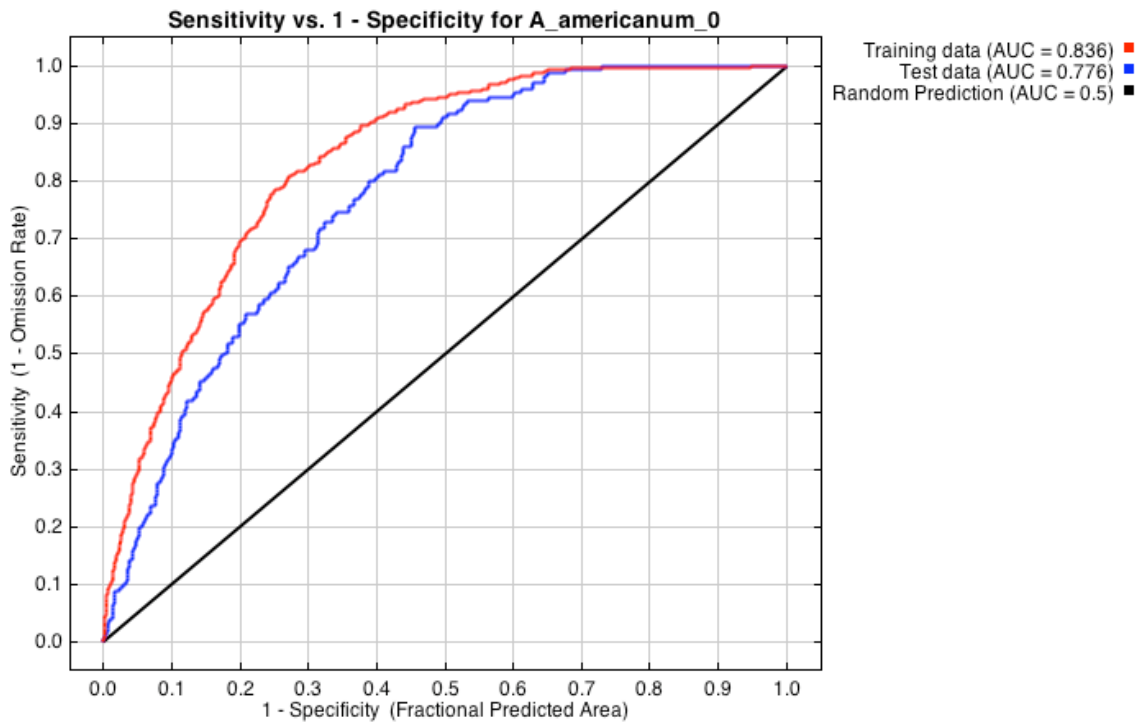


Figure 3: Receiver Operating curve for sensitivity. The red line shows the "fitness" of the model to the training data, and the blue line shows the "fitness" of the model to the testing data. The green line represents a completely random relationship.

Among the models tested, the best-fit model predicted the most geographically narrow distribution of the Lone Star tick. Some of the models with AUC values of .75 had the niche of the tick in much larger geographical ranges than the model that will be used to model future distribution. This may give a more conservative prediction for future range than some other models may have predicted.

The best-fit current niche model predicts many areas in California and throughout the West Coast that are ideal locations for the Lone Star tick (Figure 4). As far as current records show, the tick has not been documented in these regions despite the potentially ideal climate. Probability of tick occurrence is minimal for

central North America. In comparison to the actual distribution map of the Lone Star tick in North America, the projections are fairly analogous. Both the statistical climate model and the actual distribution map show areas of less tick occurrence near Ohio, and West Virginia, and areas of high tick distribution in Missouri, Kansas, and Texas regions.

The probability for tick occurrence is shown to be highly likely in already established regions of the United States, but the current niche model also predicts areas of higher tick occurrence probability to be in Western United States (figure 4). The purple region shows the actual occurrence data, while the white pixels show background data points used to generate the model, which include climactic inputs. The red regions are areas with better predictions for colonization of the Lone Star tick. Blue regions are the regions of lowest probability of colonization by the tick based on the environmental conditions given. Average temperature of the warmest quarter was found to be highly predictive of tick distribution based on the model. Areas with moderate temperatures of warmest quarter values corresponded with higher tick occurrence probabilities (Figure 5). Darker red regions have the highest average temperatures for the warmest quarter, and blue region have cooler average maximum temperatures.

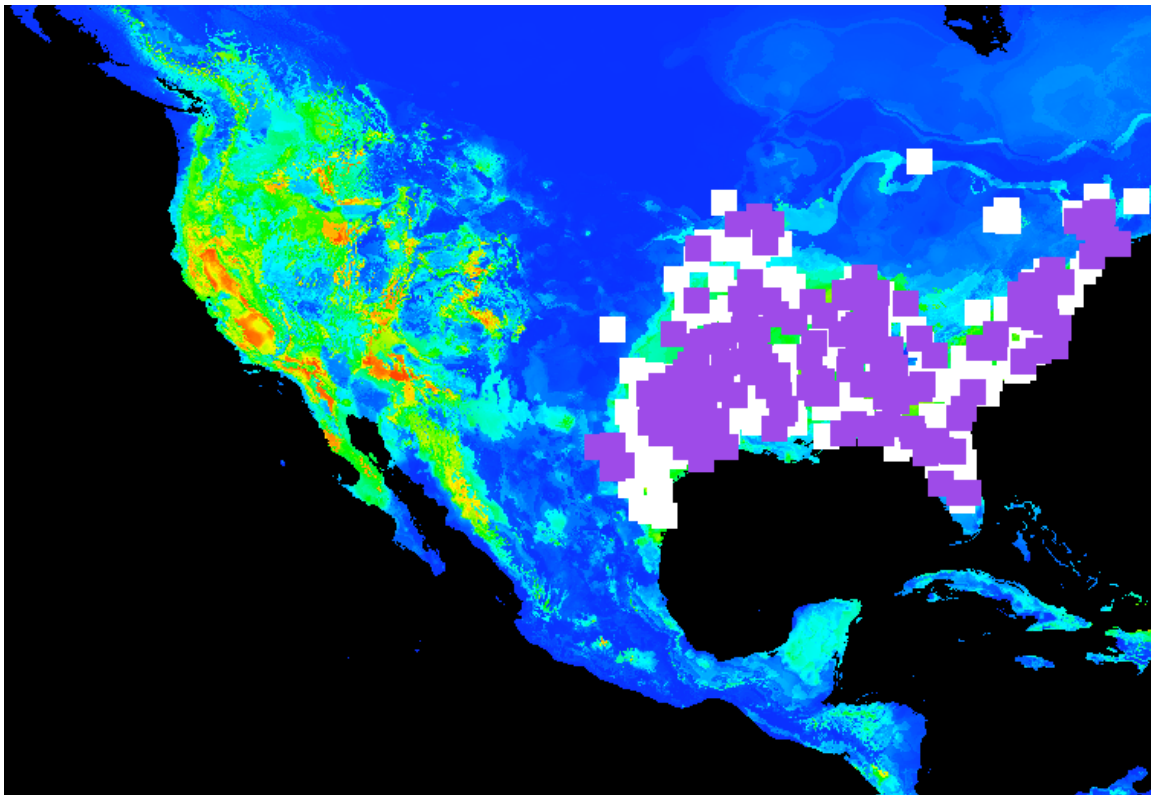


Figure 3: Lone Star Global Niche Model: This map shows the probability distribution for occurrence of the Lone Star tick based on climate conditions and known distribution in North America. Red regions are high probabilities, and blue regions are lower.

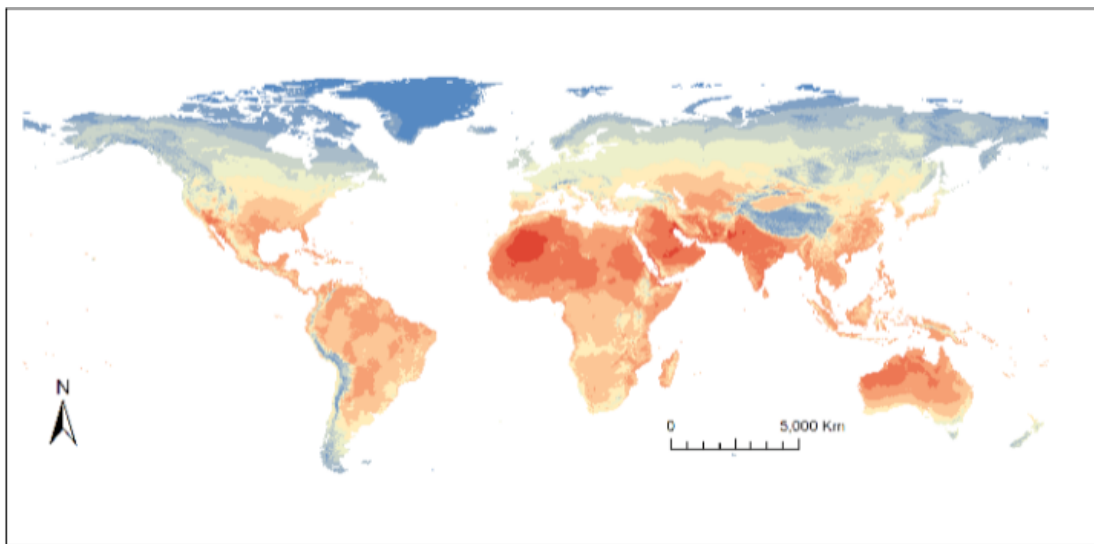


Figure 4: A map of climate records for highest average temperatures of warmest quarter. Dark red regions have records of higher average temperatures of warmest quarter, and blue regions are cooler average records for warmest quarter.

A critical step in the modeling process involved determining which of the variables were most strongly correlated with the species' distribution. After running the maximum entropy model with all of the climate variables and the tick distribution, the model gave a list of the climate variables, their "percent contribution" and their "permutation importance." The permutation importance values showed how important particular climate variables were for the final model developed, and not the path taken to get there. The percent contribution was calculated by changing the climate covariables (independent variables) included in the test model, and measuring the resulting decrease in AUC values (Phillips, 2008). The variables that seemed to correlate the highest with tick distribution were:

1. Mean temperature of warmest quarter (permutation importance = 22.6)
2. Precipitation of coldest quarter (permutation importance = 13.6)
3. Temperature Seasonality (permutation importance = 14.1)
4. Minimum temperature of coldest month (permutation importance = 10.9)
5. Precipitation of Wettest Quarter (permutation importance = 7.9)
6. Precipitation of warmest quarter (permutation importance = 5.6)
7. Annual temperature range (permutation importance = 2.1)

One thing to note about using "Precipitation of coldest quarter" in comparison to precipitation in any given month is that over time, extreme temperature events may

shift in the yearly time-frame, so standardizing extremes by quarters is more useful than assigning extremes to months which may vary year to year.

Future Models

The future niche projection models all showed varying predicted niche distributions depending on the year, climate model, and IPCC scenario. There were some differences between different future model projections depending on the variables. In general, the more conservative greenhouse gas emission scenarios for shorter future time periods had greater probabilities for tick expansion. Models with the most aggressive global warming scenarios predicted a contraction of tick range in the United States.

CSIRO Global Climate Model Niche Projections:

The predicted future niche of the Lone Star tick based on the CSIRO global circulation model shows a trend of greater future niche range prediction with the least extreme warming scenario (Figure 10). The A2A scenarios show less predicted range expansion than the B2a scenarios (figure 10).

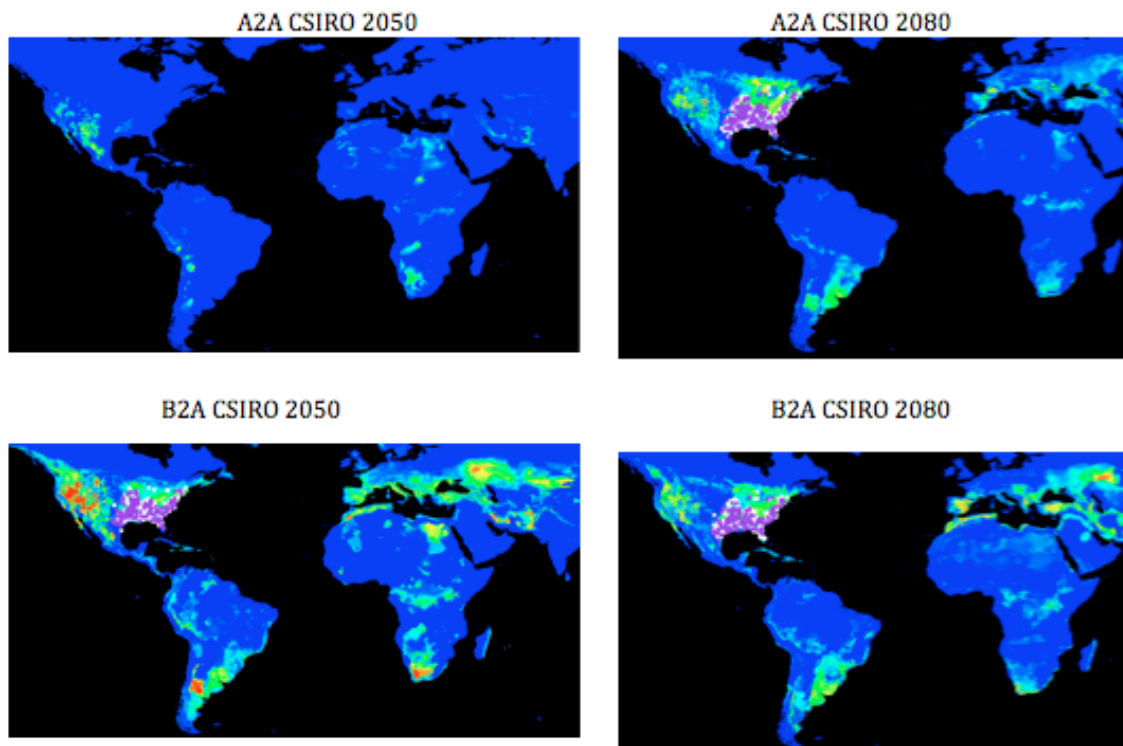


Figure 6: CSIRO Global Climate model future global niche projections. Top left, A2a, 2050; Top right A2a 2080; Bottom left B2a, 2050; Bottom right B2a, 2080.

The model for 2050 with the B2a (conservative emissions scenario) predicted the broadest niche for the Lone Star tick. In fact the same model for 2080 had the niche of the tick shrinking relative to the analogous model for 2050. The expansion for the B2a CSIRO 2050 was the most significant—especially in North America. The amount of land that had a high probability for tick occurrence increased significantly from the original present day niche model. The A2a CSIRO model for 2050 showed the least probability for tick expansion into North America, with only moderate probabilities for occurrence in the central part of California (figure 6).

The predicted tick distribution for the year 2050 with the A2a IPCC scenario and the CSIRO global climate model, was a much more conservative prediction for tick occurrence, and showed a lower probability for tick expansion into western United States than some of the other models (figure 7).

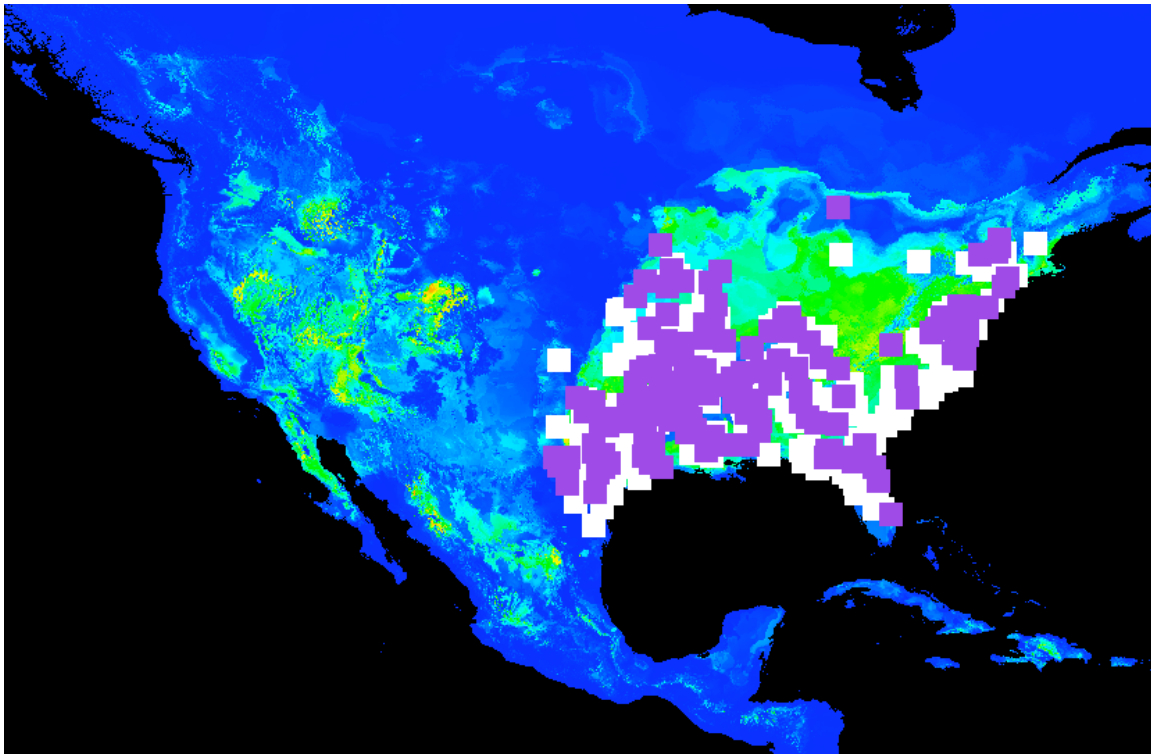


Figure 7: Niche map of the CSIRO A2a 2050 future global projection. This model projects moderate occurrence probabilities for Midwestern United States.

The B2a IPCC scenario for 2050 with the CSIRO global climate model had the most extreme predicted probability for tick expansion throughout the United States (figure 8).

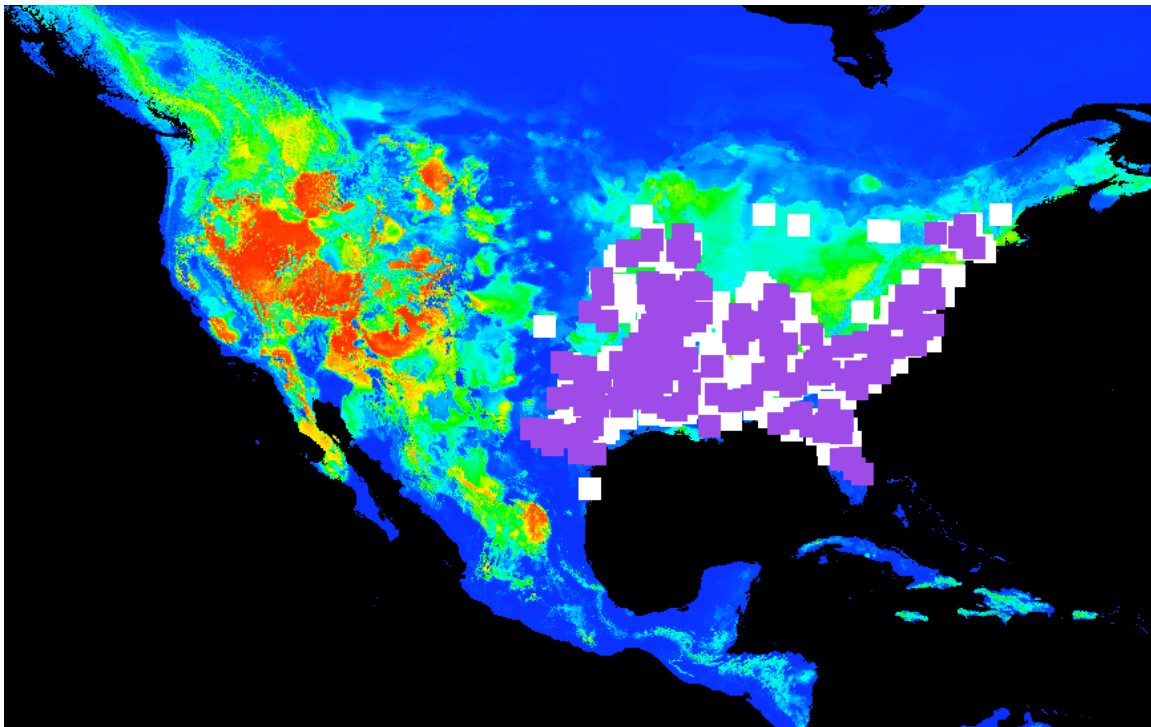


Figure 8: Future niche projection for the CSIRO B2a, 2050 model. There is a high predicted probability of tick occurrence throughout North America. This is one of the more ambitious models with high probability for expansion into North America.

With this future model there is a vast range of land that has a high probability of tick occurrence, especially throughout the western United States including parts of California, Arizona, Utah, Nevada, and Colorado (figure 12).

Hadley (HCCPR) Global Climate Model future niche projections

The Hadley model had slightly different future niche projections than the CSIRO global climate models. The Hadley model predicted the greatest probability for tick range expansion with the B2a IPCC scenario for 2050 (figure 13). The A2a scenario for 2050 had a very small probability for tick range expansion into the rest of the United States, although there was an expansion of the ticks' distribution into higher latitudes (figure 9).

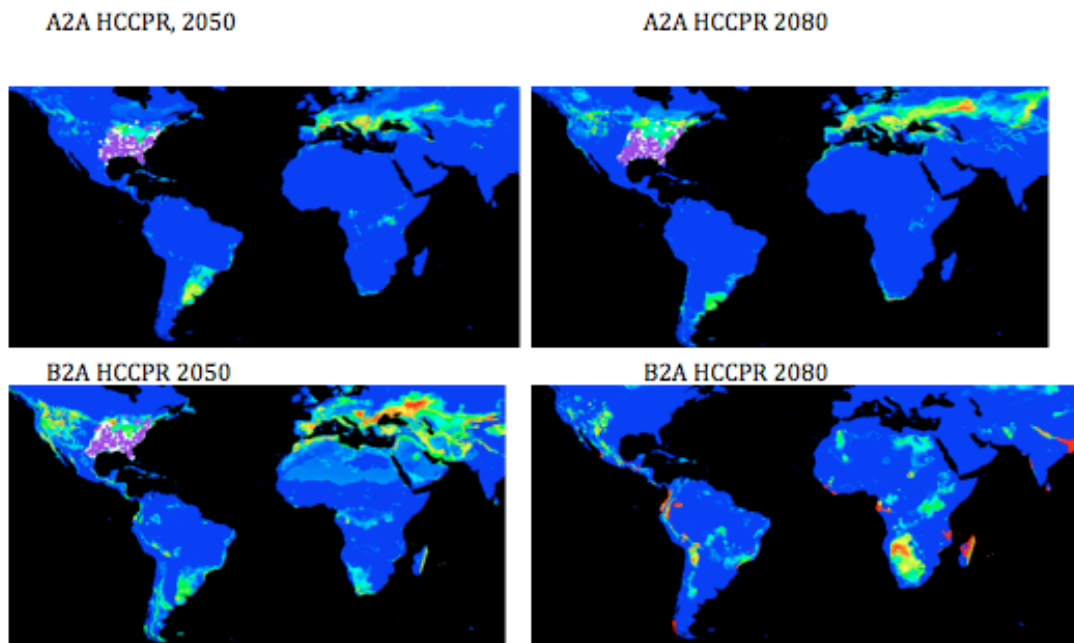


Figure 9: Global future niche projections for the Hadley (HCCPR) Global Climate Model. Top left A1a, 2050; top right A2a, 2080; bottom left B2a, 2050; bottom right B2a, 2080.

The Hadley global climate model indicated a lower probability of tick expansion in North America than the CSIRO global climate model. The B2a 2050 Hadley (HCCPR) model showed the greatest range of high probability for tick expansion, which is an analogous situation to the CSIRO model. The model future model, B2A, 2050, HCCPR had the greatest probability for tick expansion into the greatest area of North America (figure 10).

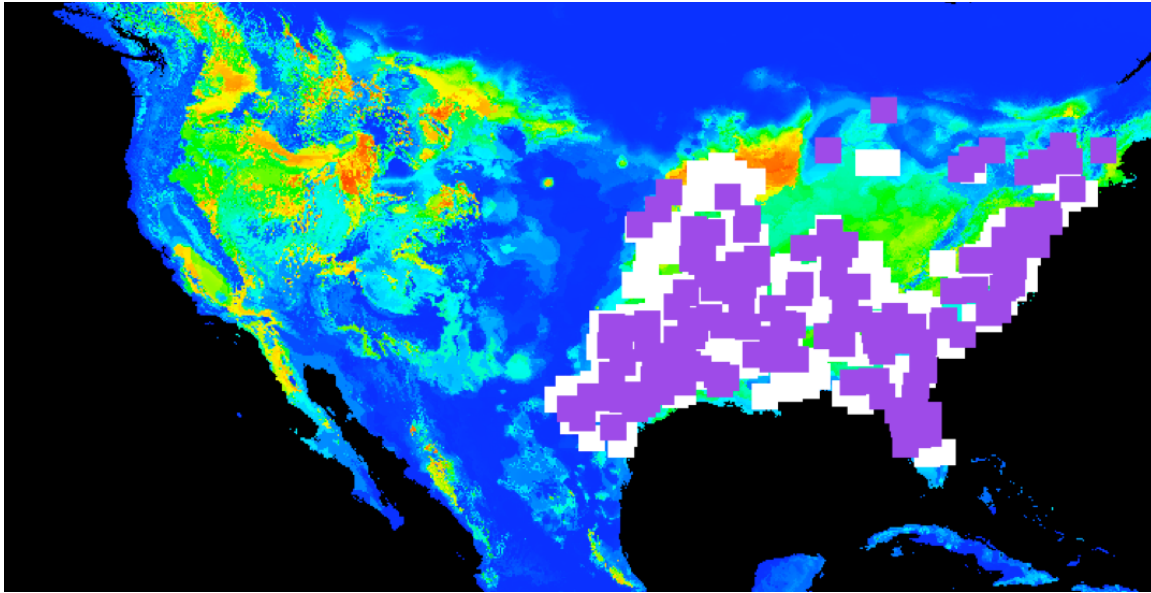


Figure 10: Future tick niche projection for Hadley (HCCPR) B2a, 2050. This model has the greatest predicted range among the Hadley model future projections.

In contrast the A2a HCCPR model for 2050 shows minimal probability for tick expansion into North America. This model was for the greater greenhouse gas emission scenario. This projection also shows a very high probability of tick distribution to higher latitudes into Canada for both eastern and western North America. The niche model for current Lone Star tick distribution and climate did not have such high probabilities for tick occurrence at such high latitudes. In contrast to the HCCPR B2a 2050 model, the projected tick distribution for A2a HCCPR 2050, which has a very minimal predicted probability for tick expansion into North America (figure 11).

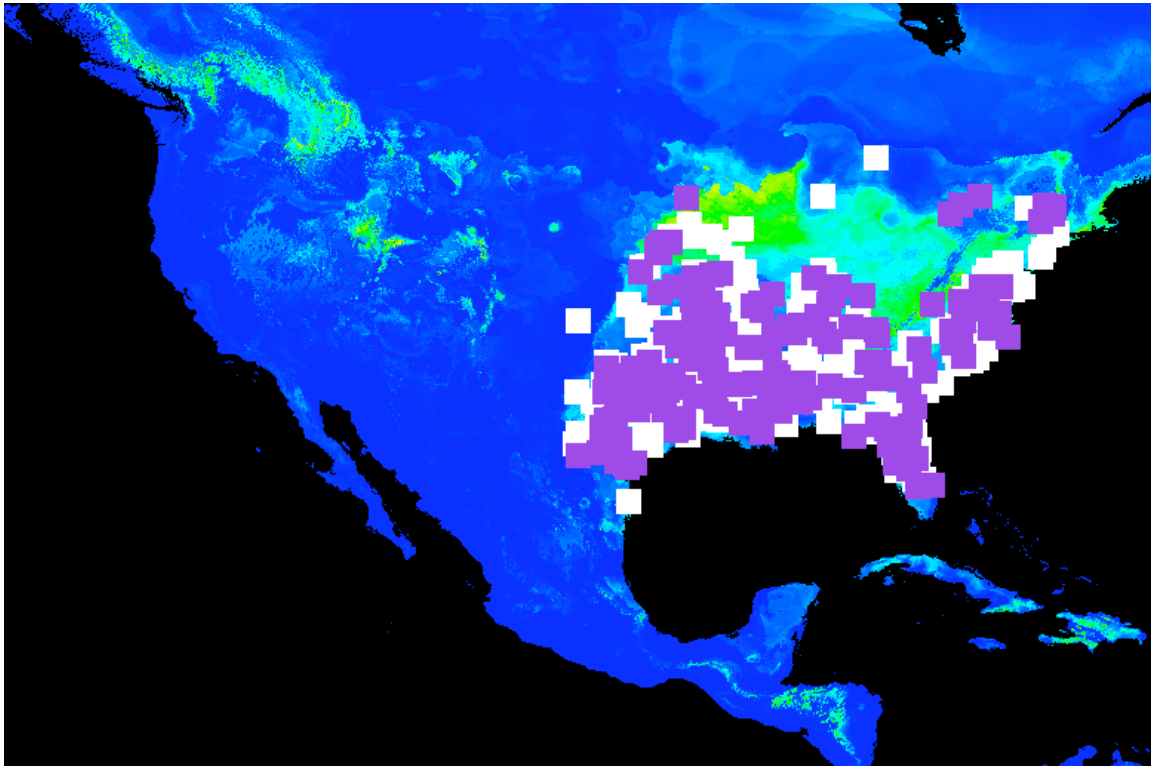


Figure 1: Future niche projection for HCCPR A2a, 2050. Minimal probabilities for tick occurrence were found throughout the rest of North America. There is a slightly greater probability of tick distribution to higher latitudes on the east coast of North America, which the current model did not have.

The future niche models were all highly variable in terms of their predictions regarding changes in distribution of the Lone Star tick. When comparing the different IPCC scenarios, both the Hadley and CSIRO models predicted much less probability for tick expansion into Western North America with the A2a IPCC scenarios than with the B2a scenarios. The Hadley model had almost no probabilities for tick expansion into North America with the A2a IPCC scenario, and the CSIRO model had very minimal probability (figure 12).

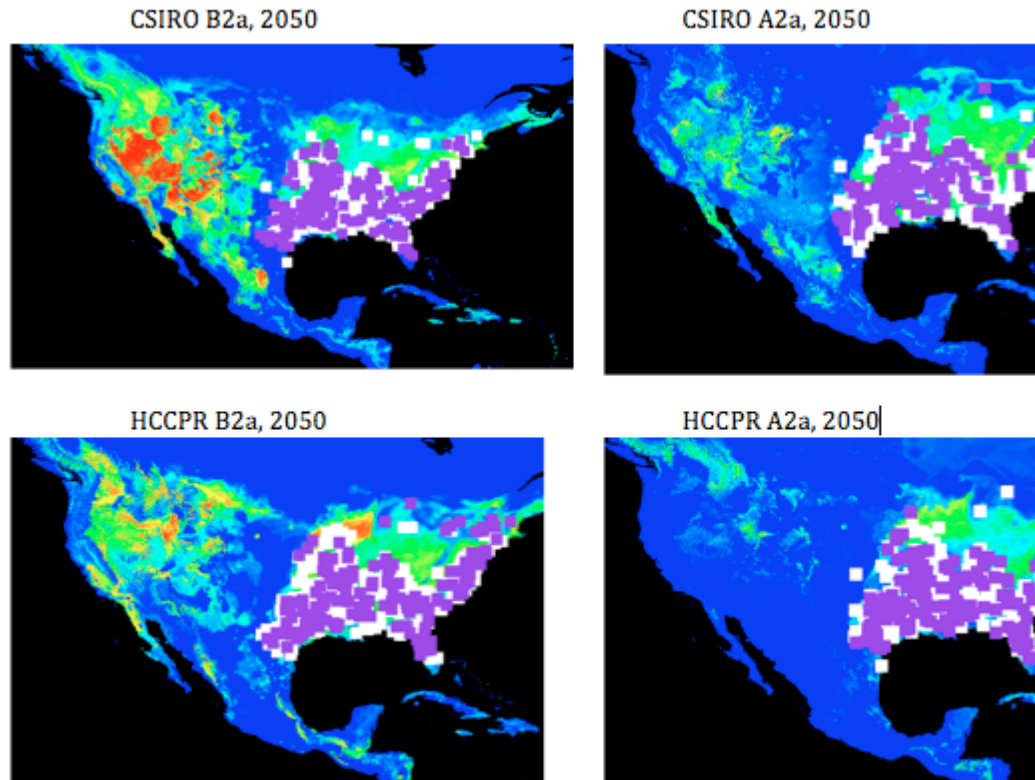


Figure 12: Comparison between A2a versus B2a IPCC emission storylines. Both the CSIRO model and the HCCPR model predict greater probability for expansion with the less extreme global warming scenario.

In addition to the differences between the two different IPCC emission scenarios, there was also a difference between the two different global circulation models (HCCPR vs CSIRO). It is evident that the HCCPR model has a much greater range expansion for the tick for the B2a scenario in 2080 than the CSIRO model does (Figure 13).

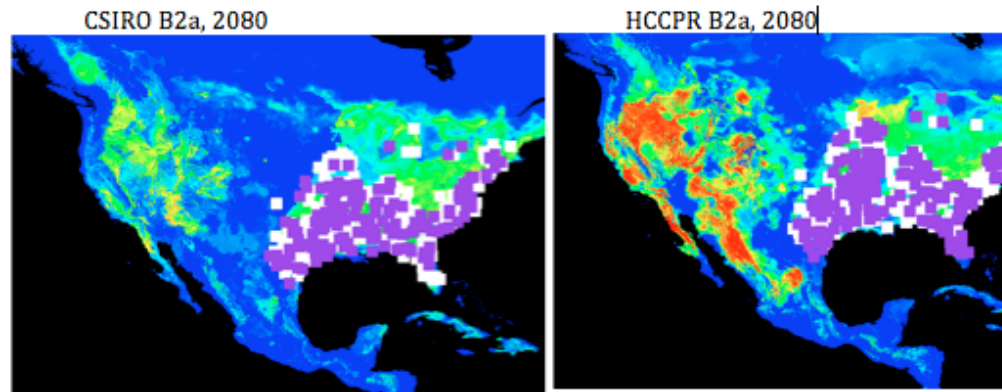


Figure 5: Comparison between Global Climate Models for the year 2080. The Hadley model shows a greater probability for expansion of the tick into North America than the CSIRO model

These were some of the major discrepancies between the predictions of future range of the tick of the different future model scenarios. Although there were some differences in the range projections there were many consistencies between the models—the greatest one being the trend for more moderate global warming scenarios having the greatest probability for tick range expansion.

Discussion:

The niche model developed for the Lone Star tick with historical climate conditions and known distribution was representative of the actual distribution of the tick. This shows that the climate model was fairly accurate and robust for predicting areas that would be suitable for tick colonization. The model predicts suitable current habitat on the east coast for areas where the tick has already been recorded. The only difference between the actual documented tick distribution and the climate model of tick distribution is that the climate model has the tick occurring in areas on the west coast of North America with a high probability. This is interesting information, because if there was a distribution event for the tick, and it

was transported into western North America, the climate model says there is a high probability for colonization (assuming that there are enough food resources and appropriate habitat in these regions). The current climate model predicts suitable climate regions for the tick in areas that it could expand to, and either by human or animal activity could cause the distribution event for this species. The current niche distribution model also has the same latitude of tick occurrence as the documented distribution of the tick shows. The consistency between upper latitude limits may also support the hypothesis that there are climatic temperature constraints for tick colonization. Higher latitudes become too cold for tick survival during winter months. In addition, the present-day climate/niche model did not show tick colonization in central regions of the United States. This region is in the leeward side of the Rocky Mountains and the associated rain shadow effect likely makes it too arid for Lone Star tick survival. The Rocky Mountains had minimal probability for tick occurrence, which could mean that higher altitudes are not ideal for tick survival in the present day. This could also provide evidence that ticks cannot colonize altitudes or latitudes that are too cold for survival.

The climatic variables that had the most statistical weight in the current distribution niche model were mean temperature of warmest quarter, precipitation of coldest quarter, temperature seasonality, and minimum temperature of coldest month. My original predictions were that annual precipitation and average temperature would be the best predictors of tick distribution. The fact that the climate variables that were most relevant for tick distribution were all “extreme” measurements may indicate that certain climate intolerances of ticks are limiting

factors of dispersal. For example, mean temperature of warmest quarter was the most important climactic predictor, suggesting that extreme heat is an important factor limiting tick distribution. If a region has relatively high temperatures during the warmest quarter ticks may be unable to survive in those locations. In addition, precipitation of coldest quarter is also an extreme parameter. Minimum temperature of coldest month was also a very important variable in the model, suggesting that ticks have a certain minimum temperature threshold that they can survive in. This factor also resonates in the map of the distribution model because ticks are not likely to be found in higher latitudes or altitudes. Temperature seasonality was also important which could mean that ticks require more consistent climates to survive. The conclusion that could be made from the most heavily weighted climate variables is that tick distribution is limited by extreme parameters of climate, including temperature extremes and precipitation extremes.

In terms of the future range models there were some notable differences between predictions associated with the two IPCC scenarios. Both the Hadley and CSIRO models predicted much lower probability for tick expansion into western North America with the A2a IPCC scenarios than with the B2a scenarios. The reason for this could be that the A2a projection assumes a greater output of greenhouse gas emission in the next century, and therefore greater global warming. Ticks are known to have a maximum optimum temperature that they can survive at before they start losing water to the environment. With too much warming, ticks may be unable to survive in many locations throughout North America. Both the CSIRO and HCCPR models have greater probability for tick expansion throughout North

America for the B2a scenario than for the A2a scenario. In fact, the HCCPR model predicts very minimal probability for tick expansion with the A2a scenario. This could be the difference between a 4.4°C warming which the B2a IPCC scenario predicts, and a 5.8°C warming that the A2a scenario predicts. An increasing in aridity with climate change in many regions of the United States may also be a predictor of why the A2a IPCC emission scenario had less of an expansion of the Lone Star tick in comparison to other models.

There was also a difference between the future niche projections for the two different global circulation models (Hadley vs CSIRO). The reason for the differences in tick niche projections between the two models could be due to differences in temperature increases between the two models. The CSIRO model has an equilibrium sensitivity to doubled CO₂ of 4.3°C, which is at the high end of the range of model sensitivities (Watterson et al., 1997; IPCC, 1992). In comparison, the HadCM2 (HCCPR) global climate model has a sensitivity to doubled CO₂ of 2.5°C, which is lower than other Global Climate Models, however the sensitivity to CO₂ for this model changes throughout time (IPCC, 1992). The differences in the sensitivity to increased CO₂ could account for the discrepancies between predicted tick distribution. Because the Hadley (HCCPR) model would be expected to have a less intense warming, more areas in the year 2080 may be suitable (not too hot) for Lone Star tick colonization.

The projections for 2080 show the Hadley model predicting greater tick expansion, but the analogous projections for 2050 show the reversed trend. The CSIRO model predicted greater expansion than the Hadley model in the year 2050.

As seen from the climate parameters that were most important in predicting Lone Star distribution, extreme temperatures are limiting factors in tick colonization. The Hadley model has less warming than the CSIRO model, so with only 40 years into the future, the climate may not have warmed enough for optimum tick expansion in the Hadley model. The CSIRO model would have greater temperature increases by 2050, which may be ideal for the tick. The CSIRO model for 2050 also shows the tick colonizing high altitude areas in the Rocky Mountains which could mean that there has been enough warming for the tick to colonize higher altitudes. The same CSIRO model for 2080 shows a range contraction in comparison to the 2050 model. This could be caused by too much warming in the CSIRO model by 2080 for tick survival. Ticks generally prefer an air temperature of 6-7°C, extreme warming could lead to an expansion of the ticks to higher altitudes and latitudes. Another modeling study showed a decline in Rocky Mountain spotted fever due to tick intolerance of high temperatures and diminished humidity (Haile, 1989). The future prediction model for 2080, with the most extreme IPCC scenario, shows only higher altitude regions in the Rocky Mountains become regions with high tick occurrence probabilities (figure 13, figure 16). This could support the hypothesis that the most severe global temperature increases will make higher altitude regions suitable for tick colonization, but previously suitable habitats may become too warm for tick survival.

Even though all of the future niche models had different projections of tick distribution, there were some general consistencies that can help determine which situation is more probable. All of the future models showed high probability for

future expansion of the tick into the western United States, and all of the models showed the greatest probability for colonization with moderate warming scenarios. This means that a little warming increases the amount of habitat that is suitable for tick colonization, but too much warming actually decreases tick distribution from the current model. With this being said, the B2a CSIRO 2050 and the B2a HCCPR 2080 models are fairly analogous in their projections, the only difference being that the CSIRO model is with a slightly accelerated warming and tick expansion. Based on the trends seen when combining all of the models, there is a likelihood for tick expansion to higher latitudes, altitudes, and farther west by 2050. It is also likely that after 2050, the Lone star tick may experience a range contraction due to too great of warming. It is likely that in the experienced global warming in the next century will be in between the CSIRO and HCCPR models. The A2a IPCC scenario is the more likely warming emission projection, because the B2a scenario is highly optimistic, which means there will probably be higher warming in the next 50 years, followed by tick expansion and then possible contraction. Areas of high-risk for future tick colonization (assuming a dispersal event) include Michigan, Wisconsin, Indiana, California, Oregon, Nevada, Utah, and Western Texas. Few models predicted high probability for Lone Star tick expansion into central North America, possibly due to the Rocky Mountains. Only the most extreme warming scenarios predicted tick occurrence in central North America. This could also be due to precipitation patterns, and the high predicted probability of drought in those regions. Areas that experience greater warming and decline in precipitation are likely to see contraction of tick distribution. Several conclusions can be made from

the results of the climate-niche modeling. First, a small increase in warming has a high likelihood for possible tick expansion to higher latitudes around already colonized areas in Eastern North America. In addition, with a dispersal event, there is also high likelihood for tick survival and colonization in many parts of western North America. With these conclusions however, it is also likely that with too much warming, the Lone Star tick will experience a range contraction. The conclusions that can be made from this modeling study are highly dependant on the ability of Global Climate Models to predict future climate. It is obvious from these results, that Lone Star tick niche is highly dependent on temperature and precipitation patterns. With these particular conclusions, however, caution should be made to prevent a human-mediated dispersal event of the tick into western United States. Due to the current absence of the tick in western United States, it does not seem to be a natural dispersal event for the tick to move West, so human activities should continue to prevent this.

There are several limitations to the study. First, habitat variables such as vegetation type and ecosystem dynamics were not included in the modeling of tick niche, and expansion of the tick could have been predicted in areas that have ideal climate, but inadequate habitat. There could also be biotic limitations to tick expansion due to competition between other species, or other limiting factors. This model is taking the realized niche of the Lone Star tick, and projecting possible the fundamental niche excluding biotic interactions. It also assumes the tick will have no evolution in terms of its tolerance to physical environmental conditions, with future climate change. In addition, the projected niche expansion was highly

variable depending on the amount of warming and future precipitation patterns. While there were a large number of inconsistent predictions between different Global Circulation Models, this also suggests that the range of *A. americanum* is strongly influenced by climate. There are also some limitations to the current niche model made, because only positive occurrence points were used, and no information on absence records were used. This model could be made potentially more robust by factoring ecological and biotic factors into the covariables, however the assumption was that tick distribution was highly dependent on climate only. This study could potentially be made more robust by building a present day niche model where tick distribution and climate data were correlated on smaller time scales. The distribution and climate data were average records for over 50 years, and being able to model potential changes in both factors with smaller time scale may lead to a more accurate model. Other statistical niche models may also be used in order to check for consistencies with the MaxEnt model. Models such as ModEco and Diva-GIS, are also valuable tools. The results of this study confirm the strong effect that climate change may have on the range of disease vectors, and it is important to acknowledge certain risk factors that may result from shifting ranges of disease vectors with climate change.

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