

# Climate change influences on the geographic distributional potential of the spotted fever vectors *Amblyomma maculatum* and *Dermacentor andersoni*

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*Amblyomma maculatum* (Gulf Coast tick), and *Dermacentor andersoni* (Rocky Mountain wood tick) are two North American ticks that transmit spotted fevers associated *Rickettsia*. *Amblyomma maculatum* transmits *Rickettsia parkeri* and *Francisella tularensis*, while *D. andersoni* transmits *R. rickettsii*, *Anaplasma marginale*, *Coltivirus* (Colorado tick fever virus), and *F. tularensis*. Increases in temperature causes mild winters and more extreme dry periods during summers, which will affect tick populations in unknown ways. Here, we used ecological niche modeling (ENM) to assess the potential geographic distributions of these two medically important vector species in North America under current condition and then transfer those models to the future under different future climate scenarios with special interest in highlighting new potential expansion areas. Current model predictions for *A. maculatum* showed suitable areas across the southern and Midwest United States, and east coast, western and southern Mexico. For *D. andersoni*, our models showed broad suitable areas across northwestern United States. New potential for range expansions was anticipated for both tick species northward in response to climate change, extending across the Midwest and New England for *A. maculatum*, and still farther north into Canada for *D. andersoni*.

1 **Climate change influences on the geographic distributional potential of the spotted**  
2 **fever vectors *Amblyomma maculatum* and *Dermacentor andersoni***

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16

**17 Abstract**

18 *Amblyomma maculatum* (Gulf Coast tick), and *Dermacentor andersoni* (Rocky Mountain  
19 wood tick) are two North American ticks that transmit spotted fevers associated  
20 *Rickettsia*. *Amblyomma maculatum* transmits *Rickettsia parkeri* and *Francisella*  
21 *tularensis*, while *D. andersoni* transmits *R. rickettsii*, *Anaplasma marginale*, *Coltivirus*  
22 (Colorado tick fever virus), and *F. tularensis*. Increases in temperature causes mild  
23 winters and more extreme dry periods during summers, which will affect tick populations  
24 in unknown ways. Here, we used ecological niche modeling (ENM) to assess the potential  
25 geographic distributions of these two medically important vector species in North America  
26 under current condition and then transfer those models to the future under different future  
27 climate scenarios with special interest in highlighting new potential expansion areas.  
28 Current model predictions for *A. maculatum* showed suitable areas across the southern  
29 and Midwest United States, and east coast, western and southern Mexico. For *D.*  
30 *andersoni*, our models showed broad suitable areas across northwestern United States.  
31 New potential for range expansions was anticipated for both tick species northward in  
32 response to climate change, extending across the Midwest and New England for *A.*  
33 *maculatum*, and still farther north into Canada for *D. andersoni*.

**34 Keywords**

35 Gulf Coast tick, Rocky Mountain wood tick, Ecological niche modeling, Climate change,  
36 GCMs, RCPs, North America.

## 37 Introduction

38 Beside the tick *Dermacentor variabilis*, *Amblyomma maculatum* (Gulf Coast tick),  
39 and *D. andersoni* (Rocky Mountain wood tick) are three North American ticks that transmit  
40 spotted fever (Boorgula et al. 2020; CDC 2018; CDC 2019). Spotted fever rickettsioses  
41 (spotted fevers) are a group of bacterial pathogens that cause disease to humans by  
42 exposure to infected ticks or mites (CDC 2019). In the United States, there are several  
43 spotted fevers: Rocky Mountain spotted fever (RMSF), which is the most documented  
44 spotted fever, caused by *Rickettsia rickettsii*; *R. parkeri* rickettsiosis caused by *Rickettsia*  
45 *parkeri*; rickettsialpox caused by *R. akari*; and Pacific Coast tick fever caused by *R.*  
46 *philippi* (CDC 2019). *Amblyomma maculatum* transmits *R. parkeri*, and *Francisella*  
47 *tularensis* which cause diseases in humans, and *Hepatozoon americanum*, which causes  
48 health problems in dogs (Sonenshine 2018). *Dermacentor andersoni* transmits *R.*  
49 *rickettsii*, *Anaplasma marginale*, *Coltivirus* (Colorado tick fever virus), and *Francisella*  
50 *tularensis* (Alkishe et al. 2021; Dantas-Torres et al. 2012).

51 *Amblyomma maculatum* and *D. andersoni* have different geographic distributions:  
52 *A. maculatum* occurs throughout the southern states of the Gulf Coast and Mid-Atlantic  
53 states (Cumbie et al. 2020), whereas *D. andersoni* occurs throughout the Rocky Mountain  
54 region, Nevada, California, and southwestern Canada (British Columbia, Alberta, and  
55 Saskatchewan; ADW 2021). Those different geographic ranges are associated with  
56 different climate conditions for each tick species (Fig. 1). *Amblyomma maculatum* is found  
57 in different months in different states with fall and winter considered as low-activity  
58 seasons for this species (Nadolny & Gaff 2018), whereas *D. andersoni* is found in hot and  
59 dry areas in summer (Wilkinson 1967).

60 Climate warming is warming North America dramatically. Mean global temperature  
61 has increased more than 1°C owing to anthropogenic greenhouse gas emissions  
62 (Djalante 2019). This increasing temperature has caused mild winters with increasing rain  
63 more than snow during winter, and more extreme drier periods during summers  
64 (Wuebbles et al. 2017). Increasing temperature can also affect vector disease survival,  
65 abundance, and activity as well as transmission dynamics, re-emergence of vector-borne  
66 diseases, and geographic expansions (Rocklöv & Dubrow 2020).

67 Here, we used ecological niche modeling (ENM) to assess the geographic  
68 potential of these two medically important vectors of diseases in North America under  
69 current conditions and then transfer those models to the future under different scenarios,  
70 with special interest in highlighting potential range new expansion areas. We also assess  
71 the model uncertainty for projected future models to highlight areas with high versus low  
72 confidence of geographic expansions.

73

74

## 75 **Methods**

### 76 **Data preparation**

77 We obtained totals of 255 and 586 occurrence points for *A. maculatum* and *D.*  
78 *andersoni*, respectively. Those data were obtained from various sources: Global  
79 Biodiversity Information Facility (GBIF; <http://www.gbif.org>), VectorMap  
80 (<http://vectormap.si.edu/>), and BISON (<https://bison.usgs.gov>) (sources summarized in  
81 supplementary file; S1). We followed Cobos et al. (2018) in cleaning the data to remove  
82 errors that clearly fall outside of the known geographic distribution of the species,

83 duplicate records, and localities with missing or meaningless coordinates such as zero  
84 degrees latitude and zero degrees longitude (0°N, 0°E), or georeferencing errors (records  
85 in ocean and far from coast). We used the spThin R package to reduce the data spatially  
86 based on a 50 km distance filter for several reasons: based on precision of the occurrence  
87 points in the area, environmental heterogeneity that present in the area, and to avoid  
88 problems with autocorrelation (Aiello-Lammens et al. 2015). In the end, we had 93 and  
89 82 occurrence points for *A. maculatum* and *D. andersoni*, respectively. We divided the  
90 final occurrence data randomly into two sets: 50% for model calibration and 50% for  
91 evaluation steps involved in model calibration. For producing final models, we used the  
92 entire cleaned occurrence points.

93

#### 94 **Delineate the calibration area**

95 The accessible area (**M**) is the set of places to which the species has had access  
96 over relevant time periods, and depends on the dispersal of the species from populations  
97 (Barve et al. 2011). Since the movement of tick species is associated with the movement  
98 of host species, we assumed ample dispersal abilities for the ticks (Nadolny & Gaff 2018;  
99 Sonenshine 2018). As such, we created 200 km buffer areas around the known  
100 occurrence points for each species (Fig. 1).

101

#### 102 **Environmental variables**

103 For the current time, bioclimatic variables were downloaded from WorldClim  
104 version 1.4, at 10' spatial resolution (Hijmans et al. 2005) (available at  
105 <http://www.worldclim.org>). We removed variables 8, 9, 18, and 19 because of known  
106 spatial artefacts (Escobar 2020). The 15 remaining variables were masked to the  
107 calibration area (**M**) for each species. We then used principal component analysis (PCA)  
108 to reduce dimensionality and multicollinearity among those variables. After having PCA  
109 results, we created 11 sets of environmental variables that represent all possible  
110 combinations of the first four principal components to test them with other parameter  
111 settings to choose best models during model calibration, following Cobos et al. (2019)  
112 (see below).

113 For future climatic conditions, we used five general circulation models (GCMs)  
114 under two representative concentration pathway scenarios (RCP 4.5, and RCP 8.5).  
115 Future climate data layers were downloaded from the Climate Change, Agriculture and  
116 Food Security (CCAFS) database at 10' resolution (available at: [http://www.ccafs-](http://www.ccafs-climate.org/data_spatial_downscaling)  
117 [climate.org/data\\_spatial\\_downscaling](http://www.ccafs-climate.org/data_spatial_downscaling)). GCMs used were (1) National Center for  
118 Atmospheric Research (NCAR\_CCISM4); (2) Met Office Hadley Centre (HadGEM2); (3)  
119 Model for Interdisciplinary Research on Climate (MIROC5); (4) Institut Pierre Simon  
120 Laplace (IPSL\_CM5A); and (5) Russian Institute for Numerical Mathematics Climate  
121 Model Version 4 (INM\_CM4). GCM choice was based on frequency of use in other such  
122 research applications, and on full availability of scenarios for both RCP scenarios.

123

## 124 **Ecological niche modeling and model transfers**

125           The combination of 11 sets of environmental variables, 15 feature classes (all  
126 combinations of linear = l, quadratic = q, product = p, hinge = h), and 17 regularization  
127 multiplier values (0.1 to 1 at intervals of 0.1, and 2 to 10 at intervals of 1) resulted in 2805  
128 candidate models for each species. We evaluated candidate models based on statistical  
129 significance (partial ROC,  $P \leq 0.05$ ; Peterson et al. 2008), predictive performance  
130 (omission rates, <5%; Anderson et al. 2003), and a criterion of minimum complexity  
131 (Akaike Information Criterion corrected for small sample sizes, AICc; Warren & Seifert  
132 2011). Specifically, we used differences between particular AICc values and the minimum  
133 values ( $\Delta\text{AICc} < 2$ ) to select best model parameter settings with which to produce final  
134 models.

135

### 136 **Final models**

137           For creating final models, we used the complete set of occurrences and the  
138 parameterizations selected during model calibration. We created 10 bootstrap replicates,  
139 and transferred the models across North America (Mexico, United States and Canada)  
140 under current and future scenarios. We calculated medians of all replicate medians from  
141 final predictions for each calibration area in which final models were produced to  
142 summarize model results. Then, we binarized models using a threshold of allowable  
143 omission error rate ( $E$ ) of 5%, assuming that as a percentage of data may have included  
144 errors that misrepresented environments used by the species.

145           We calculated differences in suitable areas between current and the two future  
146 scenarios RCP (4.5, and 8.5). For representing changes of suitable areas, we used the

147 agreement of changes (stable, gain, loss) among the five GCMs per RCP scenario.  
148 Simply, for each RCP scenario, we took all projections to future conditions based on  
149 distinct GCMs and compared against the current projection, and quantified the agreement  
150 of gain and loss of suitable areas, as well as the stability of suitable and unsuitable  
151 conditions. All modeling analysis steps were done in R 3.5.1 (R Core Team. 2018) using  
152 Maxent 3.4.1 (Phillips et al. 2017), implemented in the kuenm package (Cobos et al.  
153 2019).

154

### 155 **Uncertainty in model projections**

156 We used the mobility-oriented parity metric (MOP, considering the nearest 5% of  
157 reference cloud) (Owens et al. 2013) to assess strict extrapolation risk. We also  
158 calculated variance arising from distinct sources (replicates, parameter settings, GCMs,  
159 and RCPs) in our model projections (Peterson et al. 2018). Both model variability and  
160 strict extrapolation were represented geographically following Owens et al. (2013) and  
161 Cobos et al. (2019), respectively.

162

## 163 **Results**

### 164 **Model calibration results**

165 From among 2805 candidate models for each of *A. maculatum* and *D. andersoni*,  
166 2728 and 2554 were significantly better than random expectations, respectively (pROC  
167 test,  $p \leq 0.05$ ). Of these models, 2129 and 761 met the omission rate criteria, (i.e.,  $OR \leq$

168 0.05) respectively. Based on AICc, 55 and two models were selected as best models for  
169 *A. maculatum* and *D. andersoni*, respectively. For *A. maculatum*, models performed better  
170 with the variables in set 1 (PC1, PC2, PC3, PC4), set 2 (PC1, PC2, PC3), set 3 (PC1,  
171 PC2, PC4), and set 6 (PC1, PC2), whereas for *D. andersoni* variables in sets 4 (PC1,  
172 PC3, PC4) and 7 (PC1, PC3).

173

## 174 **Current and future potential distribution**

### 175 ***Amblyomma maculatum***

176 Current model predictions for *A. maculatum* showed suitable areas across the  
177 southern United States (Florida, Georgia, South and North Carolina, Virginia, West  
178 Virginia, Maryland, Delaware, Kentucky, Tennessee, Arkansas, Alabama, Mississippi,  
179 Louisiana, Oklahoma, and Texas), and in the Midwest (Missouri; eastern Kansas;  
180 southern Illinois, Indiana, and Ohio), and restricted areas of northeastern states (New  
181 Jersey and Pennsylvania). Suitable areas extend to include areas in western states  
182 (Arizona, California, Oregon, and Washington), although those areas are not likely  
183 accessible to the species (Fig. 2). Our models also showed suitable areas for the species  
184 across parts of eastern, western, and southern Mexico (Quintana Roo) (Fig. 2).

185 Future model transfers showed stable suitable areas (i.e., suitable in current time  
186 and in the future time) across the South, Midwest, and the Northeast, in the of United  
187 States (Fig. 2). Areas of range reduction (loss) were in restricted areas in Kansas,  
188 Oklahoma, and Texas. Range expansion (gain) was anticipated in the northeastern  
189 (Pennsylvania, New York, Connecticut, Rhode Island, Massachusetts, Vermont, New

190 Hampshire, Maine) and midwestern states (Kansas, Missouri, Nebraska, Iowa, Illinois,  
191 Indiana, Ohio, Michigan, Wisconsin) (Fig. 2). In general, we noted greater agreement  
192 among models in terms of losses and gains in the RCP 8.5 scenario compared to RCP  
193 4.5.

194

### 195 ***Dermacentor andersoni***

196 Current-time range predictions for *D. andersoni* showed broad suitable areas  
197 across Washington, Idaho, Oregon, California, Montana, Nevada, Utah, Wyoming, and  
198 Colorado, in cases where this species is known to occur in the United States. Climatically  
199 suitable areas extended across the Midwest, and Northeast and in some southeastern  
200 states (Fig. 3), although these areas are not likely accessible to the species. Currently  
201 suitable areas were also observed in parts of central and western Canada (British  
202 Columbia, Alberta, Saskatchewan, and restricted areas in Manitoba) (Fig. 3).

203 Future model transfers showed stable suitable areas across the states listed  
204 above, with some degree of reduction in suitable areas in the western states including  
205 much of Washington, Oregon, California, Nevada, Arizona, New Mexico, and Utah, and  
206 restricted areas in Colorado, Idaho, and Montana (Fig. 3). Predictions for the two RCP  
207 scenarios showed closely similar patterns of range stability, expansion, and loss, with  
208 more agreement among models in the RCP 8.5 scenario (Fig 3).

209

### 210 **Model uncertainty**

211 MOP results for *A. maculatum* showed that strict extrapolative areas among future  
212 scenarios were concentrated in northern parts in North America, particularly in Canada,  
213 and in some restricted areas of the United States and southern Mexico (Fig. 2). Model  
214 variability results showed almost no variation coming from replicates and RCPs, but high  
215 contribution to variation from GCMs and parameter choice (Supplementary material; Fig.  
216 S3).

217 In *D. andersoni*, we noted high agreement of strictly extrapolative areas in both  
218 southern and northern North America, and in lesser degree in the eastern United States  
219 and Canada (Fig. 3). High model variability came mainly from parameter choice in the  
220 eastern United States; we noted low variation deriving from GCMs, RCPs, and replicates  
221 (Supplementary material; Fig. S4).

222

## 223 Discussion

224 The geographic distributions of *A. maculatum* and *D. andersoni* are much wider  
225 today than they were in the recent past. For example, *A. maculatum* has expanded its  
226 geographic range from the southeastern United States to become well established in the  
227 Northeast in Connecticut (Molaei et al. 2021), and in the Midwest in southern Illinois  
228 (Jolley 2020). Beside the movement of tick adults for long distances via their hosts to new  
229 areas, immature *A. maculatum* can also access new areas with the help of migratory  
230 birds; larvae and nymphs can move thousands of miles during bird migratory seasons  
231 from the southern United States north to southern Canada (Florin et al. 2014; Teel et al.  
232 2010). Cuervo et al. (2021) showed similar suitable ranges using current time predictors,

233 and demonstrated that levels of niche conservatism differed among different members of  
234 *A. maculatum* group (*A. tigrinum* and *A. triste*).

235 This study is the first to assess the geographic distributions of the spotted fever  
236 vectors *A. maculatum* and *D. andersoni* in North America under current and future climate  
237 conditions. We included uncertainty analyses (MOP analysis and model variability) in our  
238 future model projections to detect areas with strict extrapolation, and to assess variation  
239 coming from multiple sources, such as different GCMs and RCPs. We considered only  
240 abiotic climatic variables such as temperature and precipitation as predictors that may  
241 influence the geographic distributions of those tick species.

242 Our models predicted that suitable areas for *A. maculatum* will remain stable in  
243 most southern and Midwestern states, whereas few reductions in suitable areas were  
244 anticipated only in western parts of Texas, Oklahoma, and Kansas (Fig. 2). Most  
245 importantly, our models predicted newly suitable areas northward in the United States  
246 successfully, to cover areas that were recently discovered to hold new populations in  
247 Connecticut and Illinois (Jolley 2020; Molaei et al. 2021) (Fig. 4). For *D. andersoni*, our  
248 models showed broader suitable areas beyond its known range (from Washington state  
249 to Colorado). Midwestern and eastern states; however, most of the anticipated reduction  
250 in ranges were in areas not known to hold this tick species. Most of the anticipated  
251 expansions in range were in northward in Canada (Fig. 3).

252 Our projections suggested higher potential of *A. maculatum* to invade new areas  
253 outside its native range mainly in the southeastern United States. For *D. andersoni*,  
254 suitable areas were mostly in northern North America (United States and Canada). We

255 also noted more extensive strict extrapolative areas for *D. andersoni* than *A. maculatum*,  
256 especially in the eastern United States, which suggested caution about interpreting those  
257 areas as suitable for *D. andersoni* (Fig. 3).

258         Several significant limitations and caveats regarding predictions emerging from  
259 ecological niche modeling that should be considered. First, a species faces dispersal  
260 limitations and biotic interactions that may prevent it from occupying the full suitable area  
261 that corresponds to its fundamental ecological niche. Second, the variation in spatial  
262 precision associated with different occurrence data records, which can cause problems  
263 for model results. Third, data availability in which biases in sampling in regions more than  
264 others can cause biases in model output (Peterson 2014). All these points have been  
265 considered in the design of our methodology to achieve the most robust model possible.

266         In the United States, numbers of documented spotted fever cases have increased  
267 in recent years, especially in 2017, with 6248 new cases (CDC 2021). Previous analyses  
268 have noted overlap between reported cases in some states and suitable areas for spotted  
269 fever vectors including *Dermacentor variabilis* (Alkishe et al. 2021; Boorgula et al. 2020).  
270 Spotted fever case data collected by the Centers for Disease Control and Prevention, and  
271 used by Alkishe et al. (2021) however, were lacking in full detail on the type of pathogen  
272 and associated tick species, which made it difficult to interpret the source of the infection.

273         In summary, using ecological niche modeling allowed us to highlight suitable areas  
274 of two medically important tick species in North America. We showed the potential for  
275 expansion of those tick vectors into new areas that were not suitable in the past with  
276 emphasis on the newly discovered dispersal of *A. maculatum* to those newly suitable

277 areas in Illinois and Connecticut. We also showed the uncertainty and variability that can  
278 come from projection models to different times and places. These results help to  
279 recognize the uncertainty and source of variability in predicting suitability.

280

### 281 **Author Contributions**

282 AA and ATP designed the work; AA performed the analysis; AA and ATP wrote the  
283 manuscript.

284

### 285 **Conflict of interest statement**

286 The authors declare that there is no conflict of interest.

287

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408 **Figure 1.** Occurrence points and calibration areas for *Amblyomma maculatum* (blue dots  
409 and blue buffer) and *Dermacentor andersoni* (red dots and red buffer) in geographic and  
410 environmental space.

411

412 **Figure 2.** Left panel: Potential suitable areas of *Amblyomma maculatum* based on  
413 binarized (5% threshold) models under current conditions (in blue and gray), and future  
414 (blue = no longer suitable, red = newly suitable) conditions. Right panel: agreement in  
415 strict extrapolation areas among the five general circulation models. Results are  
416 presented for RCP 4.5 (top) and RCP 8.5 (bottom).

417

418 **Figure 3.** Left panel: Potential suitable areas of *Dermacentor andersoni* based on  
419 binarized (5% threshold) models under current conditions (in blue and gray), and future  
420 (blue = no longer suitable, red = newly suitable) conditions. Right panel: agreement in  
421 strict extrapolation areas among the five general circulation models. Results are  
422 presented for RCP 4.5 (top) and RCP 8.5 (bottom).

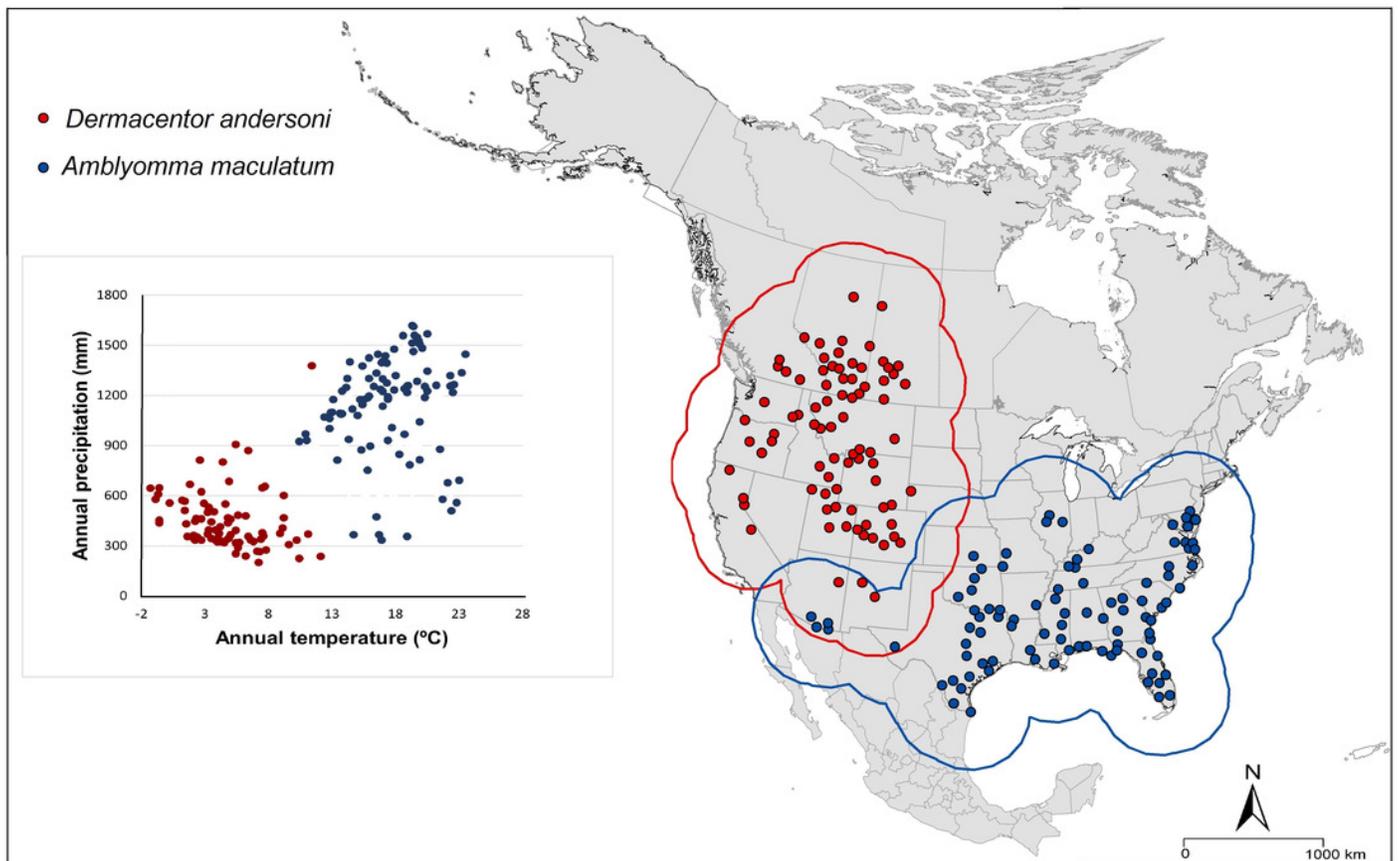
423

424 **Figure 4.** Detail of figure 2, showing the most recent confirmed established populations  
425 of *Amblyomma maculatum* in counties of Illinois and Connecticut in the United States  
426 (light blue boundaries) (Jolley 2020; Molaei et al. 2021). Gray indicates suitable areas  
427 under current and future conditions. Red color indicates newly suitable areas with climate  
428 change.

# Figure 1

Figure 1

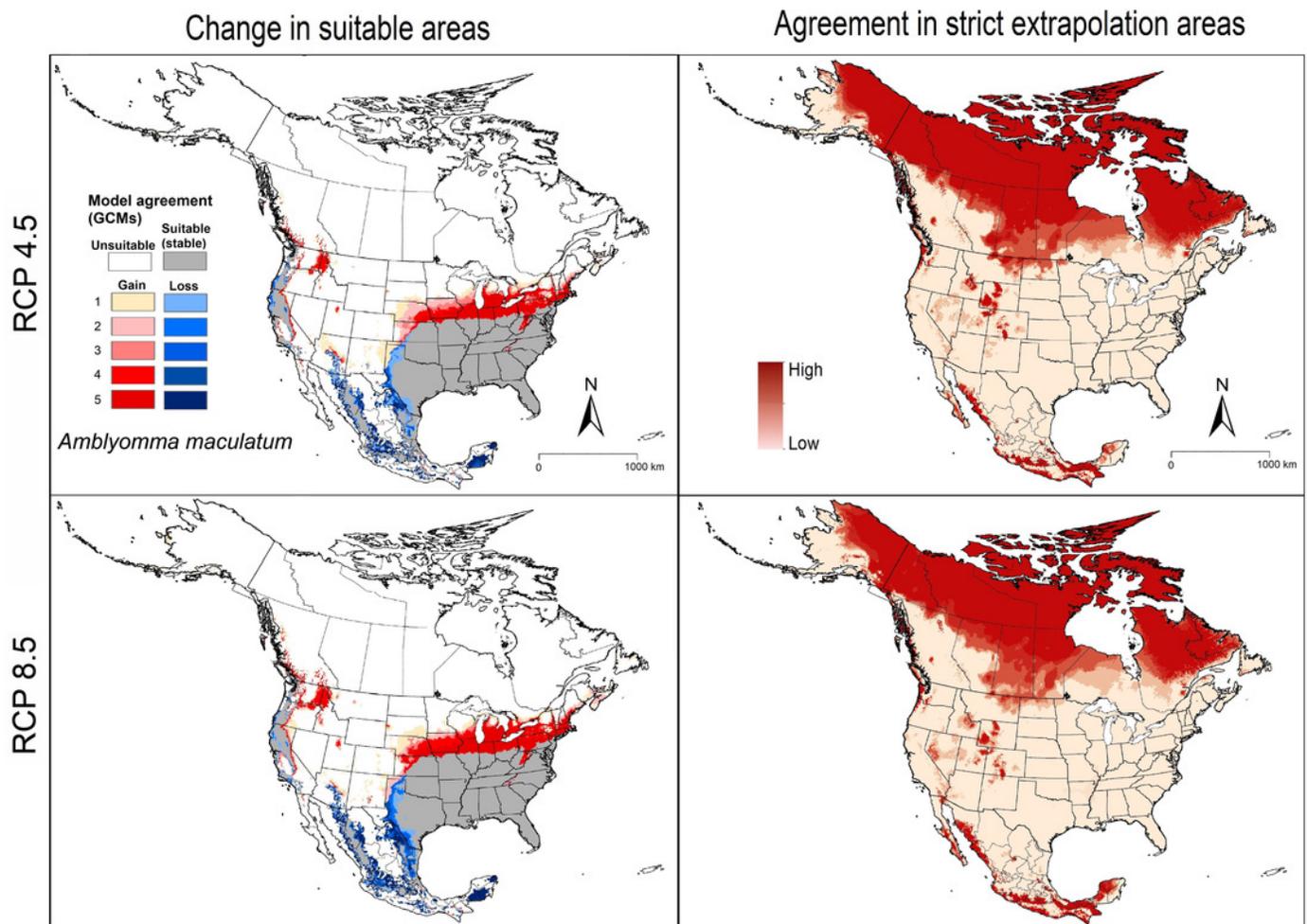
Occurrence points and calibration areas for *Amblyomma maculatum* (blue dots and blue buffer) and *Dermacentor andersoni* (red dots and red buffer) in geographic and environmental space.



## Figure 2

Figure 2

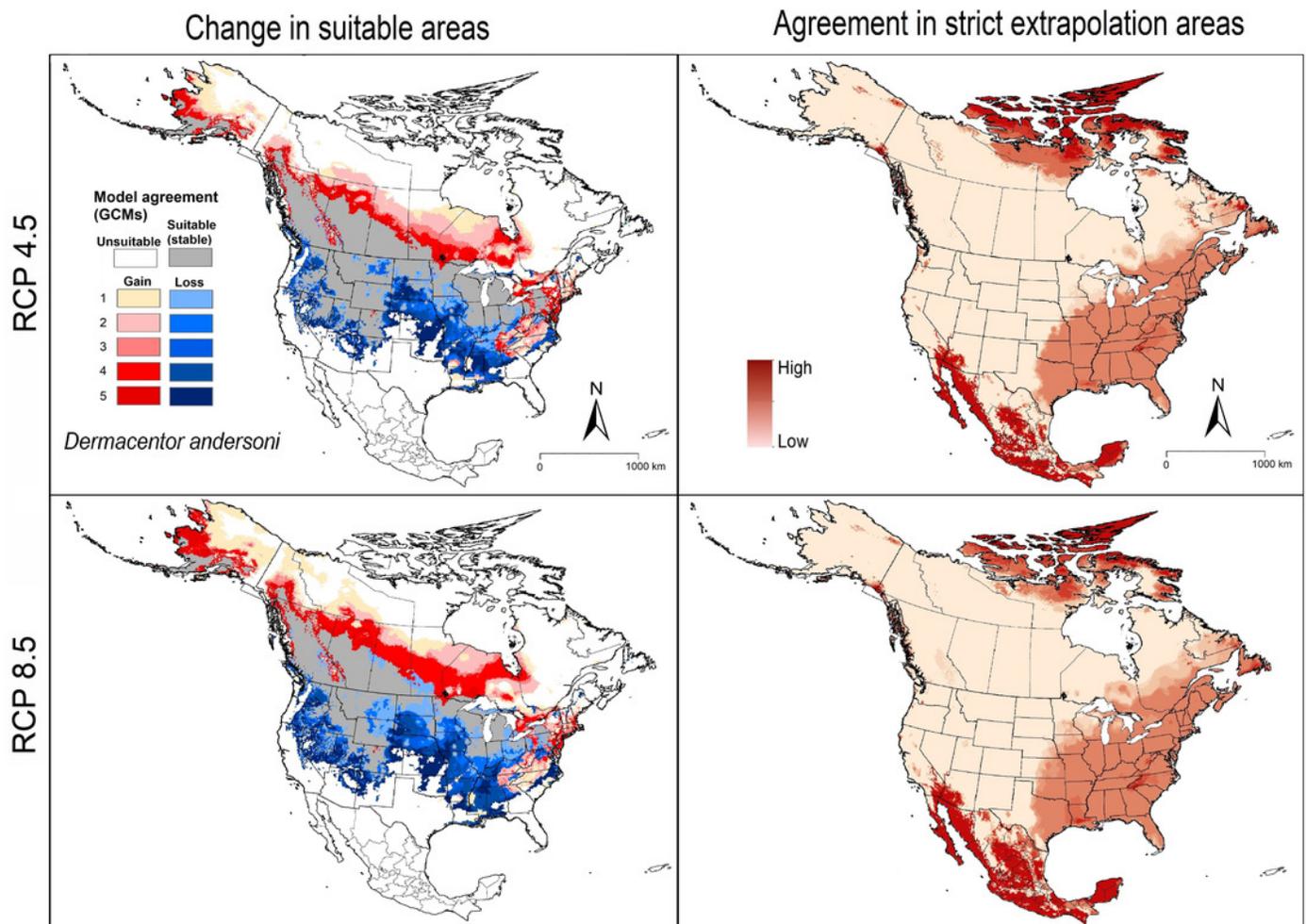
Left panel: Potential suitable areas of *Amblyomma maculatum* based on binarized (5% threshold) models under current conditions (in blue and gray), and future (blue = no longer suitable, red = newly suitable) conditions. Right panel: agreement in strict extrapolation areas among the five general circulation models. Results are presented for RCP 4.5 (top) and RCP 8.5 (bottom).



## Figure 3

Figure 3

Left panel: Potential suitable areas of *Dermacentor andersoni* based on binarized (5% threshold) models under current conditions (in blue and gray), and future (blue = no longer suitable, red = newly suitable) conditions. Right panel: agreement in strict extrapolation areas among the five general circulation models. Results are presented for RCP 4.5 (top) and RCP 8.5 (bottom).



## Figure 4

Figure 4

Detail of figure 2, showing the most recent confirmed established populations of *Amblyomma maculatum* in counties of Illinois and Connecticut in the United States (light blue boundaries) (Jolley 2020; Molaei et al. 2021). Gray indicates suitable areas under current and future conditions. Red color indicates newly suitable areas with climate change.

