



Amblyomma ticks and future climate: Range contraction due to climate warming



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ARTICLE INFO

Keywords:

Tick-borne diseases
Ecological niche modeling
Maxent
Spotted fever
Climate change

ABSTRACT

Ticks of the *Amblyomma cajennense* species complex are important vectors of spotted fever in Latin America. Environmental conditions determine the geographic distribution of ticks, such that climate change could influence the distribution of tick-borne diseases. This study aimed to analyze the potential geographic distribution of *A. cajennense* complex ticks in a Brazil region under present-day and future climate models, assuming dispersal limitations and non-evolutionary adaptation of these tick populations to climate warming. Records of *A. cajennense sensu stricto* (s.s.) and *Amblyomma sculptum* were analyzed. Niche models were calibrated using Maxent considering climate variables for 1950–2000 and projecting models to conditions anticipated for 2050 and 2070 under two models of future climate (CCSM4 and HadGEM2-AO). Broad suitable areas for *A. cajennense* s.s. and *A. sculptum* were found in present-day climate models, but suitability was reduced when models were projected to future conditions. Our exploration of future climates showed that broad areas had novel climates not existing currently in the study region, including novel extremely high temperatures. Indeed, predicted suitability in these novel conditions would lead to biologically unrealistic results and therefore incorrect forecasts of future tick-distribution. Previous studies anticipating expansions of vectors populations due to climate change should be considered with caution as they assume that model extrapolation anticipates that species would evolve rapidly for adaptation to novel climatic conditions.

1. Introduction

Ticks of the genus *Amblyomma* are important parasites of domestic animals and humans in the Neotropical region (Guglielmono et al., 2006). They are also the principal vectors of the zoonotic bacterium *Rickettsia rickettsii*, the etiological agent of spotted fever in parts of South and Central America (Labruna 2009). The taxonomic status of *A. cajennense* was recently reassessed by Nava et al. (2014). They proposed recognition of six species in the complex in populations distributed across the Americas. This proposition has seen support from other

studies and shows the diversity of *A. cajennense* lineages in the Neotropical (Labruna et al., 2011; Mastropaolo et al., 2011; Beati et al., 2013).

Empirical studies have shown that environmental conditions determine geographic distributions of tick species such that they also shape areas of risk for emergence of tick-borne pathogens (Mather and Howard 1994; Glass et al., 1995; Guerra et al., 2002; Estrada-Peña et al., 2012). Climate is recognized as a major determinant of infectious disease distributions (Peterson 2006) and climatic data have been used to predict geographic distributions of tick species (e.g., Estrada-Peña

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2008).

Predictive models have been developed using future climate scenarios to assess and understand potential distributional changes of ticks (e.g., Lindgren and Gustafson 2001; Estrada-Peña 2008; Porretta et al., 2013; Estrada-Peña et al., 2015). However, previous studies did not incorporate the implicit uncertainty in the forecasts (Beale and Lennon 2012). In addition, models aiming to predict species distributions in future climates should consider niche conservatism, which has been demonstrated on the local, regional, and global scales, showing evidences that many species have a very limited capacity of adaptation to novel environmental conditions (see Crisp et al., 2009; Soberón and Peterson, 2011).

Previous evaluations have shown that failing to consider niche conservatism may result in predicting survival of tropical vectors even at freezing and boiling temperatures (Owens et al., 2013), generating ecological niche models with lack of biological realism. That is to say, adaptation to novel climates is a slow process (e.g., hundreds of centuries; Peterson 2011), thus, models ignoring niche conservatism assumes that species will evolve fast (~50 years) to be adapted to the current trends of climate warming. An alternative to these artifacts is to assume niche conservatism to avoid model extrapolation under novel climatic conditions (see Anderson 2013; Owens et al., 2013). However, the current practices for modeling vector distributions under future climate conditions fail to consider impacts of model extrapolation in novel climates (e.g., Fischer et al., 2013). Previous models also assumed high dispersal potential of ticks and dramatic range shifts in short terms (i.e., decades). Good practices of vectors modeling under future climates should include estimations of the dispersal potential of species, explorations of several emission scenarios and climate models, ecological niche model transference (i.e., restriction of predictions to environments analogous between calibration and projection areas), uncertainty estimation, and identification of non-analog environmental conditions for more robust conclusions (Soberón and Peterson 2011). As such, the aim of this study is to analyze the potential geographic distribution of two species of ticks of the *A. cajennense* complex (i.e., *A. cajennense* (sensu stricto) (s.s.) and *A. sculptum*), to explore how future climate scenarios by 2050 and 2070 can shape the distribution of these species in Brazil. We assumed non-adaptation of these ticks to climate warming (i.e., niche conservatism) and limited dispersal abilities (see below).

2. Methods

We modeled the distribution of ticks under present-day climate conditions based on a proxy of the potential dispersal of their populations in Brazil, assuming limited dispersal of these populations. Models were then projected to future climate models under different emission scenarios as summarized in a workflow diagram (Fig. 1).

2.1. Dispersal potential

The modeling followed the BAM framework (Peterson et al., 2011), which is a generalization of the factors shaping the geographic distributions of organisms in terms of biotic relationships (B), abiotic constrains (A), and the dispersal potential or movement of species (M). Thus, $A \cap B \cap M$ is the geographic area where the organism of interest occurs (Soberón and Peterson 2005). Models were calibrated based on our hypotheses of dispersal potential, M, for the target population of each tick species (Barve et al., 2011). Briefly, to approximate the dispersal potential of tick populations, we used the average geographic distance between a centroid point among populations and all the most distant reports in the study area as described by Poo-Muñoz et al. (2014). Occurrences were restricted to populations of *A. cajennense* (sensu stricto) (s.s.) and *A. sculptum* species in Brazil to resemble the climatic signature of the populations in this region. We estimated a distance of 7.14 geographic degrees for *A. cajennense* s.s. and 7.74 for *A.*

sculptum. These distances were then used to create buffers around occurrences for each population as an approximation of M, these areas were then used as model calibration regions (Fig. 2).

2.2. Input data

Occurrence data were obtained from the scientific literature (Nava et al., 2014; Martins et al., 2016) including taxonomic assessments of the *A. cajennense* complex in Brazil, focused on two species, *A. cajennense* s.s. and *A. sculptum*. Occurrence reports were converted to geographic coordinates (WGS 84) in decimal degrees format. In all, after removing duplicates and allowing only one occurrence per grid cell of the environmental layers, 60 confirmed single records of *A. cajennense* s.s. and 122 of *A. sculptum* were used to calibrate the models (Fig. 2).

To characterize environmental conditions across the study region, we explored seven climatic variables that we considered relevant to the species biology in terms of their physiological tolerance: annual mean temperature, mean diurnal temperature range, maximum temperature in the warmest month, minimum temperature in the coldest month, annual precipitation, and precipitation in the wettest and driest months. These variables had been also used in previous studies of the biology of vectors and reservoirs of tropical diseases in Brazil (Gurgel-Gonçalves et al., 2012; Oliveira et al., 2013). We obtained these data layers from WorldClim at approximately 5×5 km spatial resolution (Hijmans et al., 2005), which depicts present-day climate conditions as the interpolation of mean monthly climatic data from meteorological stations over 30–50 (1950–2000) years. Models were calibrated using these variables with original values, however, for visualization of the environmental distribution of the species in present-day climatic conditions, we performed a principal component analysis (PCA) to reduce dimensionality and collinearity of the environmental variables. We estimated convex polyhedrons around available occurrences for each tick species in an environmental space defined by the first three principal components generated from the PCA as these contained 92.43% of the information for *A. cajennense* s.s., and 88.73% of the information for *A. sculptum* from the seven original bioclimatic variables (Supplementary Material S1); both procedures were performed using NicheA software version 3.0 (Qiao et al., 2016a).

Greenhouse gas emissions scenarios proposed by the Special Report of Emission Scenarios of the Intergovernmental Panel on Climate Change (IPCC) were included as representatives of possible future climate conditions (IPCC, 2007; Moss et al., 2008). Specifically, we used the 8.5 representative concentration pathway (RCP 8.5) which incorporates demographic, socioeconomic, and land use patterns to estimate future gas emissions (Moss et al., 2010). RCP 8.5 is a high radiative forcing pathway reaching more than 8.5 W/m^2 by 2100 with higher temperature increases (Riahi et al., 2011). We explored the RCP 8.5 given that previous conservative scenarios of climate (e.g., RCP 2.5) have been proposed as implausible considering recent emissions records (Rahmstorf et al., 2007; Raupach et al., 2007; Manning et al., 2010). Indeed, after a detailed assessment of models considering socioeconomic trends, the RCP 8.5 scenario seems to be the most realistic (Munoz, 2010; Caceres and Nunez, 2011; Noboa et al., 2012). The RCP 8.5 was based on the socio-economic and demographic background, assumptions, and technological approach of the A2 model and is considered and updated and revised quantification of the original IPCC A2 SRES (Riahi et al., 2011), thus, resembling the limited adoptions of green technologies (Snover et al., 2013; Melillo et al., 2014). Models were projected to the RCP 8.5 scenario for 2050 (average for 2041–2060) and 2070 (average for 2061–2080). Because climate models present inherent differences based on the algorithms and assumptions employed (Harris et al., 2014), we explored two different climate models that allowed us to capture variability in forecasts, C-ISM4 and HadGEM2-AO, available at the WorldClim repository (Hijmans et al., 2005).

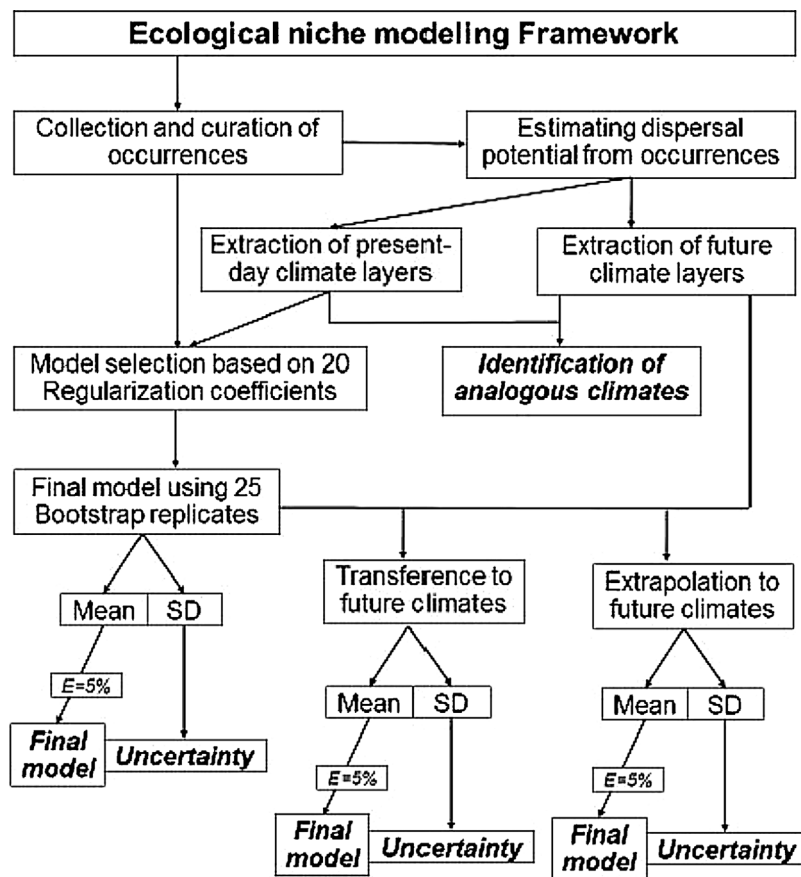


Fig. 1. Ecological niche modeling framework. The workflow summarized in this diagram includes management of occurrences for model calibration and study area delimitation, use of the study area to delineate present-day and future climate layers, and model calibration to develop final present-day and future climate models. Outputs are denoted in bold and italics to represent the results of the comparison of present-day and future climates. Models were transferred (not predictions in novel climates) and extrapolated (predictions allowed in novel climates) to future climates. Future climate models included CCSM4 and HadGEM2-AO. All models were converted to binary maps based on the suitability values of 95% of all the occurrences used during model calibration (i.e., $E = 5\%$). The standard deviation (SD) of 25 model replicates was used as a proxy of uncertainty values.

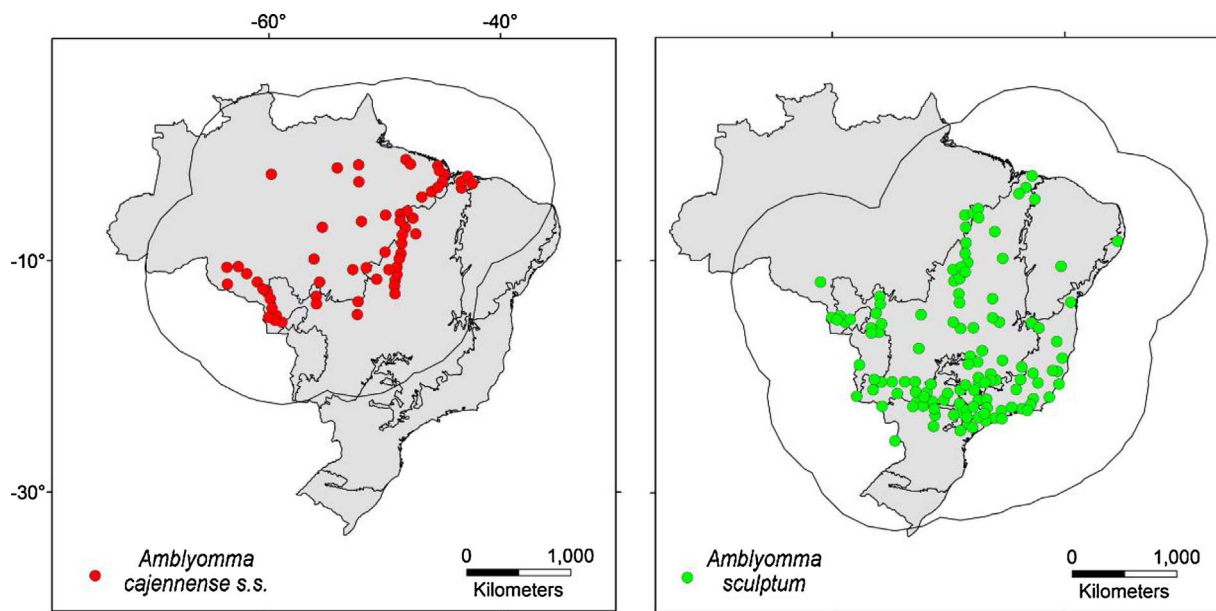


Fig. 2. Study area and occurrences of *Amblyomma cajennense s.s.* and *Amblyomma sculptum* used for ecological niche modeling. The occurrences for *A. cajennense s.s.* (red) and for *A. sculptum* (green) available for Brazil (gray) were used to estimate accessible areas (M) for each species (solid line), which were used as areas for model calibration. Within-country outlines denote biome borders (See Supplementary Material S3). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Future climate models in some areas can contain novel climatic values that may be not available under present-day conditions. Models projected into these novel climates would result in predictions based on strict extrapolation: forecasts in temperature or precipitation values above or below the range of values in the model calibration area

available for the species. Because novel climates would be potentially available in the future, we identified analogous environments in the study area by comparing present-day and future climate dataset using the extrapolation detection software Exdet of Mesgaran et al. (2014). Exdet uses Mahalanobis distance to assess similarity of conditions in

two different environmental data sets. Using Exdet, we estimated Type I novelty (i.e., environmental values of future climates, falling outside the range of values of present-day climate) for each environmental layer (see Mesgaran et al., 2014). Present-day ecological niche models were projected to future climates under strict ‘model transference’ i.e., predictions without extrapolation in novel climates. In other words, future climate models predict only in analogous environments that are also available in the calibration data, truncating predictions in novel environments, while extrapolation and clamping (a type of sustained extrapolation) allow prediction in novel climates (Anderson 2013).

2.3. Ecological niche modeling

Ecological niche models were calibrated using Maxent version 3.3.3k (Phillips et al., 2006). To assure good fit of models to our samples, models were calibrated with different regularization coefficients from 0.1 to 2 (i. e., 20 coefficients; Merow et al., 2013). Those with adequate levels of complexity and fit with the data were selected using the Akaike Information Criterion corrected for sample size (AICc; Warren and Seifert, 2011) using ENMTools 1.4.4 (Warren et al., 2010). We also assessed if the best regularization parameters were able to predict independent data better than random predictions for each species. For this, coordinates were divided in four quadrants based on their latitudinal and longitudinal location using one off diagonal set of occurrences for calibration and other for evaluation (Supplementary Material S1), following the methods described by Peterson (2012). The ability of the selected parameters to predict independent data was estimated using the Partial ROC metric described and tested elsewhere (Peterson et al., 2008); Partial ROC assesses a ratio from the number of evaluation occurrences predicted correctly and the proportion of area predicted suitable—a ratio with values ≤ 1 reflects predictions indistinguishable from random predictions, while a ratio > 1 suggests predictions better than by random (Peterson et al., 2008; Peterson, 2012).

The best regularization coefficient for each species was then used to develop final present-day models. For the final models, we selected logistic values as final output and bootstrap replicates (Elith et al., 2011). Bootstrap replicates have been used recently to map Ebola in Africa; their application allows to develop a series of models under different scenarios of data availability to develop dimensions of uncertainty (Peterson and Samy 2016). Using random seed, we constructed 25 model replicates calibrated with 80% of the data available. Uncertainty maps were generated based on the standard deviation of the bootstrap replicates. The average of replicates was selected as final model and converted to binary to generate binary maps of environmental suitability and unsuitability. The threshold to construct the binary maps was the minimum logistic value of suitability from 95% of all the occurrences used for model calibration under present-day climatic conditions. This threshold takes into consideration an estimate of the likely amount of error among occurrence data and thus removes 5% of occurrences with the lowest suitability values ($E = 5\%$) (Peterson et al., 2008).

Final models were then projected to future climatic conditions via deactivating clamping and extrapolation in Maxent, for a strict model transference avoiding predictions in environments not available in the calibration region (Anderson 2013; Owens et al., 2013; Merow et al., 2013; Escobar et al., 2015). To further visualize the effects of uncontrolled model projections to future climate, we also developed Maxent predictions allowing predictions in novel climates (i.e., clamping and extrapolation activated) for all future models.

3. Results

We forecasted present-day and future potential distributions and their associated uncertainty in estimations for *A. cajennense* s.s. and *A. sculptum* (Fig. 3). Based on our evaluation of model parameterizations,

the best regularization coefficients for *A. cajennense* s.s. and *A. sculptum* were 1.9 and 2.0, respectively (Supplementary Material S2). Model evaluations using Partial ROC resulted in ratios above 1, thus indicated that predictions using these parameters were better than random expectations (Supplementary Material S1). In geographic space, *A. cajennense* s.s. showed a broad potential distribution in the Amazon and Amazon-Cerrado transition zones. *Amblyomma sculptum* was estimated as ranging somewhat farther south, in the Pantanal, Cerrado, and Atlantic Forest biomes (Fig. 3; Supplementary Material S3).

When comparing present-day and future potential distributions, we found that suitable areas for the populations of *A. cajennense* s.s. and *A. sculptum* (red in Fig. 3) will be reduced based on model projection with strict transference (‘Strict transference,’ pink in Figs. 4 and 5). However, if models are allowed to predict in novel climates via clamping and extrapolation activated, models predict that species will increase their ranges to broad areas with novel environments expected for the region (‘Clamping and Extrapolation,’ pink in Figs. 4 and 5). Environments in both CCSM4 and HadGEM2-AO models did not match present-day climatic conditions in the calibration region, and HadGEM2-AO model had more pixels with Type I novelty (‘Novel environments,’ red in Figs. 4 and 5). The novel climate assessment, confirmed that using Maxent transference, predictions were correctly truncated in novel environmental conditions, generating outputs only in analogous climates and suggesting an agreement in the identification of novel climates by Maxent and Exdet (‘Strict transferences’ pink vs. ‘Novel environments,’ gray in Figs. 4 and 5). Within regions climatically analogous, the future prediction for *A. cajennense* s.s. was restricted to small areas for CCSM4 in the Cerrado and Amazonia and was particularly restricted in 2070 in the HadGEM2-AO model (Fig. 4). Future suitability predicted for *A. sculptum* comprised a broader area than for *A. cajennense* s.s., but only the latter species was predicted to occur in the northern parts of the study region.

Uncontrolled exploratory models using clamping and extrapolation activated predicted broad areas of suitability in the zone of potential dispersal for both species in all future models (‘Clamping’ and ‘Extrapolation,’ pink Figs. 4 and 5). However, Exdet maps showed pixels corresponding to novel environments in the areas predicted suitable by Maxent extrapolative, thus warning about unrealistic interpretation in these regions (‘Novel environments,’ red in Figs. 4 and 5).

4. Discussion

During the projection of models to future climate, restricted only to areas where analogous environments are anticipated, we estimated a reduction of areas suitable for the target populations of *A. cajennense* s.s. and *A. sculptum* in Brazil. This contrasts with other studies proposing an expansion of suitable areas for ticks such as *Rhipicephalus bursa*, *R. turanicus*, and *Hyalomma marginatum* under future climate conditions in Mediterranean regions (Estrada-Peña and Venzal, 2007) and *Ixodes ricinus* in Eurasian regions (Porretta et al., 2013). Thus, this study can be incorporated to the growing body of literature suggesting that, as has been reported for other taxa, climate change can negatively impact parasites and, in turn, generate dramatic cascade effects on food webs (Cizauskas et al., 2017).

Informing health agencies and decision makers with artifactual forecasts suggesting dramatic increases of vectors distribution could result in the inappropriate prioritization of risk areas. Recent efforts for more objective explorations of the effect of climate change on the burden of vector-borne diseases suggest that under controlled methodologies climate change would result in reductions in the burden of specific vector species (Escobar et al., 2016). Peterson (2009) also reported that the burden of malaria in Africa could reduce in number of cases if vectors shift their distribution in response to warming climates. Complementary, Ryan et al. (2015) forecasted a net decrease of areas suitable for malaria vectors in Africa. Similarly, Liu-Helmerson et al. (2014) proposed that vectors’ capacity to transmit dengue virus would

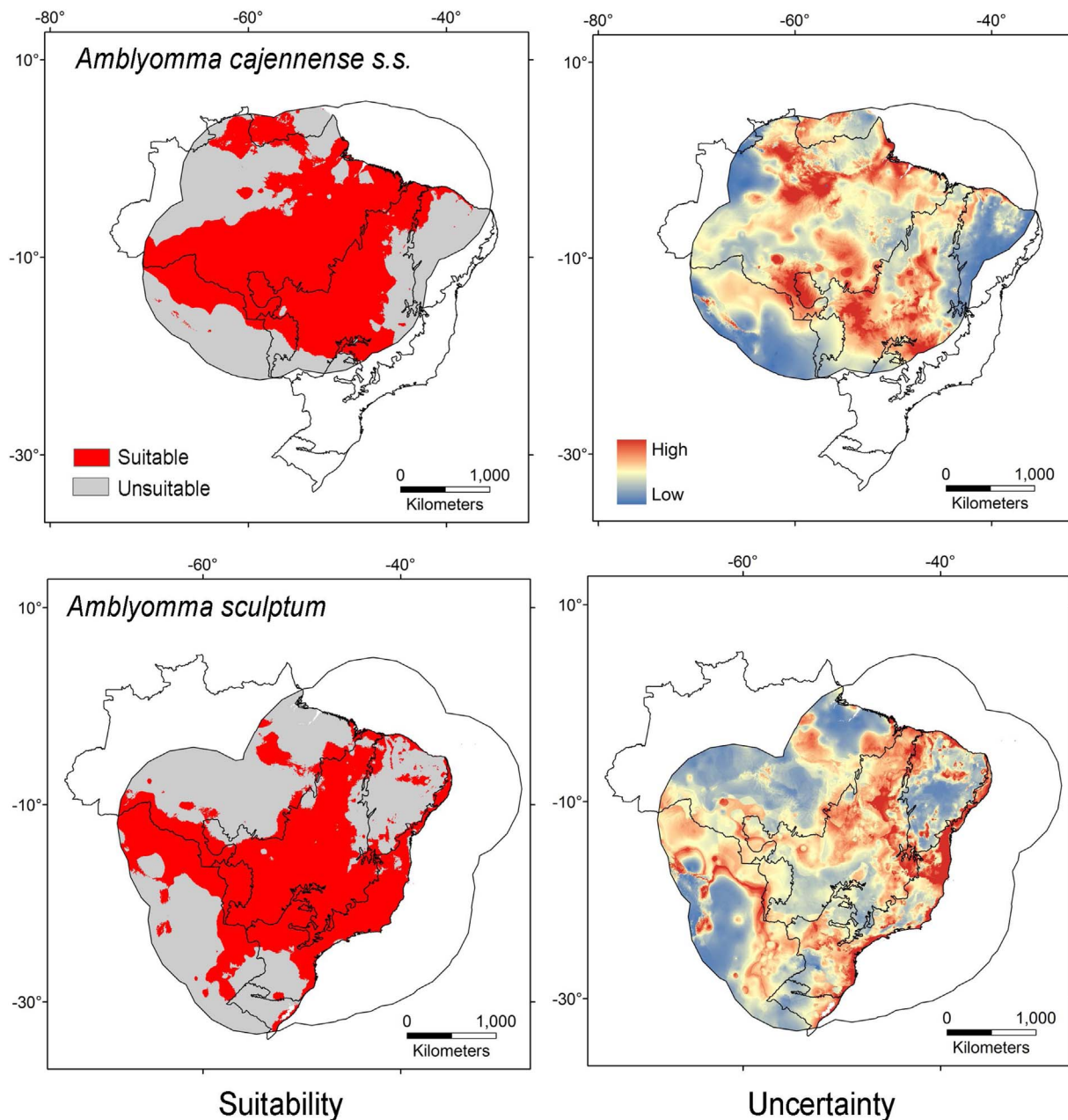


Fig. 3. Ecological niche models for *Amblyomma cajennense s.s.* and *Amblyomma sculptum* under present-day climatic conditions. Left: areas predicted suitable (red) and unsuitable (gray) for each species were identified across the calibration area M (buffer). Right: areas with high (red) and low (blue) uncertainty were also identified to provide more information during model interpretation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

be reduced with the expected raise of temperatures in future years. These patterns have been supported by recent findings in *in vivo* experiments showing a decline of fitness in insects due to increased temperatures. For example, Kellermann et al. (2012) found that *Drosophila* flies are unable to adapt to warming temperatures in laboratory conditions. Also, Murdock et al. (2016) reported that increments of temperature in laboratory experiments reduce the competence of malaria vectors.

While we anticipate a reduction on the spatial range of the tick species explored, we also recognize that this reduction should not be strictly interpreted as a reduction of spotted fever transmission risk. Thus, even if geographic ranges of vectors contract, spotted fever burden can still increase as a result of climate change. For example, climate change can affect the community composition in some areas generating unexpected disruptions in parasite traits (e.g., host switching, infection of immunologically naïve populations, increased

parasite fecundity; Cizauskas et al., 2017). In consequence, we argue that the effects of climate change on the burden of spotted fever cannot be inferred from range contractions only and more fine-scale information is necessary to infer risk reduction (or increase) due to warming temperatures.

Our models were focused on Brazilian tick populations, excluding the entire species range. Recent experiments showed that dispersal potential could limit the ability of populations to reach suitable environments due to climate change, driving extinction of local populations (Qiao et al., 2016b). Thus, our models reflect the existential niche of these ticks in Brazil, i.e., a portion of the niche occupied by the populations explored (Peterson 2011). Different patterns could emerge if dispersal limitations are ignored and the entire range of the species is used during model calibration under the assumption, however, of unlimited displacement of individuals.

More efforts are needed to understand the potential effects of

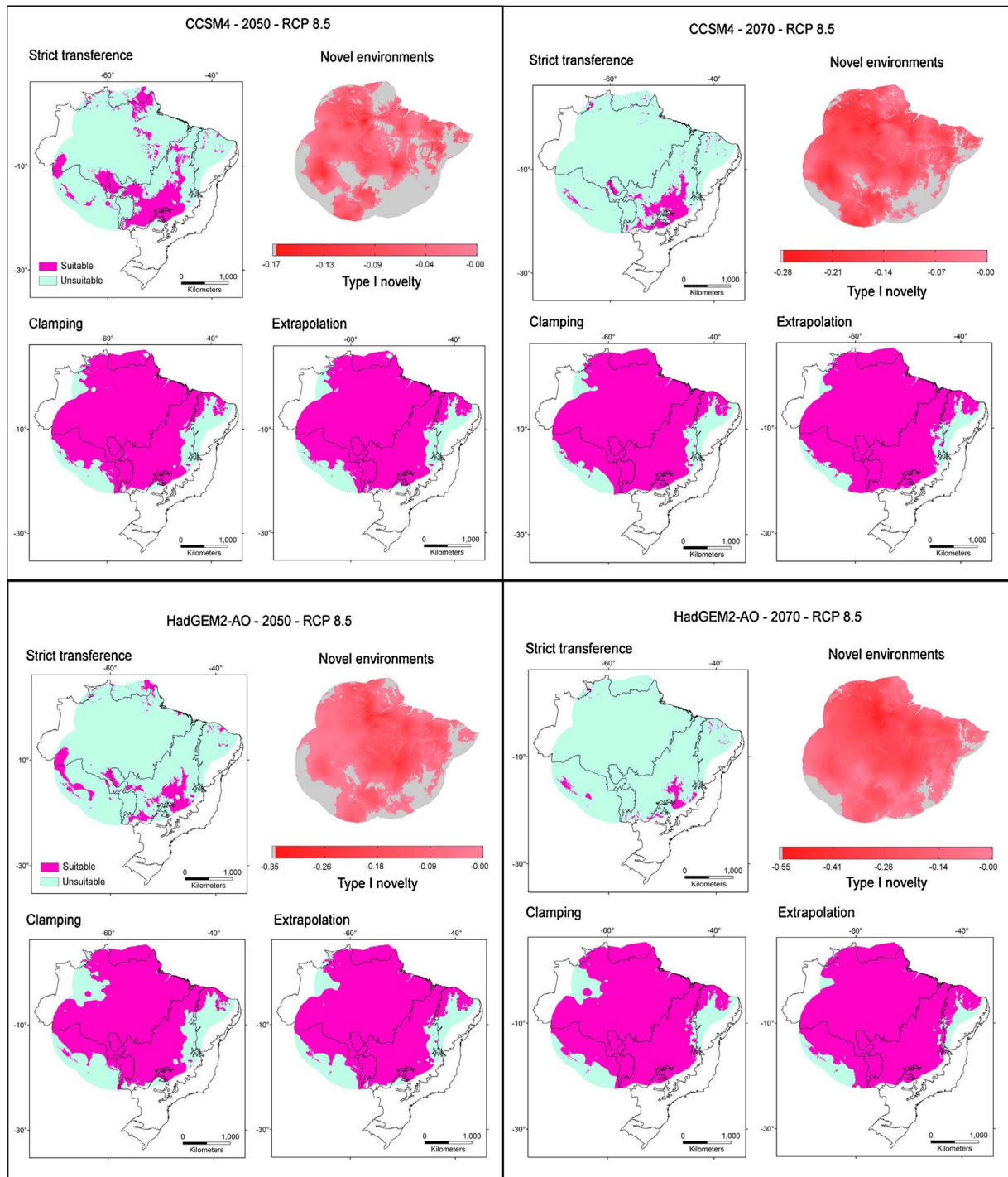
Amblyomma cajennense s.s.

Fig. 4. Ecological niche models for *Amblyomma cajennense* s.s. in 2050 and 2070 according to future climate models CCSM4 and HadGEM2-AO. **Strict transference:** Suitable (pink) and unsuitable areas (light blue) predicted for 2050 (left) and 2070 (right) in analogous environmental conditions between present-day climate and future climate models CCSM4 (top) and HadGEM2-AO (bottom). Predictions were truncated in non-analogous environments to avoid extrapolation. **Novel environments:** Areas with future climates conditions not presently available in the study area are in red (Type I novelty). Areas with analogous environments are in gray. **Clamping:** Models with clamping activated in Maxent were allowed to predict suitability (pink) in novel conditions. **Extrapolation:** Models with clamping and extrapolation activated in Maxent were allowed to predict suitability (pink) in novel conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

climate change on the epidemiology of tick-borne diseases including phylogeographic assessments to elucidate if, across the entire range of the *A. cajennense* complex, lineages differ in their physiological tolerances to climate. This information would help to better define dispersal regions, *M.* Future lines of research could also include assessing the effects of climate change on parasite survival on different life stages

(e.g., larva vs. nymph vs. adults), which may differ. Estimating tolerance limits to temperature for both, parasites and hosts, would help to determine temperatures in which hosts will be free of parasites (host's thermal refugia *sensu* Cizauskas et al., 2017). Here we assumed that ticks would be able to find suitable conditions in tandem with host, which may be an overestimation of the potential distribution of ticks.

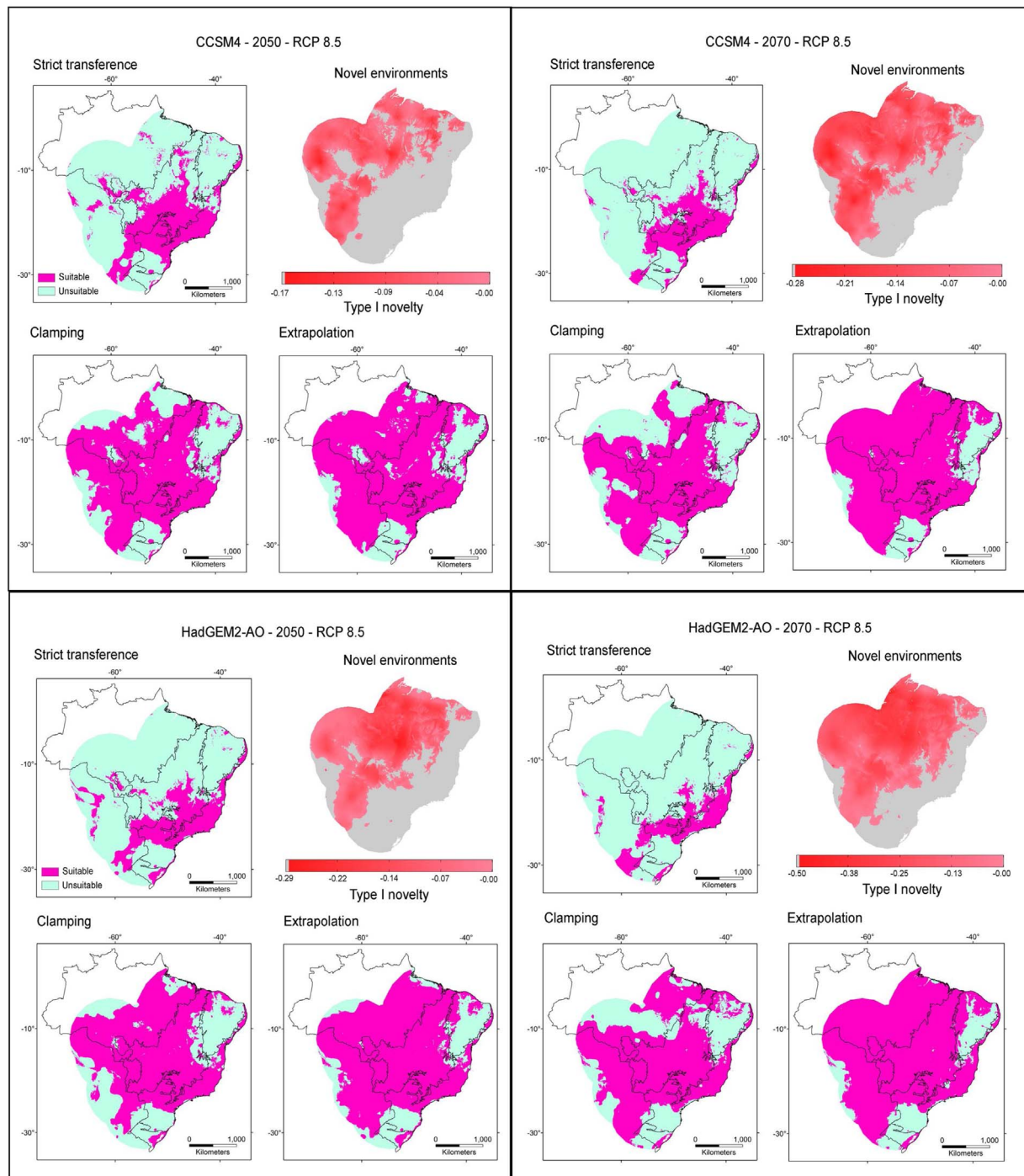
Amblyomma sculptum

Fig. 5. Ecological niche models for *Amblyomma sculptum* in 2050 and 2070 according to future climate models CCSM4 and HadGEM2-AO. **Strict transference:** Suitable (pink) and unsuitable areas (light blue) predicted for 2050 (left) and 2070 (right) in analogous environmental conditions between present-day climate and future climate models CCSM4 (top) and HadGEM2-AO (bottom). Predictions were truncated in non-analogous environments to avoid extrapolation. **Novel environments:** Areas with future climates conditions not presently available in the study area are in red (Type I novelty). Areas with analogous environments are in gray. **Clamping:** Models with clamping activated in Maxent were allowed to predict suitability (pink) in novel conditions. **Extrapolation:** Models with clamping and extrapolation activated in Maxent were allowed to predict suitability (pink) in novel conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Thus, future models should explore the co-occurrence of host species in areas predicted suitable for ticks (Cizauskas et al., 2017).

Ecological niche models for *A. cajennense* s.s. and *A. sculptum*, under present-day conditions, had impressive spatial heterogeneity in the uncertainties, both in suitable and unsuitable areas. We included maps of uncertainty in predictions to highlight the areas that should be

considered with special caution. The quality of occurrences may be an important source of uncertainty in the ecological niche models (Beale and Lennon, 2012). Errors of georeferencing and the inclusion of false positive occurrences would add error to the calibration process, incrementing uncertainty. In this sense, our study used information on the distribution of the species from populations in Brazil with extreme

precaution to assure precision in the geolocation and identification of the individuals (Martins et al., 2016). Variable selection can also contribute to generate uncertainty. For example, using many highly-correlated variables will result in models with high overfit (Peterson 2014). To avoid this, we used a reduced number of uncorrelated environmental variables. Finally, different algorithms can generate different results (Qiao et al., 2015), we mitigated this by exploring 20 different parameter values selecting the model configuration with the best fit to the data. Providing uncertainty estimates of forecasts provides information to identify areas with high accuracy for model interpretation (Reeves et al., 2015). Here, uncertainties were apparently associated with regions with low number of records.

Our maps of suitability and uncertainty could be used in tandem to identify areas where spotted fever is not reported yet, but in which models predict, with high accuracy, suitable conditions for the vectors. On the other hand, sites predicted suitable but with high uncertainty should be considered with caution when assigning public health resources. The need of reporting model uncertainty in a spatial context is a recent practice in ecological niche modeling of infectious diseases (e.g., Peterson and Samy 2016) and should be adopted as a common practice when mapping disease transmission risk. Public health authorities, as well as journal reviewers, could help in the task of making uncertainty maps an essential condition of present-day and future maps of vectors' potential distribution.

An additional source of uncertainty is the prediction in novel environments based on the extrapolative behavior of models in conditions beyond the range of values available in the calibration data; maps identifying novel climates should support the forecasts of vectors distributions in novel areas and future climates to determine regions of extrapolation and perilous predictions (Mesgaran et al., 2014). Thus, we also propose that reporting areas with novel environments should be indispensable in studies aiming to predict distribution of species under future climate models, otherwise, interpretation lacks critical information.

In conclusion, suitable areas for *A. cajennense* s.s. and *A. sculptum* populations in Brazil may be expected to decrease under current trends of climate change. Decreases were associated to novel climates across the species distributions and our assumption of niche conservatism (i.e., no adaptation of species to novel climates). Previous studies anticipating expansions of vector populations due to climate change should be considered with caution as they may assume that model extrapolation correctly anticipates species response to novel climates and that species would evolve rapidly for adaptation to warming conditions.

Competing interests

The authors have declared that no competing interests exist.

Funding

SVO received financial support (scholarship) from CAPES, Brazil (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, www.capes.gov.br). RGG was supported by a fellowship from CNPq, Brazil. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Acknowledgments

We are thankful to the staff of the Unidade Técnica de Vigilância de Zoonoses of Ministry of Health, Brazil. We thank A. T. Peterson for reviewing the manuscript. Christine Lee and Melissa Joy Oubre provided critical comments to this manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the

online version, at <http://dx.doi.org/10.1016/j.actatropica.2017.07.033>.

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