

## **Influence of anthropogenic factors on the geographical distribution of triatomine vectors of Chagas Disease**

### **Influência de fatores antropogênicos na distribuição geográfica de triatomíneos vetores da Doença de Chagas**

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## ABSTRACT

Previous work on Chagas disease at large spatial scales has not explored how interaction with humans can affect projections for geographical distribution of environmental suitability of vector species. Here, we compare niche-based species distribution models with climatic variables as predictors ( $SDM_{Clim}$ ) and with climatic variables + human population density ( $SDM_{Human}$ ). Our results show that accounting for human population density helps refine the models to finer geographical scales. Also, different spatial patterns of accumulated environmental suitability were obtained by  $SDM_{Clim}$  and  $SDM_{Human}$ . Moreover, projections were more accurate for  $SDM_{Human}$  than for  $SDM_{Clim}$ . Our results show that considering human populations in SDMs for epidemiologically relevant triatomine species can improve our understanding of macroecology and biogeography of environmental suitability for vectors of Chagas disease.

**Keywords:** disease ecology, ecological epidemiology, infectious diseases, neglected tropical diseases, maxent.

## RESUMO

Estudos anteriores sobre a doença de Chagas em grandes escalas espaciais não exploraram como a interação com humanos pode afetar as projeções para a distribuição geográfica da aptidão ambiental das espécies de vetores. Aqui, comparamos modelos de distribuição de espécies usando apenas variáveis climáticas como preditores ( $SDM_{Clim}$ ) com modelos que incluem variáveis climáticas + densidade populacional humana ( $SDM_{Human}$ ). Nossos resultados mostram que considerar a densidade da população humana ajuda a refinar os modelos para escalas geográficas mais finas. Além disso, diferentes padrões espaciais de adequabilidade ambiental acumulada foram obtidos por  $SDM_{Clim}$  e  $SDM_{Human}$ . Ainda, as projeções foram mais precisas para  $SDM_{Human}$  do que para  $SDM_{Clim}$ . Nossos resultados mostram que considerar fatores antropogênicos em SDMs para espécies de triatomídeos epidemiologicamente relevantes pode melhorar nossa compreensão da macroecologia e biogeografia para vetores da doença de Chagas.

**Palavras-chave:** ecologia de doenças; epidemiologia ecológica; doenças infecciosas; doenças tropicais negligenciadas; maxent.

## 1 INTRODUCTION

Infectious diseases cause approximately 9.6 million deaths each year, resulting in economic costs which can reach the order of billions of dollars/year and invaluable social costs (Lozano et al. 2012; Hotez et al. 2014; Murray et al. 2015; Stephens et al. 2016). From this universe, a group of etiological agents that have been little studied makes a disproportionate contribution to the global burden of human disease, being reported by the World Health Organization (WHO) as neglected tropical diseases (NTDs) (Murray et al. 2015; WHO 2015). They are among the major diseases affecting poor populations around the world, being estimated that about 1 billion people are infected by one of the 17 NTDs (Hotez et al. 2014; WHO 2015; WHO 2012).

In Latin America, Chagas disease, or American Trypanosomiasis, is the main NTD in most countries, presenting the greatest social impacts among all infectious diseases (Lozano et al. 2012; Hotez et al. 2014; WHO 2015). In Brazil, the South American country with the greatest number of NTDs, Chagas disease is the one with the highest case fatality rate (Lozano et al. 2012; Hotez et al.

2014; WHO 2015; WHO 2012; Coura & Borges-Pereira 2010). The human infections can occur by blood transfusion and by ingestion of food infected with the etiologic agent (the protozoan parasite *Trypanosoma cruzi*), however the primary form of transmission occurs by the bite of triatomine hematophagous insect, popularly called “kissing bugs” (Hemiptera, Reduviidae) (Coura & Borges-Pereira 2010). Due to the lack of vaccine and efficient chemotherapeutic treatments, epidemiological control strategies are focused on the control of vector infestations (Ministério da Saúde do Brasil 2015; Fikho et al. 2016). Despite the relative success of these actions, *T. cruzi* infection through triatomine vectors continues to represent a critical transmission route for the epidemiology of Chagas disease, with occurrences of home and peridomestic infestations, as well as records of new acute cases each year (Pereira et al. 2013). In this context, research that contributes to increase the consistency of the theoretical background of vector control practices remains needed.

Most ecological studies on the vectors of Chagas disease focus on small-scale, environmental factors affecting species distribution and abundance locally (i.e., household, peridomestic and wild microenvironments) (Dias et al. 2016; Bezerra et al. 2014; Waleckx et al. 2015; Costa & Lorenzo 2009; Diotaiuti et al. 1993; Coura et al. 1999). Previous studies have shown that triatomines can have different levels of adaptation to anthropogenic environments (Waleckx et al. 2015; Bustamante et al. 2007). They are organisms that can move around actively looking for microenvironments that meet their ecological demands and, thus, the species can infest best suited household and peridomestic areas (Bustamante et al. 2007; Parra-Henao et al. 2016). These different levels of successful colonization of anthropic environments can be interpreted as different levels of ecological interaction between different species of triatomine vectors and the human species. Given the prevalence of humans in the Earth's ecological systems, this interaction may represent a critical aspect of the niche of these species, influencing environmental suitability throughout geographical space and, potentially, affecting the spatial pattern of species distribution.

In this context, in the present study our objective was to investigate the influence of human species on environmental suitability of kissing bugs, triatomine vectors of Chagas disease. Specifically, we focused on epidemiologically relevant species in Brazil and assessed how the inclusion of spatial data of human population density affect the projections of niche-based spatial distribution models (SDMs) based in climate variables. Considering the relevance of Chagas disease in Latin America, the results of such analysis are important to the consistency of the knowledge that underpins the decisions regarding epidemiological control strategies.

## 2 MATERIALS AND METHODS

### 2.1 OCCURRENCE DATA

Through the platforms Species Link ([www.specieslink.org.br](http://www.specieslink.org.br)), GBIF (Global Biodiversity Information Facility – [www.gbif.org](http://www.gbif.org)), as well as searching directly in the literature, we obtained a total of 609 occurrence records for 14 of the 15 triatominae species reported as epidemiologically relevant by the Brazilian Department of Health Surveillance (*Panstrongylus geniculatus*, *P. lutzi*, *P. megistus*, *Rhodnius nasutus*, *R. neglectus*, *R. robustus*, *R. pictipes*, *Triatoma infestans*, *T. brasiliensis*, *T. maculata*, *T. pseudomaculata*, *T. rubrovaria*, *T. sordida* e *T. vitticeps*) (Ministério da Saúde do Brasil 2015; Fikho et al. 2016). Considering the findings of other authors (specially van Proosdij et al. 2016), we assumed 20 records as the minimal sample size for our analysis. So, *Triatoma rubrofasciata* was not considered in our analysis because we were able to compile less than five records throughout our study area. Records not identified at taxonomic level of species (e.g., identified at genus taxonomic level), with uncertainty in coordinates greater than 5 km, points of occurrence outside of continental areas, as well as repeated points at the same site (i.e., same pixel in our raster layers, having a resolution of 2.5 minutes – details in the next section), were excluded from our datasets. Our final datasets are provided at Supplementary Material. All procedures were performed in R software environment, using packages `rgibif` (<https://CRAN.R-project.org/package=rgibif>) and `raster` (<https://CRAN.R-project.org/package=raster>).

### 2.2 CLIMATIC VARIABLES AND HUMAN POPULATION DENSITY DATA

Following other authors (Diniz-Filho et al. 2013; Ceccarelli & Rabinovich 2015; Parra-Henao et al. 2016), we have modeled the niche of each one of our 14 triatomine species using species distribution models (SDMs) built upon climatic variables related to temperature (in °C) and precipitation (in mm). So, we used the 19 bioclimatic variables of the World Clim ([www.worldclim.org](http://www.worldclim.org); Hijmans et al. 2005), with resolution of 2.5 minutes ( $\approx 5\text{km} \times 5\text{km}$  in equatorial regions). In order to minimize multicollinearity, we employed a stepwise procedure to exclude highly correlated variables (i.e.,  $r > 0.7$ ). Specifically, first we calculated Pearson pairwise correlation among the 19 bioclimatic variables. Then, the employed algorithm finds the pair of variables which has the higher correlation and exclude one of them which has greater VIF (variance inflation factor). This procedure is iterated until no highly correlated variables remains. For convenience, we used the functions from `usdm` package (<https://CRAN.R-project.org/package=usdm>) in R software environment for our implementation of variable selection. After this procedure, the following variables were selected: Bio 2, Bio 3, Bio 8, Bio 10, Bio 11, Bio 12, Bio 13, Bio 14, Bio 15, Bio 16, Bio 18, Bio 19 (respectively, mean diurnal range, isothermality,

mean temperature of wettest 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 warmest quarter, precipitation of coldest quarter).

Human population density data were obtained from Gridded Population of the World, Version 4 (GPWv4) (Center for International Earth Science Information Network 2017), a spatially explicit database of human population (<http://sedac.ciesin.columbia.edu/data/collection/gpw-v4>). We used the most recent available data (which currently is for the year of 2015), at 2.5 arc-minutes and clipped for South America. All described procedures were performed in R software environment, using packages raster and usdm (<https://CRAN.R-project.org/package=usdm>).

### 2.3 MODELS OF SPECIES DISTRIBUTION

The niche-based species distribution models (SDMs) for each one of our 14 studied triatomine species were implemented with Maxent (Phillips et al. 2004; Phillips et al. 2006), using the package dismo (<https://CRAN.R-project.org/package=dismo>) in R software environment. To consider the interaction with humans in the SDMs we rely on the framework provided by Anderson (Anderson 2017). Relying on this conceptual framework, we built two types of models for each of the triatomine species: the  $SDM_{clim}$ , only with climatic variables; and the  $SDM_{Human}$ , with climatic variables + human population density.

To implement each type of model, for each species we generate background points through sampling 10,000 points across South America geographical area using a bias layer (Phillips et al. 2009; Kramer-Schadt et al. 2013; Fourcade et al. 2014). This procedure is one of the most recommended frameworks when accounting for spatial bias in the focal species occurrence data (Kramer-Schadt 2013; Fourcade et al. 2014). Our bias layer was produced using a spatial kernel density estimation algorithm (specifically, we used the function `kde2d` from the package MASS, in R software environment) and employing data for all Reduviidae occurrences available at GIBIF. Presences and background points were grouped together to form a consolidated dataset (i.e., one dataset for each one of our 14 focal triatomine species). Posteriorly, the set of points in each dataset were splitted in geographical blocks (or bins) with approximately sizes. So, the model can be calibrated using data from three blocks and validated with data from remaining one. This process was iterated until each block were used in the validation step. Also, we employed the partial area under the Receiver Operating Characteristic curve (pROC) as a measure of model performance. In practical terms, pROC allows the modeler to define a biologically acceptable level of omission in the performance of the SDM. In the present work, we use an acceptance limit of 5% of omission

error. Here, we used the R function `PartialROC` from the package `ENMGadgets` (<https://github.com/narayanibarve/ENMGadgets>) to compute pROC for each species-specific SDM.

Regarding Maxent parametrization, we assessed model complexity (i.e., combinations of Maxent features and regularization multipliers; see Moreno-Amat et al. 2008, Anderson & Gonzalez 2011) testing over each possible combination of features (being allowed linear, linear + quadratic, hinge, linear + quadratic + hinge, linear + quadratic + hinge + product, linear + quadratic + hinge + product + threshold, respectively) and regularization multipliers (ranging from 0.5 to 5.5, by steps of 0.5). The outputs of each model parametrization were compared through AICc scores and the one with the lowest scores were used. Then, for each species, SDMs with the selected parametrization were used to implement spatial projections of environmental suitability (using all occurrence data) along the geographical area inside an estimated accessible area. Following other authors (e.g., Poo-Muñoz et al. 2014), we hypothesized that the accessible area for one species is that within the minimum convex polygon described by its occurrence points in the geographical area plus a buffer equal to the mean distance between each occurrence point and the centroid of the set of points. Finally, SDMs' projections were converted in binary maps (0=non-habitat; 1=suitable habitat) using species specific threshold based on omission error (Peterson et al. 2008). In the present study, we used an omission error level of 5%.

All procedures described here were performed in R software environment using the packages `ENMeval` (<https://CRAN.R-project.org/package=ENMeval>), `ENMGadgets` (<https://github.com/narayanibarve/ENMGadgets>) and `raster`.

Given that human population data could be considered as a scenopoetic predictor variable in the SDMs, we infer ecological influence of human density on environmental suitability for each tritaomine species in terms of Maxent metrics of variable importance. Specifically, we rely on Maxent's permutation importance metric as a measure of the relative influence of each predictor variable for the SDMs.

For suitability maps, we measured the pixel-by-pixel difference between  $SDM_{Human}$  and  $SDM_{Clim}$ , i.e.,  $SDM_{Human}$  minus  $SDM_{Clim}$ , allowing us to map (species specific) geographical discrepancies in modeled suitability with the inclusion of human density in the models. Here, such maps are filled with values ranging from -1 to 1 (naturally, sites where  $SDM_{Human}$  and  $SDM_{Clim}$  project similar suitability values are mapped with values closer to zero). Also, we mapped the overlap between binary maps for  $SDM_{Clim}$  and  $SDM_{Human}$  of each species, inspect the result visually, and calculate the proportion of concordance between maps (which were measured using the overlap area between binary maps produced by  $SDM_{Human}$  and  $SDM_{Clim}$  for each species, as well Pearson correlations for environmental suitability maps produced by each one of this model types for the

species). Finally, the accumulated suitability across species (i.e., pixel-by-pixel sum of suitability maps for the modeled species – divided by 14, as for 14 species this is the maximum possible value when summing up suitability from each species; hence our accumulated suitability map can be presented ranging from 0 to 1) were mapped for both kinds of SDMs, allowing us to inspect geographical patterns of environmental suitability for the focal triatomine species. As an additional assessment, we perform a Spatial Autoregressive Regression (SARs) model between records for new cases of Chagas disease and accumulated suitability projections produced by  $SDM_{Human}$  and by  $SDM_{Clim}$ . We used data for Brazilian municipalities for the last 10 years (2007-2017), made available by Sistema de Informação de Agravos de Notificação at <http://datasus.saude.gov.br/> (see Supplementary Material). The spatial autocorrelation of residuals of models were analyzed from spatial correlogram of Moran's I. The software SAM 4.0 was used for SAR (Rangel et al. 2010).

### 3 RESULTS

Our assessment of  $SDM_{Clim}$  and  $SDM_{Human}$  showed that human population density represents an important variable for the models. For most modeled species, SDMs have better performance when human population density is considered among the predictor variables, increasing pROC by 26.68% on average. Moreover, human population density always performed as one of the main variables of the set of the predictor variables used, being the most important one for most of the species (9 of 14 triatomine species). Among this last group of species, the largest differences in model performance (i.e.,  $\Delta pROC$ ) were observed for *P. geniculatus* and *T. infestans*.

Table 1: Performance metrics (pROC) for the implemented species distribution models (SDMs). Species names are arranged in the rows, models and performance metrics are arranged in the columns of the table.  $SDM_{Clim}$  and  $SDM_{Human}$  are the models with and without human population density as a predictor variable, respectively (see Material and Methods section);  $\Delta pROC$  stands for the difference of pROC between the different models (values in bold represents loss in performance when human population density is added to the SDM); the permutation importance of human population density as a predictor variable in the  $SDM_{Human}$  were computed by the Maxent algorithm and are provided in the last column.

Species	pROC		$\Delta pROC$	Permutation importance of human pop. density in $SDM_{Human}$
	$SDM_{Clim}$	$SDM_{Human}$		
<i>Panstrongylus geniculatus</i>	0.578	0.982	0.404	90.813
<i>Panstrongylus lutzi</i>	0.836	0.987	0.151	95.536
<i>Panstrongylus megistus</i>	0.686	0.979	0.293	88.034
<i>Rhodnius nasutus</i>	0.792	0.993	0.201	70.068
<i>Rhodnius neglectus</i>	0.759	0.992	0.233	38.106
<i>Rhodnius pictipes</i>	0.736	0.863	0.127	44.538
<i>Rhodnius robustus</i>	0.842	0.917	0.075	27.464
<i>Triatoma brasiliensis</i>	0.764	0.99	0.226	92.154
<i>Triatoma infestans</i>	0.635	0.941	0.306	23.041
<i>Triatoma maculata</i>	0.901	0.886	<b>-0.015</b>	3.900
<i>Triatoma pseudomaculata</i>	0.827	0.979	0.152	90.685
<i>Triatoma rubrovaria</i>	0.822	0.904	0.082	7.065
<i>Triatoma sordida</i>	0.789	0.994	0.205	55.192
<i>Triatoma vitticeps</i>	0.747	0.972	0.225	72.310

Geographically, considering the human population density in triatomines SDMs increased to spatially heterogeneous projections of suitability. While  $SDM_{Clim}$  tended to project suitability more continuously distributed across large geographical areas,  $SDM_{Human}$  tended to produce more discontinuous projections throughout the space. This can be verified through the overlap between binary maps (Figure 1; Table S2 in Supplementary Material) and the distribution of suitability difference (Figure 2) between  $SDM_{Clim}$  and  $SDM_{Human}$  of each species.



Figure 1: Results of Maxent models for the 14 triatomine species considered in this study.  $SDM_{Human}$  and  $SDM_{Clim}$  are compared through overlapping binary maps of each species.

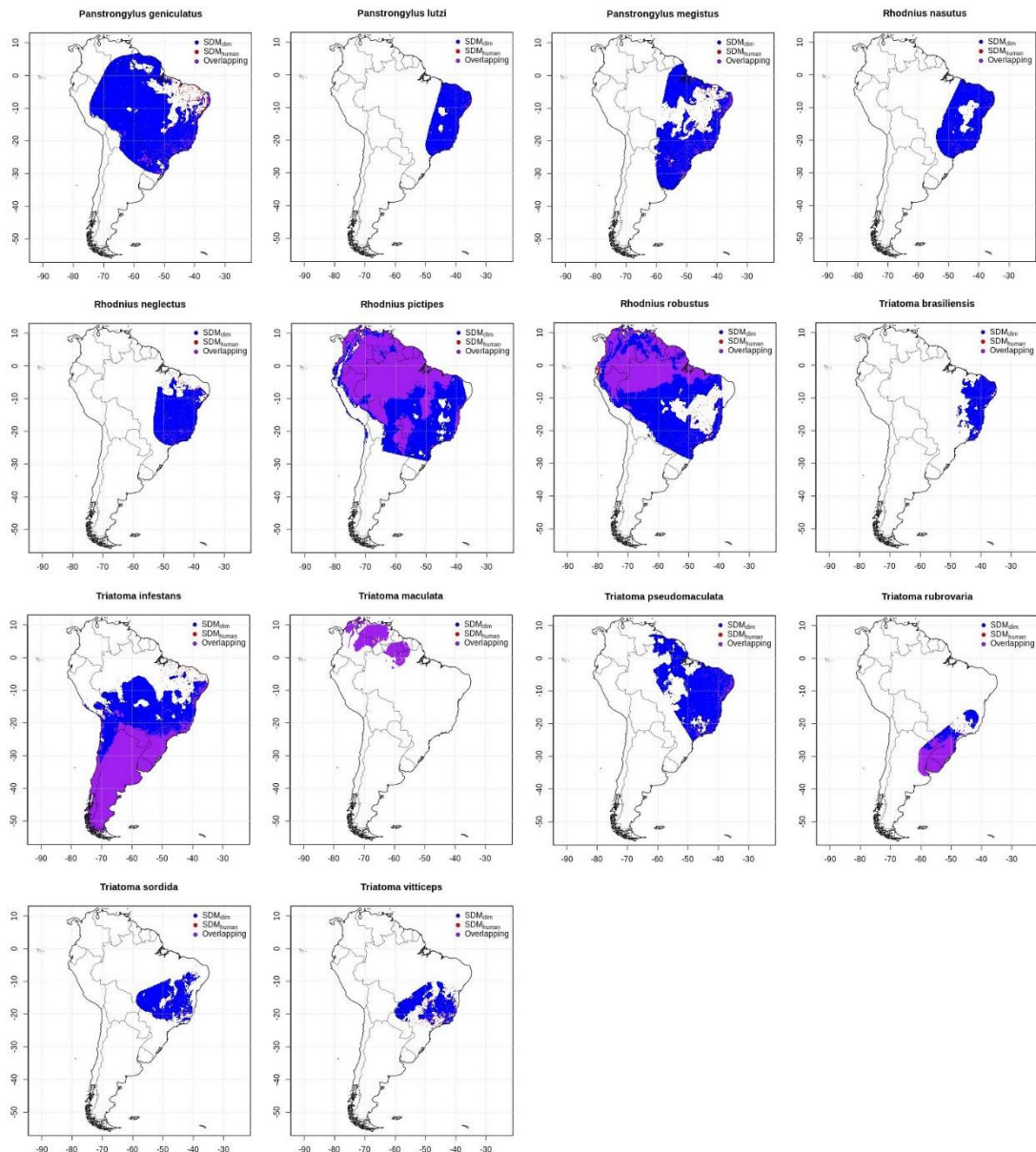
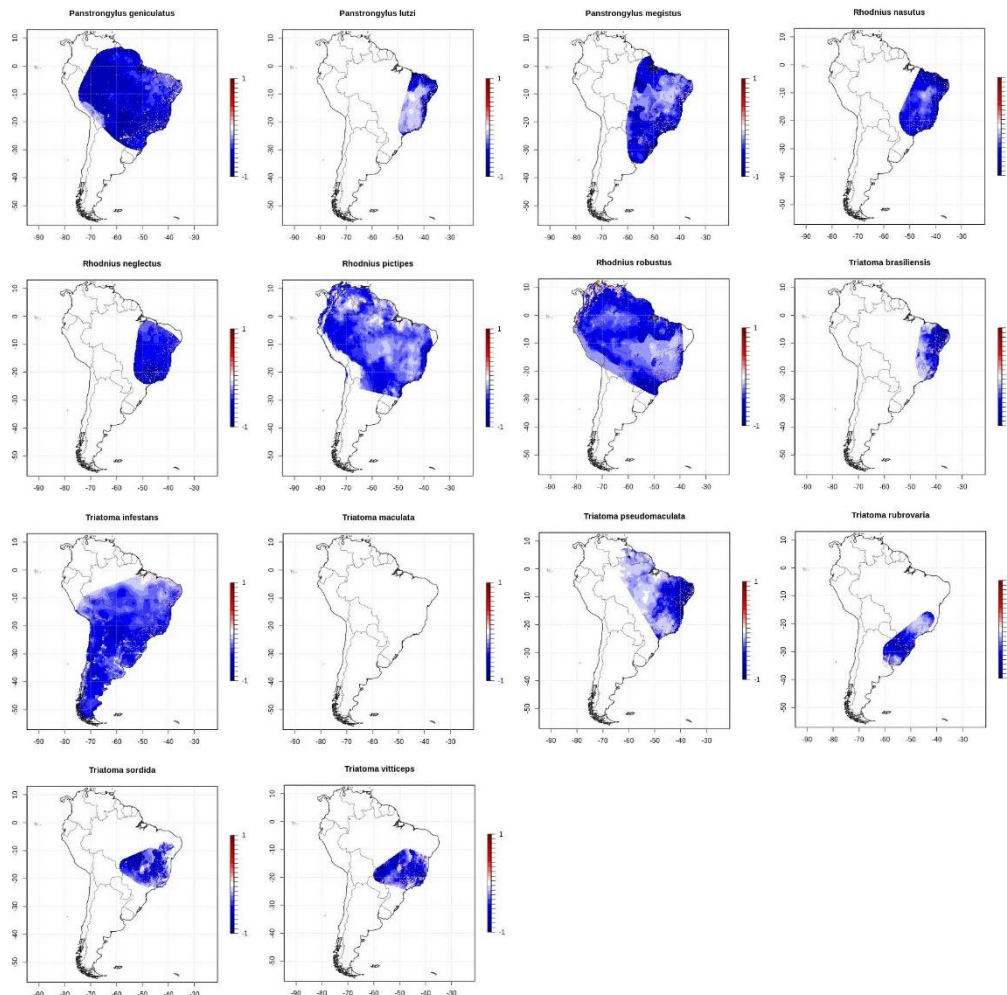


Figure 2: Results obtained from the (pixel-by-pixel) difference between projections of  $SDM_{Clim}$  and  $SDM_{Human}$  for each triatomine species (i.e., suitability map obtained with  $SDM_{Human}$  minus suitability map obtained with  $SDM_{Clim}$ ). Values in the maps range from -1 (blue) to 1 (red). So, regions where the inclusion of human density in SDMs led to lower predictions of suitability are mapped in blue tons. Regions where accounting for human density increases modeled suitability are mapped in red tons.

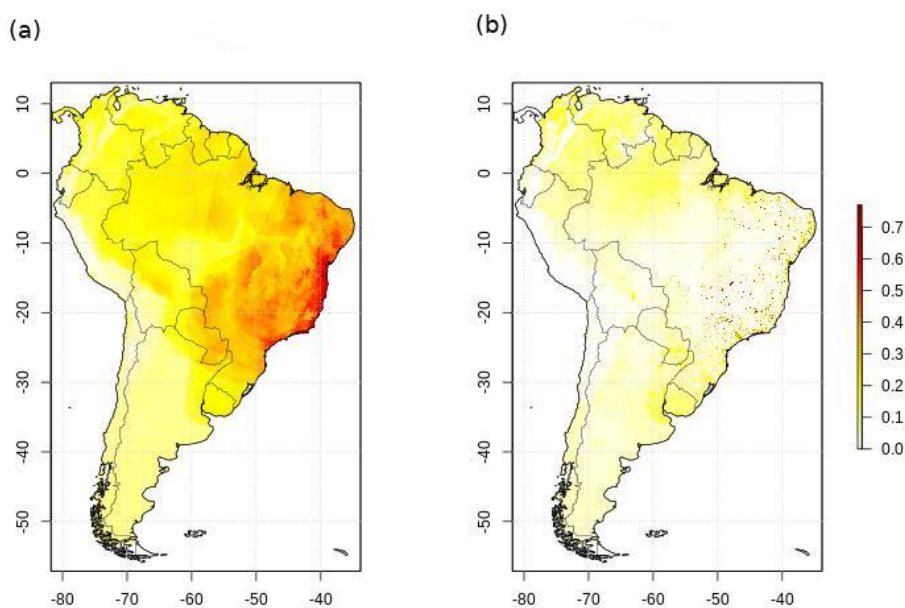


Comparatively, for the species which human population density have higher influence in the models' performance we observed the lowest overlay in binary maps. For example, for *P. lutzi* and *T. pseudomaculata* we obtained a permutation importance of 91.913 and 88.502 for human population density and binary maps overlap were 0.049 and 0.096, respectively. For *T. rubrovaria* and *T. maculata* we obtained 0.429 and 2.989 for permutation importance and 0.647 and 0.917 for binary maps overlap, respectively. However, in general, this does not represent improvement in SDM performance. The  $\Delta pROC$  were 0.051, 0.028, 0.008, -0.008 for *P. lutzi*, *T. pseudomaculata*, *T. rubrovaria* and *T. maculata*, respectively. Apparently, species with higher delta pROC are the ones with higher differences between  $SDM_{Clim}$  and  $SDM_{Human}$  projections, in terms of geographical extension. However, this is not conclusive.

Beyond the differences in terms of geographical areas, human population density affected environmental suitability distribution (as a continuous response variable) throughout the overlapping areas projected by  $SDM_{Clim}$  and  $SDM_{Human}$ . In this sense, we observed that suitability was higher at the southern portion of the modeled distribution of *T. rubrovaria* when human density is considered in the SDM. For *T. maculata*, higher suitability throughout the whole modeled distribution area is obtained with  $SDM_{Human}$ . For other species with higher overlap (i.e., *R. pictipes*, *T. infestans*, *R. robustus*) no clear or relevant patterns were observed.

The results for accumulated suitability (Figure 3) shows that high quality habitats for most of the species analyzed are located at northeastern and south-eastern Brazil, despite the consideration of human population density in SDMs. Accounting for human density, we observed that most of the accumulated environmental suitability are associated to localities populated by humans. The accumulated environmental suitability throughout northern and southern Brazil were lower and exhibits a more continuous distribution, not associated to human populated localities. Spatial Autoregressive Regression between records of new Chagas disease cases (for Brazilian municipalities, between 2007 and 2017) and accumulated suitability obtained from  $SDM_{Human}$  showed a statistically significant positive slope (0.621, p-value < 0.05), being positive but not statistically significant (0.622, p-value > 0.05) when projections from  $SDM_{Clim}$  were used. Detailed results are available in Supplementary Material.

Figure 3: Map of accumulated environmental suitability for epidemiologically relevant triatomine species in Brazil. Each map was produced by adding the suitability map projected for each triatomine species using Maxent. Results for  $SDM_{Clim}$  (a) and  $SDM_{Human}$  (b) are presented. Higher values indicate locations with greater accumulation of suitability (considering the 14 epidemiologically relevant triatomine species studied here) and are indicated in darker shades of red.



#### 4 DISCUSSION

Together, our results showed that the inclusion of the human population density can affect the projections of environmental suitability obtained from SDMs. Ecologically, human density performs as a relevant environmental covariate for the niche of the analyzed triatomine species. So, on the one hand, human populations trigger a range of environmental alterations which biologically favor (at least) most of the analyzed studied species. These environmental alterations comprehend an amalgam of local conditions, being not it possible here to specify which dimensions of the triatomine species niche were decisive for the differences observed between  $SDM_{Clim}$  and  $SDM_{Human}$ . On the other hand, it is precisely the generality of such environmental alteration that allows us to argue that the ecological interaction among human density and triatomine species may represent a relevant aspect for the ecological niche of these vector species. Future work that seeks to thoroughly analyze the nature of anthropogenic environmental changes and how they affect the availability of conditions and resources for triatomine vectors may advance and deepen our results, paving the way for highly detailed projections in time and space to become possible and benefiting the accurate identification of sites with high suitability for proliferation of triatomine vectors.

Despite our focus in triatomine species with epidemiological relevance for Brazil (see Ministério da Saúde do Brasil 2015 and Fikho et al. 2016), the geographical patterns of accumulated environmental suitability mapped by  $SDM_{Clim}$  is concordant with patterns of species richness provided by other authors who investigated the triatomine group more comprehensively. The most

extensive studies were Diniz-Filho et al. (2013) and de la Vega et al. (2015), the first providing an analysis of the species richness patterns of 115 species for the whole Western Hemisphere and the second assessing the thermal tolerance of two species (*T. infestans* and *R. prolixus*), bringing insights into the distribution of the triatomine group as a whole. Specific studies were carried out for Venezuela (Ceccarelli & Rabinovich 2015; Medone et al. 2015), Argentina (Medone et al. 2015), Colombia and Ecuador (Cajo et al. 2016). For Brazil, in particular, Pereira et al. (2013) analyzed the distribution of eight species in the center-west region and de Melo-França et al. (2014) analyzed the distribution of the species complex *T. brasiliensis*, which occurs mainly in the Brazilian northeast. Such results are in consonance with the species distributions and the patterns of environmental suitability obtained through  $SDM_{Clim}$ .

As evidenced in our results, human population density can affect model projections for geographical distribution of environmental suitability of Chagas disease vectors. Despite of that, even before the advent of large-scale, macroecological studies on triatomine distribution and richness, *T. infestans* was recognized as an emblematic example of the potential of human influence on the geographical distribution of vector species in this group (Waleckx et al. 2015). This is a species with wide distribution in South America, which is pointed out in the literature as a consequence of its high association with humans (Waleckx et al. 2015; Waleckx et al. 2011). Due to its ability to completely perform its life cycle and establish persistent populations in anthropic environments, this triatomine species was the main target of measures of epidemiological control of Chagas disease over the last decades (Ministério da Saúde do Brasil 2015; Fikho et al. 2016; Waleckx et al. 2015). However, *T. infestans* are not among the species most influenced by human population density in our analysis. In fact, isothermality (i.e., variable Bio 3 variable in our SDMs) was the most influential predictor in the SDMs for this species. We highlight that such apparent discrepancy relies on the different spatial scales involved, which was continental scale in our implemented models whilst classical works on *T. infestans* ecology focused on local scale. This species has historic occurrence records from central Argentina and north Bolivia to the Brazilian Atlantic coast, and the west coast of southern Peru (Schofield 1994; Galvão 2014). So, niche-based models, focusing on Grinnellian niche, should capture the range of climate conditions in which the species can maintain viable populations (Peterson et al. 2012). In the case of *T. infestans*, the influence of human species at local spatial scales does not scale up to macro-spatial scales, where climate conditions tend to be critical. This draws attention to the fact that the influence of biotic interactions may not be linearly transposed between different spatial scales during construction and interpretation of environmental suitability models.

It has been widely recognized that the global climate change will have broad impact in the distribution of the infectious diseases (Ceccarelli & Rabinovich 2015; Altizer et al. 2013). The extent to which human populations will suffer the adverse effects of this biogeographical reorganization of diseases depends closely on the consistency of the knowledge that underpins decision makers in public health systems (Ceccarelli & Rabinovich 2015). Previous works show that, unlike diseases with direct transmission among humans, zoonoses are not uniformly distributed on the globe, presenting strong geographical bias (Jones et al. 2008; Smith et al. 2014). Furthermore, zoonoses account for most of the emerging infectious diseases in humans (Jones et al. 2008; Smith et al. 2014). In this context, the macroecology and biogeography of species that are related to the epidemiological cycle of etiological agents of infectious diseases assumes a critical aspect in epidemiology. Moreover, it is important to emphasize that both vector species and reservoir species may present different levels of ecological interaction with humans, and accounting for such nuances in SDMs can yield new insights in spatial epidemiology of vector born infectious diseases.

Our results show that more detailed information about the distribution of environmental suitability and accumulated environmental suitability throughout geographical space can be obtained from niche-based species distribution models when human population density is taken into account. Finally, our findings may serve to subsidize better estimates of areas vulnerable to Chagas disease, as well as to highlight that environmental variables related to human populations should be progressively explored in upcoming macroecological and biogeographical research on vector ecology.

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