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Potential distributions of the parasite *Trypanosoma cruzi* and its vector *Dipetalogaster maxima* highlight areas at risk of Chagas disease transmission in Baja California Sur, Mexico, under climate change

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Abstract

Dipetalogaster maxima is a primary vector of Chagas disease in the Cape region of Baja California Sur, Mexico. The geographic distribution of *D. maxima* is limited to this small region of the Baja California Peninsula in Mexico. Our study aimed to construct the ecological niche models (ENMs) of this understudied vector species and the parasite responsible for Chagas disease (*Trypanosoma cruzi*). We modelled the ecological niches of both species under current and future climate change projections in 2050 using four Representative Concentration Pathways (RCPs): RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5. We also assessed the human population at risk of exposure to *D. maxima* bites, the hypothesis of ecological niche equivalency and similarity between *D. maxima* and *T. cruzi*, and finally the abundance centroid hypothesis. The ENM predicted a higher overlap between both species in the Western and Southern coastal regions of the Baja California Peninsula. The climate change scenarios predicted a Northern shift in the ecological niche of both species. Our findings suggested that the highly tourist destination of Los Cabos is a high-risk zone for Chagas disease circulation. Overall, the study provides valuable data to vector surveillance and control programs.

KEYWORDS

Abundance, climate change, *Dipetalogaster maxima*, ecological niche modelling, population risk, *Trypanosoma cruzi*

INTRODUCTION

Trypanosoma cruzi (Chagas 1909) is the parasite responsible for Chagas disease (CD). Chagas disease affects 6–7 million people worldwide and causes approximately 10,000 deaths annually (WHO, 2021). It is currently the most common parasitic infection in Latin America and the third most important worldwide (Pinazo & Gascon, 2015; WHO, 2021). The annual incidence of Chagas disease in the Americas alone reaches 30,000 cases and leads to 14,000 deaths (González-

Zambrano et al., 2020). The global economic burden of CD is approximately estimated as \$7.19 billion USD per year (Lee et al., 2013). The disease has no vaccine or specific drug treatment (Lidani et al., 2019). The World Health Organization (WHO) protocol recommended the combinations of benznidazole and nifurtimox to successfully treat CD (Thakare et al., 2021). This current treatment regimen is likely associated with some efficacy limitations in the chronic phase of CD infection and side effects in its prolonged therapy (Thakare et al., 2021). The disease can be transmitted via various routes; however, the edical and Veterinary

vector-borne disease (VBD) transmission of *T. cruzi* is the main route of new infections (WHO, 2021). *Trypanosoma cruzi* is transmitted through the exposure of the bite site to the infected faeces and urine of triatomine bugs or through the consumption of food that is contaminated with the infected bug faeces (WHO, 2021). There are approximately 130 indigenous species of triatomine bugs (i.e., kissing bugs) (Hemiptera: Reduviidae) in the Americas. These reduviid bugs have been reported as primary vectors of *T. cruzi* (Galvão et al., 2003; WHO, 2021). The geographic distribution and vectorial capacity of these bug species are crucial to define the most effective means of CD control based on vector-control programs (Rassi Jr. et al., 2010).

The Cabo region of Baia California Sur (BCS) is home to the endemic triatomine species Dipetalogaster maxima (Uhler, 1984). This vector species has epidemiological implications in CD transmission since it has been found to naturally carry T. cruzi (Jiménez et al., 2003). Surprisingly, very few studies have attempted to study the natural habitats of D. maxima (Jiménez et al., 2003; Jiménez & Palacio, 1999; Ryckman & Ryckman, 1967). These studies are necessary to assess the distributional potential and abundance of the vector species and their key roles in CD transmission in Mexico. One of the few D. maxima studies reported that the species can inhabit peridomestic and intradomestic rural areas and has been reported to be a very aggressive bug species that ingests large blood meals during daylight (Jiménez & Palacio, 1999). These traits are probably the main drivers explaining the previous efforts of using D. maxima for xenodiagnosis purposes (Cuba et al., 1979; Marsden, 1986; Raul et al., 2012); the species has the natural ability to adapt to artificial conditions in the laboratory. Dipetalogaster maxima is also susceptible to infection with diverse strains of T. cruzi (Marsden, 1986; Raul et al., 2012).

Ecological niche modelling (ENM) was previously used to assess the distributional potential of T. cruzi and its triatomine vectors (Altamiranda-Saavedra et al., 2020; Eberhard et al., 2020; Parra-Henao et al., 2016; Peterson et al., 2002, 2011; Villalobos et al., 2019). Thus, ENM is used as a fundamental approach to better understand and manage CD in a particular geographic area (Altamiranda-Saavedra et al., 2020; Eberhard et al., 2020; Parra-Henao et al., 2016; Peterson et al., 2002, 2011; Villalobos et al., 2019). Overall, the evaluation of the risk and efficacy of any control measures for CD is challenging due to the lack of studies that encompass most of the parameters playing a role in the disease transmission cycle (e.g., the ENMs of the vectors, hosts, parasite, proximity to human populations, and environmental conditions). Knowledge of both the parasite T. cruzi and its 31 autochthonous triatomine vector species in Mexico remains incomplete. Geographic areas have been underrepresented in CD studies. This hinders the evaluation of the risk of VBD transmission in certain areas. The tourist destination of Cabo area of the southernmost region of the Baja California Peninsula is one of these areas. In 2018, this tourist destination received more than 950,000 visitors, marking it the second most important tourist destination of Mexico (http://www.wttc.org/). ENM can identify active transmission areas (Moo-Llanes et al., 2021) and provides important means to identify areas of vector surveillance and control priorities for successful vector control programs.

Recently, climate changes derive shifts in the distributional potential of vector-borne diseases via variations in the ecological niches of vectors, hosts, and parasites (Garza et al., 2014). A recent study reported significant shifts in the transmission of *T. cruzi* across North America based on the future climatic conditions in 2050 and 2070, resulting in an increased risk of VBD transmission in human populations (Carmona-Castro et al., 2018). Data pertaining to the infection rate of *T. cruzi* in *D. maxima* throughout its geographic distribution allows the estimation of the ENM of both the vector and the parasite in the BCS region under current climate patterns and under diverse climate change models.

An additional important question is the hypothesis of consistent relationship of the vector species density and the distance from the centre of the estimated geographic and climatic niche range (Martínez-Meyer et al., 2013; Yañez-Arenas et al., 2012). However, the distance-density question is still unresolved, some studies supported that the species are most abundant towards the centre of their niche or geographic range (Martínez-Meyer et al., 2013; Yañez-Arenas et al., 2012) and others failed to detect these consistent distance-density relationships (Dallas et al., 2017; Murphy et al., 2006). This relationship has epidemiological implications, particularly if higher vector densities derive the higher risk of Chagas disease circulation.

Thus, this study aimed to (1) construct the ENMs of *D. maxima* and *T. cruzi* in the Cape region; (2) assess the niche equivalency and similarity of *D. maxima* and *T. cruzi*; (3) assess the niche centroid and abundance hypothesis in the Cabo region of BCS; (4) construct the baseline maps to assess the climate change influences under diverse climate change scenarios; and finally (5) assess the population at risk of exposure to the bites of *D. maxima*.

MATERIALS AND METHODS

Study area

The southern region of BCS in Mexico has an annual average temperature of 22-24°C, and weather ranging from hot and arid to very hot and very arid according to Köppen's classification (García, 1973). The triatomine collection sites were selected based on previous sampling efforts in the area (Jiménez et al., 2003), emphasizing sites with exfoliative rocks and large boulder piles. The collection efforts were expanded to include broader areas outside the historical known distribution of D. maxima (File S1). These areas confirmed the limited geographical distribution of D. maxima in the southern region of BCS (Ryckman & Ryckman, 1967). The sites where D. maxima individuals were found fall within two types of vegetation: tropical deciduous forest and sarcocaulescent shrubland (de la Luz et al., 2000). The tropical deciduous forest vegetation has an average of 200-400 mm of annual precipitation, whereas the sarcocaulescent shrubland vegetation has an average annual precipitation of 200 mm (de la Luz et al., 2000; GonzáLez-Abraham et al., 2010).

Species occurrences and accessible regions

A database of D. maxima (N = 46), and T. cruzi (N = 14) occurrence records was compiled from scientific publications (Bello-Bedoy et al., 2019; Jiménez et al., 2003; Ramsey et al., 2015), our surveillance efforts (Flores-López et al., 2022), and the Global Biodiversity Information Facility database (https://doi.org/10.15468/dl.sa59ay). The identification of *D. maxima* was identified based on the previously published key (Usinger, 1939). Data were collected to only include the BCS region of Mexico. The occurrence records of T. cruzi are exclusively based on the presence of the parasite in triatomine vectors. The records of T. cruzi were cleaned to include only records identified via a T. cruzi-specific polymerase chain reaction using the previously published protocol (Rivas-García et al., 2020). All occurrence records are available in supporting information materials (File S1 and Figure S1). The occurrence datasets were subjected into two cleaning steps to reduce the effect of spatial autocorrelation: (1) all duplicate records were omitted, and (2) all records were thinned based on a distance filter of 1 km (a single unique record/pixel). The final datasets of occurrence records were randomly split into two subsets: training data (70%) and testing data (30%) using the random k-fold method (Moo-Llanes et al., 2021). The latter method partitions the occurrence localities randomly into a user-specified number of (k) bins as described in detail in the previous protocol (Muscarella et al., 2014). The accessible region "M" (Barve et al., 2011) was hypothesized to include a 5-km radius buffer around the occurrence records and was subsequently overlayed on the ecoregion shapefile of the World Wildlife Fund (Olson et al., 2001). The selection of a 5-km radius buffer was based on the sustained flying activity of the vector D. maxima, allowing only limited dispersal of the species in this area (Cavagnari et al., 2000). The accessible region "M" represents the areas to which a species has had access over a relevant time period because of its movement and colonizing capacities and the structure of barriers and distances (Barve et al., 2011). The accessible area is a critical determinant to the outcome of model calibration, model evaluation, and model comparison (Barve et al., 2011).

Model covariates

Fifteen out of 19 bioclimatic variables (WorldClim version 2.0) were used to construct ENMs (Fick & Hijmans, 2017). We excluded the variables that combine temperature (mean temperature of the wettest quarter, and mean temperature of the driest quarter) and precipitation (precipitation of the warmest quarter and precipitation of coldest quarter) owing to their spatial artefact (Escobar et al., 2014). All variables had a spatial resolution of $\approx 1 \text{ km}^2$. We used four sets of environmental predictors presenting diverse combinations of bioclimatic variables. Set 1 used 15 bioclimatic variables from WorldClim (Moo-Llanes et al., 2021): Bio 1 = Annual Mean Temperature, Bio 2 = Mean Diurnal Range; Bio 3 = Isothermality; Bio 4 = Temperature Seasonality; Bio 5 = Maximum Temperature of Warmest Month; Bio 6 = Minimum Temperature of Coldest Month; Bio 7 = Temperature Annual

Range; Bio 10 = Mean Temperature of Warmest Quarter; Bio 11 = Mean Temperature of Coldest Quarter; Bio 12 = Annual Precipitation; Bio 13 = Precipitation of Wettest Month; Bio 14 = Precipitation of Driest Month; Bio 15 = Precipitation Seasonality; Bio 16 = Precipitation of Wettest Quarter; and Bio 17 = Precipitation of Driest Quarter. Set 2 used jackknife processes in MaxEnt to select the distinct sets of variables that contributed most to the models (>90%), using the Pearson correlation (r < 0.8) to eliminate one variable per pair. The variable with the lowest spatial autocorrelation along (1) the pair of variables to be evaluated and: (2) other combinations of bioclimatic variables were eliminated (Moo-Llanes et al., 2020a, 2013, 2021, 2020b); Set 2 included Bio 1, Bio 4, Bio 5, Bio 6, Bio 7, Bio 12, Bio 13, Bio 14, and Bio 15. Set 3 included variables used to construct ENMs of diverse medically important disease vectors (Moo-Llanes et al., 2020a, 2021, 2020b): Bio 4, Bio 10, Bio 12, Bio 13, Bio 15, and Bio 17. Finally, Set 4 used the variance inflation factor (VIF) (De Marco & Nóbrega, 2018; Estrada-Peña et al., 2013), which is a measure of levels of multicollinearity between pairs of variables in the usdm package in R. Values of VIF > 10 denote a potentially problematic correlation between covariates, indicating that these covariates should be carefully evaluated in model development (Moo-Llanes et al., 2021); Set 4 used five variables including Bio 1, Bio 4, Bio 7, Bio 12, and Bio 15.

Climate change scenarios

The ENMs were estimated based on the current climatic conditions and then projected into four scenarios of Representative Concentration Pathways (RCPs) for the year 2050. ENMs were projected using the four RCPs from the Fifth Assessment Report, representing the lowest to highest estimated greenhouse gas emissions: 2.6 (>430 ppm CO₂), 4.5 (580-720 ppm CO₂), 6.0 (720-1000 ppm CO₂), and 8.5 (>1000 ppm CO₂) (Intergovernmental Panel on Climate Change, 2013.). We used the European Centre Hamburg Model (ECHAM6) general circulation model (GCM) that performs overall favourably compared to other GCMs (Rackow et al., 2018). This GCM has an improved representation of radiative transfer in the short wave (or solar) part of the spectrum, a completely new description of aerosol effects, and improved representation of surface albedo, including the treatment of melted ponds on sea ice, and a vastly improved representation of the middle atmosphere as part of the standard model (Stevens et al., 2013).

Ecological niche modelling

We created 992 ENMs in the *kuenm* R package based on MaxEnt algorithm. We allowed MaxEnt runs based on different model settings: (1) combinations of four sets of bioclimatic variables; (2) 10 values of regularization multiplier (1, 2, 3, 4, 5, 6, 7, 8, 9, 10); and (3) all 29 possible combinations of five feature classes (linear, quadratic, product, threshold, and hinge) for each species (Cobos et al., 2019). The best candidate model was selected based on three criteria: (1) significance based on partial ROC and 5% omission rates of predictive ability; (2) performance-based on Akaike Information Criterion corrected (AICc) for small sample sizes; and (3) the Akaike information criteria (AIC): AICc, delta AICc, and AICc weights according to the previous protocol (Cobos et al., 2019). The AICc provide explicit criteria for selecting models of appropriate complexity. This metric is assessed by standardizing raw scores for each ENM so that all scores within the geographic space sum up to 1 and then by calculating the likelihood of the data given each ENM by taking the product of the suitability scores for each grid cell containing a presence. Both training and test records are used in calculating likelihoods. The number of parameters is measured simply by counting all parameters with a nonzero weight in the lambda file produced by MaxEnt. a small text file containing model details that MaxEnt produces as part of the modelling process (Warren & Seifert, 2011). The final model was based on the criteria described above and established by the early published protocol (Cobos et al., 2019). After model calibration, we created final models with the selected parameter values, using all occurrences after the corresponding thinning process, with 10 bootstrap replicates and logistic outputs (Cobos et al., 2019). To further visualize the effects of uncontrolled model projections on the future climate, we also developed projections allowing predictions in novel climates (i.e., extrapolation with activated clamping) for a transferred-use type of extrapolation with clamping to the RCPs (Intergovernmental Panel on Climate Change, 2013). We performed a mobility-oriented parity (MOP) analysis (Owens et al., 2013) comparing the environmental breadth of predictors in the "M" region (10% reference points sampled) with that in the projection area using the MOP function available in the kuenm R package (Cobos et al., 2019). The risk of extrapolation analysis defines the areas with strict extrapolation to avoid the risk of over-prediction in non-analogous environments (Owens et al., 2013).

Data analysis

We carried out three post-analyses: (a) evaluation of the exposed Mexican human population in BCS to CD via the bites of D. maxima; (b) niche conservatism and similarity to assess the overlap between D. maxima and T. cruzi; and (c) assessing the centroid-abundance hypothesis based on *D. maxima* niche. The human population at risk was estimated based on converting the continuous ENM into a binary map. The models were converted into binary maps based on the minimum allowable omission rate of 5% (E = 5%) (Peterson et al., 2008). The Mexican human population data were obtained from the Instituto Nacional de Estadística y Geografía (Available at www.inegi.gob.mx) (Moo-Llanes et al., 2013). We tested the niche conservatism to assess the overlap between D. maxima and T. cruzi using ENMTools in R (Warren et al., 2008). We tested the identity and background tests to assess if the pairs of niches are identical or similar than expected by chance alone based on Schoener's D statistics (Warren et al., 2008). This analysis allows comparing pairs of species (i.e., the vector D. maxima and the parasite T. cruzi) to assess the significant overlap between

species pairs based on the environmental space available for each species. The null hypothesis of niche equivalence and similarity was rejected if the Schoener's D values fell below the fifth percentile of the random-replicate distribution values. We also visualized the environmental space of both vector and parasite ENMs in the software Niche Analyst available at http://nichea.sourceforge.net/ based on the first three principal components out of the principal component analysis of the bioclimatic variables (Qiao et al., 2016). The Niche analyst allowed visualization of the niche overlaps of different species in environmental space (Qiao et al., 2016). Finally, we assessed the relationship between the geographic abundance patterns of D. maxima and the position in environmental space: this assessed the assumption of the possible decline in abundance towards the edges of their ecological niches (Altamiranda-Saavedra et al., 2020; Chaiyes et al., 2020; Martínez-Meyer et al., 2013). The niche and its centroid were attained by using abundance data (File S2) in 37 sites and measuring the distances between observations of population abundances and the niche centroid. The abundance of the triatomines was constructed based on the spontaneous collections in many field trips across the study area. The abundance of D. maxima was recorded in diverse georeferenced locations. A minimum-volume ellipsoid (MVE) in ntbox package in R was used (Osorio-Olvera et al., 2020). A total of 2450 candidate models were fit, in addition to the MVEs generated for all possible combinations of two or three variables selected from among 15 bioclimatic variables. The Mahalanobis distance to the niche centroid (DNC) and environmental values of population abundance records were computed using the niche centroid and minimum-volume covariance matrix of the selected MVEs. Finally, the Spearman correlations between the DNC and population abundance were calculated using the cor.test function in R to assess the relationship between the distance from the niche centroid and the abundance (Altamiranda-Saavedra et al., 2020).

RESULTS

A total of 1984 candidate models were built for the two species. Only 445 models were statistically significant, and six models met the omission rate, and AICc criteria were statistically significant. Finally, each species ENM met three selection criteria and was identified as the best candidate model based on its performance. The best models with their parameters are illustrated in Table 1 for each species. The ENM of D. maxima was anticipated in a large part of Los Cabos, mainly in the coastal zone. There is high suitability in tourism areas such as La Paz, El Centenario, Mátape, San Pedro, San Marcos, El Carrizal, Todos Santos, El Pescadero, San Rafael, La Tinaja, Cabo San Lucas, El Tule, Palmilla, San Jose del Cabo, Los Frailers, La Rivera, and El Sargento (Figure 1a). The ENM of T. cruzi (Figure 1b) showed high environmental suitability in areas on the West coast of Los Cabos from El Centenario, Mátape, San Pedro, San Marcos, El Carrizal, and Todos los Santos to San Jose del Cabo. The results of the MOP analysis between the accessible area "M" and the projection area in the current climate revealed a strict extrapolation in a limited geographic pocket in the western region of BCS (Figure 2).

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TABLE 1 Best candidate models of the vector Dipetalogaster maxima and the parasite Trypanosoma cruzi

Species	SBV	SSM	BCM	RM	FC	pROC	O. rate 5%	AICc	ΔAIC	AICc.W	Number of parameters
D. maxima	Set 4	208	4	2	Linear	1.17	0.00	775	0.00	0.24	2
				1	Linear, product	1.20	0.00	775	0.07	0.28	2
				2	Linear, quadratic	1.18	0.00	775	0.24	0.19	2
				1	Linear	1.12	0.00	775	1.82	0.14	3
T. cruzi	Set 4	208	2	1	Quadratic	1.33	0.00	236	0.00	0.37	2
				1	Linear, quadratic	1.33	0.00	236	0.00	0.29	2

Note: number of parameters column summarizes the combination of environmental variables, multiple regularizations, and features other than 0 that provide information for the construction of the model based on lambdas.

Abbreviations: Δ AlCc, delta Akaike information criterion corrected; AlCc, Akaike information criterion corrected; AlCc.W, Akaike information criterion corrected weight; BCM, number of best candidate models; FC, features classes; O. rate 5%, omission rate 5%; pROC, partial receiver operating characteristic; RM, regularization multiplier; SBV, sets of bioclimatic variables; SSM, number of statistically significant models.



FIGURE 1 Ecological niche modelling of the vector *Dipetalogaster maxima* (a), and the parasite *Trypanosoma cruzi* (b) in Baja California Sur, Mexico, based on environmental suitability of *D. maxima* and *T. cruzi* occurrences, respectively. The dotted points represent the occurrences of *D. maxima* and *T. cruzi*, respectively. The grey background presents areas with unsuitable conditions where the probability of species occurrence is zero. The photo on the right of the ecological niche of *D. maxima* represents an original photo of *D. maxima* taken by one of our coauthors (C.A. F.-L).



FIGURE 2 Extrapolation risk in the model projection of *Dipetalogaster maxima* and *Trypanosoma cruzi*. Extrapolation risk analysis is based on a mobility-oriented parity (MOP nearest 10% of reference points) in the present-day climatic conditions. The risk of extrapolation analysis defines the areas with strict extrapolation (i.e., extrapolation analysis represents the degree of similarity between conditions in accessible area "M" and projection area "G", and values of zero correspond to areas of strict extrapolation) to avoid misinterpreting the risk of over-prediction in non-analogous environments. The black points represent the occurrence records of *D. maxima* and *T. cruzi*.

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We estimated an overall total of 658,657 inhabitants (\approx 97.35%) of BCS population at the risk of potential contact with *D. maxima*. There were 1234 urban areas, of which 715 were geographically overlapped in areas with projected predictions of *D. maxima*. The five most densely inhabited cities co-localize with *D. maxima* presence, with an estimated exposed human population of 583,847 inhabitants (Figure 3). In 2050,



FIGURE 3 Binary map of *Dipetalogaster maxima* prediction based on the present-day climatic conditions. The red background presents areas where the species occurs, and the yellow background presents areas where the species is absent. The size and colours of the solid points correspond to the human population density in these locations; these points present three gradients of human populations, and the size of the points is directly proportional to the human population density.

the ecological niche models of *D. maxima* showed an increase in suitability in the North region of the accessible area "*M*" (Figure 4), primarily the Gulf of California coast region. The increase in suitability was similar among diverse RCPs so that there were no much variations in *D. maxima* predictions among diverse RCPs (Figure 4). The ecological niche model of *T. cruzi* showed higher environmental suitability in the southernmost region of BCS and the Pacific Ocean based on the current climatic conditions. Under diverse future climatic conditions (RCPs), there was a decrease in suitability across the southernmost area of BCS; and increased suitability across the northern region of accessible area and the Gulf of California coast (Figure 4). The distributional patterns of *T. cruzi* were also similar among diverse RCPs (Figure 4).

The niche overlap analyses could not reject the null hypotheses of niche equivalence and similarity between *D. maxima* and *T. cruzi* (Figure 5). Thus, the ecological niche of *D. maxima* and *T. cruzi* may share similar niches than expected by chance alone. When comparing the niche overlap between the two species (*D. maxima* and *T. cruzi*) in the Los Cabos region, the niches showed a broader characteristic overlap between the vector *D. maxima* and the parasite *T. cruzi* responsible for the circulation of CD in most of the species distributional range (Figure 5). Finally, we could not validate the hypothesis of niche centroid versus abundance (r = 0.20; p = 0.212); this result reflected no characteristic relationships between the centroid of *D. maxima* and its abundance.

DISCUSSION

Risk maps of *D. maxima* and *T. cruzi* are crucial to identify the areas of surveillance and control priorities of CD in BCS region of Mexico. This



FIGURE 4 Ecological niche modelling of the vector *Dipetalogaster maxima*, and the parasite *Trypanosoma cruzi* in Baja California Sur, Mexico under diverse climatic change scenarios. (a) ENM of *D. maxima* under present-day conditions; (b) ENM of *D. maxima* in RCP 2.6; (c) ENM of *D. maxima* in RCP 4.5; (d) ENM of *D. maxima* in RCP 6.0; (e) ENM of *D. maxima* in RCP 8.5; (f) ENM of *T. cruzi* under present-day conditions; (g) ENM of *T. cruzi* in RCP 2.6; (h) ENM of *T. cruzi* in RCP 4.5; (i) ENM of *T. cr*



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Dipetalogaster maxima vs Trypanosoma cruzi

FIGURE 5 Niche conservatism and niche overlap of the vector *Dipetalogaster maxima*, and the parasite *Trypanosoma cruzi* in Baja California Sur, Mexico. (a) The chart corresponds to the distribution of random replicates of the two types of hypotheses: niche equivalence (identity test) and niche similarity (background test). The vertical axis presents the frequency, and the horizontal axis represents the Schoener *D* values. The vertical arrow of 0.92 value represents the estimated value of the observed niche overlap based on Schoener *D* statistic. (b) The right ellipsoids represent the environmental space of *D. maxima*, and *T. cruzi* ENMs based on the minimum-volume ellipsoid in *NicheA*. The axes PC1, PC2, and PC3 represent the first principal components.

study was the first to anticipate the distributional potential of *D. maxima* and the parasite *T. cruzi* in BCS, Mexico. Although, the endemic range of *D. maxima* is limited to the Cabo region of Baja California (Jiménez et al., 2003; Ramsey et al., 2015), modelling the risk of CD transmission in this area is essential given that BCS is a significant destination for tourists from many countries in Europe and North America. More than 90% of tourists come from the USA, Canada, Spain, France, and the United Kingdom (http://www.wttc.org/). The ENM of *D. maxima* anticipated higher suitability of its occurrences in most districts across the study region. These areas corresponded to many areas with tourist activities and highland and maritime characteristics. Our study placed both local and tourist populations at risk of *D. maxima* infected with *T. cruzi* in these tourist areas.

Dipetalogaster maxima is exclusively inhabiting areas with exfoliative rocks and large boulder piles based on the previous studies on this species (Cuba et al., 1979; Jiménez et al., 2003; Marsden et al., 1979; Ryckman & Ryckman, 1967) and our 3-year field observations associated with this study (Flores-López et al., 2022). Moreover, since these habitat traits are intermittent in the BCS landscape, only certain outdoor activities (e.g., hiking, camping near rocky sites, or rock climbing) may derive a moderate risk to contract CD by infected populations of D. maxima in BCS. In comparison, the risk for local populations might be restricted to rural dwellings located near rocky sites. Dipetalogaster maxima occurred in representative habitat traits (i.e., living exclusively in exfoliative rocks and large boulder piles), so, the risk of CD transmission in BCS driven by D. maxima is probably low. The presence of 97.3% of populations at risk of contact with D. maxima is not surprising particularly if D. maxima niche revealed its most abundance close to urban centres. The higher percentage of populations at risk of D. maxima contact did not necessarily reflect higher infection rates of T. cruzi in D. maxima populations. The latter is based on the presence of infections in mammalian populations but also other factors including biting rates, vector behaviour, and vector dynamics of D. maxima. These habitat characteristics should be

assessed based on physicochemical properties of the soil, greenness, and host populations on a more local scale to better understand the vector dynamics in BCS region. However, these data are lacking in this finer resolution, further evidence of the local limiting factors of *D. maxima* should provide baseline data to characterize the ecological niche of the species in Mexico.

A recent study called to reduce the active circulation of CD in California, USA (Valdez-Tah & Ibarra-Cerdeña, 2021). Results from this latter study revealed the importance of tracking the disease in Mexico, considering the importance of the country as a well-known tourist destination. Active exchanges of tourists among countries allow active circulation of CD within Mexico and among other countries (USA, Canada, Spain, France, and the United Kingdom), particularly with the availability of other triatomine vector species (Ramsey et al., 2015). The dimensions of this problem in BCS are complicated by the characteristic aggressive behaviour of D. maxima in blood feeding and its adaptability to inhabit peridomestic and intradomestic rural areas (Jiménez & Palacio, 1999). Trypanosoma cruzi was alternatively anticipated to occur in higher densities across southern and western areas of BCS. The latter distributional pattern marked the difference between D. maxima and T. cruzi suitability in the Eastern borders of BCS. However, it should be noted that the sampling effort of T. cruzi in our study area is significantly smaller than the data available for D. maxima. Few studies have reported natural infections of T. cruzi in the vector populations of D. maxima in BCS (Jiménez et al., 2003; Marsden, 1986; Ryckman & Ryckman, 1967). The infection of T. cruzi that has been reported in this study and elsewhere suggested lower rates of infections in D. maxima. All these factors contributed to the lower sampling efforts of T. cruzi versus D. maxima. Thus, the T. cruzi ENM predictions should be corroborated in the coming future by increasing the sampling efforts in the Eastern areas of BCS.

Furthermore, the presence of other CD vectors in our study area (Ramsey et al., 2015) could potentially affect the distributional potential of *T. cruzi* and consequently the risk assessment of CD in the region. However, the other triatomine vectors (*Triatoma rubida* and Royal Entom Societ

Triatoma peninsularis) that have been reported in BCS have a very close association with woodrats (*Neotoma lepida*), living almost exclusively within the rat nests (Ryckman & Ryckman, 1961). Consequently, the probability of human contact with these other species is most likely low. Thus, the risk of CD transmission by vectors other than *D. maxima* in BCS is probably small.

Interestingly, the distributional patterns of *D. maxima* and *T. cruzi* were slightly different under diverse climatic scenarios based on diverse trajectories of CO2 emissions. However, D. maxima experienced higher suitability across the entire study area, whereas the future predictions of T. cruzi under distinct climate changes experienced different distributional potential among diverse areas (i.e., reduction of suitability in southern areas of BCS and expansion in high suitable areas in the northern region and the Gulf of California coast of BCS). These distributional patterns were driven by climatic factors alone; however, other factors may derive these patterns too, for example, human population activity and house hygiene. Higher housing standards in the USA derived lower occurrences of domestic triatomines and human CD (Valdez-Tah & Ibarra-Cerdeña, 2021). Several previous studies assessed the effect of climate changes on the distributional potential of other triatomine species (Garrido et al., 2019; Garza et al., 2014; Medone et al., 2015) across different countries. These latter studies revealed a northward shift of these species like the pattern observed in our study for D. maxima. Another study identified elevated temperature as a key driver to the elevated numbers of reduviid bugs and CD (Tamayo et al., 2018). The parallel agreement between our study and the previously published studies (Garrido et al., 2019; Garza et al., 2014; Medone et al., 2015; Tamayo et al., 2018) revealed the importance of climatic variables as predictors to the distributional potential of D. maxima and T. cruzi.

Our study anticipates the future predictions of *D. maxima* and *T. cruzi*. These predictions provide baseline information to infer disease risk under climate change. Thus, they will identify the areas of surveillance and control priorities and place guidelines to the national and international regulations to reduce the incidence of CD, particularly in areas where tourism activities occur. Our study also observed an overlap between both vector and parasite in Los Cabos region. These latter findings placed this area at risk of active CD circulation, particularly with the co-occurrence of both parasite and vector. Several previous studies identified Los Cabos region as a key endemic area of CD in BCS.

This study represents a piece of baseline information for the distributional potential of *D. maxima* and *T. cruzi* in BCS, Mexico and marked one of the first efforts to map the potential distribution of this vector in this key endemic region. A recent study developed by one of our coauthors (C.A.F.-L) found that *T. cruzi* infection rate in *D. maxima* is significantly lower than other triatomine species (Flores-López et al., 2022). This supports the previous hypothesis that *D. maxima* might feed on reptiles and mammals (Galvão et al., 2003; Ramsey et al., 2015). Furthermore, establishing the biological and abiotic factors that influence the infection rate will be vital for developing effective public health control measures for CD. Interestingly, both *D. maxima* and *T. cruzi* are possibly sharing similar niches raising the importance of this vector to infer the distributional potential of CD in this region, particularly, if the data of *T. cruzi* are lacking from animal and human hosts.

However, this study is important and provides baseline maps of the vector D. maxima and the parasite T. cruzi, the study still sees some caveats that should be properly addressed in our future analyses; (1) adding additional biotic factors to construct the ENMs of the vector and parasite; (2) adding other candidate triatomine vectors to better understand the epidemiology of CD in the region. The early attempts of ENM approach were based entirely on scenopoetic factors; however, species niche is limited by a set of abiotic, biotic, and dispersal factors (Barve et al., 2011). Recent studies increasingly raised the role of biotic factors to shape the species distributions (Anderson, 2017; Lewis et al., 2017; Simões & Peterson, 2018); however, these same studies identified no clear guidelines for integrating abiotic and biotic factors into correlative ecological niches (Anderson, 2017; Lewis et al., 2017; Simões & Peterson, 2018). Integrating biotic data is based mainly on the availability of these data which is always required at a microscale level, so, their availability is lacking in many cases. Unfortunately, this current analysis used the climatic factors as the main limiting factors to the distributional potential of *D. maxima* and *T. cruzi*: however, future studies should bring host population data also to improve the ENM predictions (Anderson, 2017). Adding other vectors to better understand T. cruzi epidemiology was limited by the nature of the habitat for other species that play a minor role in transmitting CD to human (Ryckman & Ryckman, 1961).

Future studies should address further details on the possible routes of invasion of the important vector D. maxima into other parts of Mexico. We also plan to focus on assessing the risk of other triatomine species (Galvão et al., 2003) in this region and the environmental and human population factors deriving the likelihood of CD transmission risk in this highly tourist destination. Further details on the occurrences of exfoliative rocks or large boulder piles at a microscale level should be considered for future modelling studies of D. maxima since it appears to play a vital role in constructing the habitat of this species. Furthermore, no data are available for the T. cruzi infection status in mammals or humans in the study region. The latter in turn limits the risk assessment, particularly if the study is mainly limited to only vector infection data. Ideally, T. cruzi data from humans and other mammalian hosts would allow a more comprehensive risk assessment. However, CD has been poorly studied in BCS, and the only T. cruzi data generated thus far is related to the vectors (Jiménez et al., 2003; Marsden, 1986; Marsden et al., 1979; Ryckman & Ryckman, 1967).

AUTHOR CONTRIBUTIONS

Conceptualization: Carlos A. Flores-López, David A. Moo-Llanes, and Abdallah M. Samy. *Methodology*: Carlos A. Flores-López, David A. Moo-Llanes, and Abdallah M. Samy. *Software*: Carlos A. Flores-López, David A. Moo-Llanes, and Abdallah M. Samy. *Validation*: Carlos A. Flores-López, David A. Moo-Llanes, and Abdallah M. Samy. *Formal analysis*: Carlos A. Flores-López, David A. Moo-Llanes, and Abdallah M. Samy. *Investigation*: Carlos A. Flores-López, David A. Moo-Llanes, Guillermo Romero-Figueroa, Aldo Guevara-Carrizales, Teresa López-Ordoñez, Mauricio Casas-Martínez, and Abdallah M. Samy. *Resources*: Carlos A. Flores-López and Abdallah M. Samy. *Data curation*: Carlos A. Flores-López, Guillermo Romero-Figueroa, and Aldo Guevara-Carrizales. *Writing—original draft preparation*: Carlos A. Flores-López, Guillermo Romero-Figueroa, and Aldo Guevara-Carrizales. *Writing—review and editing*: Carlos A. Flores-López, David A. Moo-Llanes, Guillermo Romero-Figueroa, Aldo Guevara-Carrizales, Teresa López-Ordoñez, Mauricio Casas-Martínez, and Abdallah M. Samy. *Visualization*: Carlos A. Flores-López, David A. Moo-Llanes, Guillermo Romero-Figueroa, Aldo Guevara-Carrizales, Teresa López-Ordoñez, Mauricio Casas-Martínez, and Abdallah M. Samy. *Visualization*: Carlos A. Flores-López, David A. Moo-Llanes, Guillermo Romero-Figueroa, Aldo Guevara-Carrizales, Teresa López-Ordoñez, Mauricio Casas-Martínez, and Abdallah M. Samy. *Supervision*: Carlos A. Flores-López and Abdallah M. Samy. *Project administration*: Carlos A. Flores-López and Abdallah M. Samy. *All authors have read and agreed to the published version of the manuscript*.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data of this manuscript are available within the manuscript text and its supplementary materials.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Figure S1. Spatial distributions of occurrence records of *Dipetalogaster maxima* and *Trypanosoma cruzi* in Baja California Sur, Mexico.

File **S1.** Occurrence records of *Dipetalogaster maxima* and *Trypanosoma cruzi* used in the construction of their ecological niche models in Baja California Sur, Mexico.

File S2. Abundance data used to assess the niche centroid and abundance hypothesis in the Cabo region of Baja California Sur, Mexico.

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