Atlas of Mexican Triatominae (Reduviidae: Hemiptera) and vector transmission of Chagas disease

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Chagas disease is one of the most important yet neglected parasitic diseases in Mexico and is transmitted by Triatominae. Nineteen of the 31 Mexican triatomine species have been consistently found to invade human houses and all have been found to be naturally infected with Trypanosoma cruzi*. The present paper aims to produce a state-of-knowledge atlas of Mexican triatomines and analyse their geographic associations with* T. cruzi*, human demographics and landscape modification. Ecological niche models (ENMs) were constructed for the 19 species with more than 10 records in North America, as well as for* T. cruzi*. The 2010 Mexican national census and the 2007 National Forestry Inventory were used to analyse overlap patterns with ENMs. Niche breadth was greatest in species from the semiarid Nearctic Region, whereas species richness was associated with topographic heterogeneity in the Neotropical Region, particularly along the Pacific Coast. Three species,* Triatoma longipennis*,* Triatoma mexicana *and* Triatoma barberi*, overlapped with the greatest numbers of human communities, but these communities had the lowest rural/urban population ratios. Triatomine vectors have urbanised in most regions, demonstrating a high tolerance to human-modified habitats and broadened historical ranges, exposing more than 88% of the Mexican population and leaving few areas in Mexico without the potential for* T. cruzi *transmission.*

Key words: Triatominae - Mexico - ecological niche models - *Trypanosoma cruzi* transmission - Chagas disease

Vector-borne transmission of Chagas disease is widespread across the Americas, from Argentina and Chile north to Mexico and the southern United States of America (USA) (Coura & Dias 2009). Recent rises in Chagas case reports in Europe and Asia derive from migrants from countries with unacceptably high incidence owing to vector-transmitted and non-vector *Trypanosoma cruzi* transmission (congenital, transfusion, transplant and oral transmission) (Gascon et al. 2010). The latest prevalence estimates for Latin America, which reflect reductions in only the Southern Cone region of South America following *Triatoma infestans* control initiatives, suggest eleven million current cases, although most countries do not have active epidemiological surveillance (Remme et al. 2006, Hotez et al. 2008, Lee et al. 2013).

Chagas disease is the most important parasitic disease in Mexico based on prevalence and disease burden (Hotez et al. 2012, Ramsey et al. 2014). However, the country has only a passive national surveillance program on paper, which is barely applied in the field, with no budget or signs of political will to develop an evidence-based strategy by which to prevent vector-borne transmission (over 96% of incidence) or to promote timely diagnosis, treatment and care of patients (Manne et al. 2013). Only a handful of states have focal interventions (i.e., sending personnel to search houses for triatomines and spraying insecticides) without follow-up evaluation when blood donation contamination is reported, and patient clinical treatment and care is remanded to the clinical care arm of the public healthcare system (PHS) or one of five other clinical care systems (Manne-Goehler et al. 2014). Between 1.5-2 million Mexicans are infected with *T. cruzi*, based on the finding that 1-1.5% of blood donations are contaminated (Guzmán et al. 1998, Ramsey & Schofield 2003, Novelo-Garza et al. 2010), with 500,000-650,000 chronic cases (of a total population of 122 million) and an estimated incidence based on a 3.57% birth rate of 65,000 new cases per year (Ramsey et al. 2003). Some estimates claim the lower prevalence of 1.1 million, which, although optimistic, is not based on representative data because the health sector has never conducted a country-wide study or included Chagas disease in any national seroepidemiological health surveys, except the first (Velasco-Castrejon et al. 1992, Hotez et al. 2012).

Independent of the exact figure, it is shocking that no systematic or formal interventions exist to reduce bug populations in human communities in Mexico. Although isolated anti-vector activities occur in a few states (Morelos, Oaxaca, Veracruz, San Luis Potosi), this disease

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remains largely unattended, with minimal access to diagnosis and treatment for those infected (Manne et al. 2013). No clinical guide exists for Chagas disease in Mexico; little or no access to medication or treatment is available to diagnosed patients and most healthcare professionals (physicians and nurses) have no knowledge of the diagnosis, treatment or follow-up required for the disease.

In all, 31 autochthonous species of Triatominae are found in Mexico (*Triatoma protracta* includes four subspecies and *Triatoma rubida* includes five subspecies) and all have been found to be naturally infected with *T. cruzi,* except for the four rarest species: *Belminus costaricensis*, *Triatoma bassolsae*, *Triatoma bolivari* and *Triatoma gomeznunezi* (Ryckman 1962, Zárate & Zárate 1985, Tay et al. 1992, Vidal et al. 2000, Magallón et al. 2001, Ibarra-Cerdeña et al. 2009). Five species do not belong to the primary genus *Triatoma*; one each belongs to the genera *Eratyrus*, *Belminus*, *Paratriatoma*, *Dipetalogaster* and *Panstrongylus*.

Mexican species of *Triatoma* belong to two subgroups: protracta and rubrofasciata (Lent & Wygodzinsky 1979). The former includes the protracta complex, with six species and four subspecies of *T. protracta* in Mexico and the lecticularia complex (principally *Triatoma lecticularia*, with one record for *Triatoma incrassata* and two for *Triatoma indictiva* in Mexico) (Ryckman 1962, Galvão et al. 2003, Kjos et al. 2009). The rubrofasciata subgroup includes the rubida complex (5 subspecies of *T. rubida*) of northern Mexico and the southern USA (Pfeiller et al. 2006), the phyllosoma complex, which is found only in Mexico (11 species including *Triatoma recurva*) and the dimidiata complex [3 haplogroups (hg) of *Triatoma dimidiata* and *Triatoma hegneri*] (Ibarra-Cerdeña et al. 2009). One species has not been assigned because only one specimen of this species has been collected (*T. gomeznunezi*) (Martínez et al. 1994). Recent studies have highlighted the need for a revision of triatomine systematics because phylogenetic results conflict with the current taxonomy (Ibarra-Cerdeña et al. 2014, Justi et al. 2014).

Most Mexican bugs are generalists, living in terrestrial, arboreal and cave mammal nests or roosts and almost all readily persist in modified habitats with domesticated mammals and humans (Becerril-Flores et al. 2007, Martínez-Ibarra et al. 2010, Medina-Torres et al. 2010, Ramsey et al. 2012, Torres-Montero et al. 2012). Nineteen species have been consistently found to invade human houses and only 12 rare sylvatic species are found only occasionally in association with humans.

Disease control strategies for vector-borne pathogens focus on vector reduction or elimination in areas of human exposure. The Southern Cone Initiative and recently the Central American Initiative for Chagas Disease Control have focused on domesticated populations of two species, *T. infestans* and *Rhodnius prolixus,* respectively (Dias 2007, Hashimoto & Schofield 2012). However, all epidemiologically relevant *T. cruzi* vector species in Mexico have been collected year-round in anthropogenic landscapes (Ramsey et al. 2012), and human feeding and contact occur both in domestic and (sometimes more so) in nondomestic habitats (Cohen et al. 2006, Stevens et al. 2014).

A necessary step towards understanding Chagas disease in Mexico and stratifying transmission risk is the development of a detailed understanding of the distribution of Triatominae across the country. To this end, modelling ecological niches at coarse scales, based on the Grinellian niche concept (Soberón 2007), attempts to discover the set of environmental conditions under which a species can maintain populations in the absence of immigration (Soberón & Peterson 2005) based on occurrence data from museum collections, field samples and the literature (Soberón & Peterson 2004) and data for environmental conditions such as climate and topography. Niche models can identify suitable areas where each species can maintain populations, even though only partial occurrence data are available or when major distributional areas of species remain unsampled (Soberón & Peterson 2005). Because zoonotic disease transmission depends on processes acting at multiple scales, niche modelling approaches incorporate different information for different taxa (Peterson 2006, Ibarra-Cerdeña et al. 2009, Costa & Peterson 2012). Niche model-based predictions of exposure areas have been developed and explored for many zoonotic diseases (Peterson et al. 2005, Lash et al. 2012, Moo-Llanes et al. 2013), including *T. cruzi* mammalian reservoirs in Mexico (Peterson et al. 2002) and *T. cruzi* vector species from Brazil, Mexico and the USA (Costa et al. 2002, Beard et al. 2003, López-Cárdenas et al. 2005, Sandoval-Ruiz et al. 2008, 2012, Batista & Gurgel-Gonçalves et al. 2009, Ibarra-Cerdeña et al. 2009, Benítez-Alva et al. 2012, Gurgel-Gonçalves et al. 2012). Spatial prediction and the stratification of vector exposure are extremely useful for epidemiological surveillance and planning, cost-efficient prevention and control activities (Tarleton et al. 2014). Given the current lack of country-wide surveillance, vector control or prevention activities for Chagas disease in Mexico and the absence of robust and geographically uniform or representative collections, such evidence-based mapping of potential vector distributions could greatly assist in identifying current and potential exposure areas.

Hence, this study aimed to produce a state-of-knowledge atlas of the geographic distributions of Mexican triatomine bugs and their associations with *T. cruzi* and human demographics, based on ecological niche models (ENMs). Transmission areas for *T. cruzi* were overlaid on the latest Mexican population census (2010) to improve our understanding of at-risk areas and identify gaps in knowledge. The maps produced are made in Geographic Information System-readable raster formats to create, in effect, a national atlas of the distributions of these vector species.

MATERIALS AND METHODS

Input data - Occurrence data were accumulated from diverse sources, including all known triatomine collection records from the literature for all of North America (PubMed using the search words "Triatominae" and "Mexico" and the scientific names of each species known from Mexico prior to 2014), publication references from reviews or publications not in PubMed prior to 2002, grey literature and government reports in Mexico, entomological collections [Biology Institute/National Autonomous

TABLE I

Mexican Triatominae, their biogeographic region, occurrence points and accuracy for ecological niche models (ENMs) of 19 species

Id	Species complex	Species	Subspecies	Region	Points	Background	p
1	Lecticularia	*Triatoma incrassata*	-	Nearctic	5	-	-
2		*Triatoma indictiva*	-	Nearctic	5	-	-
3		*Triatoma lecticularia*	-	Nearctic	30	9,230,464	6.01^{E-02}
4	Protracta	*Triatoma barberi*	-	Nearctic/Neotropical	369	10,069,567	3.91^{E-21}
5		*Triatoma neotomae*	-	Nearctic	10	-	-
6		*Triatoma nitida*	-	Neotropical	7	-	-
7		*Triatoma peninsularis*	-	Nearctic	10	9,230,464	1.45^{E-33}
8		*Triatoma protracta*	*T. p. protracta*	Nearctic	177	9,230,464	1.63^{E-07}
9			*T. p. nahuatlae*				
10			*T. p. woodi*				
11			*T. p. zacatecensis*				
12		*Triatoma sinaloensis*	-	Nearctic	5	-	-
13	Rubida	*Triatoma rubida*	*T. r. cochimiensis*	Nearctic	121	9,283,966	4.74^{E-24}
14			*T. r. jaegeri*				
15			*T. r. rubida*				
16			*T. r. sonoriana*				
17			*T. r. uhleri*				
18	Phyllosoma	*Triatoma bassolsae*	-	Neotropical	1	-	-
19		*Triatoma brailovskyi*	-	Neotropical	11	652,655	6.68^{E-01}
20		*Triatoma bolivari*	-	Neotropical	4	-	-
21		*Triatoma gerstaeckeri*	-	Nearctic	164	9,270,987	1.88^{E-17}
22		*Triatoma longipennis*	-	Nearctic/Neotropical	233	10,069,567	1.14^{E-14}
23		*Triatoma mazzottii*	-	Neotropical	80	696,139	9.36^{E-03}
24		*Triatoma mexicana*	-	Nearctic/Neotropical	271	10,069,567	5.96^{E-22}
25		*Triatoma pallidipennis*	-	Neotropical	291	690,750	1.79^{E-26}
26		*Triatoma phyllosoma*	-	Neotropical	40	650,095	4.11^{E-03}
27		*Triatoma picturata*	-	Neotropical	16	680,567	2.87^{E-04}
28		*Triatoma recurva*	-	Nearctic	33	9,275,367	4.29^{E-08}
29	Dimidiata	*Triatoma dimidiata* hg 1	-	Neotropical	77	650,095	4.78^{E-11}
30		*Triatoma dimidiata* hg 2	-	Neotropical	485	701,541	6.60^{E-14}
31		*Triatoma dimidiata* hg 3	-	Neotropical	42	650,039	2.71^{E-07}
32		*Triatoma hegneri*	-	Neotropical	6	-	-
33		*Belminus costaricensis*	-	Neotropical	2	-	-
34		*Dipetalogaster maximus*	-	Nearctic	6	-	-
35		*Eratyrus cuspidatus*	-	Neotropical	13	650,095	1.44^{E-05}
36		*Panstrongylus rufotuberculatus*	-	Neotropical	9	-	-
37		*Paratriatoma hirsuta*	-	Nearctic	56	9,230,464	6.69^{E-02}
38		*Triatoma gomeznunezi*	-	Neotropical	1	-	-
	Total	-	-	-	2,580	-	-
		Trypanosoma cruzi	-	Nearctic/Neotropical	669	10,069,567	4.48^{E-50}

University of Mexico, National Museum of American History/Smithsonian Institution, Global Biodiversity Information Facility (gbif.org)] and personal collections (JMR). ENMs were developed for Mexican species for which ≥ 10 unique collection data points were available in North America. Twenty species met this criterion, but *Triatoma neotomae* had 10 occurrence points divided between two distant regions, producing unsatisfactory models, so this species was not included.

ENMs were calibrated using all occurrence points in North America because major portions of the species distributions for the lecticularia and protracta complexes fall outside Mexican national boundaries (Peterson et al. 2011). A total of 2,580 occurrence points were available for 38 species and subspecies: *Belminus* (1 species), *Dipetalogaster* (1 species), *Eratyrus* (1 species), *Panstrongylus* (1 species), *Paratriatoma* (1 species) and *Triatoma* (26 species and 7 additional subspecies). Based on the range of known occurrences, species were classified according to biogeographic region as Neotropical (16 species), Nearctic (12 species + 7 subspecies) or both (3 species), using regionalisation layers defined by Olson et al. (2001). A total of 2,519 occurrence points corresponded to the 19 species for which ENMs were developed. ENMs for *T. protracta* and *T. rubida* included occurrences of the type subspecies (*T. p. protracta* and *T. r. rubida*); the three hg of *T. dimidiata* (hg1, hg2 and hg3) were modelled separately (Table I).

An additional dataset was constructed for Mexico and the USA for known *T. cruzi* occurrences using infections in reservoirs, triatomines and human cases georeferenced to communities across Mexico from the Institute for Epidemiologic Diagnosis and Reference, National Center for Preventive Programs and Disease Control, published reports and unpublished data of the first author, which totalled 669 records from 1936-2014. All occurrence data for Triatominae and *T. cruzi* are available on DRYAD for open access and use by the broader community (doi: 10.5061/dryad.rq120).

ENMs - Ecological niches were calibrated using DesktopGarp (Genetic Algorithm for Rule Set Prediction) (nhm.ku.edu/desktopgarp/), an evolutionary computing software package available for public download (Stockwell & Peters 1999). Specifically, GARP relates the ecological characteristics of known occurrence points to those of points randomly sampled from the remaining calibration area, seeking to develop a set of decision rules that best summarise factors associated with the species' presence (Peterson et al. 2002). In GARP, input occurrence data are divided into calibration (70%) and evaluation (30%) subsets (Anderson et al. 2003). GARP works in an iterative process of rule selection, evaluation, testing and incorporation or rejection. A method is chosen from a set of possibilities (i.e., logistic regression, bioclimatic rules), it is then applied to the calibration data and a rule is developed or evolved. Rules may evolve by a number of means that mimic DNA evolution: point mutations, deletions, crossing over etc. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model and the algorithm runs either 1,000 iterations or until convergence. We used 13 data layers to characterise ecological landscapes: four layers summarising aspects of topography (elevation, slope, aspect and topographic index) from the US Geological Survey's Hydro-1K data set (usgs.gov/) and nine climate variables from WorldClim (Bio 1, 4, 5, 6, 7, 12, 13, 14, 15) (worldclim.org/) selected based on low inter-correlations ($r < 0.75$) in an analysis of multicollinearity (Moo-Llanes et al. 2013). All variables had a spatial resolution of 0.0083° (~1 km^2).

We assigned species to biogeographic regions for calibration areas if more than 80% of the data points fell inside one region (Neotropical or Nearctic); three species (*Triatoma longipennis*, *Triatoma mexicana*, *Triatoma barberi*) were classified as Nearctic/Neotropical because occurrences fell in both regions. Additionally, species were assigned to biogeographic subgroups based on overall range areas, such that *Triatoma peninsularis* was assigned to subgroup 1 of the Nearctic Region (Nearctic 1) due to its exclusive presence in the Baja California Peninsula. All other Nearctic species were assigned to subgroup 2 (Nearctic 2). Neotropical species were also divided into two subgroups based on overall ENM areas: smaller than 70,000 km^2 (Neotropical 1) or greater than 100,000 km^2 (Neotropical 2). To avoid potential modelling bias related to an important component of model calibration, the accessible region "M" (Barve et al. 2012) was taken as the biogeographic region of known occurrence. The occurrences of each species were assessed to determine whether data points were within 100 km of the biogeographic region border: such species were *Triatoma brailovskyi*, *T. dimidiata* hg2, *Triatoma gerstaeckeri, Triatoma mazzottii*, *Triatoma pallidipennis, Triatoma picturata, T. recurva* and *T. rubida*. A 100-km radius buffer was created around each occurrence point of these species to extend the limits of the calibration region (Owens et al. 2013).

Model accuracy was assessed by examining the omission rates associated with the evaluation points (Anderson et al. 2003). ENMs were thresholded such that at least 95% of the occurrence points were within the predicted area and these thresholds were used to convert model outputs into binary maps (presence/absence). To test model significance, we compared the predictive success of the models against null expectations using a cumulative binomial test (Peterson et al. 2011).

The range size of each species modelled was calculated as the number of pixels covered by its suitable area within M (Moo-Llanes et al. 2013). To calculate the elevational ranges for each species, we combined the elevation layer for each vector with model predictions and the elevation layer for *T. cruzi*. We excluded the lower and upper 5% of

TABLE II

Reclassification of the National Forestry Inventory for conserved and modified land use

Land use	Conserved	Modified
Agriculture (seasonal)	-	x
Agriculture (irrigation and humidity)	-	x
No apparent vegetation	-	x
Human settlement	-	x
Deciduous and semi-deciduous	x	-
Conifers	x	-
Conifers-broadleaf evergreen forest	x	-
Broadleaf evergreen forest	x	-
Xerophilous scrubland	x	-
Mesophilous mountain	x	-
Mezquite	x	-
Other vegetation	x	-
Grasslands	x	-
Perennial and sub-perennial	x	-
Planted forest	-	x
Hydrophilic vegetation	x	-

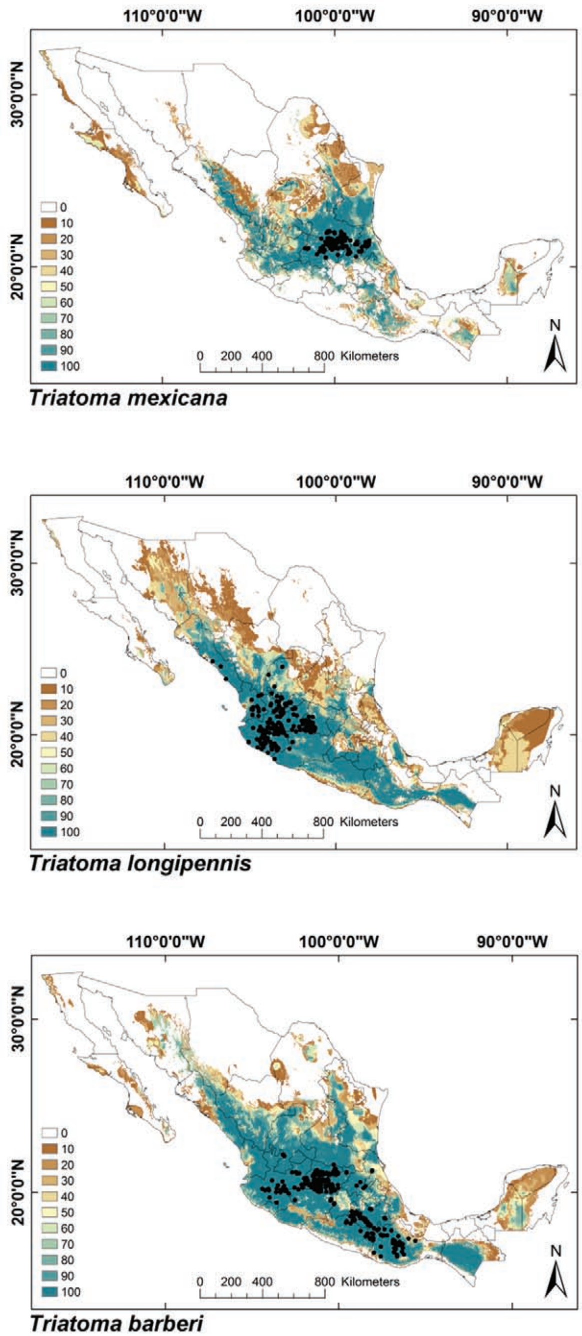

Fig. 1: ecological niche models for Mexican Triatominae distributed in both Nearctic and Neotropical regions. Colour brown to blue for increasing best subset models, black dots are occurrence points.

the distribution to remove outliers. The average elevation was calculated as the geometric mean elevation of pixels classified as suitable (Moo-Llanes et al. 2013). Land use data from the National Forestry Inventory (SEMARNAT-NFI 2007) were reclassified into "conserved" and "modified" categories (Table II). All ENMs were combined and the binary presence/absence raster was overlaid on the forestry classification data to map and calculate the proportion of pixels in each category.

ENMs for the 19 Mexican triatomine species were combined with that for *T. cruzi* to develop a map summarising coincidence and the potential for transmission by each species. Each map was combined with the Mexican census database (inegi.gob.mx) to link to all registered communities in Mexico (192,246 total) (doi: 10.5061/dryad.rq120) and calculate the resident population at risk for *T. cruzi* vector transmission for rural (< 10,000 inhabitants) and urban (> 10,000 inhabitants) categories, as reported in Moo-Llanes et al. (2013).

Triatomine species richness and T. cruzi vector-transmission - To estimate current triatomine species richness across Mexico, the 19 triatomine ENMs were adjusted to include only the portion of the ENM covered by 100-km buffers surrounding known occurrences (estimate of M) for each species, thereby eliminating areas that were likely unoccupied by species (Olson et al. 2001). Occurrence point buffers (100-km, based on appropriate environmental space models) were created for the remaining 12 species and seven additional subspecies of *T. protracta* and *T. rubida* and these buffers were overlain with the 19 adjusted ENMs. A *T. cruzi* vector transmission map was developed using the triatomine species richness model and the *T. cruzi* ENM. The two binary models were combined (arithmetic sum of binary classification) using the Map Algebra function of the Spatial Analyst of ArcGIS v.10.0 to project the current exposure for *T. cruzi* vector transmission.

Data analyses - Differences for ENM mean breadth, mean elevation, modified and conserved land coverage, conserved/modified land cover index, rural/urban population index, rural population, land cover and conserved/modified land cover index among the biogeographic regions were evaluated using one-way ANOVA (Tukey's F for comparison of means) using R software v.2.15.1 (r-project.org/).

RESULTS

ENMs - The binomial tests of the ability to predict known distributions were significant ($p < 0.05$) for all but three species: *Paratriatoma hirsuta, T. lecticularia* and *T. brailovskyi* (Table I). ENMs for the 19 triatomine species analysed are presented according to biogeographic region, with occurrence data points shown in Figs 1-5. The species with the broadest geographic distributions in Mexico were those from the Nearctic Region (Nearctic 2) (Fig. 4), with *T. protracta*'s distribution being the largest (55.1% of the country) and *T. peninsularis*'s (Nearctic 1) (Fig. 5) being the smallest (1.2%) (Table III). Species occurring in both regions had the second broadest ENMs (Fig. 1), followed by the principal Neotropical group (Neotropical 2) (Fig. 3); the Nearctic 2 region had a mean range size that was significantly higher than those of all other groups (Table IV) (df = 3, F = 8.8, p = 0.0016). The potential distributions of Nearctic 2 species covered the greatest proportion of the country (average 36.5%), whereas species in Nearctic/Neotropical cover an average 19% and the principal Neotropical Region 2, 12.4% of Mexico (Table IV). Generally, all *Triatoma* complexes had similar ranges: the protracta complex species covered between 1.2-55.1% of the country, the phyllosoma complex species covered between 1.7-43.8% and the dimidiata complex species covered between 3.2-20.1% of the country.

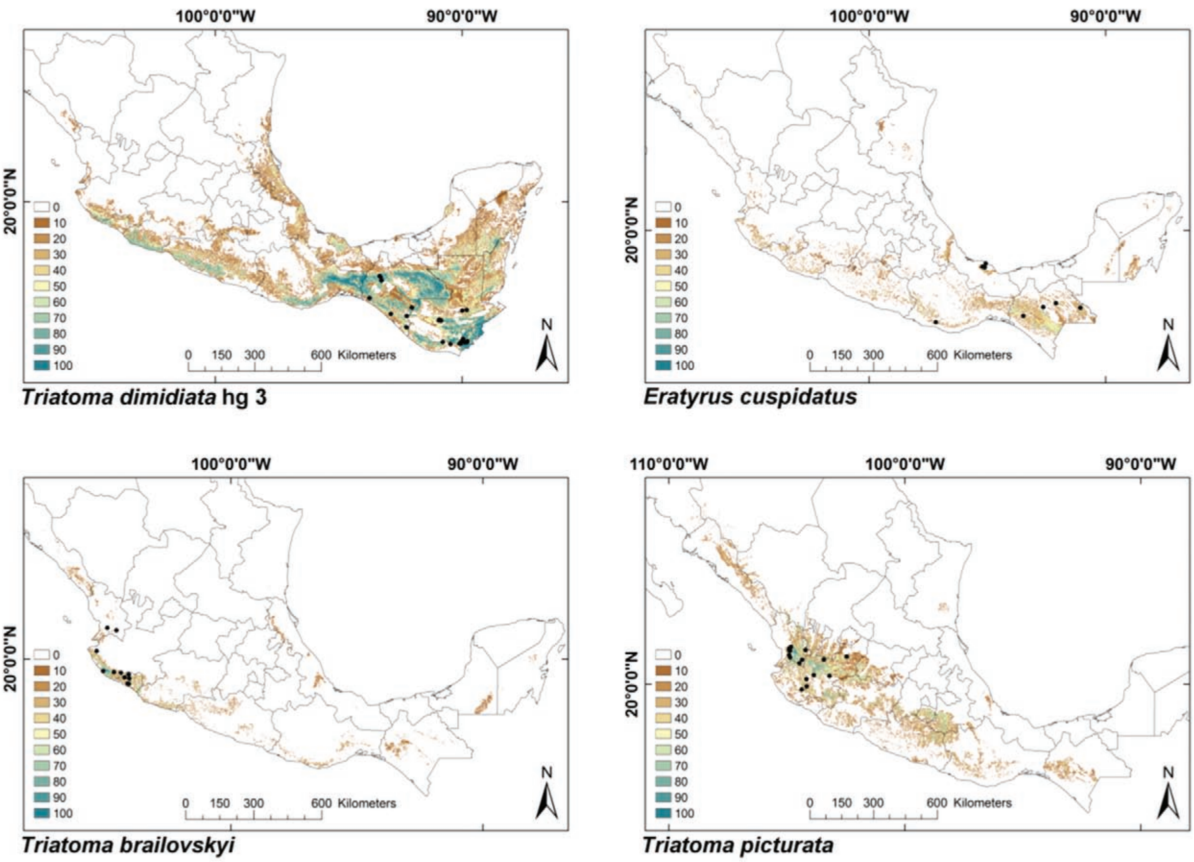

Fig. 2: ecological niche models for Mexican Triatominae distributed in the Neotropical Region, subgroup 1. Colour brown to blue for increasing best subset models, black dots are occurrence points.

The mean elevation for ENMs varied from 44 m (*T. dimidiata* hg1) to 1,751 m (*T. barberi*) (Table III). The highest mean elevation was observed for species located in both Nearctic/Neotropical regions, followed by the Neotropical Region which had lowest niche breadth (Neotropical 1); mean elevation of the Nearctic/Neotropical regions was significantly higher than all others (Table IV) (df = 3, F = 4.50, p = 0.021). Species of both Nearctic regions had the lowest mean elevations.

The ENMs of Nearctic 2 triatomine species had predominately conserved land cover (79.2%) (Fig. 6), whereas other regions had equivalent proportions of conserved and modified land cover: 59.9%, 61.2% and 59.1% for conserved land cover in the Nearctic/Neotropical, Neotropical 2 and 1 regions, respectively (Fig. 7, Table IV) (df = 3, F = 10.2, p = 0.0008). The conserved/modified land cover index for the Nearctic 2 region was significantly different from that of the other three regions (df = 3, F = 19.4, p < 0.0001). The modified land cover area was similar between the Nearctic 2 group and the Nearctic/Neotropical regions, both of which were slightly lower than that of the Neotropical 2 group (df = 3, F = 5.0, p = 0.001). *T. picturata* had the smallest area of conserved land cover (0.80), whereas *T. peninsularis,* which is highly sylvatic and reduced to the Baja California Peninsula, had the highest conserved/modified land cover ratio (28.6).

Triatomine exposure of the Mexican population - *T. cruzi*'s ENM was found to cover 91.2% of Mexico (Fig. 8). The total Mexican population with vector exposure for at least one bug species was 99,911,867 inhabitants, which is 88.9% of the current Mexican population. This coverage was similar for rural (88.1%) and urban populations (89.4%) (Table V). More than 90.1% of the communities in the country are located in potential vector distribution areas. Vector transmission models were overlaid onto the 2010 census database to stratify exposure for all communities in the country (doi: 10.5061/dryad.rq120): the exposed population was highest where triatomines covered both biogeographic regions (*T. longipennis, T. mexicana* and *T. barberi),* followed by regions where Nearctic 2 and Neotropical 2 species occur. The mean exposed populations were significantly different among biogeographic regions (Table IV) (df = 3, F = 3.64, p = 0.04).

Although the average exposed population in urban and rural areas as well as rural and urban communities was the highest for species occurring in both biogeographic regions, the group with the highest rural/urban index was the smaller of the Neotropical groups (Neotropical 1) (Fig. 2, Table V). In this group, more inhabitants from rural than urban communities were exposed (rural/urban index = 1.31). None of the other biogeographic groups had an index above 1, indicating that more inhabitants in

TABLE III

Niche breadth and elevation for ecological niche models of the 19 most abundant Mexican triatomine species

Id	Species	Biogeographic region	Background model	Niche breadth Mexico	ENM Mexico (%)	Elevation mean (m)	Elevation range (m) (min-max)
1	*Triatoma peninsularis*	Nearctic 1	9.230	20,892	1.2	102	(0-225)
2	*Triatoma brailovskyi*	Neotropical 1	0.652	28,735	1.7	409	(39-1,041)
3	*Triatoma picturata*		0.680	39,457	2.3	1,286	(718-1,731)
4	*Triatoma dimidiata* hg 3		0.650	55,391	3.2	658	(88-1,395)
5	*Eratyrus cuspidatus*		0.650	64,912	3.8	877	(342-2,289)
6	*Triatoma dimidiata* hg 1	Neotropical 2	0.650	99,969	5.8	44	(1-190)
7	*Triatoma phyllosoma*		0.650	144,082	8.4	832	(18-1,850)
8	*Triatoma pallidipennis*		0.690	153,414	8.9	1,210	(622-1,781)
9	*Triatoma mazzottii*		0.696	321,170	18.7	838	(22-1,785)
10	*Triatoma dimidiata* hg 2		0.701	344,142	20.1	259	(10-1,045)
11	*Triatoma mexicana*	Nearctic/ Neotropical	10.069	206,127	12	1,371	(113-2,107)
12	*Triatoma longipennis*		10.069	338,878	19.7	1,354	(377-2,084)
13	*Triatoma barberi*		10.069	435,238	25.4	1,751	(1,047-2,321)
14	*Triatoma lecticularia*	Nearctic 2	9.230	166,837	9.7	433	(92-975)
15	*Triatoma recurva*		9.275	751,620	43.8	768	(14-1,587)
16	*Triatoma gerstaeckeri*		9.270	434,242	25.3	792	(18-1,598)
17	*Triatoma rubida*		9.283	832,345	48.5	607	(1-1,325)
18	*Triatoma protracta*		9.230	945,643	55.1	946	(28-1,889)
19	*Paratriatoma hirsuta*		9.230	625,625	36.5	896	(48-1,642)
-	*Trypanosoma cruzi*	Nearctic/ Neotropical	10.069	1,565,392	91.2	786	(10-1,900)

background model expressed values in millions of pixels. ENM: ecological niche model.

TABLE IV

Niche breadth, elevation, population coverage and land use indices for biogeographic regions

	Biogeographic region						
	Nearctic 1	Neotropical 1	Neotropical 2	Nearctic/Neotropical	Nearctic 2		
Species (n)	1	4	5	3	6	F	p
Mean breadth (km^2)	20,892	47,124^a	212,555^a	326,748^{a,b}	626,052^b	8.79	1.60^{E-03}
Coverage for Mexico (%)	1.2	2.7^a	12.4^a	19^{a,b}	36.5^b	8.78	1.60^{E-03}
Mean elevation (m)	102	807^{a,b}	637^a	1,492^b	740^a	4.50	2.06^{E-02}
Total range elevation (m)	225	1,317^a	1,196^a	1,658^a	1,469^a	0.68	5.78^{E-01}
Rural population (n)	330,244	3,980,399^a	11,348,692^{a,b}	25,390,610^b	8,844,201^{a,b}	3.63	3.96^{E-02}
Rural/urban population index	0.09	1.31^b	0.75^{a,b}	0.48^a	0.37^a	5.66	9.40^{E-03}
Rural communities (n)	4,320	21,326^a	55,614^{a,b}	116,848^c	64,329^b	10.97	6.00^{E-04}
Urban communities (n)	16	83^a	251^a	640^b	236^a	20.58	0
Modified land cover (km^2)	703	18,725^a	85,670^{a,b}	127,948^b	126,098^b	5.00	1.18^{E-02}
Conserved land cover (km^2)	20,078	28,399^a	126,671^a	193,957^a	501,454^b	10.20	8.00^{E-04}
Conserved/modified index	28.56	1.57^a	1.63^a	1.49^a	3.91^b	19.39	0

a, *b*: statistically different (p < 0.05). *Triatoma peninsularis* (Nearctic 1) is not included in analyses.

urban communities were exposed to vector transmission than those in rural populations in these regions; the rural/urban index was significantly different among biogeographic groups (Table IV) (df = 3, F = 5.66, p = 0.009). The highest proportion of exposed urban population was found in the Nearctic 2 region, followed by that from species covering both regions and the Neotropical 2 group, which was similar to the trend for niche breadth.

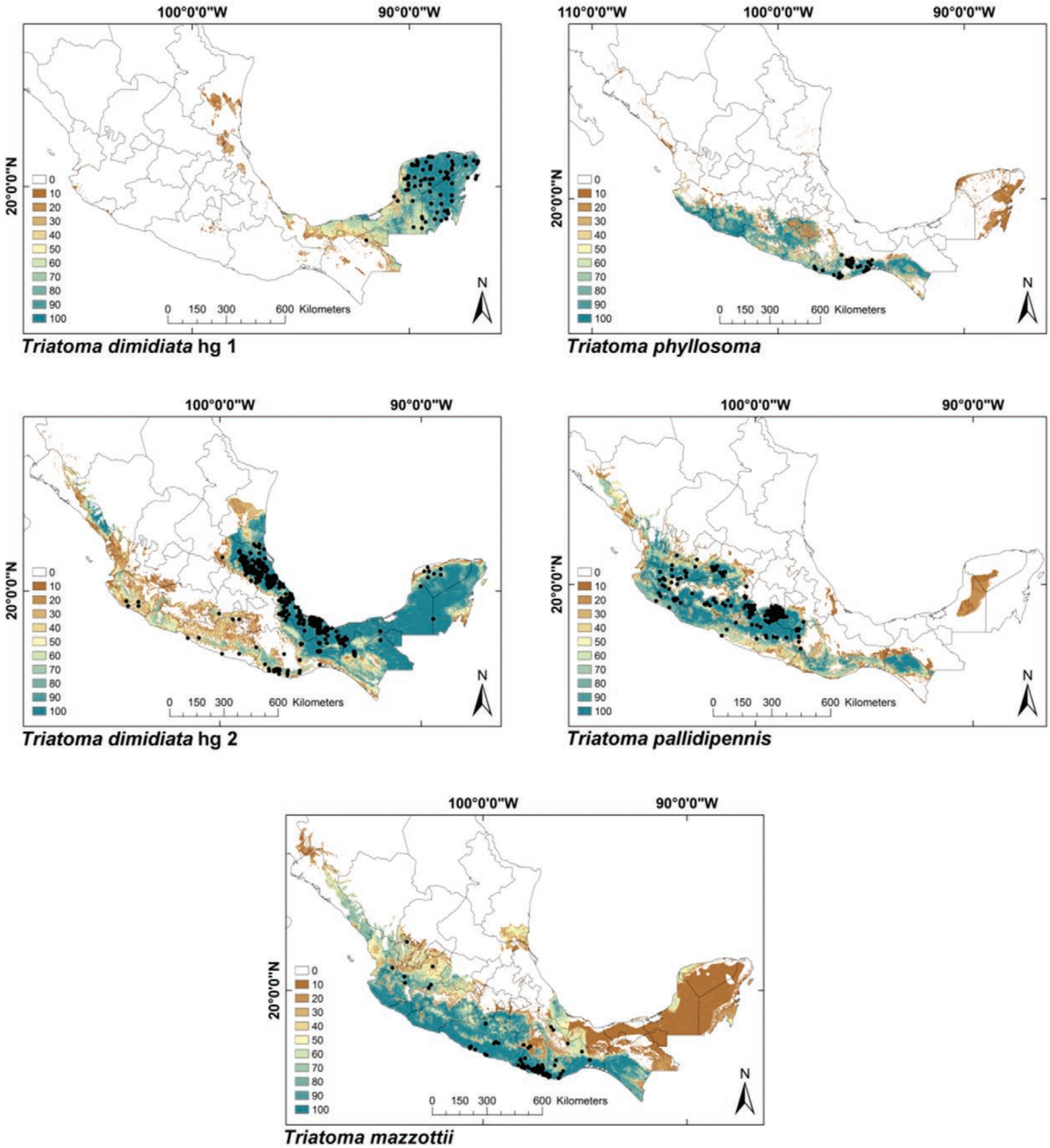

Fig. 3: ecological niche models for Mexican Triatominae distributed in the Neotropical Region, subgroup 2. Colour brown to blue for increasing best subset models, black dots are occurrence points.

Triatomine species richness and T. cruzi transmission niche - Species richness for Mexican Triatominae based on adjusted ENMs (for current and not potential distributions) was higher in the Neotropical Region than in the Nearctic Region (Fig. 9). The areas of the greatest species richness were the Sierra Madre Oriental, the Transverse Neovolcanic Belt, northern Sonora, along the Pacific Coast and the Sierra Madre Occidental, the Balsas Basin and the Sierra Madre del Sur and Oaxaca Coast.

The vector transmission map suggests that the greatest exposure of human populations to infected triatomine species occurs in Nuevo Leon, Tamaulipas, Sinaloa, Durango, Nayarit, Jalisco, Guanajuato, Michoacan, Oaxaca and Chiapas (Fig. 10). All human communities in nine states (of 32), Aguascalientes, Coahuila, Guanajuato, Hidalgo, Morelos, Nayarit, Querétaro, San Luis Potosi and Tlaxcala, are at risk for the potential vector-borne transmission of *T. cruzi* by at least one infected bug species (doi: 10.5061/dryad.rq120).

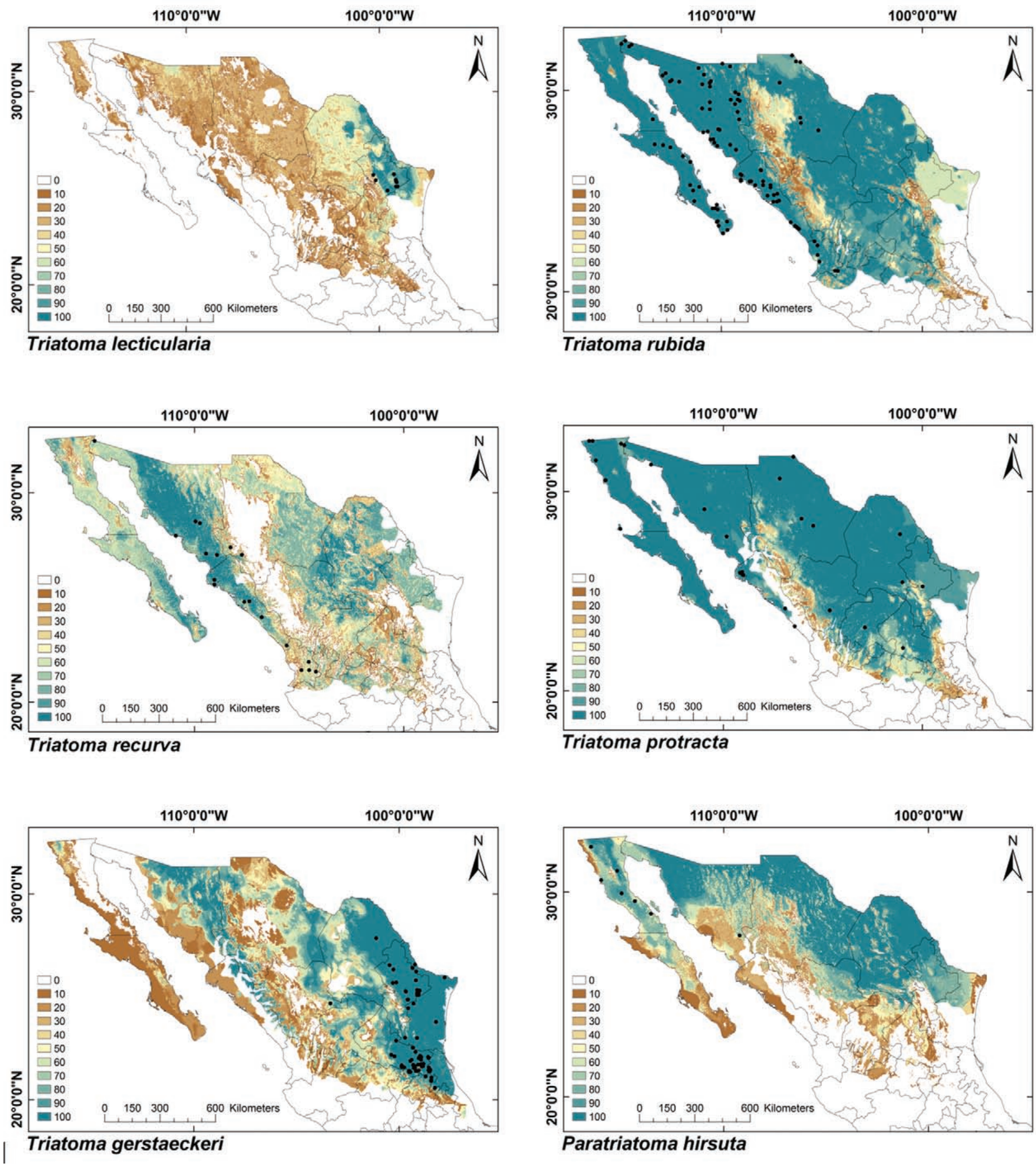

Fig. 4: ecological niche models for Mexican Triatominae distributed in the Nearctic Region, subgroup 2. Colour brown to blue for increasing best subset models, black dots are occurrence points.

DISCUSSION

Species distributions of triatomines have been modelled previously in several Mexican states: Guanajuato (López-Cárdenas et al. 2005), Puebla (Sandoval-Ruiz et al. 2008), Veracruz (Sandoval-Ruiz et al. 2012), Aguascalientes, Chiapas, Guerrero, Jalisco, Michoacan and Oaxaca (Benítez-Alva et al. 2012). However, most of these studies did not use representative occurrence datasets covering the complete range of the species modelled or they failed to specify background areas to calibrate their models, resulting in calibration bias (Owens et al. 2013). The present study separately modelled the 19 most abundant and epidemiologically relevant triatomine vector species in Mexico, providing individual species maps and exposure databases, which can be used by Mexico's PHS vector prevention and control program to stratify *T. cruzi* transmission. These maps and demographic ex-

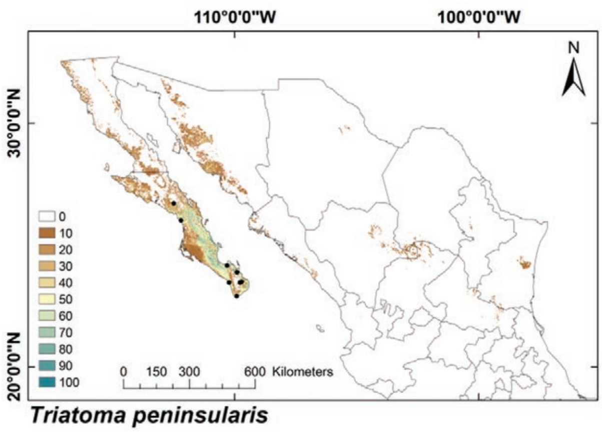

Fig. 5: ecological niche models for Mexican Triatominae distributed in the Nearctic Region, subgroup 1. Colour brown to blue for increasing best subset models, black dots are occurrence points.

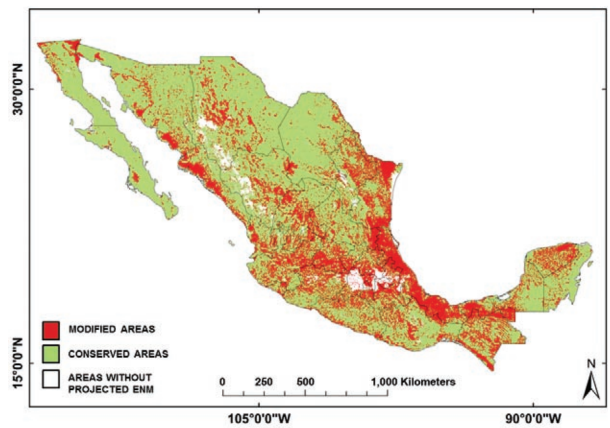

Fig. 6: composite binary map of all Triatominae ecological niche models (ENM) classified according to modified (red) or conserved (green) landscape cover.

TABLE V

Urban and rural population and communities exposed to Triatominae in Mexico

Vector	Total population (n)	Urban population (n)	Rural population	Rural/urban population index	Urban communities (n)	Rural communities (n)
Triatoma peninsularis	3,992	3,661	0.330	0.09	16	4,320
Triatoma brailovskyi	1,132	0,339	0.792	2.33	11	5,494
Triatoma picturata	13,499	8,511	4.988	0.59	152	23,997
Triatoma dimidiata hg 3	12,534	5,018	7.516	1.50	114	41,254
Eratyrus cuspidatus	5,802	3,178	2.623	0.83	55	14,561
Triatoma dimidiata hg 1	8,415	4,810	3.604	0.75	79	17,314
Triatoma phyllosoma	16,634	9,783	6.850	0.70	159	34,431
Triatoma pallidipennis	29,214	17,860	11.354	0.64	290	52,898
Triatoma mazzottii	42,598	24,639	17.958	0.73	412	87,962
Triatoma dimidiata hg 2	34,715	17,740	16.974	0.96	313	85,467
Triatoma mexicana	67,005	47,514	19.491	0.41	496	93,638
Triatoma longipennis	80,904	54,292	26.611	0.49	702	121,520
Triatoma barberi	85,684	55,614	30.069	0.54	722	135,386
Triatoma lecticularia	22,460	16,275	6.184	0.38	168	43,740
Triatoma recurva	29,868	21,531	8.337	0.39	230	60,065
Triatoma gerstaeckeri	38,047	26,350	11.696	0.44	274	80,422
Triatoma rubida	42,942	31,601	11.340	0.36	301	79,886
Triatoma protracta	37,460	27,226	10.234	0.38	263	73,506
Paratriatoma hirsuta	24,896	19,624	5.271	0.27	177	48,355

urban communities are classified as ≥ 10,000 inhabitants. Population is expressed in millions of inhabitants.

posure predictions reflect the potential geographic distributions for all epidemiologically relevant species and their interactions with *T. cruzi* and can be used to stratify vector transmission interventions if the political will exists and normative guidelines are followed.

Mexico is located in both the Neotropical and Nearctic regions, which have different topography, vegetation, climates and demography as well as high heterogeneity and landscape types (Olson et al. 2001, Morrone 2005, Rzedowski 2006). We noted significant differences in

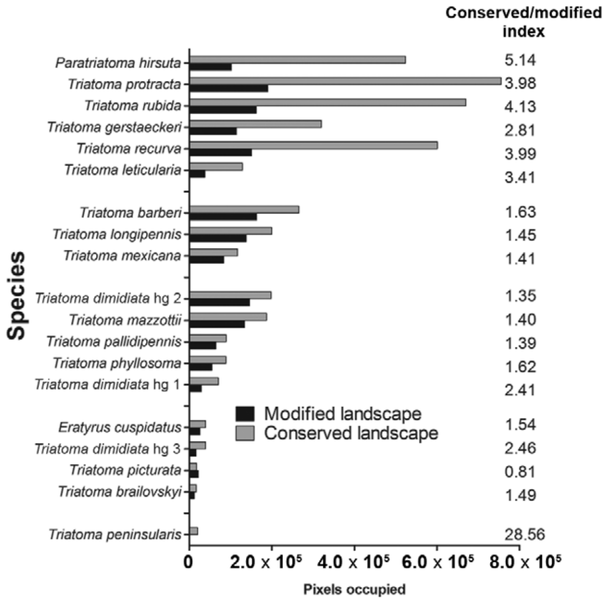

Fig. 7: landscape cover types and conserved/modified index for Mexican Triatominae ecological niche models.

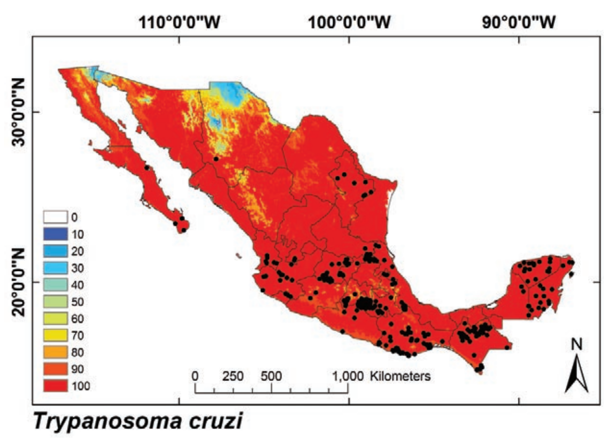

Fig. 8: ecological niche model for *T. cruzi*. Black dots are occurrence points for the species from bugs, humans and other mammals.

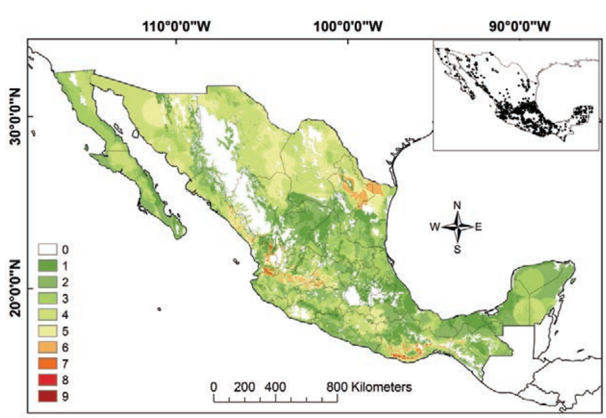

Fig. 9: species richness of Triatominae in Mexico. Insert map illustrates all data points used in modelling. Colours green to red represent number of species present.

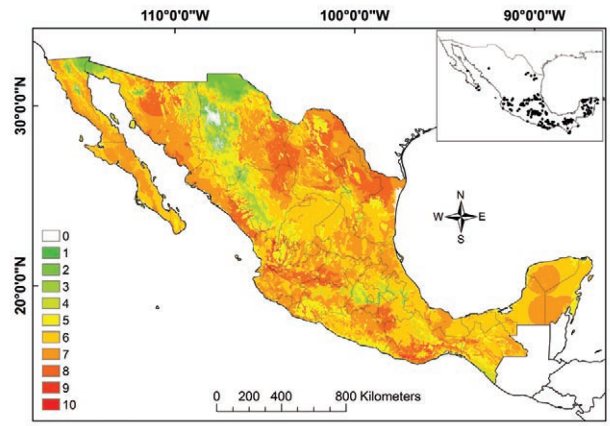

Fig. 10: *Trypanosoma cruzi* vector transmission map for Mexico. Insert map represents all data points used in modelling. Colours green to red represent increasing number of ecological niche model best subsets.

distribution potential among species occurring in different biogeographic regions, with species in the semiarid and arid Nearctic Region having the broadest distributions. However, species richness was highest in the Neotropical Region, which has greater topographic complexity, particularly along the Pacific Coast. It is interesting that the broadest potential vector distributions in the Nearctic Region coincided with the higher conserved/modified land cover index values, probably owing to vast areas of arid vegetation with low population density, as evidenced by the inverse association with the rural/urban population index. Recent studies on triatomines from the Nearctic Region of Mexico report the domestication of vector species such as *T. rubida* and *T. protracta* in urban areas, which was almost unheard of two decades ago (Pfeiller et al. 2006).

It is clear that the geographic ranges of three principal triatomine species, *T. longipennis*, *T. mexicana* and *T. barberi* occur at higher elevation and expose more rural and urban communities to *T. cruzi*, even though the rural/urban population index in this region is the lowest. For these three species and for the most important species from the Neotropical 2 region, these data suggest that the vectors have tolerated landscape modification and urban development and are not limited to rural populations. More than 75% of the Mexican population now resides in urban communities. This urbanisation process, along with strong cultural ties to ancestral communities, may provide mechanisms for continuous human-assisted vector dispersal. Most Mexican vectors have tolerated landscape modification and as true opportunists, take advantage of alternative resources and refuges to maintain populations in human-modified habitats. Because the PHS vector-borne disease program in Mexico is currently almost singularly focused on dengue, which is principally urban, a Chagas disease prevention and control program, if it were to become effective in Mexico, may not need to shift current personnel or their work areas. However, this strategy may broaden the gap between urban and rural PHS coverage, thereby increasing current inequities in health services access in dispersed and marginalised rural areas where investment in prevention and control is minimal and will be far more costly to maintain.

The present analysis provides an atlas of the current knowledge regarding potential distributions and hence the potential exposure of human populations to *T. cruzi*-infected vectors in Mexico. This information can be used to engage communities regarding Chagas disease and to analyse social, cultural and economic vulnerability components that contribute to vector transmission risk. We have related triatomine distribution patterns to the most recent demographic census in Mexico to provide Chagas state program coordinators with a blueprint with which to stratify, study and plan future activities. Stratification should be conducted based on vector capacity, domesticity and the degree of habitat modification. Current models can be improved *via* a concerted effort to generate distribution and abundance information in communities and in conserved areas. Although information regarding wildlife reservoirs of *T. cruzi* is increasing and will assist in understanding the ecology of *T. cruzi* vector-borne transmission, the current information void (for the Mexican population and professionals in PHS) regarding the vectors and the parasite is the primary impediment to understanding vector transmission risk.

The Chagas disease transmission map developed herein was adjusted to reflect the current infected vector distributions and hence is immediately applicable to the unaddressed *T. cruzi* vector transmission problem in Mexico. Few areas in Mexico do not have the potential for vector transmission exposure and vectors have already demonstrated the capacity to persist in human-modified habitats and communities, which in most Nearctic and Neotropical regions provide the greatest year-round resources. If this exposure hazard continues and human vulnerability remains unabated, the risk for vector transmission in Mexico will continue to rise, affecting economic development and broadening the social inequities already affecting most of the population in both rural and urban areas (Ramsey et al. 2014). This study has developed immediately usable products for the PHS to study, plan and intervene against the vector-mediated transmission of *T. cruzi*. How many more Mexicans must become infected before health agencies abide by their legal mandate to prevent, control and turn their attention to Chagas disease in the country?

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