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En fin, Gracias!

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RESUMEN

Los triatomíneos son insectos hematófagos con importancia médica ya que son vectores de *Trypanosoma cruzi*, parásito causante de la enfermedad de Chagas. Investigué patrones de la ecología geográfica de estos vectores, en particular relacionados con el conservadurismo de nicho y las interacciones vector-hospedero. Los objetivos fueron: (1) Investigar la historia natural de los triatomíneos de Norteamérica; (2) Poner a prueba la hipótesis del conservadurismo de nicho en los triatomíneos en un contexto filogenético; y (3) Analizar las relaciones geográficas entre los vectores y sus hospederos conocidos y potenciales. Para esto, realicé una revisión de literatura, compilé y genere bases de datos de distribuciones y de secuencias de DNA de los triatomíneos de Norte América y realicé análisis filogenéticos, modelos de nicho ecológico y modelos basados en algoritmos de teoría de redes complejas. Encontré que los triatomíneos están ampliamente dispersos en México y sur de Estados Unidos y la riqueza de especies se concentra en el Eje Neovolcánico y las costas del Pacífico y Golfo de México. Las especies no tuvieron nichos idénticos, sin embargo, la divergencia de sus nichos no corresponde con la divergencia esperada por modelos nulos, por lo que no se rechaza la hipótesis de conservadurismo. Las interacciones conocidas vector-mamífero y parásito-mamífero fueron predichas correctamente por los modelos inferenciales de interacciones. Los resultados mostraron que las especies sinantrópicas de vectores y mamíferos y particularmente aquellos que son reservorios de *T. cruzi*, tienen un efecto clave en la topología y estabilidad de la red de interacciones. Con esta tesis se expandió el conocimiento de la ecología geográfica de los triatomíneos. Los resultados pueden ayudar a generar modelos de riesgo epidemiológico realistas e inferir el efecto potencial del cambio climático en los rangos de distribución de vectores, ya estas especies son poco propensas a la evolución del nicho.

ABSTRACT

Triatomines are blood sucking insects with medical importance due their interaction with *Trypanosoma cruzi*, the parasite of Chagas disease. Geographical ecology of these insects where investigated particularly those related with niche conservatism and vector-host interactions. The objectives where: (1) To investigate the known natural history of North American triatomines; (2) To test the niche conservatism hypothesis in a phylogenetic context; and (3) To analyze the geographical associations between vectors and hosts. I found that epidemiologically relevant species inhabit open habitats as grasslands, croplands, lowland forests and avoid dense stands of rain forest. I compiled DNA sequences to reconstruct the vectors phylogeny and to recover sister species to test niche conservatism. Results strongly suggest that niche conservatism is occurring as a general pattern since all species had more similar niches than expected by null models. I generated a inferential interaction network for vectors and hosts based on their co-distributional patterns. All known vector-hosts and parasite-hosts interactions were correctly predicted. Results showed that synanthropic species had a significant effect on the network structure. More over, the independently identified reservoirs of *T. cruzi* were the key species of that structure. With this investigation the knowledge of geographical ecology of triatomines, and the results can be applied to develop epidemiological risk models and to infer the potential effect of climate change on distribution range of vectors.

PALABRAS CLAVE

Enfermedad de Chagas, Conservadurismo de nicho, Interacciones vector-reservorio,

INTRODUCCIÓN

La subfamilia Triatominae es un grupo de insectos hematófagos que incluye a 140 especies (Lent & Wygodzinsky 1979; Schofield & Galvão 2009). Más de 20 especies de este grupo tienen importancia médica debido a que son vectores reconocidos de *Trypanosoma cruzi*, el agente etiológico de la enfermedad de Chagas (EC). Aunque la importancia epidemiológica entre triatominos varía enormemente, todas las especies tienen el potencial de convertirse en vectores sinantrópicos de este parásito (Zeledon & Rabinovich 1981; Noireau et al. 2009). Además de la transmisión vectorial, la EC se puede transmitir por vía congénita o transfusional, sin embargo estos mecanismos alternativos tienen una importancia marginal desde el punto de vista eco-epidemiológico (Dias et al. 2002; Ramsey & Schofield 2003; Schmunis & Yadon 2010; Sánchez & Ramírez 2012). La transmisión vectorial de la EC está ligada a condiciones de pobreza en poblaciones rurales en las que los triatominos pueden establecer poblaciones, refugiarse en casas construidas principalmente con madera o barro y alimentarse de la sangre de personas y animales domésticos (Cohen & Gürtler 2001; Tarleton et al. 2007). La domesticación de triatominos comprende procesos de inmigración, establecimiento y colonización, pero los mecanismos por los cuales estos procesos se favorecen han sido entendidos sólo de manera superficial (Abad-Franch et al. 2010). La modificación de hábitat y la alteración de la comunidad de hospederos son probablemente los factores más comúnmente asociados a la domesticación de vectores de enfermedades (Keesing et al. 2006; Blaustein et al. 2010), mientras que el cambio climático (CC) por efectos antropogénicos tiene un efecto notable en el incremento en las áreas de distribución (Ostfeld 2009; Smith & Guégan 2010). Siendo el principal factor de riesgo para la transmisión de *T. cruzi* (Martins-Melo et al. 2012a, 2012b) y debido a la amplia distribución de casos de esta enfermedad en Latinoamérica, es de suma importancia conocer los factores evolutivos y ecológicos que están asociados a la presencia de vectores del parásito, para identificar áreas de riesgo de exposición (Stevens 2000; Beard et al. 2003; Lehane 2005; Lopez-Cardenas et al. 2005; Sarkar et al. 2010; Stevens et al. 2011; Gourbière et al. 2011; Gurgel-Goncalves et al. 2012).

El modelado de nicho ecológico se ha convertido en una herramienta fundamental para la generación de mapas de riesgo (Gurgel-Goncalves et al. 2012). Debido a su naturaleza inferencial, no solamente es útil para predecir la distribución de especies en sitios en donde no había registros previos (Raxworthy et al. 2003), sino que también se ha utilizado con bastante precisión para predecir cambios potenciales en la distribución de enfermedades debidos al CC (Nakazawa et al. 2007). No obstante, este enfoque puede presentar errores cuando sus supuestos y consideraciones metodológicas no son tomados cuidadosamente en cuenta (Araujo et al. 2005; Araujo & Peterson 2012; Pearson et al. 2006).

Uno de los supuestos en los que se basa la predicción del efecto del CC sobre la distribución de especies es la del conservadurismo de nicho (Peterson et al. 1999; Wiens & Graham 2005). Esta hipótesis argumenta que después del proceso de especiación, las especies retienen sus atributos fisiológicos que restringen su rango de tolerancia a las condiciones climáticas. Si el nicho se conserva, es posible predecir el cambio en la distribución de una especie debido a que únicamente se modifican las condiciones climáticas y no el perfil de nicho climático de las especies (Wiens & Graham 2005; Wiens et al. 2010). Si bien se ha acumulado evidencia en diversos grupos taxonómicos que sustenta esta hipótesis, la tasa de divergencia del nicho ecológico a través del tiempo no es uniforme (Kozak & Wiens 2010; Peterson 2011), por lo que no es recomendable asumir que el conservadurismo de nicho está ocurriendo en el grupo de estudio (Losos 2008). Otro elemento importante a tomar en cuenta es la contribución de las

interacciones bióticas en la configuración histórica de la distribución de especies. Aunque se ha considerado que las interacciones tienen un efecto poblacional a escalas locales y no macroecológicas (Soberón 2007), contribuciones conceptuales recientes desafían este supuesto (González-Salazar et al. 2013). En el caso de la transmisión de un parásito, es el patrón geográfico de las interacciones vector-hospedero las que finalmente determinarán su distribución espacial (Peterson 2008).

En esta tesis investigué los patrones de la ecología geográfica de los vectores de *T. cruzi* relacionados con la hipótesis del conservadurismo de nicho y las interacciones vector-hospedero a una escala macroecológica. Los objetivos fueron (1) investigar el estado del conocimiento sobre los Triatomíneos de Norteamérica con el fin de refinar las hipótesis concretas sobre la historia natural de este grupo; (2) poner a prueba la hipótesis del conservadurismo de nicho en los triatomíneos de Norte y Centro América en un contexto filogenético; y (3) analizar las relaciones geográficas entre la distribución de vectores en México y sus hospederos conocidos y potenciales.

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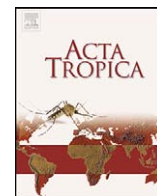
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CAPÍTULO 1



Ecology of North American Triatominae

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ABSTRACT

In all, 40 native triatomine species and subspecies occur in NA, belonging to six genera from the Triatomini (*Triatoma*, *Paratriatoma*, *Panstrongylus*, *Dipetalogaster*, *Belminus*, *Eratyrus*), and one genus from the Rhodniini (represented by one non-native species *Rhodnius prolixus*, formerly occurring exclusively in domestic habitats); 28 species are found exclusively in Mexico (and/or Central America), eight are shared between the United States (US) and Mexico, and four occur exclusively in the US. The genus *Triatoma* is the most diverse with 26 species belonging to the species groups *protracta*, including the species complexes *protracta* and *lecticularia*, and *rubrofasciata*, which includes the species complexes *rubida*, *phyllosoma* and *dimidiata*. Triatomine species richness declined both at higher (south US) and lower (south of the Isthmus of Tehuantepec, Mexico) latitudes. *Triatoma* species are found predominantly in cropland, grassland, wooded grassland and woodland landscapes. Land cover types were most similar among the *lecticularia*, *protracta*, and *rubida* complexes, in contrast to the *phyllosoma* and *dimidiata* species complexes. The land cover types having highest suitability for most species were wooded grassland, followed by woodland for the *phyllosoma* and *dimidiata* species complexes, and open and closed shrubland and cropland for the remaining three species complexes. A principal component analysis was used to demonstrate differences in the potential range for use of environmental conditions: *protracta* and *phyllosoma* complexes occupy the broadest niches. The present study represents a primary stratification of potential triatomine dispersal areas, based on species and species complexes, and based on predicted niche, a method which has already proven to be highly significant epidemiologically.

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1. Introduction

A high diversity of triatomine species (Reduviidae: Hemiptera) has been reported in North America (NA), including species in six genera from the Triatomini (*Triatoma*, *Paratriatoma*, *Panstrongylus*, *Dipetalogaster*, *Belminus*, *Eratyrus*), and one genus from the Rhodniini (represented by a non-native species *Rhodnius prolixus*, formerly occurring exclusively in domestic habitat) (Lent and Wygodzinsky, 1979). In all, 40 triatomine species and subspecies have been found in NA, of which 28 are found exclusively in Mexico and/or Central America, eight are shared between the United States (US) and Mexico, and four occur exclusively in the US. The genus *Triatoma* is the most diverse, with 26 species (two species include nine subspecies), belonging to the *lecticularia*, *protracta*, *rubida*, *phyllosoma*, and *dimidiata* species complexes.

Many *Triatoma* species have been incriminated as primary vectors for *Trypanosoma cruzi* transmission, and Chagas disease in NA (Ramsey et al., 2003; Vidal-Acosta et al., 2000). The *phyllosoma* com-

plex, the largest of the NA species complexes, includes most of the epidemiologically important vectors in Mexico, which together are responsible for an estimated 74% of vectorial transmission of Chagas disease (Ramsey et al., 2003). Most recently, two more species – *Triatoma gerstaeckeri* and *Triatoma recurva* – have been tentatively assigned to this complex, vectors in northeast and northwest Mexico, respectively (Sainz et al., 2004; Garcia et al., 2001; Pfeiler et al., 2006). *T. dimidiata* and its multiple genotypes, all of which transmit *T. cruzi* (estimated 21% of transmission altogether) were previously included in the *phyllosoma* complex, but are now considered to form the distinct *dimidiata* complex (Dorn et al., 2007; Panzera et al., 2007; Bargues et al., 2008). The *rubida* complex is the subject of recent concern in the states of Sonora and Sinaloa in northwest Mexico due to its increasing invasion of domestic habitats (Paredes et al., 2001). Recent phylogenetic studies now also suggest a structured complex for *Triatoma rubida*, with at least two defined species (Pfeiler et al., 2006). The *protracta* complex has six species and three subspecies, although only one, *Triatoma barberi*, has been incriminated as a primary Chagas disease vector (Salazar et al., 1988; Zarate and Zarate, 1985; Peterson et al., 2002; Ramsey et al., 2003). Although species from the *lecticularia* complex have been found infected with *T. cruzi*, their role in Chagas

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transmission seems limited (Ramsey et al., 2003; Dujardin et al., 2002).

In North America, sylvan and domestic transmission cycles are hypothesized to have either separate or overlapping habitats, where vector populations and vertebrate hosts of *T. cruzi* have complex and changing interactions. A crucial question is whether parasite transmission flows regularly back and forth between these habitats, or if it is constrained within habitats with little or no interchange (Pacheco, 2004). Domestic transmission cycles in Mexico are characterized by the maintenance of high and long-term *T. cruzi* parasitaemias, and may thus depend on secondary mechanisms such as congenital transmission in sylvan fauna. *T. cruzi* infection in triatomines is known to depend on environmental factors, although direct association of these factors to infection prevalence is mainly due to host availability (Giojalas et al., 1990; Asin and Giojalas, 1995; Ramsey et al., 2003). Many mammals act as *T. cruzi* reservoirs (Ryckman, 1986), including rodents, bats, mustelids, marsupials, canids, and xenarthans, among others. In Mexico, little information is available regarding *T. cruzi* infection in reservoirs from sylvan (Magallón-Gastélum et al., 2004; Ramsey et al., 2000; Ruiz-Pina and Cruz-Reyes, 2002; Zavala Velásquez et al., 1996; Peterson et al., 2002) or domestic habitats (Montenegro et al., 2002; Ramsey et al., 2005). In the US, studies have been conducted in the southeastern (Hall et al., 2007; Hancock et al., 2005; Karsten et al., 1992; Pung et al., 1995; Yabsley and Noblet, 2002; Yabsley et al., 2001), and southwestern regions (Ryckman, 1962, 1971, 1982; Ryckman and Ryckman, 1967a) identifying multiple host species for *lecticularia* and *protracta* species complexes.

New approaches for ecological niche modeling (ENM) can provide insights into species distribution and ecology (Soberón and Peterson, 2004). Niche models summarize ecological requirements of species, and can be projected onto landscapes to identify potential geographic distributions (Peterson, 2003, 2008). Briefly, these approaches involve data inputs of known occurrence points for species, digital data sets that summarize relevant environmental parameters (e.g., climate and topography), and algorithms for fitting niche models in the environmental spaces. Ecological niche modeling has been applied to a variety of spatial biodiversity phenomena (Anderson et al., 2003; Peterson et al., 2005; Thuiller et al., 2005), and also to the projection of vector-borne disease transmission (Beard et al., 2002; Peterson et al., 2002, 2003, 2004a,b, 2006; Peterson and Shaw, 2003; Levine et al., 2004a,b, 2007; Sánchez-Cordero et al., 2005; Peterson, 2006, 2008; Nakazawa et al., 2007; Williams et al., 2008). Although general habitat information exists for some NA triatomines, information on geographic distribution, host associations, and key abiotic or biotic environmental parameters is restricted to a very few species (Lent and Wygodzinsky, 1979; Ryckman, 1986; Ramsey et al., 2000). In the *protracta* species complex, host associations had been previously reported to be specific to particular species of woodrats of the genus *Neotoma* (Ryckman, 1962); an ENM application was recently used to predict these associations based on geographic distributions of triatomines and of woodrats (Peterson et al., 2002).

Generally, the bionomics, behavior, population ecology, and population genetics of most NA triatomines remain poorly studied, despite the epidemiological importance of Chagas disease vectors and the vectors' dispersal and ability to adapt to domestic habitats. Study of the natural and domestic ecology of these species, and the ecological mechanisms associated with their domestication and geographic expansion, may contribute to understanding the basic processes by which certain species of Triatominae invade new habitats, colonize human domiciles, and maintain gene flow between habitats. In light of renewed efforts to focus the control of Chagas disease transmission in both endemic and non-endemic countries (Jannin and Villa, 2007), the present study provides an overview of

the geographic distributions and niche of NA triatomines, particularly as related to identifying foci of species richness.

2. Materials and methods

2.1. Data sources

We compiled a database of known point occurrences for all triatomine species and subspecies from the literature (complete data search in PubMed, 1955–2006), state and federal Mexican healthcare system collection records until 2007, museum collections (Instituto de Biología, UNAM), all historical data for species presence from scientific literature since 1938, and our own field collections in NA (Table 1). The complete database for North America (including the geographic region covering the countries of USA and Mexico) contains 1629 records, covering the 40 species and subspecies present (or previously present) in the region. All collecting point locations were georeferenced to 0.001° resolution based on reference to fallingrain (<http://www.fallingrain.com/world>) and Geolocate (<http://www.museum.tulane.edu/geolocate/>) when locality names, states and country were specified, and Google earth

Table 1

List of NA Triatominae, indicating total unique collection sites per species or subspecies, species for which ecological niche models were generated (ENM), and species for which landscape analysis (LCA) was conducted using occurrence site polygons.

Species complex	Species	Unique data points	ENM	LCA
Lecticularia	<i>Triatoma incrustata</i>	4	X	x
	<i>Triatoma indictiva</i>	2	–	x
	<i>Triatoma lecticularia</i>	7	X	x
	<i>Triatoma sanguisuga</i>	18	X	x
	<i>Triatoma barberi</i>	83	X	x
Protracta	<i>Triatoma neotomae</i>	6	X	x
	<i>Triatoma nitida</i>	3	–	x
	<i>Triatoma peninsularis</i>	5	X	x
	<i>Triatoma sinaloensis</i>	4	–	x
	<i>Triatoma protracta protracta</i>	155	X	x
	<i>Triatoma p. nahuatlae</i>	5	X	x
	<i>Triatoma p. woodi</i>	10	X	x
	<i>Triatoma p. zacatecensis</i>	5	X	x
Rubida	<i>Triatoma rubida rubida</i>	17	X	x
	<i>Triatoma r. sonoriensis</i>	50	X	x
	<i>Triatoma r. cochimiensis</i>	2	–	–
	<i>Triatoma r. jaegeri</i>	1	–	–
	<i>Triatoma r. uhleri</i>	20	X	x
Phyllosoma	<i>Triatoma bolivari</i>	7	–	x
	<i>Triatoma brailovskyi</i>	5	X	x
	<i>Triatoma gerstaeckeri</i>	74	X	x
	<i>Triatoma longipennis</i>	117	X	x
	<i>Triatoma mazzottii</i>	49	X	x
	<i>Triatoma mexicana</i>	100	X	x
	<i>Triatoma pallidipennis</i>	268	X	x
	<i>Triatoma phyllosoma</i>	43	X	x
	<i>Triatoma picturata</i>	18	X	x
	<i>Triatoma bassolsae</i>	2	–	–
<i>Triatoma recurva</i>	27	X	x	
Dimidiata	<i>Triatoma dimidiata (Yuc)</i>	32	X	x
	<i>Triatoma dimidiata (Gulf)</i>	409	X	x
	<i>Triatoma dimidiata (Pacific)</i>	46	X	x
	<i>Triatoma hegneri</i>	5	X	x
–	<i>Belminus costaricensis</i>	1	–	x
–	<i>Dipetalogaster maxima</i>	8	X	x
–	<i>Eratyrus cuspidatus</i>	4	–	x
–	<i>Panstrongylus geniculatus</i>	1	–	x
–	<i>Panstrongylus rufotuberculatus</i>	16	X	x
–	<i>Paratriatoma hirsuta</i>	57	X	x
–	<i>Rhodnius prolixus</i>	9	X	x
Total	40	1629		

(<http://earth.google.com/>) when collection points were referred to as distances from a specific reference point.

Data sets (raster GIS layers) describing the ecological landscape were drawn from a variety of sources. For topographic information, we used the Hydro-1K data set (<http://edcdaac.usgs.gov/gtopo30/hydro/index.asp>), which includes elevation, slope, aspect, and an index of tendency to pool water (topographic index), all at a native resolution of 30" pixels. For climatic data, we used the Worldclim data base (Hijmans et al., 2005), including annual mean temperature, mean diurnal temperature range, isothermality, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, annual temperature range, mean temperature of wettest quarter, mean temperature of driest 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 driest quarter, and precipitation of warmest and coldest quarter.

Because most of the triatomine collection records were related to domestic or peridomestic collections, we derived a landscape characterization for each region of collection in order to minimize this collection bias. To obtain the profile of landscape characteristics for each collection point, we calculated a 5 km buffer around each collecting locality (78.54 km²) using ArcMap version 9.0. We then recorded land cover types for each of these occurrence polygons (i.e., within the buffer), which were obtained from Internet sources (<http://glcf.umiacs.umd.edu/data/landcover/>). Species were then grouped into complexes and a Least Square Analysis was used to assess their association with each habitat type.

2.2. Ecological niche modeling and species distributions

The Genetic Algorithm for Rule-set Prediction (GARP) was used to model ecological niches for each species; these models were subsequently projected as potential distributions. GARP divides occurrence data randomly into the genetic algorithm for model development and an independent data set ("extrinsic testing data") for evaluation of model quality; the input data are further subdivided into training data (for rule development), and intrinsic testing data (for evaluation of rule predictivity). Spatial predictions of presence and absence can include two types of error: omission (areas of actual presence predicted absent) and commission (areas of actual absence predicted present) (Fielding and Bell, 1997). Changes in predictive accuracy (i.e., avoidance of both error types) from one iteration to the next are used to evaluate whether particular rules should be incorporated into the model or not, and the algorithm runs either 1000 iterations or until convergence (Stockwell and Peters, 1999). The final rule-set is then projected back onto the environmental data sets input into the algorithm in order to identify areas fitting the model parameters, thus deriving a hypothesis of the potential geographic distribution of the species.

Given the stochastic nature of GARP (both via sampling of occurrence data and the genetic algorithm itself), it produces distinct results for different runs based on the same input data, representing alternative solutions to the optimization challenge. Following recently proposed best-practice approaches (Anderson et al., 2003), we developed 1000 replicates of each model; of these, we retained the 20 models with lowest omission error, and then discarded the 10 models of the 20 that presented the most extreme values of area predicted present [commission error index (Anderson et al., 2003)]. These "best subset" models were summed to produce final predictions of potential distributions. We considered areas identified by ≥ 8 of the 10 best subset models as predicted present, and areas predicted by fewer models considered as predicted absent.

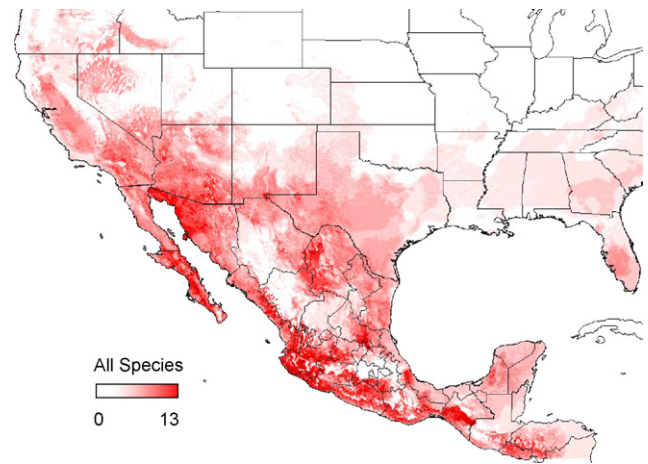


Fig. 1. Species richness for North American Triatominae, based on niche model projections (ENM).

To evaluate ecological differences between triatomine complexes, we performed a principal-components analysis (PCA) on the correlation matrix of 21 environmental data layers (see the list of variables in Table 4). We generated 250 random points within the area predicted for presence for each species, and then grouped the species into their respective complexes to explore their environmental characteristics in both raw environmental dimensions and the PCA-rotated space. ANOVA was then applied to the first two components of the PCA.

3. Results

3.1. Distributional patterns of NA triatomine species

From a total of 1629 point localities for NA Triatominae, only 94 (6%) represented the six least-documented genera (*Dipetalogaster*, *Eratyrus*, *Paratriatoma*, *Panstrongylus*, *Belminus*, *Rhodnius*). With the exception of *Paratriatoma hirsuta*, all of these species have restricted habitats. On the other hand, one genus, *Triatoma*, contained 85% of all species (33/39), some of which have a high degree of epidemiological importance for *T. cruzi* transmission to humans in Mexico (Table 1).

Triatomine species richness was generally high across Mexico, except in limited portions of high-elevation regions of the Sierra Madre Occidental, desert areas of Durango and Chihuahua in northern Mexico, and the southern edge of the Transvolcanic Belt in central Mexico. Triatomine species richness declined both at higher (south US), and lower (south of the Isthmus of Tehuantepec in Mexico) latitudes (Fig. 1).

All *Triatoma* species complexes are found in cropland, grassland, wooded grassland, and woodland landscapes, although few or none are found in mixed forest land cover types (Fig. 2). Land cover types were most similar among the *lecticularia*, *protracta*, and *rubida* complexes, as compared with the *phyllosoma* and *dimidiata* species complexes (Table 2). The *lecticularia*, *protracta*, and *rubida* complexes were not found in deciduous or evergreen broadleaf forest, although the *phyllosoma* and *dimidiata* species complexes were present in these cover types. Conversely, the *phyllosoma* and *dimidiata* complexes appear naturally absent from bare ground, urban and built environments, and open shrubland, where the remaining species complexes are found. The *rubida* complex shared evergreen needle-leaf forest land cover types only with the *phyllosoma* and *dimidiata* species complexes. The land cover types showing highest suitability for most species were wooded grassland, followed by woodland for the *phyllosoma* and *dimidiata* species complexes, and

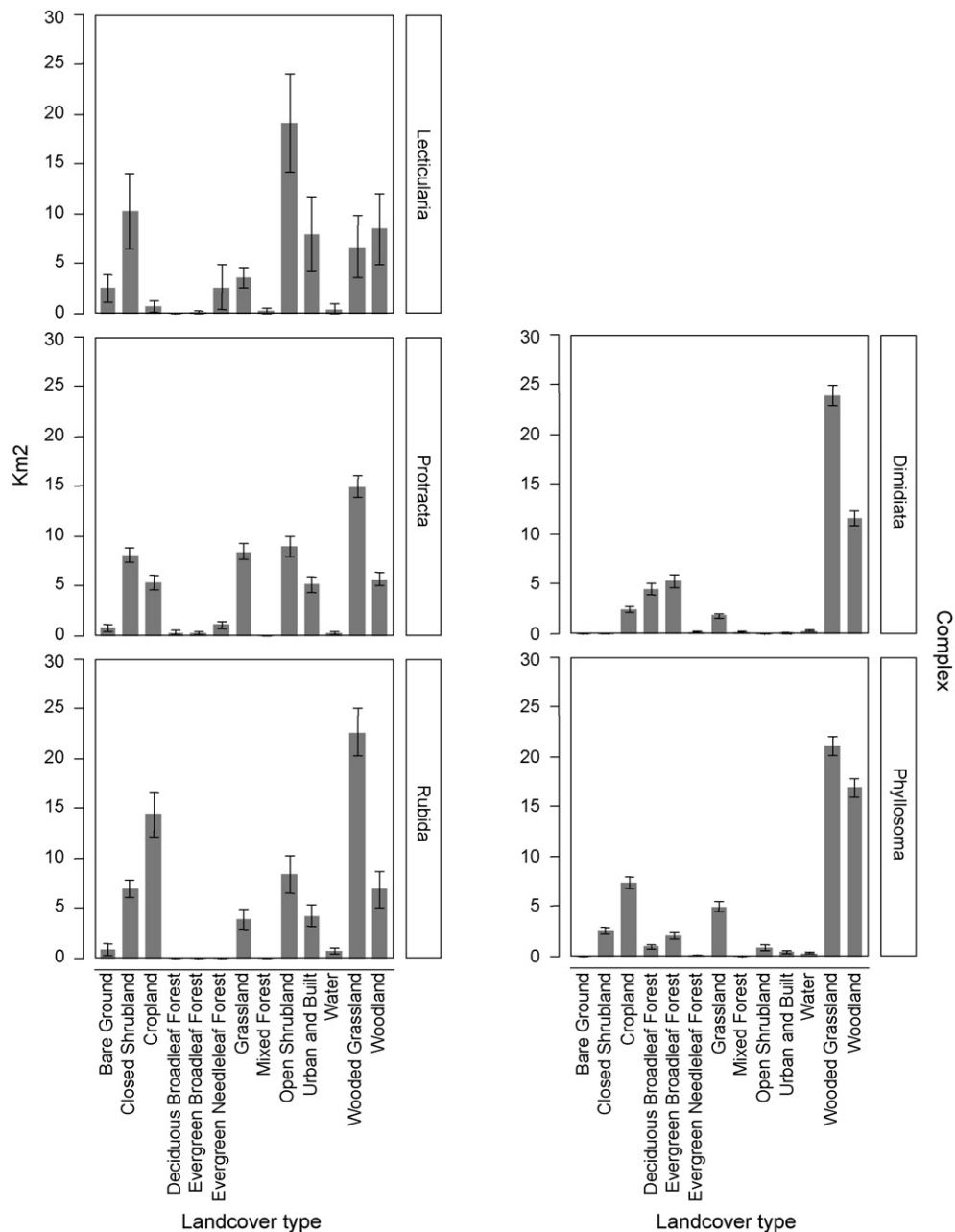


Fig. 2. Land cover types associated with NA *Triatoma* species complexes. Bars represent mean area (km²) ± S.E. for each land cover type, for all species combined within each complex.

open and closed shrubland and cropland for the remaining three species complexes.

3.2. Vector-host associations of NA *Triatominae*

Few studies have identified mammal hosts of *Triatominae* in NA, and most of these represent individual reports, or the analysis of few specimens (Table 3). Vector-host associations have only been studied extensively for the *protracta* complex (Ryckman, 1986), which is strongly associated with rodents of the family Cricetidae, compared with the more generalist associations of the *dimidiata* and *phyllosoma* complexes, which feed on mammals from three or more orders: Carnivora, Didelphimorpha and Rodentia, and Cingulata, Chiroptera, Didelphimorpha and Rodentia, respectively. Within the Rodentia, the family Cricetidae is the most associated with *Triatoma* species, with the genera *Neotoma*, *Peromyscus* and *Sig-*

modon being the more important hosts in sylvan and disturbed habitats.

3.3. Ecological niche models

We were able to model ecological niche for 30 species for which more than five unique occurrence localities were available (Table 1). *Rhodnius prolixus* was not included for ENM analysis since it is no longer found in Mexico, and because it was never collected outside the domestic habitat when it was present. ENMs for *Paratriatoma*, *Panstrongylus*, and *Dipetalogaster*, based on minimal numbers of point localities are shown in Fig. 3. *Paratriatoma hirsuta* is the only species in this group that appears to have a broad potential niche, which supercedes its current distribution. In contrast, *Dipetalogaster maxima* and *Panstrongylus rufotuberculatus* have restricted potential niches, restricted to Baja California

Table 2
Analysis of variance relating land cover types with the five *Triatoma* species complexes from North America (*** $P < 0.0001$). NS = differences not significant. LSM = mean of least squares and S.E. = standard error; different letters (A, B and C) represent statistical significant differences ($P < 0.05$ with Tukey's test).

Landcover type	F	P	Complex									
			Lecticularia		Protracta		Rubida		Phyllosoma		Dimidiata	
			LSM	S.E.	LSM	S.E.	LSM	S.E.	LSM	S.E.	LSM	S.E.
Bare ground	8.44	***	2.56 A	0.64	0.79 A	0.17	0.90 A,B	0.31	0.02 B	0.14	0.00 B	0.14
Closed shrubland	67.77	***	10.25 B,C	1.57	8.15 B	0.42	6.92 A	6.92	2.63 B	0.34	0.05 C	0.34
Cropland	24.50	***	0.71 A,B	2.54	5.35 B	0.68	14.42 A	1.26	7.4 B	0.55	2.40 C	0.55
Deciduous broadleaf forest	17.47	***	0 A,B	1.73	0.36 B	0.46	0 B	0.85	0.99 B	0.37	4.44 A	0.37
Evergreen broadleaf forest	16.14	***	0.18 A,B	2.04	0.32 B	0.55	0.00 B	1.01	2.14 B	0.44	5.31 A	0.44
Evergreen needleleaf forest	6.03	***	2.65 A	0.80	1.11 A	0.21	0 B,C	0.39	0.14 C	0.17	0.18 C	0.17
Grassland	21.73	***	3.64 A,B,C	2.10	8.46 A	0.56	3.92 B,C	1.04	4.99 B	0.45	1.81 C	0.45
Mixed forest	1.83	NS	0.31 A	0.25	0.01 A	0.07	0 A	0.12	0.03 A	0.05	0.19 A	0.05
Open shrubland	52.94	***	19.17 A	2.35	8.96 B	0.63	8.36 B	1.16	0.89 C	0.50	0 C	0.51
Urban and built	36.49	***	8.01 A	1.52	5.16 A	0.41	4.27 A	0.75	0.49 B	0.25	0.01 B	0.33
Water	1.24	NS	0.49 A	0.39	0.3 A	0.10	0.75 A	0.19	0.34 A	0.08	0.30 A	0.08
Wooded grassland	11.45	***	6.70 A	4.42	15 A	1.18	22.66 B	2.18	21.1 B	0.95	23.92 B	0.95
Woodland	22.71	***	8.50 A,B,C	3.61	5.66 C	0.98	6.92 B,C	1.78	16.89 A	0.77	11.62 B	0.78

and southern Mexico, respectively. ENM results for *Triatoma* species are shown as combined potential niche in Fig. 4A; patterns for individual *Triatoma* species complexes are depicted in Fig. 4B–F. The *protracta* complex (Fig. 4D) showed the broadest distribution of all, extending from the southwestern US, throughout the

northwest US, northeast US, and the Transvolcanic Belt in central Mexico. Only *T. barberi* in this complex is predicted to occur south of the Isthmus of Tehuantepec, even though this species has never been collected south of the central plains of Oaxaca (Fig. 4D). Predicted niche distributions for the *lecticularia* species complex

Table 3
Host species associated with NA *Triatominae*.

Complex	Triatominae species	Host mammal species	Reference
Lecticularia	<i>Paratriatoma hirsuta</i>	<i>Neotoma lepida</i> <i>Neotoma albigula</i> <i>Neotoma mexicana</i> <i>Neotoma</i> spp.	Ryckman and Ryckman (1967b) and Ryckman (1971)
	<i>Triatoma sanguisuga</i>	<i>Neotoma micropus</i>	Burkholder et al. (1980), Davis et al. (1943), Eads (1960), Pippin et al. (1968), Lent and Wygodzinsky (1979) and Usinger et al. (1966). Wood (1941)
	<i>Triatoma indictiva</i> <i>Triatoma lecticularia</i>	Domestic and peridomestic animals <i>Didelphis marsupialis</i> <i>Neotoma</i> spp. <i>Spermophilus variegatus</i>	Lent and Wygodzinsky (1979) Ryckman and Ryckman (1967b) Packchianian (1939)
	<i>Triatoma neotomae</i>	<i>Neotoma micropus</i> <i>Neotoma albigula</i>	Eads (1957), Thurman (1944) and Usinger et al. (1966) Ryckman (1962)
	<i>Triatoma p. protracta</i>	<i>Neotoma fuscipes</i>	Ryckman (1962) Ryckman (1962)
	Protracta	<i>Triatoma p. woodi</i>	<i>Neotoma lepida</i> <i>Neotoma micropus</i> <i>Neotoma albigula</i>
<i>Triatoma barberi</i>		<i>Sciurus variegatus</i> <i>Mus musculus</i> <i>Didelphis marsupialis</i> <i>Sigmodon hispidus</i> <i>Baiomys musculus</i> <i>Peromyscus levipes</i> <i>Liomys irroratus</i>	Tay (1969) and Salazar et al. (1987) Salazar et al. (1988) Zarate and Zarate (1985) Zarate and Zarate (1985) and Mota et al. (2007) Mota et al. (2007) Mota et al. (2007)
<i>Triatoma rubida uhleri</i>		<i>Neotoma albigula</i>	Ryckman and Ryckman (1967b)
<i>Triatoma longipennis</i> <i>Triatoma mazzottii</i> <i>Triatoma pallidipennis</i>		<i>Dasytus novemcinctus</i> <i>Dasytus novemcinctus</i> <i>Baiomys musculus</i> <i>Dasytus novemcinctus</i>	Ryckman and Ryckman (1967b) Biagi et al. (1964) Mota et al. (2007) Brumpton et al. (1939)
Phyllosoma		<i>Didelphis marsupialis</i> <i>Myotis</i> sp. <i>Neotoma alleni</i> <i>Sigmodon hispidus</i>	Zarate and Zarate (1985) Mota et al. (2007) Brumpton et al. (1939) Mota et al. (2007)
	<i>Triatoma phyllosoma</i> <i>Triatoma recurva</i>	<i>Baiomys musculus</i> <i>Neotoma albigula</i>	Mota et al. (2007) Ryckman and Ryckman (1967b)
	<i>Triatoma dimidiata</i>	<i>Didelphis marsupialis</i> <i>Didelphis virginiana</i> <i>Peromyscus leucopus</i> <i>Peromyscus yucatanicus</i> <i>Sigmodon hispidus</i> <i>Urocyon cinereoargenteus</i>	Zavala Velásquez et al. (1996) Ruiz-Pina and Cruz-Reyes (2002) Zavala Velásquez et al. (1996) Zavala Velásquez et al. (1996) Mota et al. (2007) Zavala Velásquez et al. (1996)
Dimidiata			

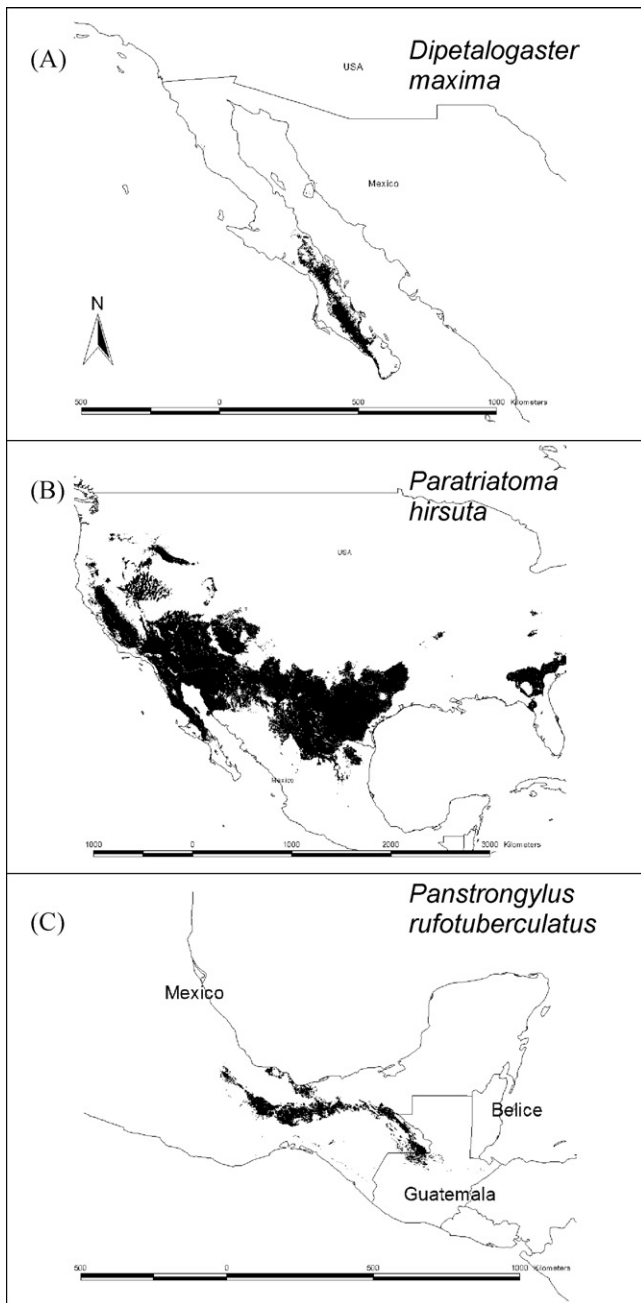


Fig. 3. Ecological niche models using GARP projected as species potential distributions for *Paratriatoma hirsuta*, *Dipetalogaster maxima*, and *Panstrongylus rufotuberculatus*.

span from west to east in the southern US, although concentrated principally in the south central and eastern states (Fig. 4B). The *rubida* species complex is restricted to the Pacific coast from the southwestern United States, south to northwestern Mexico, Baja California, and northeastern Mexico (Fig. 4C). The most speciose of the complexes, *phyllosoma*, has been collected only from Mexico, although its predicted niche distribution extends north into the southwestern United States and south into Central America (Fig. 4E). Predicted niche distributions of the *dimidiata* species complex followed a typical Neotropical pattern, along the southern Gulf and Pacific Mexican coasts, across southern Mexico (Fig. 4F). Potential niches for *dimidiata* complex species also occur in Florida, although none of the *dimidiata* genotypes have been collected in the US to date.

Table 4

Principal component analysis which reflects the importance of the environmental variables used to produce the ecological niche models, projected as potential distributions of the five *Triatoma* species complexes in North America. PC1 accounted for most of the explained variation (see Fig. 5).

Environmental variables	PC 1	PC 2
Mean temperature of coldest quarter	0.31199	-0.1768
Precipitation of wettest quarter	0.30779	0.10759
Annual precipitation	0.30627	0.1608
Precipitation of wettest month	0.30442	0.12343
Isothermality	0.30273	-0.1282
Precipitation of warmest quarter	0.28127	0.1126
Annual mean temperature	0.2453	-0.2441
Mean temperature of driest quarter	0.17101	-0.1906
Precipitation seasonality	0.15292	-0.3672
Mean Temperature of wettest quarter	0.13982	-0.2125
Precipitation of coldest quarter	0.10393	0.40189
Precipitation of driest quarter	0.10301	0.45452
Topographic index	-0.0301	0.00875
Elevation	-0.0444	0.01771
Mean temperature of warmest quarter	-0.05949	0.28778
Precipitation seasonality	-0.07278	0.2077
Max temperature of warmest month	-0.13614	-0.2424
Mean diurnal range	-0.22812	-0.2314
Temperature seasonality	-0.32289	0.06575
Temperature annual range	-0.33226	-0.0025

A principal component analysis (PCA) was developed to explore the degree to which environmental conditions used by different *Triatoma* complexes were similar (Table 4). The first and second principal components explained 41% and 17.2% of the overall variance, respectively. PC1 was dominated by humidity-related variables (e.g., precipitation of wettest month, precipitation of wettest quarter, annual precipitation, and also isothermality), whereas PC2 was dominated by drought and high temperature conditions (e.g. precipitation of driest quarter, precipitation of coldest quarter and mean temperature of warmest quarter (Table 4). The *phyllosoma* and *protracta* complexes had the greatest divergence in their environmental ranges, covering the complete range of all other complexes combined, even though the core region for each was distinct in terms of humidity and temperature variables. The PCA1 correlated with latitude for the *lecticularia* and *protracta* complexes in the drier habitats, and with decreasing latitude for the *rubida*, *phyllosoma* and *dimidiata* complexes in order of increasing humidity (Fig. 5). Along PC1, all complexes were distinct ($F=2119$, $P<0.0001$), except for *rubida* and *protracta* complexes (Tukey test $P>0.05$), although all complexes were different along PC2 ($F=799$, $P<0.0001$).

4. Discussion

Very few studies have been published regarding the ecology of NA triatomines, and each of these uses different methods and ecological criteria. The present study attempts to analyze geographic distribution patterns and ecological affinities for triatomine diversity from a continental perspective. Since most NA triatomine specimens have been collected from domestic habitats, it is assumed that these point localities also represent their occurrence in surrounding sylvan habitats, and consequently their infection due to zoonotic *T. cruzi* (Ramsey et al., 2000; Breniere et al., 2007; Salazar Schettino et al., 2007). The lack of interest in the dynamics of *T. cruzi* transmission via epidemiological surveillance (in Mexico) or the paucity of vector transmission of Chagas disease (in the US), has biased attention and collections away from more complete sylvan collections, which implies the need to use robust models to predict and analyze spatial and temporal distributions, and eventually, abundance.

Predominant land cover types are different for each *Triatoma* species complex, with low variance for four of these complexes

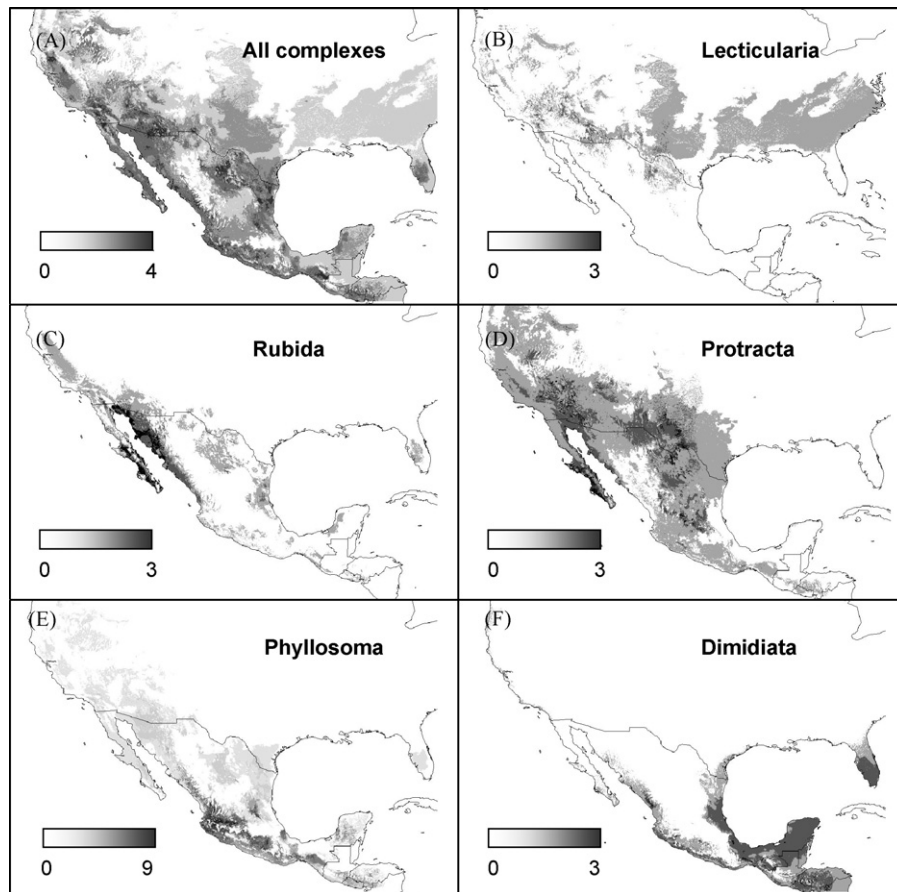


Fig. 4. Ecological niche modeling projected as potential distributions for all NA *Triatoma* species complexes, combined and individually for: *lenticularia*, *protracta*, *rubida*, *phyllosoma*, and *dimidiata* complexes, respectively.

(*protracta*, *rubida*, *phyllosoma*, *dimidiata*), indicating general niche agreement among species currently assigned to each complex. In the last decade multiple genetic marker studies have shed light on phylogenetic affinities for some of these species. Recent stud-

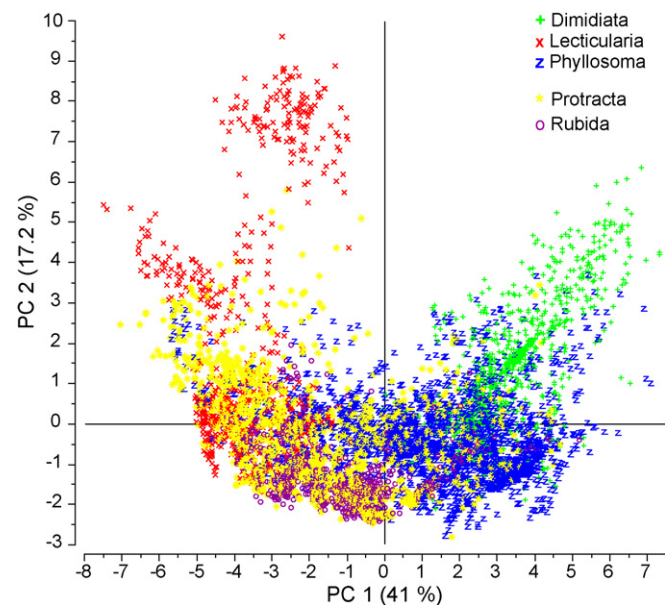


Fig. 5. Principal component analysis (PCA) of environmental variables and geographic distributions of the five *Triatoma* species complexes occurring in North America: *lenticularia*, *protracta*, *rubida*, *phyllosoma* and *dimidiata*.

ies using mtDNA markers have indicated that *T. recurva*, previously unassigned to any of the other NA species complexes, has a high degree of sequence homology with species of the *phyllosoma* complex (Pfeiler et al., 2006). In addition, ITS-2 analysis (rDNA) indicates a close phylogenetic relationship between *T. gerstaeckeri* and the *phyllosoma* complex (Marcilla et al., 2001). These data were used in the present analysis to include *T. gerstaeckeri* and *T. recurva* in the *phyllosoma* complex, and to separate the *dimidiata* from the *phyllosoma* complex. The present study indicates that there is no niche restriction or variation of either *T. recurva* or *T. gerstaeckeri* compared to that of the other members of the *phyllosoma* complex, thereby supporting their inclusion in the *phyllosoma* complex. In the present analysis, the *lenticularia* complex had the highest land cover variance. The *lenticularia* complex had previously included *Triatoma lenticularia*, *Triatoma indictiva* and *Triatoma sanguisuga*, with uncertain assignment of *Triatoma incassata* (Lent and Wygodzinsky, 1979); all four species were included in this analysis of the species complex.

Triatoma rubida includes five subspecies based on morphological criteria and lack of reproductive barriers (Adams and Ryckman, 1969). However, recent analyses indicate that at least one of the subspecies, *T. rubida cochimiensis*, has greater than 9% sequence divergence for cyt b and COI from *T. r. uhleri* and *T. r. sonoriana* (Pfeiler et al., 2006). Most genetic markers indicate that the *rubida* complex is more closely related to the *protracta* and *lenticularia* complexes than to the *phyllosoma* and *dimidiata* complexes (Sainz et al., 2004; Pfeiler et al., 2006). Landcover types analyzed in this study indicate high similarity between the *rubida* complex and the *protracta* and *lenticularia* complexes, while predicted ecological niche patterns for the *rubida* complex indicate greater niche simi-

larity with both *phyllosoma* and *dimidiata* complexes. Future genetic marker studies of all species and subspecies of this complex will be required to ascertain phylogenetic affinities.

The *lecticularia*, *protracta* and *rubida* complexes are generalists in terms of land cover, having an equivalent proportional coverage of over 5 or 6 landcover types (generally open and closed shrubland, cropland, urban and built areas, wooded grassland and woodland). However, the *phyllosoma* and *dimidiata* complexes showed a quantitative bias for only two landcover types, both associated with the previous three complexes, although not with the same intensity (wooded grassland and woodland). In addition, and despite an apparent high level of ecologic plasticity based on current species domestication of *phyllosoma* and *dimidiata* complexes, they were not found in highly urbanized or barren polygons, which correlates with the negative relationship observed between *Triatoma pallidipennis* infestation indices and human housing density in the Cuernavaca metropolitan area (Ramsey et al., 2005).

The principal component analysis was useful to measure the niche amplitude for each complex, as well as niche divergence between the *Triatoma* species complexes. The maximum variation in niche amplitude occurred along the first axis, associated with seasonal precipitation-humidity variables. The *protracta* and *phyllosoma* complexes had the greatest niche amplitude, possibly due to their high number of subspecies and species, respectively, adapted to different humidity regimes.

Despite the lack of epidemiological surveillance for Chagas disease in Mexico, human infection prevalence estimates, based on seropositivity in transfusion donations and/or specific seroepidemiological studies and predicted distributions of vector species, indicate that areas where *phyllosoma* complex species predominate represent 74% of vector transmission (including *T. gerstaeckeri*). The *dimidiata* complex is responsible for 21% of transmission, while the *protracta* complex accounts for 3%, and between the *rubida* and *lecticularia* complexes 2% of vector transmission (Ramsey et al., 2003). However, these estimates were compiled prior to reports confirming widespread domestication of species of the *rubida* complex. Vector transmission in the northern areas of Mexico including Chihuahua and the Rio Bravo Valley, and the southern US, may be more active than previously expected, due to massive habitat modifications in these areas in the last decades (Beard et al., 2002).

The Mexican population has become highly urbanized in the last decade, with continuous population migration back and forth from rural to urban areas, and the associated growth of urban areas, with parallel modification of surrounding rural and sylvan habitats. This has provided opportunity for most members of the *Triatoma* species complexes to adapt to domestic habitats, with at least nine of these now playing a primary role in *T. cruzi* transmission. Surprisingly, however, *Dipetalogaster*, *Panstrongylus* and *Eratyrus* are also now being collected in domestic habitats, indicating a previously unrecognized potential for domestication, correlating with their association with urbanized or barren land cover.

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CAPÍTULO 2

**MONOPHYLY AND NICHE CONSERVATISM IN NORTH AND CENTRAL
AMERICAN TRIATOMINE BUGS (HEMIPTERA: REDUVIIDAE: TRIATOMINAE),
VECTORS OF CHAGAS' DISEASE**

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Abstract

Niche conservatism, the hypothesis that closely related species tend to have similar niches, has been studied mainly in evolutionary, conservation biology and ecology and provides a framework to predict potential impacts of environmental change on biodiversity. Herein, we use multilocus phylogenetic analysis, niche modeling and randomization tests to study whether niche conservatism is occurring across triatomine vector species of *Trypanosoma cruzi*. Chagas disease, caused by this parasite, is the most important vector-borne disease in Latin America and transmission control is focused on vector population reduction. We first analyzed the evolutionary history of New World vector species to substantiate ecological niche comparisons within a clade composed of North and Central American species. Niche similitude correlated inversely with divergence times in six sister species pairs. However, niche conservatism occurs across these pairs, as demonstrated using randomization tests of niche comparisons. This is the first phylogenetic analysis to provide robust evidence of monophyly for North and Central America triatomine species and to analyze niche conservatism patterns on a sub-continental basis. This analytical framework can now be used to analyze long-term patterns in species' niche evolution of different vector-borne species to better understand potential changes in niche breadth and distribution due to large-scale environmental changes.

Keywords: Niche conservatism, vector-borne disease, Chagas Disease, Triatominae, evolutionary history, disease biogeography, multilocus phylogeny.

Introduction

Molecular sequence data and geographic species' distributions provide insight regarding their evolutionary history and biogeography (Fitzpatrick & Turelli 2006; Lemmon et al. 2007; Eaton et al. 2008; Peterson & Nyári 2008; Ree & Smith 2008; Lemmon & Lemmon 2008). Recent development of computational and algorithm applications for evolutionary biology now also provide better tools for integrated analysis of these data (Kozak et al. 2008, Sidlauskas et al. 2010). In particular, phylogenetic and biogeographic studies of species involved in pathogen transmission are useful to understand the patterns and processes behind specific biotic and abiotic relationships that cause their spread (Gaunt et al. 2001; Rigaud,

Perrot-Minnot, and Brown 2010; Biek and Real 2010; Crawl et al. 2008; Lafferty et al. 2010; Duffy et al. 2012; Hall et al. 2007; Hall et al. 2008; Jones et al. 2008).

Triatomines are vectors of *Trypanosoma cruzi*, the etiological agent of Chagas disease, which is the most common parasitic disease in the Americas (WHO 2004; 2010). Although Chagas disease can occur without the vector via congenital and blood transmission (Schmunis 2007, Yadon & Schmunis 2009, Schmunis & Yadon 2010), the proportion of non-vector risk is comparably minimal (Ramsey et al. 2003). Vector occurrence, therefore, is still considered the primary risk factor for *T. cruzi* transmission and Chagas disease (Schofield et al. 2006, Dias 2007, Martins-Melo et al. 2012), and triatomine bionomics are the primary determinants for Chagas disease exposure hazard (Ibarra-Cerdeña et al 2009, Stevens et al. 2011; Gourbière et al. 2011). Triatominae is a subfamily that belongs to the large family of assassin bugs (Reduviidae) (Schuh & Slater 1995), with more than 6600 species grouped in 21 subfamilies (Weirauch 2008). Triatomine bugs are characterized by their obligate hematophagy (Lehane 2005), which is considered to have evolved once or twice in this group (Weirauch & Munro 2009, Hwang & Weirauch 2012). With 140 described species grouped in 11 genera (Schofield & Galvão 2009), triatominae are the least diverse among the more phylogenetically closer reduviid subfamilies (Weirauch 2008, Weirauch & Munro 2009), such as Reduviinae (more than 140 genera), Stenopodainae (113 genera), Salyavatinae (16 genera), and Physoderinae (at least 11 genera) (Schuh & Slater 1995).

The Triatominae are distributed in the New World, except for seven species found in Southeast Asia. In North, Central and South America, triatomines occupy tropical and subtropical areas approximately between the 40° parallels in both hemispheres (Rodríguez & Gorla 2004). Despite wide environmental variation across North America (Badgley & Fox 2000), triatomine species shows a considerable environmental overlap on their distributional ranges (Ibarra-Cerdeña et al. 2009). This pattern could be explained by niche conservatism, the idea that closely related species tend to have similar niches (Peterson et al. 1999). Despite ecological niches diverge across the evolutionary history of lineages (Losos 2008), the rate of that divergence depends upon clade divergence times (Peterson 2011). Different macroevolutionary models have been proposed to explain niche conservatism patterns and divergence rates (drift, phylogenetic inertia, niche filling/shifting, evolutionary rate, and niche retention; Cooper et al. 2010). The niche retention model proposes lower expected divergence (Cooper et al. 2010) which could be the result of stabilizing selection or evolutionary constraints such as those imposed by developmental, physiological or population-level genetic factors (Wiens et al., 2010; Wiens, 2004; Wiens & Graham, 2005). It has been argued that sister species maintain key aspects of their environmental tolerances after speciation, thereby preventing species from occupying regions where niche conditions are not satisfied (Holt 2009, Wiens et al. 2010). Niche retention can be tested by comparing niche similarity of accessible areas for dispersal (“M” for “mobility” in Soberón & Peterson 2002) among sister species. Niche conservatism analysis using the M region within an evolutionary meaningful time span (Peterson et al. 2011) could have a profound impact on hypothesis testing (Anderson & Raza 2010, Barve et al. 2011). Niche conservatism by means of niche retention occurs when the empirical niche model of the sister pair of species are more similar than niche models that are extracted randomly from their respective “M” regions (Warren et al. 2008). Niche conservatism rather than niche divergence is proposed to play an important role in allopatric speciation (Kozak & Wiens 2006), a plausible mechanism for dominant speciation

events of North and Central American (NCA) triatomines. In vector-borne disease systems, vector niche conservatism patterns could influence a particular suite of processes in pathogen dynamics (i.e. *Trypanosoma cruzi*), for instance, to which areas dispersal occurs and/or with what hosts they interact.

We present here a framework to study the evolutionary trends in ecological niches of triatomines considering phylogenetic and biogeographical characteristics of species. Particularly, we asked if niche conservatism is a common pattern for triatomines inhabiting the continuous landmass of the North and Central American sub-continent. Since the phylogenetic relationships within triatomines are a matter of debate (Hypsa et al. 2002; Weirauch 2008; Schofield & Galvão 2009; Weirauch & Munro 2009; Patterson & Gaunt 2010), and only a small subset of NCA triatomines have been included in phylogenetic studies, we started with a reconstruction of the phylogenetic relationships of New World triatomines and tested whether phylogeny of NCA triatomines had a biogeographical association that could indicate that bioclimatic niches evolved in a continuous historically accessible landmass and provide an approximate time-scale for the divergence periods of sister pairs that lead to the interpretation of evolutionary pattern in niche evolution. Then, based on the relationships recovered within our NCA clade, sister species were used to test for niche conservatism across this group.

Materials and Methods

1. Taxon sampling

Our taxon sampling covered species belonging to the Triatominae subfamily, distributed within the American continent, for which DNA sequences of at least three of six gene markers (see below) are published in GenBank. A total of 53 triatomine species from seven genera (*Dipetalogaster*, *Eratyrus*, *Mepraia*, *Paratriatoma*, *Panstrongylus*, *Rhodnius*, and *Triatoma*) were analyzed. This database represents 40% of all described species of the subfamily for the American continent, and all of the primary Chagas disease vectors.. *Triatoma* species from North, Central and South America were assigned as currently classified (Lent and Wygodzinsky 1979). *Triatoma dimidiata* was divided into three terminal taxa (Pacific, Gulf and Yucatan regions) based on previous studies (Dorn et al. 2007; Barges et al. 2008; Stevens et al. 2011; Gourbière et al. 2011). We also include six species (*Dipetalogaster maximus*, *Eratyrus mucronatus*, *Mepraia spinolai*, *Panstrongylus herreri*, *Panstrongylus megistus*, *Paratriatoma hirsuta*), of five small triatomine genera from the American continent, as well as seven species of *Rhodnius* (Rhodniini tribe). Two species belonging to Reduviinae (*Zelurus petax* and *Reduvius personatus*), were used as subfamily outgroups (Hypsa et al. 2002, de Paula et al. 2005, Patterson & Gaunt 2010), using both species to root all trees. In all, sequences for 54 species were compiled (87% of species had sequences for 16S, 63% for 12S, 52% for Cytb, 48% for COI, 37% for 18S, and 30% for 28S). A list with the species included and GenBank accession numbers for all sequences used is included in Appendix 1 and a list of their references is presented in Appendix 2.

2. Phylogenetic analyses

Previously published (GenBank) sequences belonging to three loci, four mitochondrial (mt) and two nuclear gene markers, were used to carry out a concatenated phylogenetic analysis. The mt markers included a fragment covering most of cytochrome oxidase I (1,494 bp), 682 bp of cytochrome *b* (*cyt b*), 375 bp of the 12S ribosomal RNA (rRNA), and 604 bp of the 16S rRNA genes. The nuclear markers selected were ~1919 bp of the 18S rRNA and ~620 bp of the 28S rRNA genes. Sequences of the six markers were used to analyse phylogenetic relationships at different taxonomic levels within the Reduviidae (see Appendix 2). Gene sequences were aligned manually and ambiguously aligned regions of rRNA genes were excised.

We carried out the concatenated analysis using the partitioned Bayesian method implemented in the MrBayes version 3.2.1 (Ronquist et al., 2011). The analysis included two independent runs of four parallel chains and 20 million generations each, using uniform priors and sampling trees every 1000 generations. Protein coding genes were divided into three partitions, based on codon positions, whereas rRNA genes were considered each as a single partition. The program JMODELTEST version 2 (Darriba et al., 2012) was employed to select the evolutionary model used for each partition following the Akaike criterion. Even though a stationary state occurred before 1 million generations, we used a conservative approach and deleted the first 5000 sampled trees. The remaining trees were used to reconstruct a tree with posterior probabilities (PP) of clades, assuming that clades with $PP \geq 0.95$ were significantly supported (Ronquist and Huelsenbeck, 2003).

We also carried out separate Bayesian and maximum likelihood analyses (ML) for those species belonging to a reconstructed NCA clade (see results) using both the *cyt b* marker and a 497 bp fragment of the nuclear ITS2 gene. The Bayesian analysis was conducted using the same parameters described above. The ML conducted in MEGA version 5 (Tamura et al. 2011) was based on the Tamura-Nei model with a bootstrap consensus tree inferred from 1000 replicates. Branches corresponding to partitions reproduced in less than 50% bootstrap replicates were collapsed. A discrete Gamma distribution was used to model evolutionary rate differences among sites (4 categories +G; Cytb parameter = 0.54; ITS2 parameter = 0.57). In the Cytb analysis, the rate variation model allowed for some sites to be evolutionary invariable ([+I], 49.9% sites). The Bayesian and ML were carried out to 19 NCA species (Appendix 1).

3. Tests of alternative topologies

We tested our recovered hypothesis of phylogeny with three alternative topologies using Bayes factors comparisons, which were calculated from estimates of marginal likelihoods using the stepping stone (ss) sampling approach (Xie et al., 2011) implemented in MrBayes version 3.2 (Ronquist et al. 2012). The three alternative topologies forced: (1) the genus *Triatoma*, (2) the NCA species of *Triatoma*, and (3) the NCA species of *Triatoma* with the inclusion of the North American *D. maximus* and *P. hirsuta*. The SS estimates were obtained running 10 million generations, followed by 50 steps with 1000 samples within each step, and eliminating the first 25% of samples from each step. Two independent runs were performed for each dataset (one for a constrained and one for a non-constrained topology). The arithmetic difference of the bayes factors of the two runs in log units constitutes the criterion employed to reject the null hypothesis (monophyly). A log difference in the range of 3–5 is typically

considered strong evidence in favor of a model, whereas a log difference above five is considered very strong evidence (Kass and Raftery, 1995).

4. *Divergence times*

We estimated divergence times of clades among the species using a relaxed molecular clock approach with BEAST version 1.7.4 (Drummond et al. 2012). We excluded *R. personatus* from this analysis to have a basal node separating the remaining *Z. petax* outgroup from the Triatominae clade. The G + I + Γ model was used for this analysis, considering each gene marker as a single partition. The analysis was run for 20 million generations, sampling trees every 1,000 generations. The first 10 million generations were discarded and the remaining trees were used to build a maximum clade credibility tree with TreeAnnotator version 1.7.4 (Rambaut and Drummond, 2008).

The most basal node indicating separation between Reduviinae and Triatominae in our BEAST topology was calibrated to have a normal prior distribution of 52.89 (MY) with 4.5 standard deviations. We set this calibration based on the divergence time estimate recovered by Hwang & Weirauch (2012) for the most recent common ancestor (MRCA) between the above two subfamilies. The MRCA of the Triatomini clade was on the other hand calibrated to have a normal prior distribution 30.0 MY with one standard deviation, based on the age of a fossil assigned to *Triatoma* from Dominican amber reported by Poinar (2005).

5. *Sister species data points and definition of the background area for each pair*

Based on our preferred estimate of phylogeny, we defined six pairs of sister species belonging to our recovered NCA *Triatoma* clade for niche conservatism analysis. Only one sister species pair was assigned using previously published single locus data, given the lack of information for at least three gene markers (*T. gerstaeckeri* – *T. mexicana*). This sister pair was, however, corroborated with our single locus phylogenetic analysis. Georeferenced occurrence locations reported elsewhere were used to build ENM models (Peterson et al. 2002, Lopez-Cardenas et al. 2005, Ibarra-Cerdena et al. 2009). Niche models were constructed using 188 data points for *T. barberi*, 378 for *T. dimidiata* Gulf, 59 for *T. dimidiata* Pacific, 253 for *T. gerstaeckeri*, 115 for *T. longipennis*, 42 for *T. mazzottii*, 265 for *T. mexicana*, 22 for *T. nitida*, 33 for *T. phyllosoma*, 154 for *T. protracta*, 44 for *T. recurva*, and 42 for *T. rubida*. We use a regional classification for the *T. dimidiata* complex based on their distribution (*T. dimidiata* “Gulf” for the species that occurs along the Gulf of Mexico in the eastern region of Mexico; *T. dimidiata* “Pacific” for the species that occurs along the Pacific coast and inland areas of southern Mexico and Guatemala. The “M” region (Soberón & Peterson 2005) or “background area” in the terminology of Warren et al. (2008), was defined for each species by plotting the species’ data points with the map of terrestrial ecoregions of the world (Olson et al. 2001), and recording the ecoregions where each species has been registered, a recommended strategy for “M” delineation (Soberón 2010, Barve et al. 2011).

6. *Ecological niche modeling*

Ecological niche models (ENM) were produced using the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell and Peters 1999). GARP is an evolutionary-computing software package available in openModeller Desktop *version*. 1.1.0 (<http://openmodeller.sourceforge.net/>). To take advantage of the random-walk nature of the GARP algorithm, we developed 100 replicate models of each species' ecological niche. We used the procedures described in Anderson et al. (2003) for choosing a 'best subset' of the 100 models based on optimal combinations of error statistics, which is also implemented in openModeller. This procedure is based on the observations that (1) models vary in quality, (2) variation among models involves an inverse relationship between error of omission (leaving out true distributional area) and of commission (including areas not actually inhabited), and (3) best models (as judged by experts blind to error statistics) are clustered in a region of minimum omission of independent test points and moderately predicted area (an axis related directly to commission error). The relative position of the cloud of points relative to the two error axes assesses the relative accuracy of each model. To choose best model subsets, we (1) eliminated all models that had omission error > 5% based on independent intrinsic test points, (2) calculated the median area predicted present among these zero-omission points, (3) identified the 10 models closest to the overall median area predicted, and (4) summed these 'best subsets' models. These latter procedures are also implemented in openModeller *ver*. 1.1.0. Finally, binary models were obtained and projected on geography as potential distribution, from the 10 best models by using a minimum presence threshold criterion in which the binary projection is a result of the percentage of model agreement that predicts the presence of all datapoints.

The WorldClim bioclimatic layers were used as variables for species distribution predictors. Since this database contains 19 bioclimatic variables, we analyzed the correlation levels between these variables and excluded from niche modeling those variables that were correlated ($r > 0.75$); variables most related with species physiological tolerances were retained. Nine bioclimatic variables were retained in model development (annual mean temperature, maximum temperature of warmest month, minimum temperature of coldest month, annual temperature range, temperature seasonality, annual precipitation, precipitation of wettest and driest months, and precipitation seasonality; Hijmans et al. 2005), as well as four topographic variables from the Hydro-1K data set (elevation, slope, aspect, compound topographic index; USGS, 2001), at the 0.01° of resolution (approx. 1km). Topographic variables can modify how a species experiences climate (e.g. north-facing slopes versus south-facing slopes) and are known to contribute positively to model quality (Giles et al. 2011).

7. Testing for niche similarity in environmental space

We measured the multidimensional niche overlapping (e-space) in each pair species. First, we sampled 15,000 random points in NCA for sister species niche analysis. The values for these geo-referenced points from bioclimatic and topographic layers were analyzed to identify principal components using a correlation matrix. Binary maps derived from the ENM's for each *Triatoma* sister species were overlain on the matrix to project points that represent the species' potential niche and those representing the North American region. The final matrix was imported into Arc Map 9.2 to draw a convex hull polygon representing environmental space (E-space) for each species. The centroid of each polygon and 100 random points within

each polygon were generated. The Euclidian distance between the centroid of each of a pair of sister species and the distance from the centroid of each species to 100 random points from the corresponding species' polygon were also calculated. All analyses were conducted in Arc Map 9.1 using Hawkth's Tools. Niche similarity in E-space was calculated by comparing the distance between each centroid and the distribution of distances from the centroid to random points. The niche of each species' pair is considered indistinguishable when distances between centroids were less than the distribution distances of each centroid to corresponding random points.

8. Testing for niche similarity in geographic space

We applied a randomization test of background similarity to compare the geographic projections of species' niches for each pair. To test if sister species' pairs had more similar ecological niche than expected by chance (Warren et al. 2008), we conducted niche similarity analysis using ENMTools *ver* 1.3 (Warren et al. 2010). Briefly, two similarity tests, "D" and "I" derived from Schoener (1968) and Hellinger distances, respectively (Warren et al. 2008), were calculated from ENM's generated in MaxEnt for each species (Phillips et al. 2006; Phillips & Dudik 2008); the "minimum presence training" threshold for each pair of sister species were projected. A null distribution for these distances was calculated from ENM's generated with random occurrence points within the M of its sister species. Random occurrence points were generated from ASCII raster file of the ecoregions defined for each species. The null hypothesis (species similarity not different than expected, based on background environment) was rejected when empirical similarity values were either significantly higher (niche conservatism) or lower (niche divergence), based on 100 random replicates (95% confidence interval, $P < 0.05$).

Results

1. Phylogenetic relationships

The Bayesian phylogram based on the concatenated analysis of cytb, COI, 12S, 16S, 18S and 28S gene markers is shown in Figure 1. The phylogram contains a considerable number of significantly supported clades (23 out of 49 clades), with three additional clades also having marginally significant PP values ($0.9 \leq PP \leq 0.94$).

Members of Triatomini and Rhodniini each appeared significantly supported as monophyletic (both with $PP = 0.96$). Specimens assigned to *Triatoma*, with the exclusion of *T. flavida*, were nested in a significantly supported ($PP = 0.96$) major clade together with two species of *Panstrongylus* (*P. herreri* and *P. megistus*), *D. maximus*, and *E. mucronatus*.

There are two weakly supported main clades within *Triatoma* ($PP = 0.43$), one composed of South American species ($PP = 0.37$), and another one with NCA species ($PP = 0.98$) species. In general, the recovered sister species of the NCA clade (Table 2 and Appendices 3 and 4) were supported by significant PP values (≥ 0.90), except for *T. protracta*-*T. barberi* ($PP = 0.56$). This latter sister species pair, however, was significantly supported ($PP = 1$; BTP = 99) in the ITS2 Bayesian and ML topologies (Table 1; Appendix 4). The cytb and ITS2 topologies (Appendices 3 and 4) also significantly supported *T. mexicana* and *T. gerstaeckeri* as sister species, and this relationship was also significantly supported in the Bayesian ITS2 analysis

(PP = 0.96).

The three Bayes factors comparisons performed with the ss approach strongly favored the relationships derived from the Bayesian concatenated analysis, which show *Triatoma*, the NCA species of *Triatoma*, and the latter species with the inclusion of *D. maximus* and *E. mucronatus*, each as non-monophyletic. In these analyses, the compared model likelihood estimates had differences higher than 81 log likelihood units (monophyletic vs non-monophyletic *Triatoma* = 28556.75 and 28475.20, respectively; monophyletic vs non-monophyletic NCA *Triatoma* = -28563.94 and -28411.77, respectively; monophyletic vs non-monophyletic NCA *Triatoma* with the inclusion of *D. maximus* + *Pa. hirsuta* = -28399.01 and -28653.88, respectively).

2. Divergence time estimates

Divergence time estimates between the triatomine species of the NCA region and South America are on the order of 14.1-22 MYA. The separation between the Central American clade (*Panstrongylus* spp. and the *rubrofasciata* complex) and the clade composed of North America including Mexico is similar (13-20 MYA). Divergence between Nearctic (*protracta* and *rubida*) and Neotropical (*phyllosoma* and *dimidiata*) complexes on the other hand was timed to the Miocene (10-16 MYA). Speciation processes within the Neotropical complexes occurred principally in the Pleistocene, in contrast to the Pliocene speciation for Neartic complexes (Figure 2).

3. NCA *Triatoma* sister species' ENM

The combined ENM for all NCA *Triatoma* species covers most of the regional territory of Guatemala, Belize, El Salvador, Nicaragua, Honduras, Mexico and the southern United States (Figure 2). There was minimal range overlap between sister species, except for *T. mazzottii*-*T. phyllosoma* (Figure 2E). The broadest potential distribution range was *T.p. protracta* in the US and Mexico, almost crossing the complete continental longitudinal gradient, while its sister species, *T. barberi*, has a more restricted ENM, covering only the highlands of the transvolcanic belt (Figure 2A). In general, sister species have allopatric potential distribution along a north/south latitudinal configuration (Figure 2A, 2B, 2C, 2D), although sub-tropical species pairs are partially sympatric (i. e. Figure 2E).

4. Niche breadth and similarity between sister pairs in E-space

All NCA sister species occupied a portion of the complete environment of the PCA range. Species such as *T. protracta*, *T. barberi*, *T. mazzottii*, and *T. dimidiata* Gulf, had broader niche range (relative polygon size), while the other species have relatively narrow niche ranges (*T. rubida*, *T. nitida*, and *T. phyllosoma*; Figure 3). There was no association of this pattern with the ecoregions where these species occur (Figures 2 and 3). NCA *Triatoma* spp. did not occupy a particular suite of environmental conditions as a group, but the environment of this genus was composed of the sum of all species' niches (Figure 3). Niche divergence among species' pairs was broad over E-space. One group of sister species pairs had non-overlapping polygons (Figures 3A, 3B, and 3C) with statistically significant differentiation (Figure 4: *T. protracta*-*T. barberi*, *T. nitida*-*T. rubida*, and *T. gerstaeckeri*-*T. mexicana*). Sister species with partial niche overlap (Figure 3D and 3E) or complete niche polygon overlap (Figure 3F) were

statistically indistinguishable (Figure 4: *T. recurva*-*T. longipennis*, *T. phyllosoma*-*T. mazzottii*, and *T. dimidiata* Gulf and *T. dimidiata* Pacific).

5. Niche similarity in G-space (accessible niche M)

The niche of all NCA *Triatoma* sister species' pairs is more similar between them, than expected by chance. There is high niche similarity between sister species ($P < 0.01$), even for those with complete E-space differentiation (red arrows in Figures 4 for E-space and Figure 6 for G-space: *T. protracta*-*T. barberi*, *T. nitida*-*T. rubida*, *T. gerstaeckeri*-*T. mexicana*).

Discussion

Evolutionary history of New World and NCA triatomine

This is the first phylogenetic analysis that provides robust evidence of monophyly for NCA species of *Triatoma*. Our study also supports a previous phylogenetic analysis based on a single locus that recovered a sister group relationship between the NCA and the South American *Triatoma* clades (Hypsa et al., 2004), and other one that recovered the latter clade (Patterson & Gaunt 2010).

Our phylogenetic study yielded a robust hypothesis that allow us to reconstruct the evolutionary history and biogeography of New World triatomines. *Triatoma* consistently appears as not monophyletic, and the bayes factors tests performed forcing its monophyly also support this (Ronquist et al. 2012). A paraphyletic *Triatoma* is therefore proposed with respect to *Eratyrus*, *Dipetalogaster*, *Paratriatoma* and *Panstrongylus*. The results consistently reaffirm the monophyly of NCA triatomines (None of all the extant species in the clade are distributed significantly beyond of the NCA region and no species outside of the clade include a significant portion of their ranges within NCA study region). However, *Triatoma* is intermingled with the two monotypic genera *Dipetalogaster* and *Paratriatoma*.

The subfamily Triatominae has been recovered both as monophyletic (Hypsa et al. 2002, Weirauch 2008, Weirauch & Munro 2009, Patterson & Gaunt 2010) or paraphyletic (De Paula et al. 2005, Schofield & Galvão 2009). In the most recent and comprehensive multilocus phylogenetic analysis of Reduviidae, the subfamily appeared paraphyletic with respect to the reduviine genus *Opisthacidius*, even though only a small sample of Triatominae species were included (less than 10% of its described species; Hwang & Weirauch 2012).

The divergence times estimates recovered within the Triatominae showed that the MRCA of the NCA and South American *Triatoma* clades originated 14.1-22 MYA, which is congruent with the recently proposed completion of the Isthmus of Panama between the early Oligocene and Miocene (Bacon et al. 2012). Hypsa et al. (2004) had proposed a Central American and/or Great Antilles origin for Triatominae. A Central American origin for the Triatominae seems more likely due to the presence in this region of many extant Triatominae species of *Eratyrus*, *Cavernicola*, *Panstrongylus*, *Rhodnius*, *Triatoma* and *Opisthacidius*.

Most of NCA species of *Triatoma* diverged during the Pliocene. This was a period of major climate and orographic changes in North and Central America (Haywood et al. 2009, Ferrari et al. 2012). These changes have been proposed to promote speciation events

throughout the continent. In particular, Ibarra-Cerdeña et al. (2009) demonstrated partial overlap of climatic niche of NA triatomines at a species complex level for the *dimidiata*, *lecticularia*, *phyllosoma*, *protracta* and *rubida* complexes.

Niche conservatism within NCA triatomines

Our concatenated phylogenetic analysis recovered six sister species pairs from NCA, all of which belong to a significantly supported clade. Niche conservatism among NCA *Triatoma* sister species occurred across different degrees of phylogenetic divergence and niche overlap patterns, representing the first evidence of niche conservatism across several species vectors of zoonotic diseases that burden human health.

Niche similarity or divergence between species are not a *per se* proof of niche conservatism or a lack thereof (Warren et al. 2008, McCormack et al. 2010, Peterson 2011). Since niche similarity between species could be a result of niche conservatism or convergence (Eaton et al. 2008), knowing the phylogenetic relations between compared taxa is crucial for interpretation of niche comparisons. In analyzing ecological niche conservatism in sibling species, at least three components must be considered: (1) compared taxa should be the most likely sister species, (2) the sister species should be located in a region of probable historical accessibility (Anderson & Raza 2010, Barve et al. 2011), and (3) niche predictor variables must be selected based on biological significance and absence of statistical redundancy (Peterson & Nakazawa 2008, Rödder et al. 2009). These three points should be considered to avoid ambiguity as a result of inconsistency in sibling species selection criteria (Silvertown et al. 2006 and a re-analysis of Ackerly et al. 2006), multi-dimensionality of dataset predictors (causing overfitting) (Fitzpatrick et al. 2007 and a re-analysis in Peterson & Nakazawa 2007), and of failure to integrate geographically explicit potential dispersal areas (Rice et al. 2003 and a re-analysis in McCormack et al. 2010).

Our study analyzed niche conservatism between sister species by first using robust selection criteria to identify species pairs, since previous works did not recover robust relationships of triatomine species in the American continent (Hypsa et al. 2002, Sainz et al. 2004, de Paula et al. 2005, Patterson & Gaunt 2010). We reconstructed Bayesian phylogeny and estimated divergence times using a concatenated data set using six gene markers that contained different degrees of missing data. Previous studies using both empirical and simulated data, however, have shown that the accuracy of phylogenetic analyses is not influenced by the inclusion of missing data but by the amount of phylogenetic signal (Wiens & Moen 2008, Wiens & Morrill 2011).

The niches of sister species' were non identical in the pairs with deep divergence times (*T. protracta* and *T. barberi*, *T. rubida* and *T. nitida*), whereas the opposite was found for the more recent split taxa (*T. dimidiata* Gulf and *T. dimidiata* Pacific). Despite the observed gradient in niche similarity in e-space, all pairs showed more similarity than expected considering a null model of background similarity (Warren et al. 2008, McCormack et al. 2010). Niche conservatism therefore occurs across the species complexes of NCA. We observed a gradient in distribution size, region of distribution, range overlapping and niche breadth in NCA triatomines. However, in each of these conditions, we found the presence of niche conservatism. This was observed even for species pairs with highly divergent

background environments (i.e. *T. protracta* and *T. barberi* or *T. rubida* and *T. nitida*) and allopatric distributions. Under the evolutionary species concept, retention of niche characteristics in highly divergent environments could promote speciation, since dispersal between geographical ranges is unlikely (Kozak & Wiens 2006, Glor & Warren 2011). Whether a deep phylogenetic niche conservatism is occurring in NCA triatomines as in other taxa (Eaton et al. 2008; Anciães & Peterson 2009), needs to be further examined. Here we tested whether niche conservatism is a general pattern for NCA triatomines regardless to the complex to which they belong (i.e. *protracta*, *phyllosoma*, etc). We found that niche similitude in e-space was related inversely to the divergence periods among sister species, however there was no evidence for ecological speciation since niche similitude among sister species was always higher than the background similarity. Allopatric species often inhabit different environmental conditions and landscapes (Peterson 2011), thereby the fact that their niches are not identical do not prove lack of niche conservatism (Warren et al. 2008, McCormack et al. 2010, Peterson 2011, Rödder & Engler 2011). Conversely, if niches of two closely related species are more similar than expected accordingly to the environmental differences of each species' regions, indicate that species retained niche traits due phylogenetic effect (Losos 2008, McCormack et al. 2010). Niche conservatism influence the possibility for population establishment in accessible areas and the trends of persistence due to ecological disturbs and climatic fluctuations (Holt 2009). In this context, climate change will affect notoriously the species-environment relationships and has been shown that some vector-borne and zoonotic disease could increase their spatial distribution (Peterson & Shaw 2003, Nakazawa et al. 2007, González et al. 2010). However, could be parasite, vectors or reservoir extinctions if species are not able to cope with climate change (Rohr et al. 2011). Knowing if niche conservatism explain the current species-environment relationships help to conduct a more realistic forecasting of future effects of climate change on vector-borne zoonotic distributions (Wiens et al. 2010).

Implications of niche conservatism in spatial epidemiology

Niche conservatism in species of public health importance has implications in spatial epidemiology. Niche conservatism could impose constraints on the the responses of vector-borne species facing climate change effects (Peterson 2006) or to adapt to new locations after natural or anthropogenic dispersal (Benedict et al. 2008). Recognizing whether niche conservatism is a dominant principle in vector-borne species will allow to anticipate the likelihood for distributional shifts owed climate change (Peterson 2009) and/or involuntary translocations due human migration (Cascio et al. 2010). Since the vector species studied here are mostly synanthropic (Guzmán-Bracho 2001, Ibarra-Cerdena et al. 2009), they are prompt to involuntary translocations owed human migration (Guhl et al. 2000). A well documented case of such dispersal process is the Central American and southern Mexico invasion of *Rhodnius prolixus* (Hashimoto & Schofield 2012). This species succeeded in tropical forest as far as South of Mexico, however did not go into the ecological zone of dry forest, possibly because niche conservatism prevented species to establish outside of their ecological requirements (Peterson 2003). Recent distributional shifts for the NCA triatomines are not being observed except for some extra-range collections for *T. dimidiata* (Martínez-Ibarra et al. 2011), *T. nitida* and *T. mazzottii* (Ramsey et al. 2000; J. Ramsey personal communication), however these localities are inside of the ecological range of species as predicted for our niche conservatism analysis. The framework used here is useful way to develop rational predictions

about the potential impact of environmental changes on the spatial distribution of the animals implicated in the transmission of diseases.

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Figure legends

Figure 1. A multilocus bayesian tree of the Triatominae subfamily and *Zelurus petax* and *Reduvius personatus* from the Reduviinae subfamily as outgroup. The geographic range for all species modeled in the genus *Triatoma* are also shown. Branch color indicates PP <0.8 in gray and ≥ 0.8 in black. Black circles indicate $PP \geq 0.95$ and black stars, $PP \geq 0.9 < 0.95$.

Figure 2. Geologic age and a BEAST tree showing the probable clades divergence times. Asterisks and black circles above branches indicate clades supported by posterior probabilities of 0.9–0.94 and ≥ 0.95 , respectively.

Figure 3. Maps depicting potential distributions for sister species from the ecological niche models. A: *Triatoma protracta* (red) and *T. barberi*; B: *T. rubida* (red) and *T. nitida* (blue); C: *T. gerstaeckeri* (red) and *T. mexicana* (blue); D: *T. recurva* (red) and *T. longipennis* (blue); E: *T. phyllosoma* (red) and *T. mazzotii* (blue); F: *T. dimidiata* Gulf (red) and *T. dimidiata* Pacific (blue).

Figure 4. E-space (PCA environment) of NCA *Triatoma* sister species. A: *Triatoma protracta* (red) and *T. barberi*; B: *T. rubida* (red) and *T. nitida* (blue); C: *T. gerstaeckeri* (red) and *T. mexicana* (blue); D: *T. recurva* (red) and *T. longipennis* (blue); E: *T. phyllosoma* (red) and *T. mazzotii* (blue); F: *T. dimidiata* Gulf (red) and *T. dimidiata* Pacific (blue).

Figure 5. Test of ecological niche similarity in E-space between the six NCA sister species pairs. The arrows indicate distances between species. Within distribution distances for each species are indicated in white and black bars.

Figure 6. Test of ecological niche similarity in G-space between the six NCA sister species pairs. Observed distances between niches are indicated with the arrows, while bars indicate the null distribution of ecological niche distance generated randomly.

Appendix 1. Accession numbers of the DNA sequences used in this study with a number code for the references.

Appendix 2. References for the DNA sequences used in this study.

Appendix 3. A Cytb bayesian and ML tree of North and Central American Triatominae using *Panstrongylus megistus* as outgroup.

Appendix 4. ITS2 bayesian and ML tree of North and Central American Triatominae using *Panstrongylus megistus* as outgroup.

Table 1. Comparative phylogenetic analysis of sibling species from NCA species complexes using concatenated multilocus or single gene locus analysis. (ML=maximum likelihood).

Sister species	Multilocus	Cytb		ITS2	
	Bayesian	Bayesian	ML	Bayesian	ML
<i>T. barberi</i> - <i>T. p. protracta</i>	✓	NS	NS	✓***	✓***
<i>T. nitida</i> - <i>T. r. rubida</i>	✓***	✓***	✓	✓***	✓*
<i>T. mexicana</i> - <i>T. gerstaeckeri</i>	ND	✓	✓	✓**	✓
<i>T. longipennis</i> - <i>T. recurva</i>	✓***	✓***	✓	NS	NS
<i>T. mazzottii</i> - <i>T. phyllosoma</i>	✓*	NS	✓	✓***	✓**
<i>T. dimidiata</i> PAC - <i>T. dimidiata</i> GULF	✓**	✓***	✓	✓***	✓**

ND: No Data

NS: Not Supported

*significance (for Bayesian: * $\geq 0.85 < 0.95$, ** $\geq 0.95 < 0.99$, *** ≥ 0.99 , for ML (%): * $85 < 95$, ** $\geq 95 < 99$, *** ≥ 99)

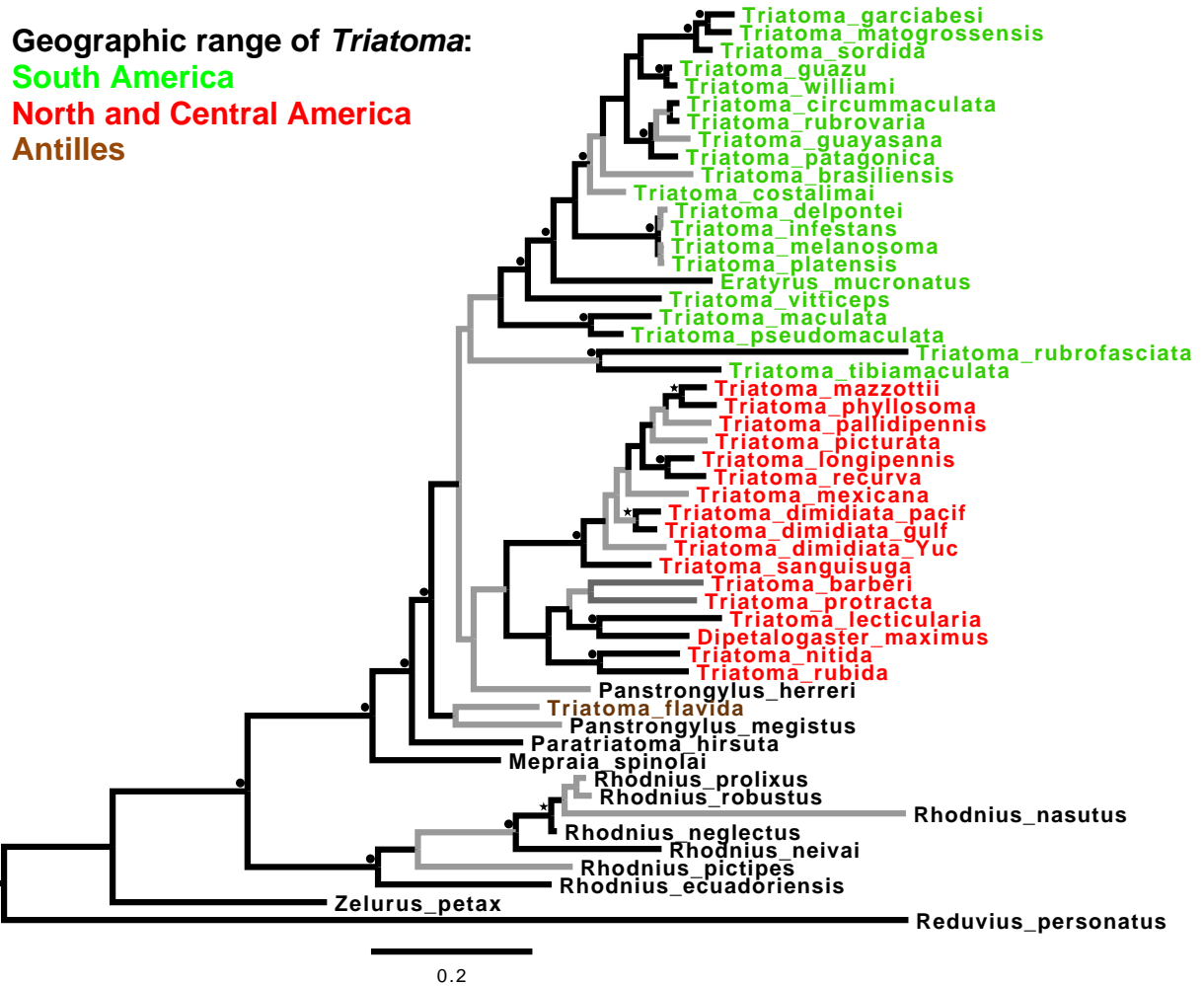


Figure 1.

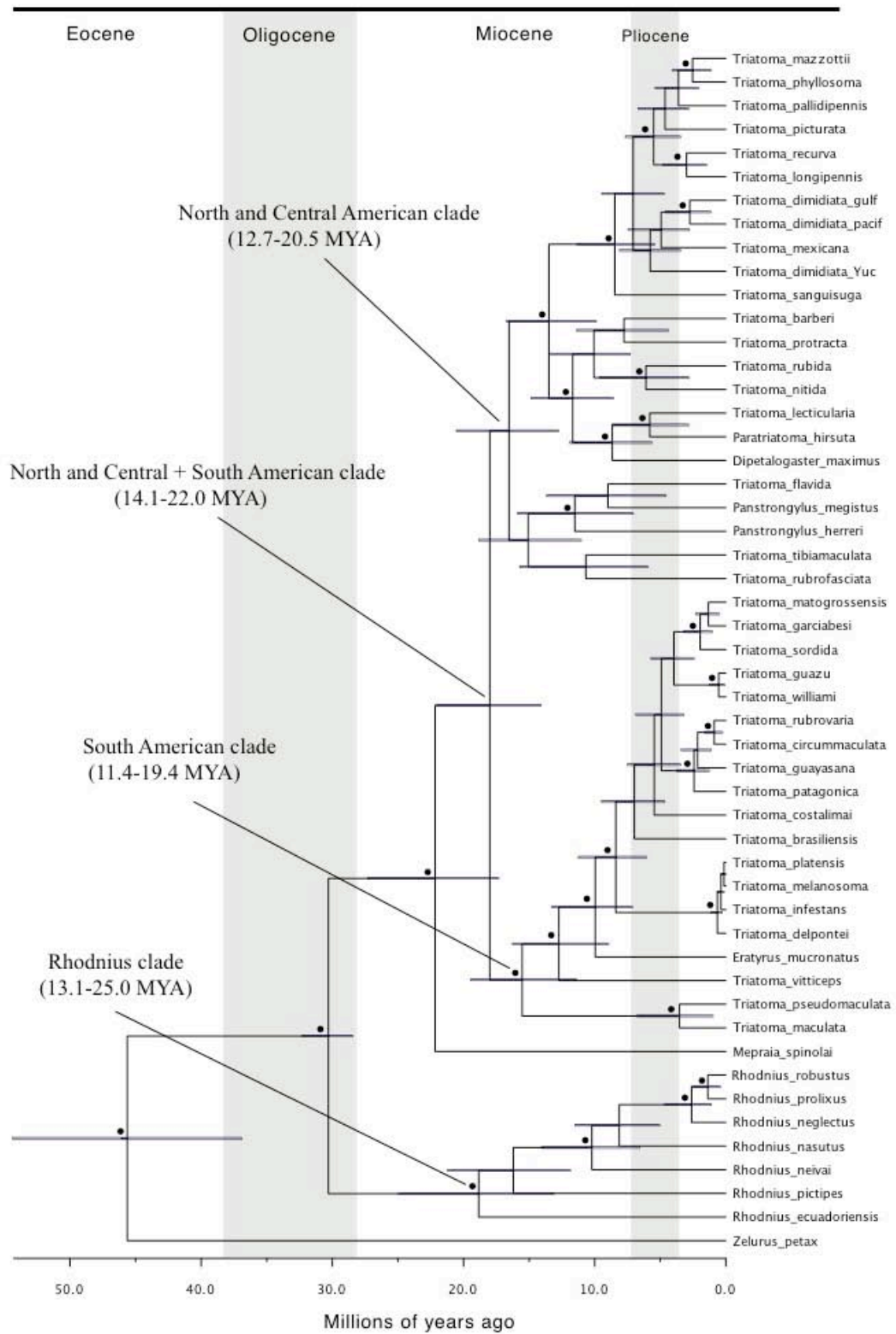


Figure 2.

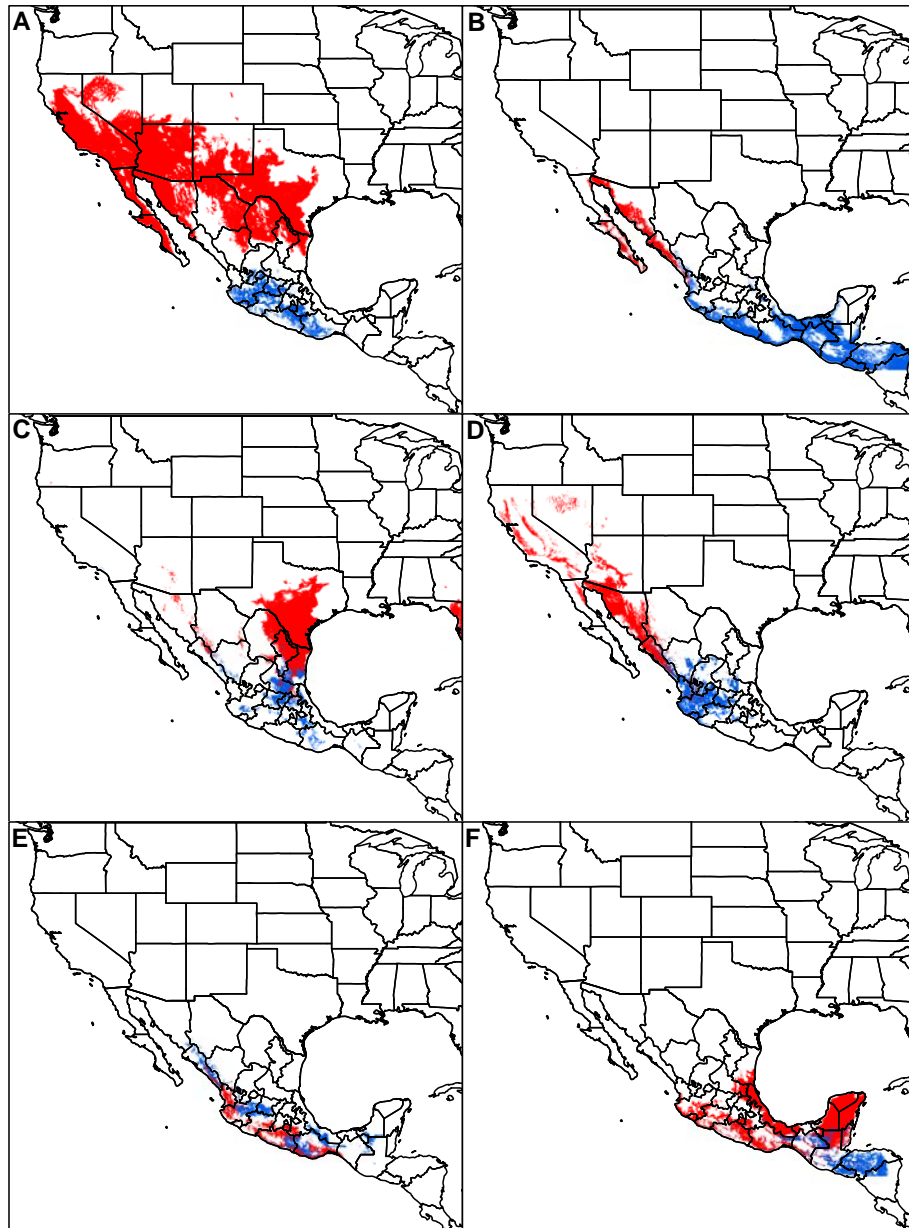


Figure 3.

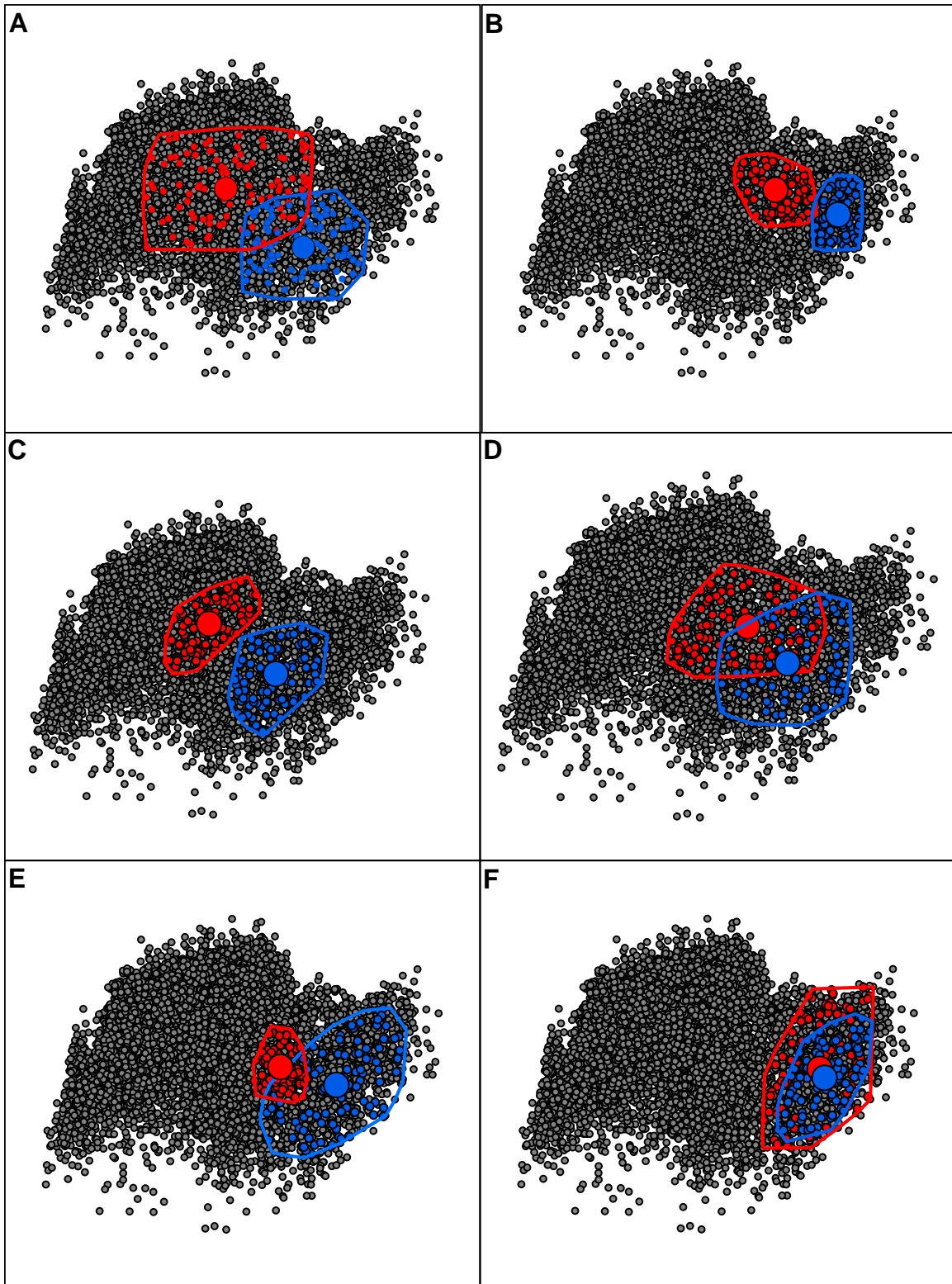


Figure 4.

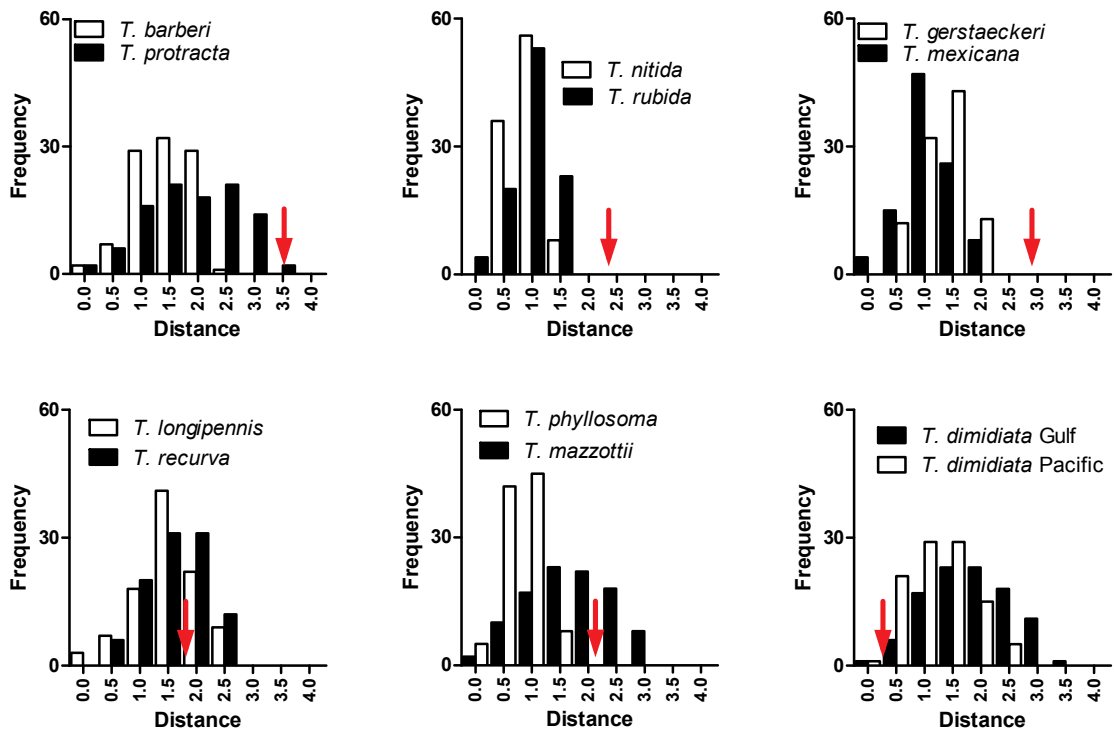


Figure 5.

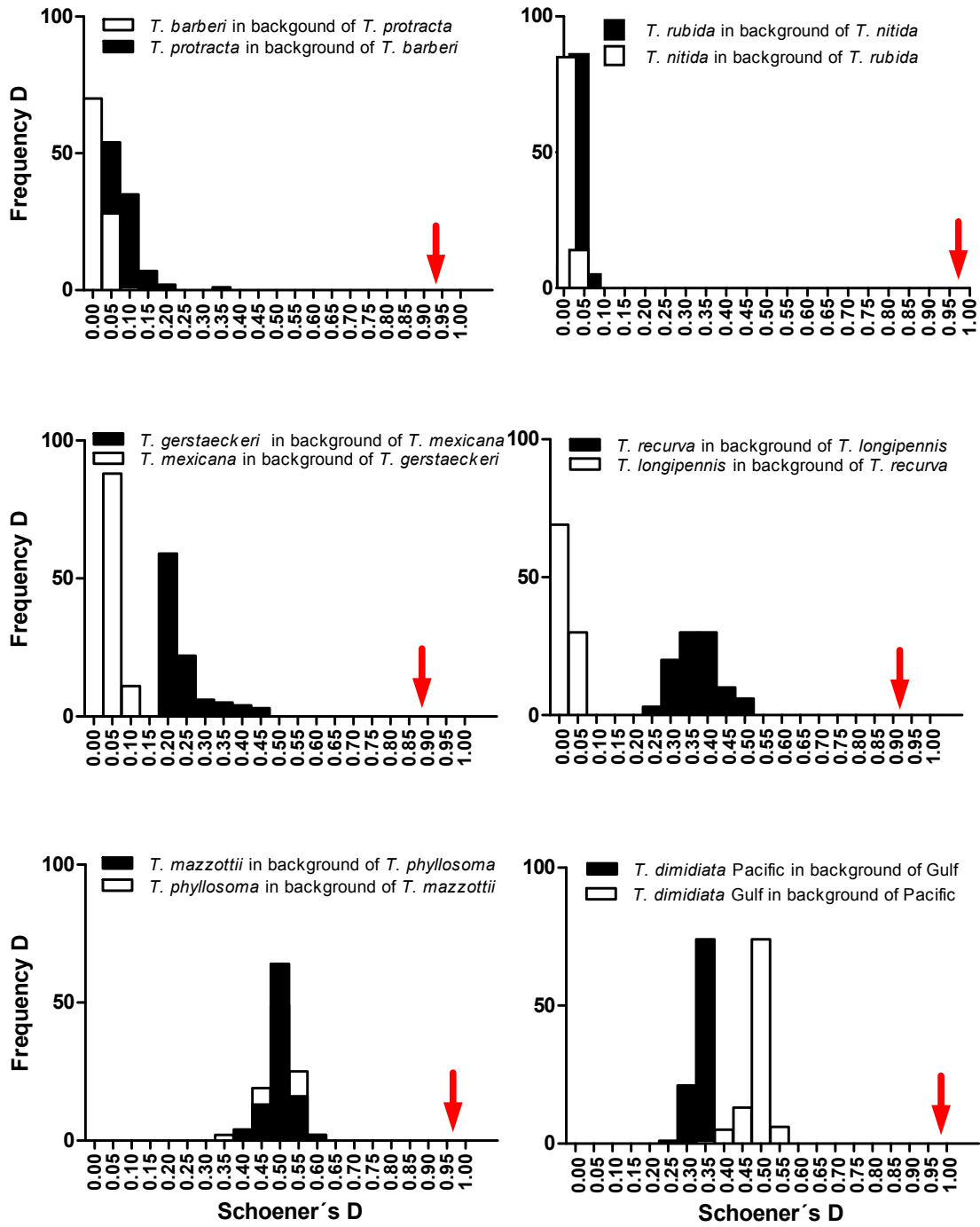


Figure 6.

Appendix 1.

Species	Locus							Phylogenetic Analysis		
	Cytb	COI	12S	16S	18S	28S	ITS2	MLocus	Cytb	ITS2
<i>T. barberi</i>	AY830137 ¹				AJ421958 ²⁸		AJ293590 ³¹	✓	✓	✓
<i>T. bassolsae</i>							AM286724 ²⁹			✓
<i>T. brasiliensis</i>	FJ594113 ²	AF021186 ¹³	AF021187 ¹³	AF021185 ¹³	AJ421957 ²⁸	GQ853395 ¹⁷		✓		
<i>T. circummaculata</i>		AF021191 ¹³	AF021190 ¹³	AF021189 ¹³				✓		
<i>T. costalimai</i>			AY185820 ²⁰	AY185834 ²⁰				✓		
<i>T. delpontei</i>	HQ333241 ³	FJ439768 ¹⁴	AF324510	AF324520 ²¹				✓		
<i>T. dimidiata Pac</i>	AY062157 ⁴			AY062139 ⁴			AM286693 ²⁹	✓	✓	✓
<i>T. dimidiata Gulf</i>	AY062149 ⁴			AY062132 ⁴			AM286714 ²⁹	✓	✓	✓
<i>T. dimidiata Yuc</i>	FJ197159 ⁵			AY062147 ⁴	AJ243328 ²⁸		FJ197152 ³⁰	✓	✓	✓
<i>T. flavida</i>				AY035451 ²³	AJ421959 ²⁸			✓		
<i>T. garciabesi</i>		EF451041 ¹⁴	AY185821 ²⁰	AY185835 ²⁰				✓		
<i>T. gerstaeckeri</i>							AM286734 ²⁹			✓
<i>T. guayasana</i>		AF021193 ¹³	AF021196 ¹³	AF021194 ¹³				✓		
<i>T. guazu</i>			AY185822 ²⁰	AY035457 ²³				✓		
<i>T. infestans</i>	AY702024 ⁶	FJ811848 ¹⁵	AY226895 ²²	EU143699 ²⁴	Y18750	GQ853397 ¹⁷		✓		
<i>T. lecticularia</i>	AY859414 ¹		AY185823 ²⁰	AY185837 ²⁰			GQ853378 ¹⁷	✓	✓	✓
<i>T. longipennis</i>	DQ198815 ⁷	DQ198804 ⁷			AJ243331 ²⁸			✓	✓	✓
<i>T. maculata</i>		AF449139 ¹⁶	AF324512 ²¹	AY035465 ²³				✓		
<i>T. matogrossensis</i>			AF394521 ²³	AY035454 ²³			GQ853398 ¹⁷	✓		
<i>T. mazzottii</i>	DQ198816 ⁷	DQ198805 ⁷	AF324514 ²¹	AF324527 ²¹	AJ243333 ²⁸			✓	✓	
<i>T. melanosoma</i>			AY185824 ²⁰	AY185838 ²⁰				✓		
<i>T. mexicana</i>	DQ118976 ¹	DQ198807 ⁷					AM286728 ²⁹	✓	✓	✓
<i>T. nitida</i>	AF045723 ⁸	DQ198806 ⁷		AF045702 ⁸			AM286733 ²⁹	✓	✓	✓
<i>T. pallidipennis</i>	EU790632 ⁹		AY185825 ²⁰	AY185839 ²⁰	AJ243330 ²⁸		AM286729 ²⁹	✓	✓	✓
<i>T. patagonica</i>			AF324515 ²¹	AY035464 ²³				✓		
<i>T. phyllosoma</i>	DQ198818 ⁷				AJ243329 ²⁸		HQ185172 ³²	✓	✓	✓
<i>T. picturata</i>	DQ198817 ⁷		AY185826 ²⁰	AY185840 ²⁰	AJ243332 ²⁸		AJ286884 ³¹	✓	✓	✓
<i>T. platensis</i>		AF021202 ¹³	AY226891 ²²	AF021201 ¹³			GQ853400 ¹⁷	✓		
<i>T. protracta</i>	AF045727 ⁸		AF324516 ²¹	AY035444 ²³	FJ230520 ²⁸	GQ853383 ¹⁷	JQ282715 ³³	✓	✓	✓
<i>T. pseudomaculata</i>			AY185827 ²⁰	AY185841 ²⁰				✓		
<i>T. recurva</i>	DQ198813 ⁷	DQ198803 ⁷		FJ230417 ²⁵	FJ230496 ²⁸	FJ230577 ²⁵	JQ282717 ³³	✓	✓	✓
<i>T. rubida</i>	DQ198808 ⁷	DQ198800 ⁷	AY185828 ²⁰	AY185842 ²⁰		GQ853391 ¹⁷	AM286735 ²⁹	✓	✓	✓
<i>T. rubrofasciata</i>		GQ869655 ¹⁷		AY035468 ²³	AJ421960 ²⁸	GQ853371 ¹⁷		✓		
<i>T. rubrovaria</i>	GQ398005 ¹⁰	AF021206 ¹³	AF021207 ¹³	GQ423626 ¹⁰				✓		
<i>T. sanguisuga</i>	AF045725 ⁸			AF045696 ⁸		GQ853392 ¹⁷		✓		
<i>T. sordida</i>	AF045730 ⁸	AF021216 ¹³	AF021211 ¹³	AF021212 ¹³	AJ421956 ²⁸			✓		
<i>T. tibiamaculata</i>			AY185829 ²⁰	AY185843 ²⁰				✓		
<i>T. vitticeps</i>		AF021219 ¹³	AF021217 ¹³	AF021218 ¹³				✓		
<i>T. williami</i>			AY185830 ²⁰	AY185844 ²⁰				✓		
<i>E. mucronatus</i>		AF449140 ¹⁶	AY185817 ²⁰	AY035450 ²³	AJ421953 ²⁸			✓		
<i>D. maximus</i>	AF045728 ⁸		AF394524 ²³	AY035442 ²³	AJ243334 ²⁸		AJ286887 ³¹	✓	✓	✓
<i>M. spinolai</i>		GQ336894 ¹⁸	AF324507 ²¹	AF324518 ²¹	AJ421961 ²⁸			✓		
<i>P. megistus</i>	AF045722 ⁸	AF021182 ¹³	AF021180 ¹³	AF045701 ⁸	AJ243336 ²⁸	GQ853381 ¹⁷	AJ306542 ³⁴	✓	✓	✓
<i>P. herreri</i>		AF449141 ¹⁶	AY185818 ²⁰	AY185833 ²⁰				✓		
<i>Par. hirsuta</i>				FJ230443 ²⁵	FJ230521 ²⁵	FJ230604 ²⁵		✓		
<i>Re. personatus</i>		AY318911 ¹⁹	AF394517 ²³					✓		
<i>R. ecuadoriensis</i>	AF045715 ⁸			AF028746 ²⁶				✓		
<i>R. nasutus</i>			AF394520 ²³	AF028749 ²⁶		AF435856 ¹²		✓		
<i>R. neglectus</i>	AF045716 ⁸			EU822951 ²⁷				✓		
<i>R. neivai</i>		AF449137 ¹⁶		AY035441 ²³				✓		
<i>R. pictipes</i>	FJ887792 ¹¹	AF449136 ¹⁶		EU827215 ²⁷				✓		
<i>R. prolixus</i>	AF421339 ¹²	AF449138 ¹⁶	AF394519 ²³	EU827206 ²⁷	AJ421962 ²⁸	AF435860 ¹²		✓		
<i>R. robustus</i>	FJ887793 ¹¹		AF394518 ²³	EU827206 ²⁷		AF435861 ¹²		✓		
<i>Z. petax</i>				FJ230416 ²⁵		FJ230576 ²⁵		✓		

Appendix 2.

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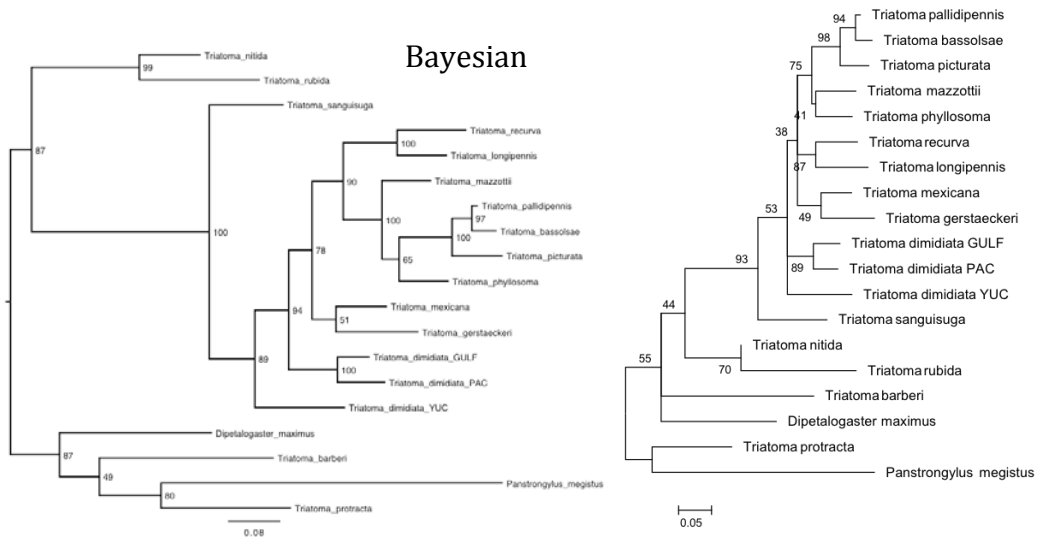
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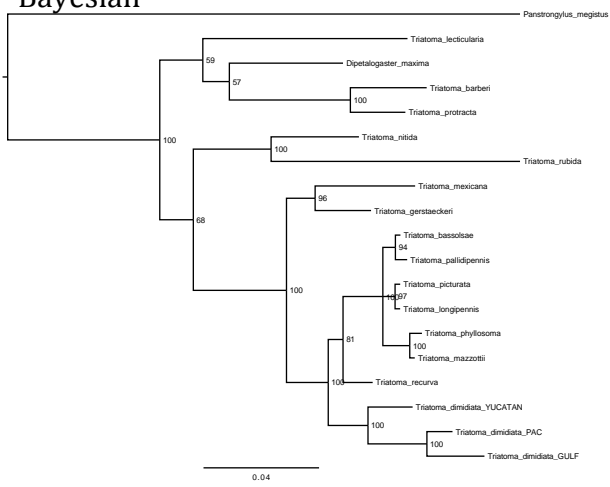
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Appendix 3.

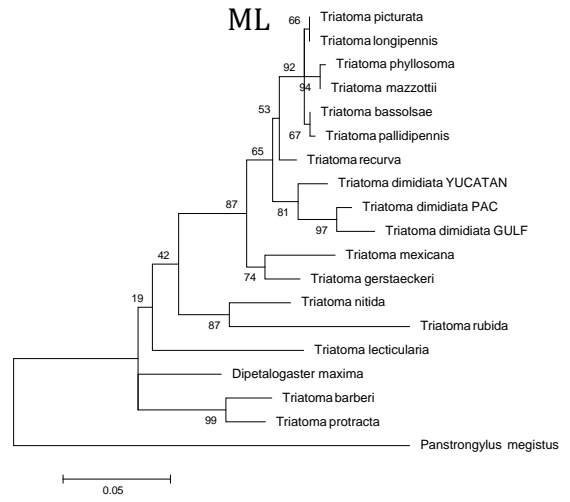


Appendix 4.

Bayesian



ML



CAPÍTULO 3

AN INTERACTION NETWORK MODEL FOR VECTORS AND HOSTS OF *TRYPANOSOMA CRUZI*, THE AETIOLOGIC AGENT OF CHAGAS DISEASE

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Introduction

A century after its discovery, Chagas' disease continues to be the principal neglected tropical disease in Latin America, based on mortality, disability-adjusted life years lost (DALY's), and at risk population¹. This chronic infectious disease is the most frequent cause of heart failure in rural populations^{2,3}. *Trypanosoma cruzi*, etiologic parasite of the disease, is transmitted via congenital⁴⁻⁶, oral⁷⁻¹⁰, blood transfusion^{11,12}, and triatomine vectors, the latter being the principal mechanism of parasite transmission¹³⁻¹⁸. A range of conditions have been identified for parasite dispersal in natural sylvatic areas¹⁹⁻²², anthropogenic ecotones^{23,24}, and rural and urban domestic habitats²⁵⁻³¹. Triatomine bugs and many mammal species act as vector and reservoirs of the generalist parasite³². The complexity of vector-reservoir assemblages (i.e. number and strength of species interactions), have been associated with a gama of transmission conditions³³. While traditional chemical interventions for domestic vector infestation have achieved relative success in reducing human exposure to domiciliated vector species (i.e. *Triatoma infestans* and *Rhodnius prolixus*)³⁴, re-infestation by sylvatic populations imposes the need for a more integrate landscape framework to interrupt domestic *Trypanosoma cruzi* transmission³⁵⁻³⁷. However, mathematical models have shown that control of vector presence is insufficient in the long-term to impede exposure to *T. cruzi* and highlight the importance of reservoirs as key factors for parasite circulation^{38,39}. The relative importance of different mammal species as reservoirs depends on susceptibility and accessibility to vectors⁴⁰. Since vectors and reservoirs are the source of the circulating parasite, the study of their interaction patterns is crucial to better understand the ecological conditions surrounding their dynamics, which could cause ecological shifts in the assemblage of these communities⁴¹.

The study of ecological interactions between species has been traditionally conducted at reduced scales of $\leq 10 \text{ m}^2$ and over periods of ≤ 5 years⁴², focusing on observable short-term ecological processes. However, the impact of environmental change and anthropogenic activities on the ecosystems, motivate more long-term and large-scale approaches⁴³. Examples of large-scale biotic interaction studies exist for competitive interactions of large⁴⁴ and small⁴⁵ mammals and birds⁴⁶. Other large-scale interaction models have been applied to infer interaction networks and their fragility due to climate change⁴⁷ or to predict reservoir species of Leishmaniasis⁴⁸.

Predictions of current and potential effects of global and habitat changes on vector-borne diseases indicate that reservoir and vector species distribution ranges effective for

disease transmission, could broaden as a result of an increase in suitable areas^{49–54}. These changes will inevitably affect the geographic patterns of vector-reservoir interactions and stimulate parasite flux across landscapes⁵⁵. Recent advances to study community complexity emerge from network theory^{56,57} which provides the opportunity to visualize and analyze communities with species as nodes connected via links that represent their biotic interactions⁵⁸. The network approach focuses on the patterns of node interactions and key components of the network architecture⁵⁷. Although links between species are often the result of intensive fieldwork observations, in less studied systems those links can be predicted by using alternative data sources^{48,59}. Community composition over spatial scales less than a few meters typically fluctuate widely over a period of a few years in response to local disturbance, In contrast, there is a more predictable and persistent pattern with a scale of a few hundred meters to thousands of kilometers⁶⁰. At these scales, metacommunities emerge when local communities are connected by dispersal of potentially interacting species. The metacommunity framework focuses on those interactions among species across a network of patches⁶¹. As an extension, species co-occurrences may reflect evolved ecological relationships that result of such long-term dispersal process^{62–65}. A network of that process would be one that takes in consideration the arrangement of geographical distributions of potentially interacting species. Information regarding the geographic structure of vector-borne disease interaction networks is a primary goal to understanding potential effects of large scale environmental factors on future changes in disease exposure^{47,66,67}.

It has been argued that host use by triatomines is influenced by the habitat they colonize, and that host accessibility is a major factor shaping the blood-foraging patterns of these bugs³³. At a coarse-grain scale, their more common hosts could be the species with the highest exposure probability and exposure could be defined as the level of geographic covariation between every bug species and every potential host. If co-occurrence patterns between triatomines and mammals are indicative of a vector-host interaction, a significant interaction should occur for those species pairs that are blood sources of triatomines and/or mammal reservoirs of *Trypanosoma cruzi*. In this study, we analyze empirically identified or evidence-based interactions and evaluate a model's performance. If the vector-host interaction is an important component for *T. cruzi* dispersal, the interaction will correlate with the probability of a mammal species being a *T. cruzi* reservoir.

Materials and Methods

1. Data

We used georeferenced data points for triatomines and terrestrial mammal collection sites in Mexico. For triatomines, we used a database that consisted of all documented data collections since 1979 (the year of publication of the first global monograph of Triatominae by Lent and Wygodzinsky) published in technical reports (National Health Secretary), scientific publications, or scientific collections (i.e. INSP, INDrE and IBUNAM), and which comprised 1600 data points for 26 Mexican triatomine species. Mammal data points were retrieved from the Global Biodiversity Information Facility (GBIF; www.gbif.org), registered for Mexican collections (last accessed in February of 2011). We obtained 36000 records for 396 mammal species which were all used for network construction.

2. Interaction model based on vector-mammal co-distributions

Triatomine species and their potential hosts are a subset of all terrestrial mammal species present in their distribution range $I' \subseteq I$. Then, the probability $P(B_i | I') - P(B_i)$, is the probability of the presence of a particular triatomine species (B_i) given the presence of a particular mammal species (I'). To calculate this probability we used a grid of size N (0.25°) that covers the area of all ecoregions where the species B_i had been reported (Figure 1A). Then, $P(B_i | I') - P(B_i) = (N_{B_i \text{ and } I'} / N_{I'}) - (N_{B_i} / N)$, where $N_{B_i \text{ and } I'}$ is the number of spatial cells where there is a co-occurrence of the taxon B_i and the taxon I' (the potential mammal host), and $N_{I'}$ is the number of cells where that host takes their stated values (a Boolean presence/absence value), within the grid (Figure 1B). In this context, $P(B_i | I_k)$ is the number of co-occurrences of the taxa B_i and I_k and, allows us to find the most important statistical associations between these pair of species distributions, however, $P(B_i | I_k)$ being a probability does not account for sample size. For example, if $P(B_i | I_k) = 1$ this may be a result of a coincidence of B_i and I_k in one spatial cell or 1000, being the latter more statistically significant. To remedy this we consider the following test statistic of statistical confidence

$$\varepsilon(B_i | I_k) = \frac{N_{I_j} (P(B_i | I_k) - P(B_i))}{(N_{I_j} P(B_i)(1 - P(B_i)))^{1/2}} \quad (1)$$

Which measures the statistical dependence of B_i on I_k relative to the null hypothesis that the distribution of B_i is independent of I_k and randomly distributed over the grid, i.e.,

$P(B_i) = N_{B_i} / N$, where N_{B_i} is the number of grid cells with point collections of species B_i

and N is the total number of cells in the grid. The sampling distribution of the null hypothesis is a binomial distribution where, in this case, every cell is given a probability $P(B_i)$ of having a point collection of B_i . Then, the numerator of equation (1), is the difference between the actual number of co-occurrences of B_i and I_k relative to the expected number if the distribution of point collections were obtained from a binomial with sampling probability $P(B_i)$. As we are talking about a stochastic sampling the numerator must be measured in appropriate “units”. As the underlying null hypothesis is that of a binomial distribution, it is natural to measure the numerator in standard deviations of this distribution and that forms the denominator of equation (1). In general, the null hypothesis will always be associated with a binomial distribution as in each cell we are carrying out a Bernoulli trial. The quantitative values of $\varepsilon(B_i | I_k)$ are interpreted in the standard sense of hypothesis testing by considering the associated p-value as the probability that $|\varepsilon(B_i | I_k)|$ is at least as large as the observed one and then comparing this p-value with a required significance level. In the case where $N_{B_i} \geq 5 - 10$ then a normal approximation for the binomial distribution should be adequate, in which case $\varepsilon(B_i | I_k) = 2$ would represent the standard 95% confidence interval. Naturally, as ε values become higher, the hypothesis of interaction becomes stronger. Note that such a statistical association does not necessarily prove that there is a direct “causal” interaction between the two taxa. Rather, it allows for a statistical inference that may be validated subsequently.

If co-occurrence patterns between Triatomines and mammals are indicative of a vector-host interaction, the significant ϵ values (≥ 2) should be showed for those species pairs that are actually blood sources of Triatomines and/or mammal reservoirs for *Trypanosoma cruzi*. As a model performance measure, we examine the ϵ value for the known interactions identified empirically and reported in the literature (Supplemental material). Usually, these reports targets on a specific triatomine species (i.e. the blood source of *Triatoma pallidipennis*, etc), therefore, we could evaluate the model performance for every species for which information was available. If, as mentioned before, the vector-host interaction is an important component of the *T. cruzi* transmission, the ϵ value should be correlated with probability for mammal species to be a reservoir for *T. cruzi*. To evaluate this, we listed all the mammal reported in the literature and conducted the same analysis as described before.

3. Validation of the interaction model

A literature search was conducted in Google Scholar for publications that report the presence of *T. cruzi* in Mexican wild mammals and vector hosts using bloodmeal analysis. We used these records to evaluate the model performance. Epsilon values of all potential mammal hosts of *T. cruzi* that were found in literature to be positive for the presence of *T. cruzi*, were divided into deciles. The 10th decile corresponds to the 10% of the highest epsilon values, the 9th decile, the next 10% with the highest epsilon values, etc. This allowed us to describe the model predictability across different epsilon deciles.

4. Description of Regional availability of vector hosts and interaction patterns

Vector host availability was measured as the number of mammal species in the distribution range of each species (the grid). This number determines the potential for vector-host interactions and the opportunity for vector specialization. A simple statistical description of frequency distribution of host availability was conducted across vector species to investigate how vectors relate with mammal species richness. The same procedure was conducted to analyze the number of mammals with which each vector had an epsilon value ≥ 2 . We extracted the mean and standard error from the group of mammals with which each vector had significant interactions to describe comparatively the strength of vector-mammal interactions.

5. Network construction

We used 26 Triatominae species and 396 mammal species (Appendix 1) for network vertices (nodes). Vertices were inter-connected representing significant triatomine-mammal geographic associations ($\epsilon \geq 2$). All species were classified using binary variables associated with their ecological tolerance for anthropogenic habitats (synanthropic vs. non-synanthropic) and with *T. cruzi* infection, the latter used for model validation (Appendix 2). We used an automatic procedure to draw the network with a force-directed algorithm that assigns forces among the set of edges and nodes. Briefly, this algorithm emulates a system as if the edges were springs and the nodes were electrically charged particles. Forces are applied to the nodes, thereby pulling them closer together or pushing them further apart. This is repeated iteratively until the system comes to an equilibrium state; i.e., their relative positions do not change from

one iteration to the next, and the graph is then drawn. The equilibrium state represents all forces in mechanical equilibrium. In the final graph the position of every node corresponds to their connectivity level, indicating that the most connected vertices are located in the center of the graph and vertices with fewer edges are the periphery⁶⁸. In order to analyze geographic patterns of vector-mammal interactions relevant for Chagas disease risk, we used modular algorithms to identify network “community structure”, which uses centrality indices to identify community boundaries. Instead of constructing a measure for edges which are central to communities (as in hierarchical clustering), focus was placed on the least centralized edges which are “between” communities. Rather than constructing communities by adding the strongest edges to an empty vertex set, they were constructed by progressively removing edges from the original graph. Vertex betweenness was used as the centrality measure, since it reflects the node influence in the network. The betweenness centrality of a vertex i is defined as the number of shortest paths between pairs of other vertices that run through i . To find which edges in a network are most between other pairs, we generalize betweenness centrality to edges and define the edge betweenness as the number of shortest paths between pairs of vertices. If there is more than one shortest path between a pair of vertices, each path is given equal weight so that the total weight of all of the paths is unity. If a network contains communities or groups that are only loosely connected by a few inter-group edges, then all shortest paths between different communities must attach to one of these edges. Thus, the edges connecting communities will have high edge betweenness. By removing these edges, we separate groups and reveal the underlying community structure of the graph⁶⁹. We further analyzed the structure of the network by disentangling the relative effect of triatomines and mammals grouped according to their habitat (synanthropic and non-synanthropic) and parasite association (*T. cruzi* and non-*T. cruzi*), in the network structure. To do this, we analyzed the mean degree of species belonging to each group. The degree of a node is the number of connections (edges) it has to other nodes in the network. Finally, we estimated the vector species’ similarity in terms of their mammal host communities using a hierarchical cluster analysis based on the 1- Jaccard similarity coefficient⁷⁰. All analysis were conducted in the statistical package R ver 2.15 (<http://www.r-project.org>), using and script developed by LV-B.

Results

The matrix of 28 triatomine species and 396 mammal species’ co-occurrence has 1200 significant links from a total 2695 (45%) of possible links. All mammal species known to be potential *T. cruzi* reservoirs had significant epsilon values with at least one vector. More the 50% of these species were among the 30% of the highest epsilon values (deciles 8th to 10th), showing the good performance of the interaction model.

Mammal species number per vector was moderately correlated with vector grid size (Spearman rank correlation coefficient $r = 0.61$, $P = 0.001$). The number of mammals to which vectors had significant epsilon was less correlated with grid size ($r = 0.5$, $P = 0.01$). Six species of the *phyllosoma* (*Triatoma pallidipennis*, *Triatoma longipennis*, *Triatoma mazzottii*, *Triatoma picturata*, *Triatoma mexicana*, and *Triatoma gerstaeckeri*), one of the *protracta* (*Triatoma barberi*), and two of the *dimidiata* complex (*Triatoma dimidiata* gulf, and *T. dimidiata* pacific), had their distributional ranges in regions significantly coincidental with a high number of mammal species (above of 95% CI range = 79-128). In contrast, eleven triatomine species had ranges in regions with significantly small number (below of 95% CI) of mammal species (*T. protracta*, *T. peninsularis*, *T. sinaloensis*, *T. neotomae*, *T. lecticularia*,

T. nahuatlae, *T. uhleri*, *T. zacatecensis*, *T. woodi*, *Dipetitolagster maximus* and *Paratritoma hirsuta*). Conversely, these latter species had significant links with a high proportion of those mammal species (above the 95% CI range of the proportion of mammals with significant links; Figure 3A). Additionally, that links had the highest mean epsilon values (Figure 3B). This pattern was inverted in vectors with high availability of mammals, given the fact that they had significant link with a small proportion of their accessible mammal hosts and a low statistical dependence with them (Figure 3B).

The kamada-kawai force-directed network shows that synanthropic species (both triatomine and mammals) are key species shaping the network structure as indicated by their position in the center of the graph, while non-synanthropic species remain in the periphery. Moreover, those mammal species that are simultaneously synanthropic and confirmed vector hosts and *T. cruzi*-infected are even more central in the network (Figure 4). This last group of mammals (simultaneously synanthropic and probable reservoirs), had proportionally more significant links than the group with species of probable reservoirs which are not synanthropic (odds ratio = 1.17, 95% IC = 1.01-1.4).

Network connectivity as measured by node degree, decreased exponentially with epsilon increase both in vectors (Figure 5A) and mammals (Figure 5B). Synanthropic vectors were more connected than non-synanthropic (Figure 5A). Synanthropic potential reservoirs of *T. cruzi* were noticeable more connected than the other categories particularly at low, yet significant, epsilon values (Figure 5B). All categories showed the same pattern of connectivity decrease with epsilon increase except for non-synanthropic potential reservoirs. Two clusters were drawn from the complete geographic model network. These clusters differed by the number of species and the regions where they are distributed. The cluster principally composed of *phyllosoma* and *dimidiata* complex species included 171 mammal and nine triatomine species, while the cluster with *protracta* and *rubida* complexes had 183 mammal and 17 triatomine species. The more representative species of this latter group are *T. rubida*, *T. uhleri* and *T. woodi*, while distinctive triatomine species of the former group are *T. dimidiata* Gulf and *T. dimidiata* Pacific.

Several mammal species and certain vector species were intermediate between the two groups and could not be assigned to either: *T. dimidiata* Yucatan, *T. barberi*, *T. longipennis*, *T. mexicana* and *T. pallidipennis* (Figure 6). These intermediate species that connect the two communities are most likely generating a metacommunity scenario in the network. Hierarchical similarity of vectors constructed from mammal hosts resulted in two main clusters. Most of synanthropic vectors were grouped in one cluster, while most of non-synanthropic were separated in a different cluster (Figure 7).

Discussion

We used a data mining modeling approach to predict vector-host interactions⁴⁸ that could be meaningful for vector transmission of *T. cruzi*. Our results strongly suggest that this approach can lead to accurate prediction of unknown interactions using freely distributed museum data⁷¹. This highlights the importance of natural history museum and scientific collections for analysis of processes affecting human populations⁷².

Our interaction model correctly predicted known mammal-parasite interactions using only geographic associations between vector species and potential mammal hosts. More over, these potential *T. cruzi* reservoirs appear more frequently in top deciles. Since epsilon value measure the statistical geographic dependence of vectors given the presence of mammal species, the result of model validation suggest that this geographic dependence is influencing local interaction patterns with an impact in parasite transmission. Stephens et al (2009), showed a same pattern using this method to find unknown potential reservoirs for Leishmaniasis, we provide here support for this methodology in finding vector-host-parasite interactions for Chagas disease. Overall, our methodology illustrate how local interactions are affected by large-scale processes, as has been demonstrated in spatial scaling models⁷³. The geographic ecology of vector-host interactions in triatomines was first studied by Peterson et al. (2002). These authors focused on the *protracta* complex which specializes on woodrats as a natural blood source⁷⁴ and analyzed the correspondence of identified hosts and vectors using climatic niche modeling and their associations to hypothesize unknown host interactions for one of the primary *T. cruzi* vector species in Mexico, *T. barberi*⁷⁵. Here we extend the study of geographic interactions to all Mexican vectors of *T. cruzi* and to all Mexican species of potential terrestrial mammal hosts. Protracta species had significant epsilon with a high proportion of the mammals inhabiting their distributional regions, sharing interactions with several species. Such a large-scale ecological similarity could be causing an ecological displacement in host selection among protracta species as proposed for lizards⁷⁶. By contrast, the neotropical vector species that are found to be more labile in host selection^{23,33}, shows an epsilon pattern consistent with low reliability on particular hosts and yet associated with synanthropic mammal species.

Synanthropic mammal species are keystone components of the geographic structure of triatomine-mammal network interactions. Synanthropy is a relatively recent phenomenon that means that fauna can co-exist with humans or with human related environments because some animals benefit from the effects of human presence such as of agriculture, food storage, garbage, livestock, land-use changes, habitat fragmentation, etc.⁷⁷⁻⁷⁹ Some species groups associated with zoonotic diseases affecting humans are fully synanthropic such as dengue⁸⁰, or partially synanthropic as American Trypanosomiasis⁸¹. A gradient of synanthropism has been found in vector species of *T. cruzi* in North America⁸² with highly synanthropic species as *Triatoma barberi*^{83,84} or *Triatoma dimidiata*^{25,29}, or partially synanthropic as *Triatoma pallidipennis*^{23,85,86}. Reservoirs such as *Rattus rattus* or *Mus musculus* could be the case for a highly synanthropic rodent species⁸⁷, and *Sigmodon hispidus* or *Liomys irroratus* as partially synanthropic, all of them implicated in the transmission of *T. cruzi*²³. These results are of high relevance for control of peridomestic processes of triatomine colonization and to understand other different processes based on species interaction scenarios^{75,88}. Evolutionary studies on *T. cruzi* diversification patterns suggests that long-term interaction with particular host species as armadillos or opossums has a profound significance on their phylogenetic history⁸⁹⁻⁹¹. However, no studies have been published that analyze this in the context of macroecological patterns of vector-host interactions. We hypothesize that this large-scale network topology is a critical point for the geographic propagation of Chagas disease, mediated mostly by a large-scale landscape transformation, and encourage research on tracing the *T. cruzi* population genetics and phylogeographic patterns using as a template the ecological network model we developed.

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Figure legends

Figure 1. Method for defining grid size for triatomine interaction analyses using *Triatoma pallidipennis* distribution data as an example (A) The ecoregions where *T. pallidipennis* has been recorded. (B) A grid generated from the sum of ecoregions where *T. pallidipennis* has been collected, and the data points of a potential host (*Baiomys musculus*). After data points are plotted in the grid and assigned to any grid cell, these turn out into the unit of analysis to construct the links.

Figure 2. Evaluation of the performance for the interaction model. *T. cruzi* potential hosts species are those mammals that were independently reported in literature to test positive to natural infection by *T. cruzi*. Gray area represents deciles with $\epsilon \geq 2$.

Figure 3. Relation of vector species with mammal host species in its distributional ranges and their interaction strengths. (A) Number of mammal species within each vector's range and proportion of these with which vectors had significant links ($\epsilon \geq 2$). Red letters indicate bars that are above (H) or below (L) the 95% confidence interval (CI) of the normal number of mammal richness per vector's range. Blue letters indicate those bars that are above (H) or below (L) the 95% CI of the normal proportion of mammal available species with which vectors had significant links. (B) Mean and SE of epsilon values for each vector species in their distribution ranges. Black letters indicate the species' vector that has mean epsilon's outside of 95% CI (H: higher and L: lower). Lack of statistical differences in epsilon values are indicated for the same color with a $P < 0.05$. (Red and blue colors are used for lower epsilon's, while green and purple are used for higher epsilon's).

Figure 4. A graph drawn using the Kamada-Kawai algorithm which represents the interaction network model of Mexican triatomines and terrestrial mammals. Red circles are synanthropic triatomines and orange circles are non-synanthropic triatomines. Red squares are synanthropic mammals that are simultaneously infected and probable reservoirs of *T. cruzi*, yellow squares are synanthropic mammals that have not been reported infected with *T. cruzi*, orange squares are mammals that have been found infected with *T. cruzi* and are not synanthropic, and green squares are mammals that are not synanthropic or have not been reported with *T. cruzi* infection.

Figure 5. Habitat affinities and *T. cruzi* relationships for vectors (A) and mammal hosts (B) in relation to node importance for the network structure.

Figure 6. Analysis of community structure in the triatomine-mammal host network model. Node size indicates the proportional contribution of each species to its group. Circles represent vectors and squares mammal hosts. Green and gray edges differentiate the two primary clusters, and yellow edges show the links that cause community intermediation. Certain primary vector *Triatoma* species are labeled, with bold names used for predominant cluster species.

Figure 7. Hierarchical clustering of mammal host similarity among vectorspecies. . Asterisk indicates synanthropic triatomine species.

Appendix 1. List of mammal species that were classified as “T. cruzi positive”

Appendix 2. List of Vector and Host species that were classified synanthropic

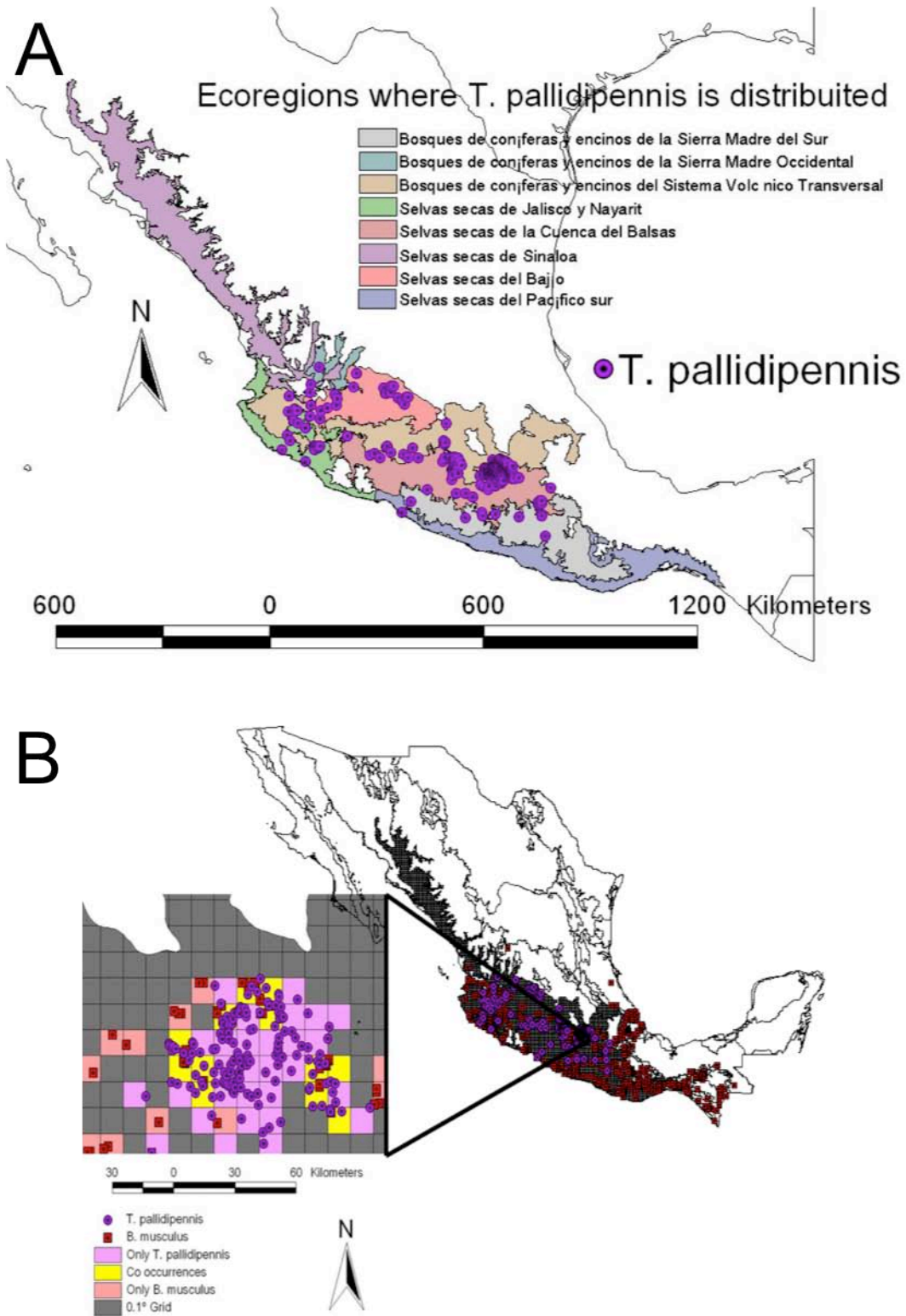


Figure 1.

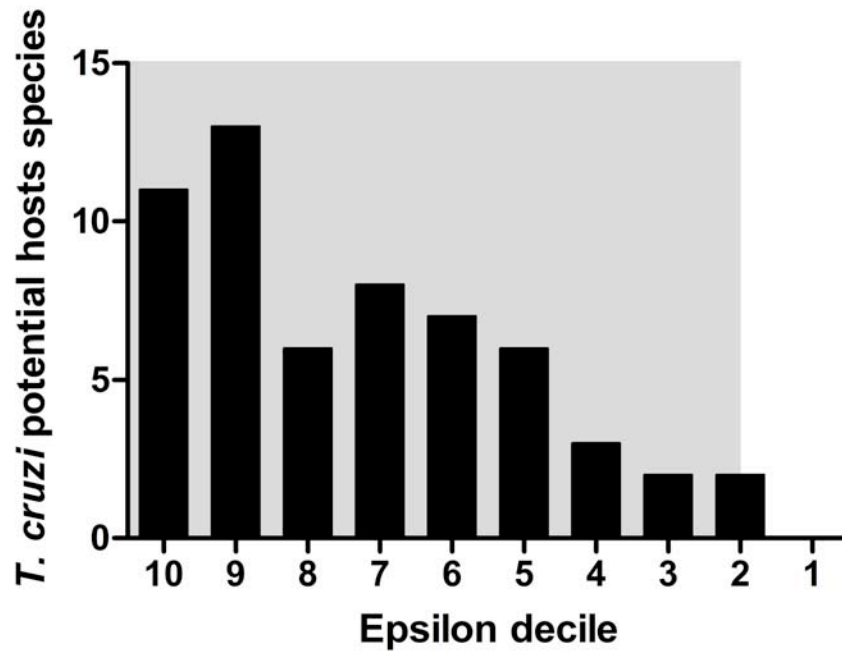


Figure 2.

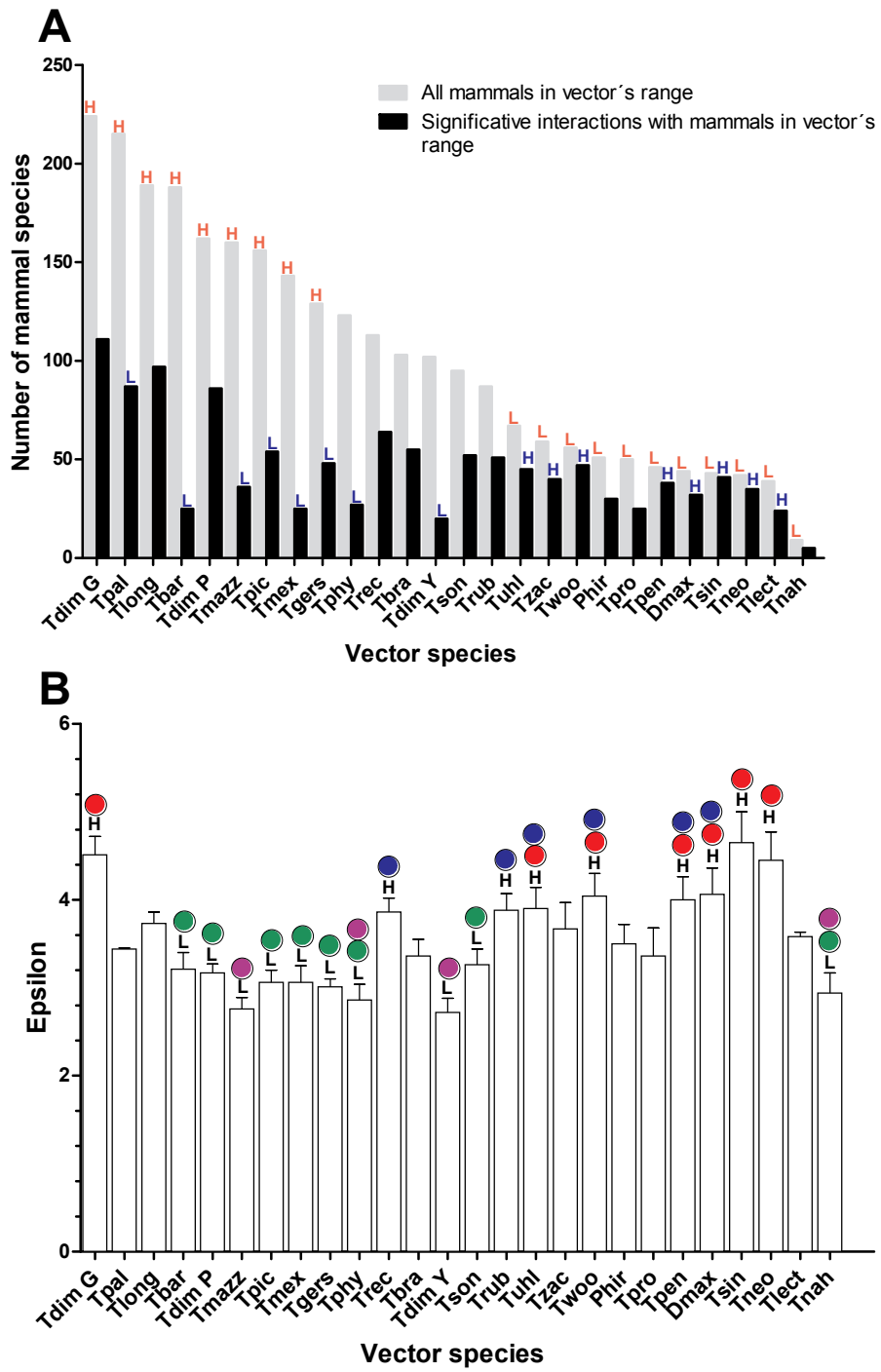


Figure 3.

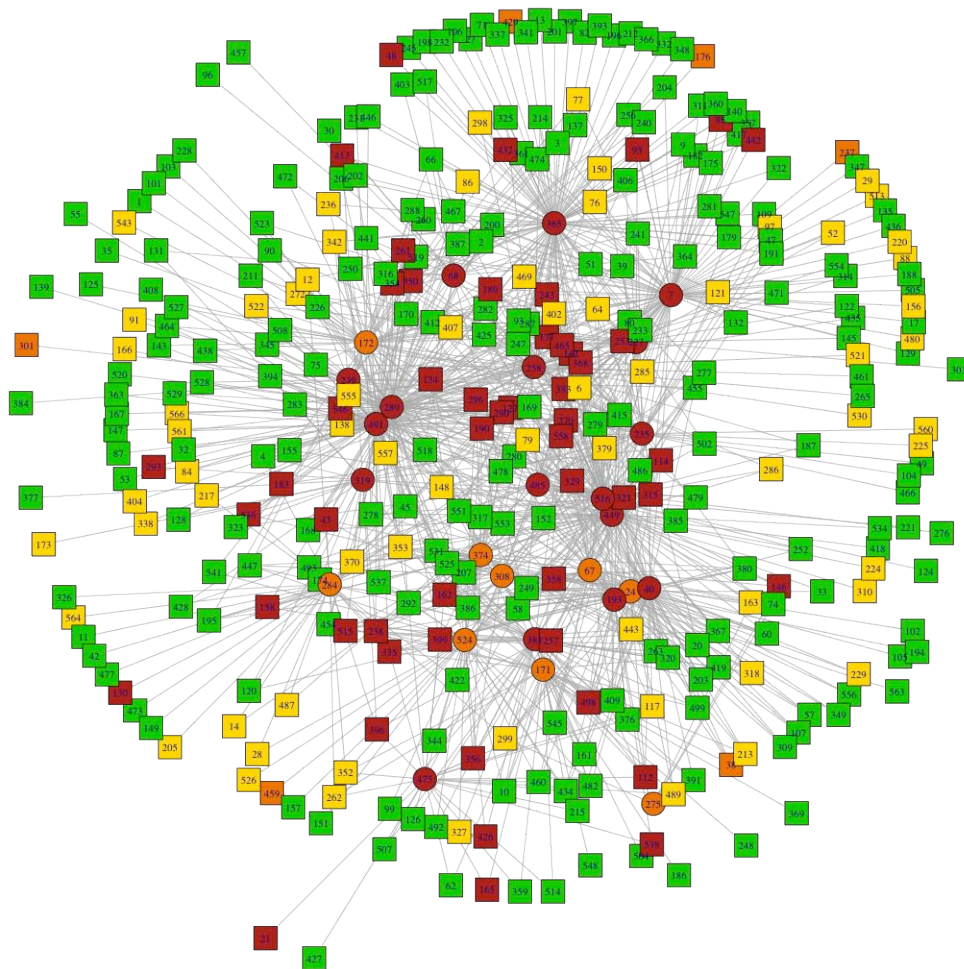


Figure 4.

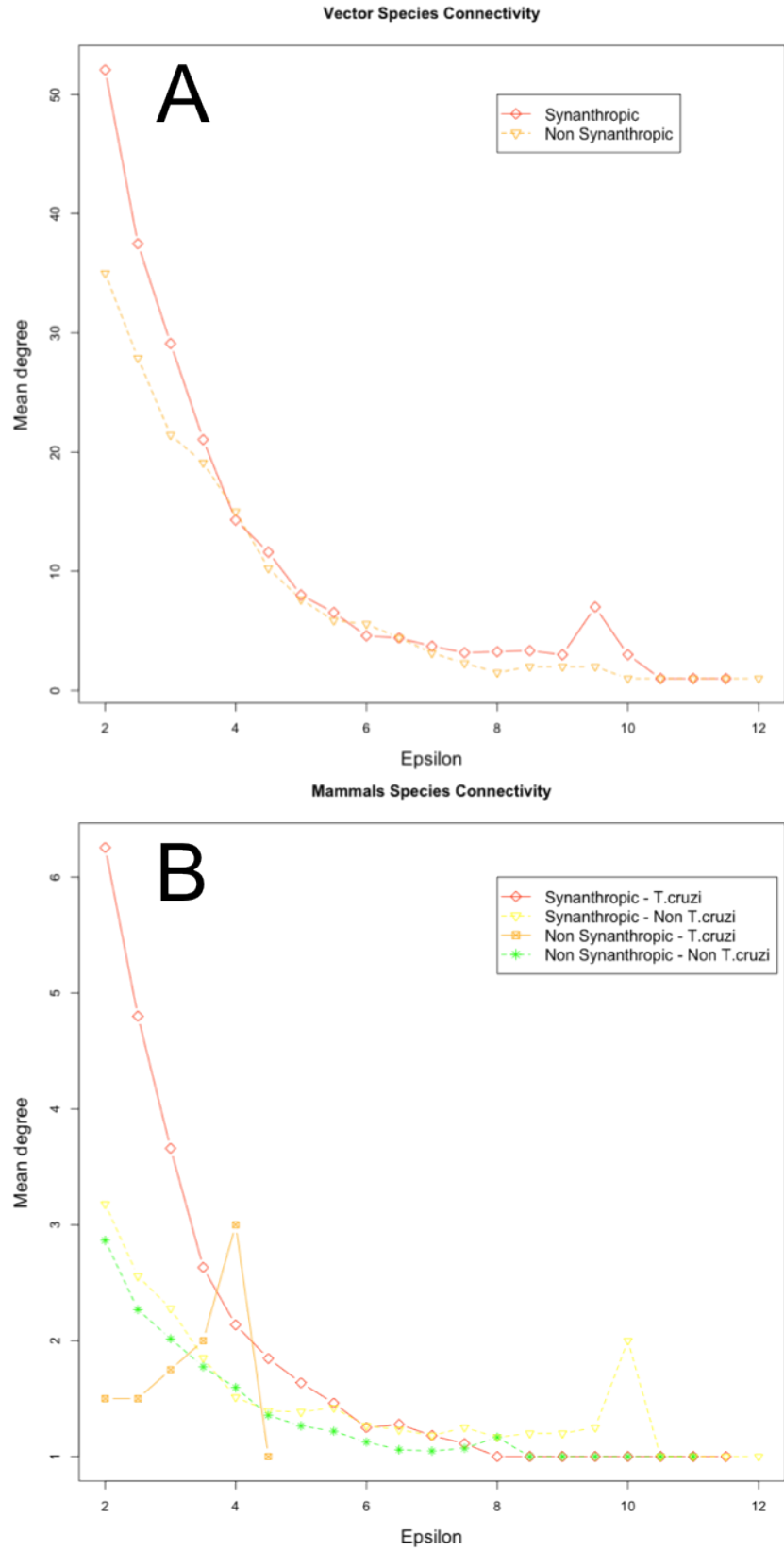


Figure 5.

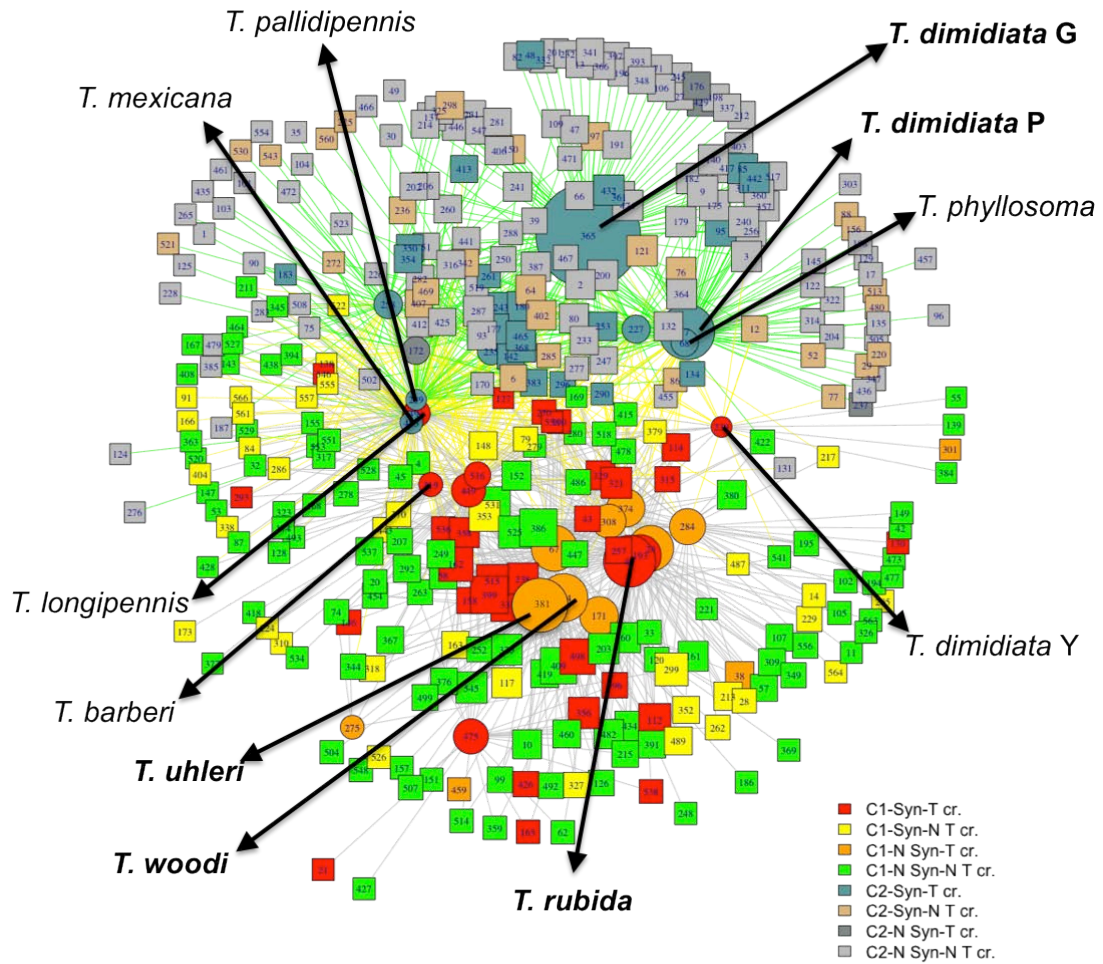


Figure 6.

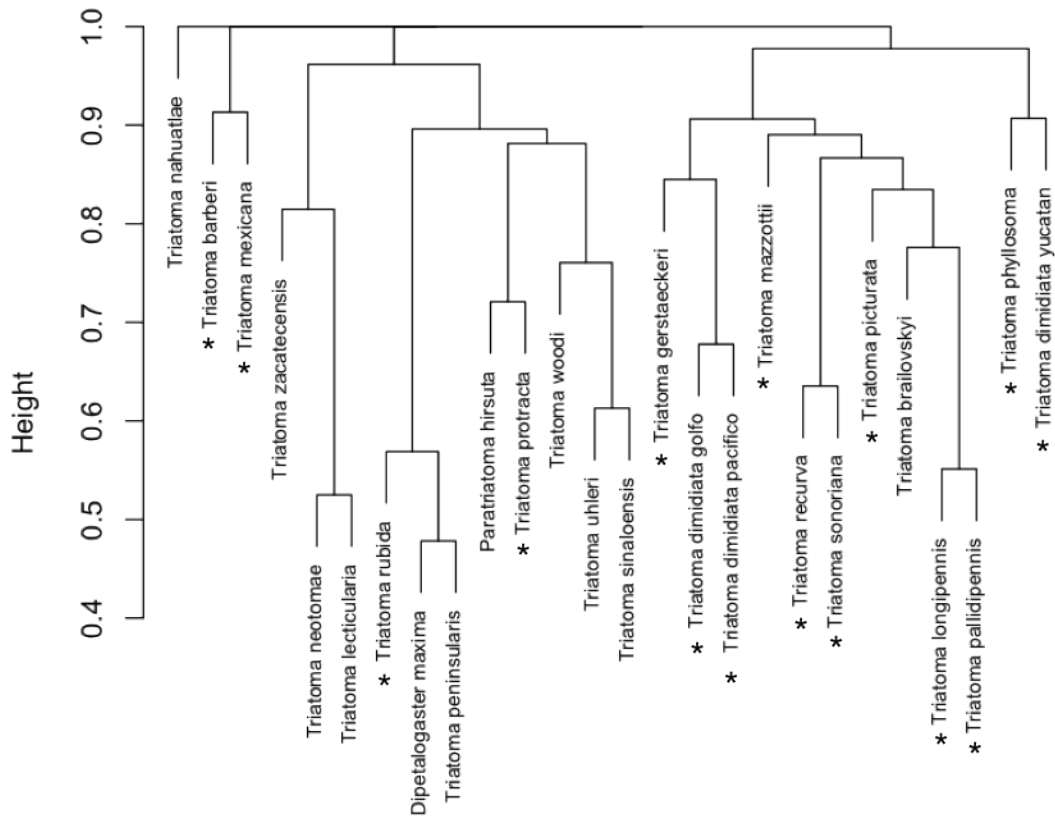


Figure 7.

Appendix 1.

Ammospermophilus leucurus

Artibeus jamaicensis

Baiomys musculus

Balantiopteryx plicata

Bassariscus astutus

Canis latrans

Carollia perspicillata

Carollia sowelli

Chaetodipus hispidus

Choeronycteris mexicana

Dasyprocta punctata

Dasytus novemcinctus

Dermanura phaeotis

Desmodus rotundus

Didelphis marsupialis

Didelphis virginiana

Glossophaga soricina

Heteromys desmarestianus

Heteromys gaumeri

Liomys irroratus

Liomys pictus

Mephitis mephitis

Mormoops megalophylla

Mus musculus

Nasua narica

Neotoma albigula

Neotoma fuscipes

Neotoma goldmani

Neotoma lepida

Neotoma mexicana

Neotoma micropus

Neotoma phenax

Onychomys leucogaster

Oryzomys couesi

Peromyscus boylii

Peromyscus californicus

Peromyscus eremicus
Peromyscus leucopus
Peromyscus levipes
Peromyscus maniculatus
Peromyscus melanophrys
Peromyscus mexicanus
Peromyscus truei
Philander opossum
Procyon lotor
Pteronotus davyi
Pteronotus parnelli
Rattus rattus
Reithrodontomys fulvescens
Sigmodon hispidus
Sigmodon mascotensis
Spermophilus beecheyi
Spermophilus variegatus
Sturnira lilium
Tadarida brasiliensis
Tadarida laticaudata
Urocyon cinereoargenteus
Uroderma bilobatum
Vampyrus spectrum

Appendix 2.

Synanthropic Species**Triatomines**

Triatoma barberi
Triatoma dimidiata Gulf
Triatoma dimidiata Pacific
Triatoma dimidiata Yucatan
Triatoma gerstaeckeri
Triatoma longipennis
Triatoma mazzottii
Triatoma mexicana
Triatoma pallidipennis
Triatoma phyllosoma
Triatoma picturata
Triatoma protracta
Triatoma recurva
Triatoma rubida
Triatoma sonora

Mammals

Artibeus intermedius
Artibeus jamaicensis
Baiomys musculus
Baiomys taylori
Balantiopteryx plicata
Bassariscus astutus
Canis latrans
Carollia perspicillata
Carollia sowelli
Choeronycteris mexicana
Conepatus leuconotus
Conepatus mesoleucus
Cratogeomys castanops
Cratogeomys fumosus
Cratogeomys gymnurus
Dasypus novemcinctus
Dermanura azteca
Dermanura phaeotis
Desmodus rotundus
Didelphis marsupialis
Didelphis virginiana

Glossophaga soricina
Heteromys desmarestianus
Heteromys gaumeri
Leptonycteris curasoae
Leptonycteris nivalis
Liomys irroratus
Liomys pictus
Liomys salvini
Mephitis mephitis
Mormoops megalophylla
Mus musculus
Nasua narica
Nasua nasua
Neotoma albigula
Neotoma fuscipes
Neotoma goldmani
Neotoma lepida
Neotoma mexicana
Neotoma micropus
Neotoma palatina
Neotoma phenax
Oligoryzomys fulvescens
Onychomys leucogaster
Orthogeomys grandis
Orthogeomys hispidus
Oryzomys alfaroi
Oryzomys couesi
Oryzomys melanotis
Oryzomys palustris
Pappogeomys bulleri
Pecari tajacu
Perognathus flavescens
Perognathus flavus
Perognathus pernix
Peromyscus aztecus
Peromyscus banderanus
Peromyscus boylii
Peromyscus californicus
Peromyscus crinitus
Peromyscus difficilis
Peromyscus eremicus
Peromyscus eva
Peromyscus furvus

Peromyscus guatemalensis
Peromyscus gymnotis
Peromyscus leucopus
Peromyscus levipes
Peromyscus maniculatus
Peromyscus megalops
Peromyscus melanophrys
Peromyscus melanotis
Peromyscus melanurus
Peromyscus merriami
Peromyscus mexicanus
Peromyscus ochraventer
Peromyscus pectoralis
Peromyscus perfulvus
Peromyscus polius
Peromyscus simulus
Peromyscus spicilegus
Peromyscus truei
Peromyscus yucatanicus
Philander opossum
Procyon lotor
Pteronotus davyi
Pteronotus parnelli
Rattus rattus
Reithrodontomys fulvescens
Reithrodontomys gracilis
Reithrodontomys megalotis
Reithrodontomys mexicanus
Reithrodontomys microdon
Reithrodontomys sumichrasti
Sciurus aureogaster
Sciurus oculatus
Sciurus variegatoides
Sciurus yucatanensis
Sigmodon alleni
Sigmodon arizonae
Sigmodon fulviventris
Sigmodon hispidus
Sigmodon leucotis
Sigmodon mascotensis
Spermophilus adocetus
Spermophilus annulatus
Spermophilus beecheyi

Spermophilus mexicanus
Spermophilus perotensis
Spermophilus pilosoma
Spermophilus tereticaudus
Spermophilus variegatus
Sturnira lilium
Tadarida brasiliensis
Tadarida laticaudata
Tamias bulleri
Tayassu tajacu
Thomomys bottae
Thomomys umbrinus
Urocyon cinereoargenteus
Vampyroides caraccioli

CONCLUSIONES

En el capítulo 1 se realizó una revisión de literatura con el objetivo de sistematizar la información disponible sobre la ecología, en sentido amplio, de los triatominos de Norteamérica (Ibarra-Cerdena et al. 2009). Encontré que si bien hay diversos trabajos publicados sobre aspectos epidemiológicos relacionados con los vectores (e.g. Guzmán-Bracho 2001), éstos estaban centrados fundamentalmente sobre la infestación por *Triatoma dimidiata* y especies del complejo phyllosoma, entre ellas *T. pallidipennis* y *T. longipennis*. Los trabajos publicados sobre ecología de interacciones vector-hospedero fueron realizados fundamentalmente por Raymond Ryckman (Ryckman 1986) durante los años 1960 y 1970, en los que se documenta la interacción especialista entre especies del complejo protracta y ratas del género *Neotoma*. En dichos trabajos se postula que las especies neotropicales de triatominos (principalmente el complejo phyllosoma), son generalistas. Al profundizar en este tema encontré que los mamíferos reportados como hospederos de los triatominos, sin excepción, son especies sinantrópicas, ya sea porque son plagas agrícolas (por ejemplo *Baiomys musculus*, *Liomys irroratus* y *Sigmodon hispidus*) o porque son comensales urbanos, semiurbanos o de poblaciones rurales (e.g. *Didelphis virginiana*, *Mus musculus* y *Urocyon cinereoargenteus*). Estas especies a su vez han sido reportados como probables reservorios de *T. cruzi* debido al hallazgo de individuos naturalmente infectados con éste parásito (e.g., Mota et al. 2007; Ramsey et al. 2012).

El patrón de interacciones vector-hospedero es en gran medida determinado por las características de la vegetación o el tipo de hábitat (González-Salazar & Stephens 2012), y en triatominos se ha encontrado que el uso de hospederos está efectivamente determinado por los hábitats que colonizan (Rabinovich et al. 2011). A partir de un análisis de la distribución de localidades de colecta de triatominos que comprendió más de 1600 registros para 40 especies y subespecies, encontré que si bien se puede decir que éstos ocupan prácticamente todos los diferentes paisajes en Norteamérica, las especies más involucradas en la epidemiología de la enfermedad de Chagas (complejos phyllosoma y dimidiata), ocupan hábitat relativamente abiertos, como pastizales, sitios agrícolas o bosques bajos y evitan los bosques lluviosos o muy densos. Los triatominos están ampliamente dispersos en México y sur de Estados Unidos y la distribución de la riqueza de especies muestra que hay áreas, particularmente en la región del Eje Neovolcánico y las costas del Pacífico y Golfo de México en las que hay mayor concentración de especies.

Posteriormente, evalué la influencia de la historia evolutiva en la distribución de los triatominos de Norteamérica (Capítulo 2). Debido a que las relaciones filogenéticas entre los triatominos y entre éstos y otros grupos de Reduidos son sujeto de debate (Hwang & Weirauch 2012), además de que las filogenias publicadas en las que se incluyen especies de Norteamérica son parciales (Hypsa et al. 2002; Sainz et al. 2004), realicé una compilación de secuencias de DNA lo más amplia posible con el fin de realizar una reconstrucción filogenética de estos insectos. A partir de dicho análisis obtuve pares de especies hermanas con alto soporte estadístico, las cuales utilicé para poner a prueba la hipótesis de conservadurismo de nicho. La propuesta de que el nicho en especies hermanas se conserva en tiempo evolutivo, tiene un profundo impacto en la conformación de los rangos de distribución ya que implica que las especies están limitadas para ocupar las áreas accesibles que resultan del proceso de dispersión (Peterson et al. 1999; Wiens 2011). Las especies comparadas no tuvieron nichos idénticos, resultado esperado debido a que los pares de especies comparados tienen distribuciones alopátricas. Sin embargo, la divergencia de sus nichos no corresponde

con la divergencia esperada con respecto a la divergencia ambiental en sus áreas de distribución. Por el contrario, encontré que el nicho de las especies estudiadas se puede considerar conservado. Este resultado es el primero que se documenta en vectores de enfermedades que ponen en riesgo la salud humana, el cual permite generar predicciones sobre el efecto que el cambio climático futuro tendría sobre la distribución de los vectores.

Si bien el clima es un factor determinante en la conformación del rango de distribución de las especies (Soberón 2007, 2010), la influencia de las interacciones bióticas tiene un impacto directo en la probabilidad de establecimiento de una población en un sitio particular (Soberón & Nakamura 2009). El estudio de los patrones geográficos de las interacciones entre vectores y sus hospederos está limitado por problemas metodológicos muy importantes. La detectabilidad de triatominos silvestres es muy baja, probablemente debido a su comportamiento de alimentación (viven en madrigueras de mamíferos para alimentarse de sangre). Asimismo, aunque se han desarrollado métodos de campo para estudiar las interacciones entre vectores y mamíferos directamente (Yeo et al. 2005), la eficiencia de éstos mínima (Víctor Sanchez-Cordero; Janine Ramsey Willoquet, Angel Rodriguez, comunicación personal). Entre los medios indirectos, la identificación de fuente sanguínea por métodos moleculares (Mota et al. 2007), ofrece ventajas sobre los métodos directos (e.g. colecta de triatominos en madrigueras de mamíferos previamente indentificados) y ha permitido estudiar la comunidad de hospederos de los que se alimentan los vectores de esta enfermedad en hábitat silvestres (Ramsey et al. 2012). No obstante, dada la diversidad de especies de triatominos en México (40 especies y subespecies) y cientos de especies de hospederos potenciales de insectos hematófagos, las posibilidades de estudiar experimentalmente los patrones de sus interacciones son prácticamente nulas. Con esto en mente, desarrollamos una metodología basada en minería de datos para generar hipótesis de interacciones con sustento estadístico que pudieran ponerse a prueba mediante un diseño experimental apropiado (Stephens et al. 2009). Este método se ha utilizado para conocer aspectos básicos de la influencia de las interacciones bióticas en la distribución de mamíferos e insectos (Sánchez-Cordero et al. 2008; González-Salazar et al. 2013). A partir del uso de localidades de colecta de triatominos y mamíferos distribuidos en México, generé una red inferencial de interacción vector-hospedero, que refleja el patrón geográfico de co-distribuciones de la mayoría de las especies de vectores y mamíferos mexicanos (Capítulo 3). Particularmente, el método utilizado busca encontrar relaciones de dependencia estadística de las especies de triatominos con respecto a las especies de mamíferos disponibles en sus áreas de distribución, sin considerar explícitamente ninguna información sobre interacciones. Con el método utilizado, tanto las interacciones conocidas para las especies analizadas como las interacciones mamífero-parásito conocidas fueron predichas correctamente. Este resultado es muy importante porque amplía el rango de usos que tienen los datos primarios disponibles en colecciones científicas y museos de historia natural (Sánchez-Cordero & Martínez-Meyer 2000; Soberón & Peterson 2004). Con base en la matriz de interacciones, utilicé algoritmos y métricas de la teoría de redes complejas (Strogatz 2001) para identificar patrones macroecológicos relacionados con la interacción entre vectores y mamíferos. Los resultados mostraron que las especies sinantrópicas de vectores y mamíferos tienen un efecto significativo en la conformación de la red. Más aún, las especies que han sido identificadas independientemente como reservorios potenciales de *T. cruzi*, son elementos clave en la estructura de la matriz. Este resultado es relevante porque implica que la mayoría de las especies implicadas en la transmisión de una enfermedad zoonótica como es la

Trypanosomiasis Americana (o enfermedad de Chagas) (Noireau et al. 2009), son tolerantes a la transformación antropogénica de sus hábitats (Ramsey et al. 2012). A partir de estos resultados se puede tener un listado de vectores y reservorios de *T. cruzi* que puede ser investigado de manera experimental. Un diseño experimental planteado con dicho propósito está actualmente en marcha y a partir de sus resultados será posible evaluar en mayor extensión la pertinencia del enfoque conceptual desarrollado en este trabajo, así como su utilidad para contar con mapas de riesgo más realistas.

Con esta tesis se expandió el conocimiento de la ecología geográfica de los triatominos de Norteamérica, vectores de una de las enfermedades tropicales más importantes en Latinoamérica (Hotez et al. 2008). Los resultados presentados en este trabajo pueden ayudar a generar modelos de riesgo epidemiológico más realistas que los basados puramente en información epidemiológica; además se puede inferir el efecto potencial del cambio climático en los cambios en rangos de distribución de Triatominos, ya que ahora sabemos que estas especies son poco propensas a la evolución del nicho (Holt & Gaines 1992). Así, el cambio climático podría propiciar que áreas no ocupadas actualmente por vectores, al no estar dentro de los rangos de tolerancia fisiológicos, se modifiquen positivamente y cambien hacia áreas propicias para el mantenimiento de poblaciones viables. Si en estas áreas están presentes los hospederos identificados de *Trypanosoma cruzi*, existe la posibilidad de que se genere un ciclo de transmisión del parásito con consecuencias epidemiológicas.

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