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Ecological and physiological thermal niches to understand distribution of Chagas disease vectors in Latin America

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Abstract. In order to assess how triatomines (Hemiptera, Reduviidae), Chagas disease vectors, are distributed through Latin America, we analysed the relationship between the ecological niche and the limits of the physiological thermal niche in seven species of triatomines. We combined two methodological approaches: species distribution models, and physiological tolerances. First, we modelled the ecological niche and identified the most important abiotic factor for their distribution. Then, thermal tolerance limits were analysed by measuring maximum and minimum critical temperatures, upper lethal temperature, and 'chill-coma recovery time'. Finally, we used phylogenetic independent contrasts to analyse the link between limiting factors and the thermal tolerance range for the assessment of ecological hypotheses that provide a different outlook for the geo-epidemiology of Chagas disease. In triatomines, thermo-tolerance range increases with increasing latitude mainly due to better cold tolerances, suggesting an effect of thermal selection. In turn, physiological analyses show that species reaching southernmost areas have a higher thermo-tolerance than those with tropical distributions, denoting that thermo-tolerance is limiting the southern distribution. Understanding the latitudinal range along its physiological limits of disease vectors may prove useful to test ecological hypotheses and improve strategies and efficiency of vector control at the local and regional levels.

Key words. CTmax, CTmin, latitudinal variation, species distribution models, thermo–tolerances, triatomines.

Introduction

Several species belonging to the subfamily Triatominae are vectors of one of the most important parasitaemia in South and Central America, the Chagas disease (Schofield *et al.*, 2006). This subfamily of insects is represented by several species across the continent, naturally ranging from tropical to temperate regions with cold winters (Moncayo, 1992; Carcavallo *et al.*, 1999). At present, this disease affects *c.* 20 million people in Latin America, and *c.* 120 million are at risk of infection. A complete understanding of the aetiology and epidemiology of Chagas disease across its distribution seems to be an elusive and complex goal, which remains under intense investigation (Patterson & Guhl, 2010). A key topic is to comprehend the abundance and distribution of disease vectors (Kitron, 1998).

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The study of distribution of the species usually involves modelling, either using correlative or mechanistic models. For the latter, some physiological traits are required (e.g. thermal tolerance limits), or demographic responses to environmental change (Evans *et al.*, 2015). For correlative models, occurrence data (presence only, presence/absence or abundance records) are used together with climatic variables to determine the realized niche (Elith *et al.*, 2006). Both approaches have been used to estimate the impact of climate on malaria vectors (Martin & Lefebvre, 1995) and it has been suggested that a combination of either one may provide a better outlook for the fundamental and the realized niche, allowing for better predictions than just using correlative models (Buckley *et al.*, 2010).

For insects, temperature affects most of the physiological processes; in fact, it is probably the most important abiotic factor determining species geographical distribution (Chown & Nicolson, 2004; Angilletta, 2009). There are many studies about the effects of temperature on physiological and behavioural processes of Chagas disease vectors (Blaksley & Carcavallo, 1968; Schilman & Lazzari, 2004; Rolandi *et al.*, 2014, among others), and several about the abiotic factors explaining their distributions (Carcavallo *et al.*, 1999; Gorla, 2002). However, there are only a few studies linking physiological traits of one (de Souza *et al.*, 2010) or two species of triatomines (de la Vega *et al.*, 2015) to their geographical distribution.

Physiological traits of species play a fundamental role in their adaptive responses to environmental changes, as well as in their geographical distribution (Spicer & Gaston, 1999; Addo-Bediako *et al.*, 2000). Knowledge of an insect's physiological tolerances, such as the thermo-tolerance range determined by both critical temperatures – maximum (CTmax) and minimum (CTmin) (Spicer & Gaston, 1999) – might help to identify their fundamental thermal niches or active areas where they can be geographically distributed (Kearney & Porter, 2009). In addition, for disease vectors it could determine potential areas of vector disease transmission risk. The ecological basis behind this idea is the climate variability hypothesis (CVH), which states that terrestrial organisms distributed in variable environments (e.g. high latitudes or altitudes), are adapted to withstand a broader range of climatic conditions than organisms in less variable environments (e.g. low latitudes or altitudes). Therefore, species living at high latitudes (or altitudes) develop a broader range of thermo-tolerance, thus becoming more extensively distributed than species at low latitudes (or altitudes) (Stevens, 1989).

The CVH hypothesis has been tested extensively on ectotherms (e.g. Addo-Bediako *et al.*, 2000; Calosi *et al.*, 2010; Araújo *et al.*, 2013), yet barely on a few disease vectors (e.g. Terblanche *et al.*, 2006; de la Vega *et al.*, 2015).

The present study aims to explore the possible relationships between the thermo-tolerance and the geographical distribution of seven species of triatomines chosen by their epidemiological relevance (Lent & Wygodzinsky, 1979; Patterson & Guhl, 2010), geographical distribution (Carcavallo *et al.*, 1999) and phylogenetic relationship (Hypsa *et al.*, 2002). We combined two different methodological approaches: species distribution models (SDMs), and individual physiological tolerances. First, we modelled the ecological niche of each species using climatic variables, identifying the most important abiotic factor for their distribution. Then, the thermal tolerance limits for all species were analysed and compared by measuring their CTmax, CTmin, upper lethal temperature (ULT), and chill-coma recovery time (CCRT). Finally, in order to unravel possible causes of the distribution of Chagas disease vectors, we analysed whether there is any link between the most important abiotic limiting factors and thermal tolerance ranges of the species to test the CVH, providing a different standpoint for the geo-epidemiology of the Chagas disease vectors.

Materials and methods

Ecological niche model

We modelled the ecological niche for seven species of triatomines, i.e. *Rhodnius prolixus*, *Triatoma dimidiata*, *T. infestans*, *T. vitticeps*, *T. sordida*, *T. delpontei* and *T. patagonica*, using random points from their geographical range distributions, which can be found in a public domain site (http://dx.doi.org/10.6084/m9.figshare.653959). The random points used include 'pseudo-presences' with the advantage that there is no sampling bias problem, although it has the disadvantage that certain points in geographical ranges may include unsuitable areas that can overestimate actual occurrences (Jetz *et al.*, 2008). To model habitat suitability and identify the potential limiting factor, we used 19 bioclimatic variables (plus altitude; see S1 in File S1) at a 0.5 arc-minute resolution from WorldClim (www.worldclim.org).

For the comparison of the physiological thermal niche limits of each species with their ecological niche model, correlative models were performed, where variables that were highly correlated ($r > 0.7$) with Bio 5 (maximum temperature of the warmest month) or Bio 6 (minimum temperature of the coldest month) were excluded in order to avoid collinearity. Matrices of Pearson's rank correlation were made for each species using function rcorr from package 'Hmisc' in R (R – Development Core Team, 2013). Furthermore, to avoid any remaining multicollinearity with the bioclimatic variables, the variance inflation factor (VIF) for each species model was calculated using the vif function from the package 'car' in R (R – Development Core Team, 2013). Any variable with a VIF > 10 was excluded (Zuur *et al.*, 2009). The remaining independent variables were used to fit species distribution models with MAXENT. This algorithmic modelling, based on machine learning and used as a method for modelling presence-only data (Elith *et al.*, 2011), was selected because it represents a niche-based model as an approximation of the ecological niche in the examined environmental dimensions being consistently competitive with the highest performing methods (Elith *et al.*, 2006). Moreover, MAXENT has shown to outperform other algorithms based on machine learning or regression methods (Aguirre-Gutiérrez *et al.*, 2013). We used the MAXENT function from the 'dismo' package in R (Hijmans & Elith, 2013) and the limiting factor analysis and maps. At each pixel, the limiting factor analysis replaces each variable predictor by its average value at occupied sites. If a change results in the highest probability of occurrence, the variable changed is then viewed as a limiting factor (see Elith *et al.*, 2010 and Hill *et al.*, 2012, as well as supporting information for more details). Final models were run with 10-fold cross-validation and the goodness of fit of the predictions, the ability to predict presence vs. absence, was evaluated by the area under the receiver operating characteristic curve (AUC) criterion. The AUC value ranges from a minimum of 0 to a maximum of 1 (perfect discrimination). Although the relative merits of this criterion have previously been discussed, because AUC values could depend on the extent of the geographical region in which background or pseudo-absence points are taken (e.g. Lobo *et al.*, 2008), it is very useful in SDMs to assess the predictive performance of each variable of the model, rather than assess the overall model performance (Elith *et al.*, 2006).

Physiological thermal niche

Experiments were performed with 1-week-old, unfed fifth-instar nymphs of *R. prolixus*, *T. dimidiata*, *T. infestans*, *T. vitticeps*, *T. sordida*, *T. delpontei* and *T. patagonica*. Insects were provided by the National Chagas Control Service (Córdoba, Argentina) as third- or fourth-instar nymphs, and reared in the laboratory at 28 °C under an LD 12 : 12 h photoperiod (light on 08.00 hours) until they emerged as the fifth instar. To determine physiological upper thermo-tolerances, we used thermo-limit respirometry (Lighton & Turner, 2004) following the protocol detailed in de la Vega *et al.* (2015). The setup consisted of a flow-through respirometry system with a CO_2 analyser (LI-6251; Li-Cor, Lincoln, NE, U.S.A.) attached to an activity detector [AD-2; Sable Systems International (SSI), Las Vegas, NV, U.S.A.] to measure real-time CO_2 production and motor activity in an unrestrained individual insect inside a respirometric chamber within a temperature-controlled cabinet (PTC-1; SSI). The temperature profile began with 15 min at 35 °C followed by a ramp of increasing temperature rate of 0.25 °C/min. Maximum critical temperature was defined by motor activity, and respiratory breakdown was defined by the inflection point in the absolute difference sum curves (Lighton & Turner, 2004). After CTmax occurred, we distinguished the ULT in the respiratory curve (see S3 in File S1 and de la Vega *et al.*, 2015 for more details).

The lower limits of the physiological thermal niche were determined by measuring the CTmin and CCRT. For CTmin, triatomines were tested on a temperature plate (Pelt-plate; SSI) connected to a temperature controller (Pelt-5; SSI), with a temperature profile beginning with a baseline of 15 min at 20 °C followed by a ramp of decreasing temperature rate of −0.25 °C/min. The CTmin was defined as the temperature at which insects stopped responding to a soft mechanical perturbation. To determine the time required to recover from cold exposure or CCRT, insects were placed individually for 4 h in small containers with melting ice (*c.* 0 °C), and then transferred to a controlled temperature cabinet at 28 °C (same reared temperature) positioned on their back at the centre of a Petri dish (70 × 10 mm). Recovery time was the time until insects assumed an upright position (visually observed through a glass), or if insects did not assume an upright position after observation for 1 h they were recorded as non-recovered. Each insect was weighed to the nearest 0.1 mg on an analytical balance (AJ100; Mettler Toledo, Columbus, OH, U.S.A.) before each assay.

Eco-physiological approach of the distribution

To compare the limits of the physiological thermal niche with the ecological niche models, the critical temperature values of each species were analysed in relation to the minimum temperature of the coldest month (Bio 6), and the maximum temperature of the warmest month (Bio 5) in areas where the probability of occurrence for each species exceeds a critical value for each model. For this purpose, an area with probability values greater than a critical value determined by the value of maximum probability of the sum of sensitivity (percentage of true positives) and specificity (percentage of true negatives) was taken (Svenning *et al.*, 2008). This limit allows us to work with presence probability uncoupled from the coordinates of 'pseudo-presence'. In addition, within this limit (i.e. where the probability of presence is between 0.35 and 1), values of Bio 5 and Bio 6 were taken from 1000 random coordinates and plotted against the critical thermal tolerances.

In relation to the CVH, if the lower thermo-tolerance depends on natural selection, species living in low-temperature environments should have better cold tolerance (i.e. lower CTmin or faster CCRT), while species that are not exposed to low temperatures should have worse cold tolerance. By contrast, if the upper thermo-tolerance is highly conserved across species, it would be expected that natural selection did not act on this trait, resulting in a weak relation between the maximum temperature and maximum thermo-tolerance (i.e. CTmax or ULT). To test these ecological hypotheses, regressions between physiological parameters (thermo-tolerances) and environmental gradients (maximum or minimum temperature) were performed. Finally, regressions between thermo-tolerances and latitudes were carried out in order to try to understand the underlying mechanisms that lead to the geographical distribution of the species. To determine the ecological niche of each insect vector, extreme temperatures and latitude were taken from the highest probability points of the distribution model.

Statistical analyses

Generalized models were used with the varIdent function from the 'nlme' package in R (R – Development Core Team, 2013) to include heteroscedasticity in the statistical model when homogeneity of variance was rejected by the Levene test or graphically examined. In addition, normality was checked with the Shapiro–Wilk test. Phylogenetic independent contrasts (PICs) were constructed for all linear regressions (See S2 in File S1 for details). Tables show means and standard deviation (SD) compared by ANOVA test. The overall error was corrected by the Bonferroni correction (12 variables for respirometry analysis, $P < 0.004$; and two variables for CTmin analysis, $P < 0.025$).

Results

Ecological niche models

The contribution of each variable and the average AUC for the SDM of each species are shown in Table 1. The minimum temperature of the coldest month (Bio 6) was the

Table 1. Relative contribution (percentage) of bioclimatic variables and area under the receiver operating curve values from MAXENT.

Variable	*T. infestans*	*Triatoma vitticeps*	*Triatoma delpontei*	*Triatoma dimidiata*	*Triatoma patagonica*	*Triatoma sordida*	*Rhodnius prolixus*
BIO 2	3.3	–	–	–	–	–	–
BIO 3	–	19.3	64.5	38.6	–	22.2	26.9
BIO 5	6.5	16.2	8.3	8.8	13.7	2.2	2.2
BIO 6	60.5	37.5	12.5	26.5	55.8	34.5	48.2
BIO 12	13.5	–	15.0	8.1	–	20.4	1.4
BIO 15	6.5	27.1	–	9.9	7.1	2.2	2.8
BIO 18	–	–	–	8.0	–	11.6	–
BIO 19	10.7	–	–	–	23.5	6.8	18.4
AUC	0.825 ± 0.01	0.970 ± 0.01	0.952 ± 0.03	0.808 ± 0.03	0.933 ± 0.01	0.843 ± 0.02	0.839 ± 0.02

Bio 2, mean diurnal range [mean of monthly (maximum temperature − minimum temperature)]; Bio 3, isothermality [Bio 2/(Bio 5 − Bio 6)](× 100); Bio 5, maximum temperature in the warmest month; Bio 6, minimum temperature in the coldest month; Bio 12, annual precipitation; Bio 15, precipitation seasonality (coefficient of variation); Bio 18, precipitation during the warmest quarter; Bio 19, precipitation during the coldest quarter.

most influential abiotic factor for triatomine distribution. For *T. delpontei*, the isothermallity (Bio 3) made a greater contribution to the final model. However, it is important to note that this variable includes the effect of Bio 6 in its formula (Bio 3 = Bio 2/Bio 5 − Bio 6 × 100). Furthermore, the permutation analysis (Table S1 in File S1) and jackknife analysis for variables on the AUC model (Figure S1 from File S1) showed variables Bio 3 and Bio 6 having a great effect in each model. The SDM showed overlapped areas with favourable environmental conditions for the establishment of more than one triatomine, but also areas with no species present (i.e. in the Andes region and some environments from the central-north part of Brazil) (Fig. 1A). Only *T. patagonica* and *T. vitticeps* appeared to be circumscribed to a single country (Argentina and Brazil, respectively) (Fig. 1A). The limiting factor for most of the distribution models was the minimum temperature of the coldest month (Bio 6; green colour in Fig. 1B).

Physiological thermal niche

The metabolic rate of triatomines can be modified by extrinsic variables such as temperature (Rolandi *et al.*, 2014), as well as intrinsic variables such as insect mass. Because there were significant differences of mass across the species studied (Table 2; $F_{6,88} = 136.08$, $P < 0.0001$), we analysed the thermo-limit parameters of mass-independent metabolic rate to compare differences across species (Table 2; see S4 in File S1 for mass-independent conversion). Thermo-limit respirometry measurements showed a dynamic response (Fig. 2) similar to that found in other insect species (Lighton & Turner, 2004). In the equilibrium phase, when insects are not moving, it is possible to measure the resting or standard metabolic rate (SMR). There were significant differences across species for the mass-independent SMR (Table 2; $F_{6,75} = 7.02$, $P < 0.0001$). The post hoc analysis showed statistically significant differences between *T. dimidiata* and *T. patagonica*, between *T. dimidiata* and *T. sordida*, as well as between *T. sordida* and *T. delpontei* (Table 2). Once the temperature ramp started, the activity and the CO_2 release increased progressively (Fig. 2). This CO_2 increase was different for the distinct species ($F_{6,88} = 17.42$, $P < 0.001$). *Rhodnius prolixus* showed the greatest sensitivity to temperature with a metabolic rate increase of $2.60 \pm 0.89\ \mu W/mg^{0.856}$ per °C (see Table 2). The post hoc contrasts evinced *R. prolixus* as the only species showing significant differences against the other triatomines (Table 2). The duration of the rise in CO_2 released was between 40 and 60 min for most of the species (Table 2), with significant differences across them. *Triatoma dimidiata* showed the shortest duration (< 30 min), and it was significantly different from the other triatomines (Table 2; $F_{6,93} = 46.35$, $P < 0.0001$). Then, the CO_2 trace reached the plateau phase and maintained a relatively constant maximum rate, even if the temperature continued increasing (Fig. 2, Phase 3). There were no significant differences in the CO_2 release between the start and the end of the plateau for each species, except for *T. delpontei* (Table S2 in File S1). The mass-independent maximum CO_2 release rate observed on the plateau (phase 3) showed differences across species ($F_{6,88} = 37.02$, $P < 0.0001$). The post hoc test showed that the significant differences were across *R. prolixus*, *T. dimidiata* and *T. delpontei* (Table 2). Furthermore, the plateau had a significant different duration for each species ($F_{6,93} = 9.48$, $P < 0.0001$), being shorter for *T. infestans* and *T. sordida* (Table 2).

After a maximum release of CO_2, a marked decrease was observed until a valley shape occurred (phase 5), where it is considered that the insect died. During the 'pre-mortal fall' in phase 4, the CTmax was determined for both traces (CO_2 emission rate ($\dot{V}CO_2$) and activity), with no significant differences between them (Table S3 of File S1). The CTmax showed significant differences across species, for both the CO_2 release and the activity (CO_2, $F_{6,92} = 33.30$, $P < 0.0001$; activity, $F_{6,92} = 20.65$, $P < 0.0001$). Post hoc analysis showed significant differences between species with the extreme values of 44.2 °C (*T. dimidiata*) and 49.5 °C (*T. sordida*; Table 2). After CTmax, if the temperature continued rising, the ULT was determined as the temperature at which individuals lost spiracle control, which was reflected on the $\dot{V}CO_2$ trace (Fig. 2, phase 5). Despite the fact that few species showed statistical differences between the ULT and CTmax (Tables 2 and S4 in File S1), the difference (ULT − CTmax) in most of species was close to 1 °C. Comparing $\dot{V}CO_2$ values in phase 5, there are significant differences between triatomines ($F_{6,88} = 14.15$, $P < 0.0001$), as well as between ULT values ($F_{6,90} = 41.01$, $P < 0.0001$). In addition, post hoc analysis showed that *T.*

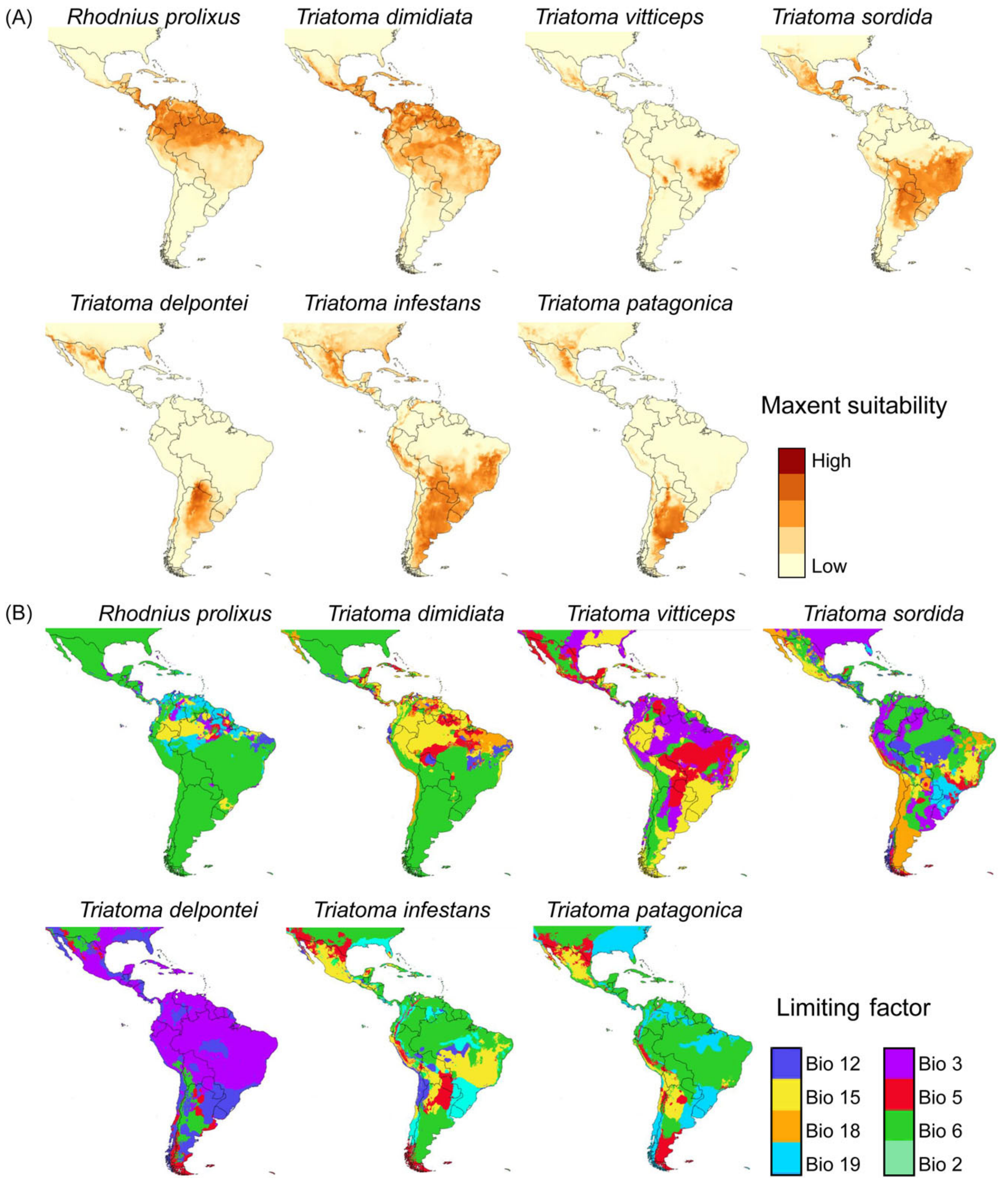

Fig. 1. Habitat suitability for the ecological niche and limiting factor maps for seven species of triatomines. (A) Maps resulting from MAXENT distribution modelling of seven species of triatomine and habitat suitability. (B) Limiting factor maps (relationship between each model performance and the predictor variables at each pixel; for details see Elith *et al.*, 2010; Hill *et al.*, 2012). Bio 2, mean diurnal range [mean of monthly (maximum temperature − minimum temperature)]; Bio 3, isothermality [Bio 2/(Bio 5 − Bio 6)](× 100); Bio 5, maximum temperature in the warmest month; Bio 6, minimum temperature in the coldest month; Bio 12, annual precipitation; Bio 15, precipitation seasonality (coefficient of variation); Bio 18, precipitation during the warmest quarter; Bio 19, precipitation during the coldest quarter. [Colour figure can be viewed at wileyonlinelibrary.com].

Table 2. Thermo-limit respirometry for seven species of triatomines.

	Rhodnius prolixus	*Triatoma delpontei*	*Triatoma dimidiata*	*Triatoma infestans*	*Triatoma patagonica*	*Triatoma sordida*	*Triatoma vitticeps*
Sample size (*n*)	16	18	11	14	13	16	10
live body mass (mg)	29.43 ± 5.48	116.16 ± 20.41	131.32 ± 29.09	72.46 ± 10.94	46.45 ± 10.98	34.28 ± 10.50	173.47 ± 23.49
	a	b	b	c	d	ad	e
Equilibration							
$\dot{V}CO_2$ equilibration (phase 1) (μL/h)	14.94 ± 10.99	51.49 ± 28.66	43.22 ± 13.74	22.92 ± 10.00	11.92 ± 5.41	8.14 ± 3.68	49.89 ± 16.73
Standard metabolic rate (μW^{-1})	4.11 ± 1.80	4.87 ± 2.03	4.46 ± 1.10	2.64 ± 1.08	2.68 ± 0.69	2.62 ± 0.88	3.91 ± 1.48
	ab	bc	b	abc	ac	a	ab
Sensitivity							
$\dot{V}CO_2$ vs temperature (phase 2) ($\mu L\ h^{-1}\ {}^{\circ}C^{-1}$)	6.96 ± 2.52	10.35 ± 3.66	11.64 ± 4.75	6.55 ± 2.31	2.66 ± 0.79	2.23 ± 0.52	10.22 ± 1.14
Mass-independent correction ($\mu W/mg^{0.856}\ {}^{\circ}C$)	2.60 ± 0.89	1.23 ± 0.36	1.28 ± 0.62	1.16 ± 0.40	0.71 ± 0.22	0.76 ± 0.10	0.86 ± 0.13
	a	b	bc	bc	c	c	c
Ramp duration (phase 3) (min)	41.82 ± 3.68	46.93 ± 4.81	28.59 ± 5.74	52.73 ± 2.44	54.45 ± 5.03	59.85 ± 8.92	51.93 ± 5.34
	a	ad	b	c	c	c	cd
Resistance							
Start plateau temperature (phase 3) (°C)	44.27 ± 0.81	45.47 ± 1.06	41.50 ± 0.98	46.51 ± 0.51	46.60 ± 1.16	48.30 ± 1.87	46.06 ± 1.12
Finish plateau temperature (phase 3) (°C)	45.81 ± 0.69	47.04 ± 1.11	43.24 ± 1.08	47.34 ± 0.40	48.03 ± 0.82	49.41 ± 1.55	47.92 ± 0.83
$\dot{V}CO_2$ plateau (phase 3) (μL/h)	80.43 ± 18.19	169.49 ± 64.10	129.01 ± 31.93	116.25 ± 29.55	43.93 ± 14.27	41.40 ± 7.24	178.34 ± 22.97
Mass-independent correction ($\mu W/mg^{0.856}$)	30.38 ± 5.53	19.92 ± 5.21	13.71 ± 2.96	20.68 ± 4.87	11.42 ± 2.89	14.42 ± 2.43	15.04 ± 1.92
	a	b	c	b	c	c	c
Plateau duration (phase 3) (min)	8.78 ± 3.67	7.95 ± 2.85	7.91 ± 5.04	3.63 ± 1.60	6.49 ± 1.51	5.05 ± 1.57	7.89 ± 4.28
	a	a	ab	b	ac	ab	a
Critical thermal							
CTmax activity (°C)	45.81 ± 0.71	47.47 ± 1.24	44.90 ± 1.54	47.21 ± 0.35	47.77 ± 1.61	49.46 ± 1.56	47.83 ± 0.82
	a	b	a	b	b	c	b
CTmax $\dot{V}CO_2$ (°C)	45.90 ± 0.68	47.18 ± 1.05	44.18 ± 0.99	47.24 ± 0.41	48.05 ± 1.01	49.45 ± 1.51	48.13 ± 1.23
	a	b	d	b	bc	b	bc
Lethal							
$\dot{V}CO_2$ valley (phase 5) (μL/h)	46.19 ± 16.98	176.44 ± 64.31	100.84 ± 29.93	104.97 ± 22.28	43.44 ± 13.28	37.44 ± 9.03	160.76 ± 39.61
Mass-independent correction ($\mu W/mg^{0.856}$)	17.59 ± 5.61	20.75 ± 5.38	10.57 ± 2.39	18.77 ± 4.17	11.32 ± 2.79	12.88 ± 2.75	13.53 ± 3.13
	ab	a	c	ab	c	c	bc
ULT (°C)	47.29 ± 0.59	47.94 ± 1.21	44.96 ± 1.32	47.92 ± 0.34	48.75 ± 0.76	50.71 ± 1.36	48.81 ± 0.67
	a	ab	d	ab	b	c	b

Different letters represent significant differences between species ($P < 0.004$). Mean values are displayed with their standard deviation.
$\dot{V}CO_2$, CO_2 emission rate; CTmax, maximum critical temperature; ULT, upper lethal temperature.

dimidiata, with the lowest mass-independent metabolic rate ($10.57 \pm 2.39\ \mu W/mg^{0.856}$), was significantly different from *T. delpontei*, *R. prolixus* and *T. infestans*, as well as having the lowest ULT (45.0 ± 1.3 °C), which was significantly different from the other species (Table 2).

The CTmin was significantly different across species ($F_{6,142} = 40.40$, $P < 0.001$; Table 3). The range of the physiological thermal niche (CTmax − CTmin) showed differences across species, with *T. sordida*, *T. patagonica* and *T. infestans* having higher tolerance range than the other triatomines (Table 3).

The CCRT, or insect's recovery time after being exposed to c. 0 °C for 4 h, showed that *R. prolixus*, *T. vitticeps* and *T. dimidiata* have the worst cold tolerance. These species did not recover during 1 h at 28 °C after being exposed to cold; however, they all recovered and none of them died after 24 h. The remaining species were able to recover before the end of the experiment (even before 20 min) ($F_{3,70} = 19.25$, $P < 0.0001$) (Fig. 3).

Eco-physiological approach for the distribution

Figure 4A–G shows the relation between the physiological thermal niche limits (CTmax and CTmin) and extreme

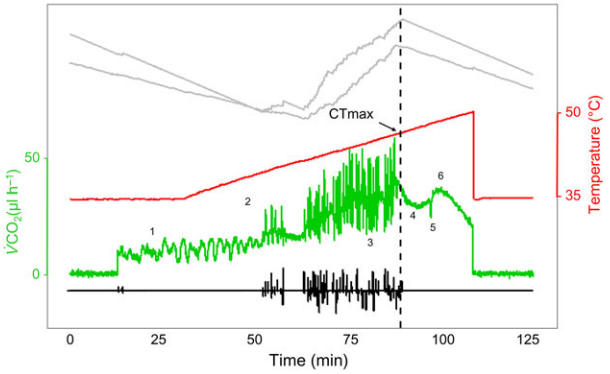

Fig. 2. Thermo-limit respirometry of a fifth-instar *Triatoma sordida* (mass = 42.6 mg). The $\dot{V}CO_2$ trace (green) shows the six stages of the response (phases 1–6; see S3 in File S1 for details and definitions). Equilibration temperature (red scale) was 34.54 °C. Ramping rate was 0.25 °C/min. The maximum critical temperatures (CTmax) were 47.05 °C (spiracular CTmax) and 47.04 °C (activity CTmax). The bottom trace in black shows activity (arbitrary units, scales not shown). Above, activity absolute difference sum (ADS) and $\dot{V}CO_2$ ADS residual lines are used to determine CTmax objectively (scales not shown). The $\dot{V}CO_2$ trace begins and ends with a baseline. [Colour figure can be viewed at wileyonlinelibrary.com].

Table 3. Summary of critical thermal minimum (CTmin) and critical temperature range for seven species of triatomines.

	Rhodnius prolixus	*Triatoma delpontei*	*Triatoma dimidiata*	*Triatoma infestans*	*Triatoma patagonica*	*Triatoma sordida*	*Triatoma vitticeps*
Sample size (*n*)	25	17	23	25	20	19	20
CTmin (°C)	6.04 ± 1.47	4.10 ± 2.61	4.23 ± 2.53	0.65 ± 1.27	0.82 ± 1.58	2.17 ± 1.48	3.90 ± 2.88
	a	ac	ac	b	bd	cd	ac
Thermo-tolerance Range (CTmax–CTmin)	39.77	43.37	40.67	46.56	46.95	47.29	43.93

Different letters represent significant differences between CTmin of species ($P < 0.025$). Mean values are displayed with their standard deviation. CTmax, maximum critical temperature.

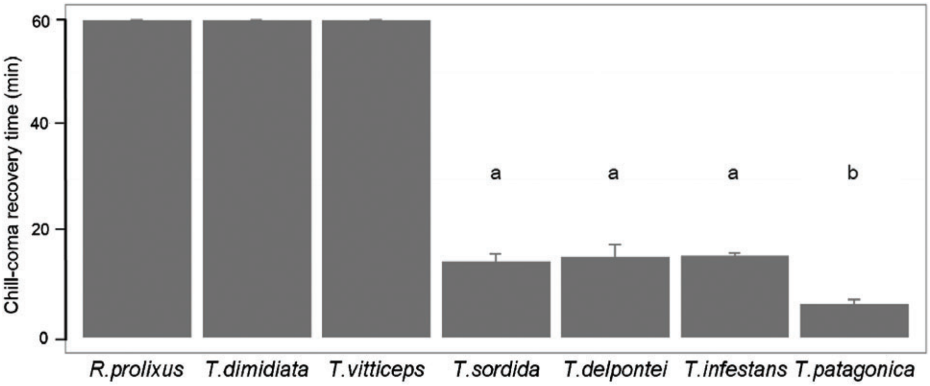

Fig. 3. Chill-coma recovery time for seven species of triatomine. *Rhodnius prolixus*, *Triatoma dimidiata* and *Triatoma vitticeps* did not recover within 1 h. Different letters indicate significant differences ($P < 0.05$); only species recovered before 1 h were statistically compared.

temperatures (Bio 5 and Bio 6) for 1000 random points on the map extent. In addition, points are depicted according to presence probability for each species and the confidence ellipse for extreme temperatures (Bio 5 and Bio 6) on a presence probability greater than a threshold (maximum sum of sensitivity, true positive rate, and specificity, true negative rate). Sensitivity and specificity values for each model and threshold values can be found in Table S5 of File S1. In terms of the maximum temperature of the warmest month, the probability of presence almost never exceeds values of temperature higher than 40 °C, being the confidence ellipses (95% of the points) more than 10° C below their CTmax. An exception was *T. dimidiata* with some high probability points in areas with temperatures higher than 40 °C, and its CTmax 7 °C higher than the maximum temperature within the confidence ellipse. On the other hand, the relationship between the minimum temperatures and the lower limit of the physiological thermal niche of *T. dimidiata*, *R. prolixus* and *T. vitticeps* confidence ellipses (95%) showed temperatures above their CTmin, and with no presence points of high probability at temperatures below 0 °C. However, the confidence ellipses for *T. delpontei*, *T. infestans* and *T. patagonica* have high probability points even in areas with temperatures lower than their CTmin, whereas *T. sordida* shows that the confidence ellipse is very close to their CTmin, with areas showing the minimum temperatures of the coldest month below 0 °C (Fig. 4A–G).

The geographical position of the maximum probability of presence for each species was taken as the 'midpoint' of their distribution, as a means of understanding the relationships between species tolerances and extreme temperatures in their distribution. As shown in Fig. 1A, *R. prolixus*, *T. vitticeps* and *T. dimidiata* have tropical distributions, whereas the other species have a high probability of presence on both hemispheres in subtropical or temperate regions. For this subtropical species, probability values in the southern hemisphere were taken. The selected species do not share the pattern proposed by Rapoport, namely that species distributed to the latitudinal extremes had a greater geographical range. At least, for these seven species of triatomines, latitudinal range does not vary as species spread southwards (latitudinal range ~ latitude = slope = 0.12, $F_{1,5} = 0.03$, $P = 0.85$, $r^2 = 0.0007$); however, the thermal amplitude decreases toward the tropics (temperature range ~ latitude = slope = −5.19, $F_{1,5} = 37.2$, $P < 0.002$, $r^2 = 0.85$). Species with southernmost distribution are exposed to lower Bio 6 than species with distribution toward the tropics (slope = 0.18, $F_{1,5} = 24.05$, $P < 0.002$, $r^2 = 0.88$), but no latitudinal variation for Bio 5 was found (slope = −0.08, $F_{1,5} = 0.20$, $P = 0.67$, $r^2 = 0.02$).

In order to understand these patterns, we assessed whether the critical temperatures (CTmax and CTmin) depend on temperature and latitude for points of maximum probability. This new analysis showed that extreme temperatures (Bio 5 or Bio 6) and latitude values of the centre of distribution have a positive linear relationship with CTmin (CTmin ~ Bio6 = slope = 0.02, $F_{1,5} = 18.74$, $P = 0.007$, $r^2 = 0.79$; CTmin ~ absolute value of latitude = slope = −0.13, $F_{1,5} = 22.15$, $P < 0.006$, $r^2 = 0.81$), but not with CTmax (CTmax ~ Bio 5 = slope = 0.01,

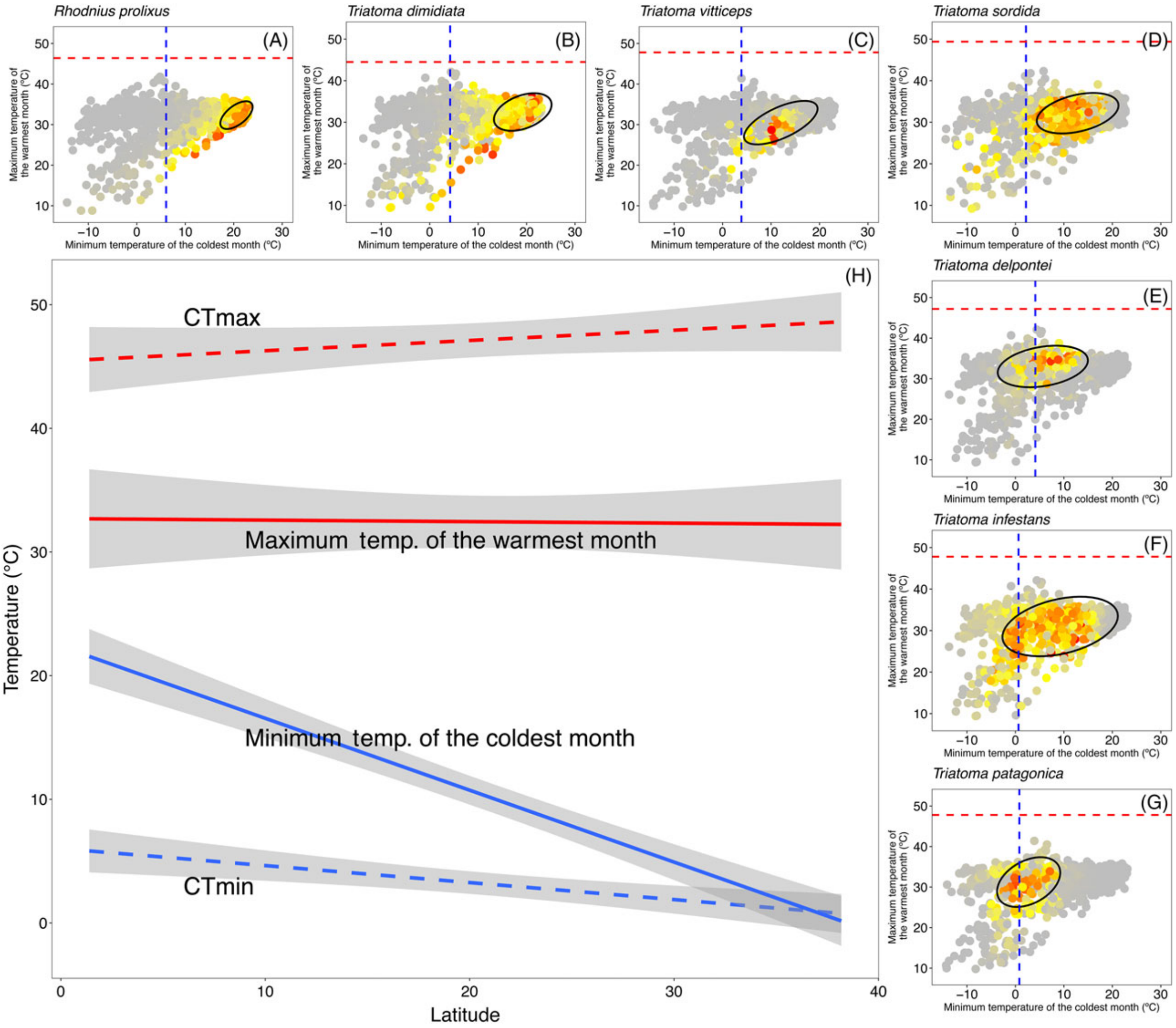

Fig. 4. (A–G) Relationship between limits of the physiological thermal niche and the ecological niche for seven species of triatomines. Thermo-limits (CTmax and CTmin) and extreme temperature variables, the minimum temperature of the coldest month (Bio 6) and the maximum temperature of the warmest month (Bio 5) for 1000 random coordinates are depicted according to the probability of the presence ('MAXENT suitability') of each species. Ellipse of confidence (95%) that the presence probability is higher than the maximum value of the sum of sensitivity (percentage of true positives) and specificity (proportion of true negatives). (H) Critical temperatures and their relationship with latitude and extreme temperatures. The regressions shown are from the relation between the minimum critical temperature (CTmin) and latitude (dashed blue line); Bio 6 from the ecological niche and latitude (solid blue line; the relation between the maximum critical temperature (CTmax) and latitude (dashed red line); and Bio 5 from the ecological niche and latitude (solid red line; ANOVA, $F_{1,5} = 0.032$, $P = 0.86$). [Colour figure can be viewed at wileyonlinelibrary.com].

$F_{1,5} = 0.21$, $P = 0.66$, $r^2 = 0.04$; CTmax ~ absolute value of latitude = slope = 0.08, $F_{1,5} = 3.50$, $P = 0.12$, $r^2 = 0.29$) (Fig. 4H). It was further noted that the thermo-tolerance range (CTmax–CTmin) maintained this positive latitudinal relationship (tolerance range ~ latitude = $F_{1,5} = 21.9$; $P = 0.005$, $r^2 = 0.77$). In a more realistic approach, when we included the phylogenetic relationship between species, the results of PIC analyses between physiological traits (CTmin, CTmax and thermo-tolerance range), and either temperature or latitude of the distribution for each species showed similar significance levels and patterns to those observed without phylogeny correction (Figure S2 in File S1).

Discussion

Ecological niche

Species distribution models were used to assess the ecological niche and geographical distribution of seven species of triatomines. Models predicted favourable environmental conditions for more than one species. When overlapping the seven models, it was possible to show two areas with high richness of species and epidemiological importance: the north-central part of Argentina and the south-central part of Brazil (Figure S3 of File S1). These regions of high vector richness match with richness maps proposed by Fergnani *et al.* (2013), in which most triatomine species are found in northern Argentina, southern Bolivia, southeastern Brazil and Venezuela. Furthermore, Rodriguero & Gorla (2004) stated that the highest density of triatomine species corresponds to a latitudinal pattern with its maximum between 5° and 10° south (*c.* 20 species) and has values close to 10 species in comparison with the richest areas found in our work (Figure S3 of File S1). In addition, the models determined that Bio 6 was one of the most important variables and limiting factors for the geographical distribution of the seven species of triatomines. The low probability of presence in the Andes and north-central areas of Brazil could be explained by the low temperatures found at high altitudes, which is consistent with the fact that most triatomine species and populations are located between sea level and 1500 m above sea level (Carcavallo *et al.*, 1999). Low probability of presence in Brazil could be understood from the maps of limiting factors (Fig. 1B). These suggest that tropical species are limited in that area by Bio 6 and temperate species where their distribution reaches the east centre of the continent, as *T. infestans* and *T. sordida* are also limited in their northern distribution by precipitation variables [mean annual precipitation (Bio 12) and precipitation during the coldest quarter (Bio 19)], although, given that there is a great richness of triatomines in South America, biotic interactions could also be affecting their distribution (Rodriguero & Gorla, 2004; Fergnani *et al.*, 2013).

In accordance with previous studies (Gorla, 2002; de la Vega *et al.*, 2015), environmental temperatures have significant effects on the distribution of triatomines. Additionally, precipitation has a great effect on the distribution of *T. vitticeps*, where seasonal precipitation [precipitation seasonality (coefficient of variation) (Bio 15)] accounts for a large percentage of this contribution (27.1%). In the same way, de Souza *et al.* (2010) showed that the annual precipitation and precipitation of the wettest quarter of the year were associated with the distribution of *T. vitticeps* in Brazil, and would be associated with the 'Atlantic forest' and 'Cerrado' biomes (Gurgel-Gonçalves *et al.*, 2012). The distribution models show the importance of low temperatures for the distribution of triatomines, as has been observed for other insect species (Warren *et al.*, 2010), particularly those species inhabiting temperate regions with cold winters.

Physiological thermal niche

The CO_2 emission profiles of triatomines revealed the same seven phases found in other insect species (e.g. ants; Lighton & Turner, 2004). As shown in Table 2, all species have relatively similar SMR at 35 °C and a rise in temperature enhances the interspecific differences in metabolic rates. At this stage of 'sensitivity', clear differences between *R. prolixus* and the rest of triatomine species for the increased rate, and between *T. dimidiata* and the other species for the ramp length were observed. A higher metabolic rate implies a higher nutrient conversion and biting frequency for these insects (Rolandi & Schilman, 2012). Thus, in terms of their importance as disease vectors, it is worth noting the thermal sensitivity of the metabolic rate of *R. prolixus* and *T. infestans*. These two species are the most important vectors of Chagas disease (Schofield *et al.*, 2006). Geographical distribution, the degree of domiciliation, anthropophily, and the time between feeding and defecation are key factors for their capacity as vectors (Lent & Wygodzinsky, 1979). So, the higher thermal sensitivity of *R. prolixus* and *T. infestans* compared with the other species could be responsible, to a certain degree, for their importance as Chagas disease vectors. The relationship between the metabolic rate increases during the ramping phase ('sensitivity') and the time during which there is a fairly constant metabolic rate, although the temperature continued to increase, during the plateau ('resistance') shown by each species, is reflected in the CTmax. In addition, after the CO_2 emission rate reached its maximum (phase 3, plateau; S3 in File S1), it decayed, except for *T. delpontei*. The CTmax values revealed that there is a small intraspecific variation in, and no significant differences between, CTmax determined by respirometry or activity. In addition, differences between CTmax and ULT were also very small (Table 2); hence the vulnerability to extreme upper-thermal conditions will mostly be given by behavioural plasticity in habitat use (Sunday *et al.*, 2014). Even though there was a higher intra- and interspecific variation for CTmin than for CTmax, in some triatomine species, the upper critical thermal tolerances were closer to the upper-lethal temperatures than was the case for CTmin and the lower-lethal temperatures. These physiological traits are consistent with results in other insect species, where the upper thermo-lethal limits show less variation than the lower ones (Addo-Bediako *et al.*, 2000; Sunday *et al.*, 2011), with the upper thermal limits having less phenotypic plasticity than the lower ones (García-Robledo *et al.*, 2016). This asymmetry could be explained because cold and heat tolerances in insects are based on different mechanisms. Cold tolerance variation is due to the specific ability to maintain ion homeostasis (MacMillan *et al.*, 2012), whereas heat tolerance can be explained by the inability to counteract deleterious effects of high temperatures on the stability of membranes and proteins (Angilletta, 2009).

Eco-physiological approach of the distribution

Ours results show that the upper limits of the physiological thermal niche for all triatomine species tested are much higher than the extreme warm temperature ecological niche. That is, triatomines are geographically distributed in areas where the maximum temperatures of the warmest month (Bio 5) are considerably lower than their respective CTmax (Fig. 4, ellipse). This could be considered an adaptive strategy to avoid exposure to temperatures near their CTmax, and therefore their ULT (*c.* 1 °C higher than their CTmax), providing a margin of safety for lethal thermal conditions. Tolerance to high temperatures will determine the survival of species under projected global warming (García-Robledo *et al.*, 2016). However, based on our results, this scenario does not seem to represent a climatic constraint for Chagas diseases vectors. Regarding the lower limits of the physiological thermal niche and the ecological niche, tropical species *R. prolixus*, *T. dimidiata* and *T. vitticeps* inhabit areas where the minimum temperatures in the coldest month (Bio 6) are greater than their CTmin. By contrast, species that are distributed in temperate and subtropical zones (*T. delpontei*, *T. infestans* and *T. patagonica*) inhabit areas where the Bio 6 values are lower than their CTmin (Fig. 4A–G, ellipse). The relationship between the minimum temperature of the coldest month and CTmin in subtropical species implies that these insects can inhabit colder areas than their CTmin, and so microclimatic conditions could be affecting their geographical distribution, especially for domiciliated species (Waleckx *et al.*, 2015). High cross-scale similarity of realized temperature niches is possible for species inhabiting ecosystems where small-scale environmental noise is low, as are the links with macroclimatic conditions (Schweiger & Beierkuhnlein, 2016). Previous results for the most important Chagas disease vector in Argentina, *T. infestans*, suggest sufficiently similar CTmin values from field populations and laboratory colonies (de la Vega *et al.*, 2015). Moreover, these temperatures are 'critical' and not 'lethal'. The lower lethal temperatures (LLTs) for *T. infestans*, *T. patagonica* and for *T. delpontei* are *c.* 10–12 °C below their CTmin [estimated to be −10 to −12 °C for *T. infestans*, −12 °C for *T. patagonica*, and −6 °C for *T. delpontei* (Blaksley & Carcavallo, 1968)]. In agreement with our CCRT results, tropical species inhabit regions where winters may not drop to temperatures below *c.* 0 °C, although for temperate species (*T. delpontei*, *T. infestans* and *T. patagonica*) this may not have important ecological consequences (Fig. 4, and Figure S4 of File S1). Even for *T. patagonica*, which recovered from chill-coma in a shorter time, minimum temperatures for the coldest month close to 0 °C are very common according to its distribution model (Figure S4 of File S1). Both, domiciliated and sylvatic populations of these subtropical vectors show a seasonal variation in population size, with few records in winters associated with the low temperatures (Gorla & Schofield, 1989; Wisnivesky-Colli *et al.*, 2003). By contrast, tropical vectors, including *T. dimidiata*, show seasonal variation related to the wet season (Dumonteil *et al.*, 2002). It is important to note that *T. dimidiata* could include presence data from multiple taxa due to the existence of several cryptic species from southern Mexico to northern Peru. Observed population dynamics could imply a reduction in meeting rates between vectors and hosts (and also transmission of the parasite *Trypanosoma cruzi*) during the cold season in subtropical regions or the dry season in tropical regions. Models of Chagas disease transmission could be improved by knowing the effects of cold temperatures on the vectors. In addition, an eco-physiological approach could help researchers to discard some false projections of geographical distribution of Chagas disease vectors due to the effect of global climate change. A suggested decreasing trend of suitability of areas that are currently considered high-to-moderate transmission risk (Medone *et al.*, 2015), and some vector species extinction, locally or completely (Escobar *et al.*, 2016), could be overestimating the tolerances of these triatomines, as well as other disease vectors. The assumption of a reduction in the distribution used by policymakers could place them at high risk of making incorrect decisions with subsequent negative consequences on health issues.

In terms of the CVH, our results fit well within the macroecological principle stating that species at higher latitudes have broader physiological thermal niches (Fig. 4H). It has been proposed that the species that inhabit a wider range of climatic gradients have higher thermal tolerance (Stevens, 1989; Addo-Bediako *et al.*, 2000; Sunday *et al.*, 2011), where the physiological niche is the key factor explaining the geographical range and its latitudinal variation (Cioffi *et al.*, 2016). However, Rapoport's rule on the geographical range and latitudinal position of species does not apply to the seven species tested in this study. In part, this may be explained by the fact that these species have been mainly chosen *a priori* for their epidemiological relevance, being only seven out of more than 140 species of triatomines.

The CTmax showed no significant latitudinal variation (in both realistic and unrealistic regression); the relationship between the tolerance range and latitude would be given by the linear regression of the lower limits of the physiological thermal niche and latitude. The realistic linear regression (Figure S2 of File S1) shows that the tolerance to low temperatures depends on thermal adaptations of species rather than being associated with ancestral inertia. Natural selection appears to modulate physiological responses to lower temperatures, but it is not observed to have an effect on higher temperatures (Araújo *et al.*, 2013). Ours results agree with findings in *Drosophila*, where phylogenetic inertia is responsible for heat resistance so that the species of this genus have a limited evolutionary ability to show variations in the upper thermal limits (Kellermann *et al.*, 2012). Hence, conservation of thermal tolerance across lineages suggests that the potential for local adaptation to alleviate the impacts of climate change may be limited. Furthermore, species with low CTmin and LLT are able to occupy higher latitudes (or altitudes), i.e. a broader range of environmental temperatures, while species with lower cold tolerance can only occupy warmer places (Araújo *et al.*, 2013).

The great importance of the minimum temperatures of the coldest month in the ecological niche models, and the results of physiological thermal niche analysis for these seven species of triatomines allow us to understand more clearly the southern limit and the distribution of these vectors. Critical thermal minimum and, to a lesser extent, CCRT are parameters that describe accurately the latitudinal variation, distribution and exposure to low environmental temperatures (Andersen *et al.*, 2015). Combining distribution patterns with physiological tolerances or mechanistic approaches allows us to understand the ecological niche of species (Warren *et al.*, 2010), therefore predicting where limiting temperatures will occur in the coming decades, and to grasp the latitudinal extent of different species. Also, such an approach meets the fundamental thermal niche and physiological limits of different species and so can serve to improve the efficiency of strategies for vector control at local and regional scales. The creation of combined models as applied here might represent a better approach to avoid the generalization of vector distribution at a local scale from a national-scale model. Models including other variables such as the number of days above or below the critical thermal values of the species could enhance distribution models for these or other disease vectors. A major challenge remains in creating predictive habitat models referred to the collection of systematic insect presence/absence data, as well as indices of triatomine population density to develop suitable statistical models for monitoring changes in Chagas disease risk, which could occur due to climate and land-use shifts in Latin America.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: DOI: 10.1111/mve.12262

File S1. Supporting information files.

Table S1. Relative importance of variables with permutation analysis.

Table S2. Differences between input and output from the plateau (phase 3) in $\dot{V}CO_2$ and temperature for seven triatomines.

Table S3. Difference between critical thermal maximum (CTmax) determination critera, $\dot{V}CO_2$ and activity, CTmax CO_2 vs CTmax ACT.

Table S4. Differences between critical thermal maximum (CTmax) and upper lethal temperature (ULT) for seven triatomines.

Table S5. Binary criterion values of probability for each model. Sensitivity or true positive rate (TPR) and specificity (TNR) or true negative rate for the threshold used. The sensitivity is the proportion of presences correctly predicted, and the specificity is the proportion of absences correctly predicted.

Figure S1. Jacknife analysis for the variables in the AUC ('area under the curve') for each species of triatomine analysed.

Figure S2. Phylogenetically independent contrasts of critical temperatures and their relationship with latitude and extreme temperatures. At the top, the phylogenetically independent contrasts (PICs) of the critical thermal minimum (PIC CTmin) and latitude as variables (PIC latitude) and minimum temperature of the coldest month (PIC Bio 6) are shown. The middle pair shows the relationship of the PICs of high critical thermal tolerance (PIC CTmax) and latitude as variables (PIC latitude) and maximum temperature of the warmest month (PIC Bio 5). The lower pair shows the linear relationship of the tolerance range (CTmax − CTmin) and latitude and also the PIC for tolerance range (PIC tolerance range) and latitude (PIC latitude). Statistical analysis for the regressions were as follows: PIC CTmin vs. PIC latitude: $F_{1,5} = 8.90$, $P = 0.04$; PIC CTmin vs. PIC Bio 6: $F_{1,5} = 38.27$, $P = 0.003$; PIC CTmax vs. PIC latitude: $F_{1,5} = 1.19$, $P = 0.33$; PIC CTmax vs. PIC Bio 5: $F_{1,5} = 1.54$, $P = 0.28$; PIC tolerance range vs. PIC latitude: $F_{1,5} = 10.34$, $P = 0.03$; tolerance range vs. latitude: $F_{1,5} = 21.9$, $P = 0.005$.

Figure S3. Triatomine richness by overlapping realized niches. Colour indicates the number of species.

Figure S4. Density function from frequency analysis for extreme temperatures (maximum and minimum) for the geographical distribution of the seven species of triatomines.

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