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Abstract	Small ectotherms, such as insects, with high surface area-to-volume ratios are usually at risk of dehydration in arid environments. We hypothesize that desiccation tolerance in insects could be reflected in their distribution, which is limited by areas with high relative values of water vapor pressure deficit (VPD) (e.g., hot and dry). The main goal of this study was to explore whether incorporation of eco-physiological traits such as desiccation tolerance in arid environments can improve our understanding of species distribution models (SDM). We use a novel eco-physiological approach to understand the distribution and the potential overlap with their fundamental niche in triatomine bugs, Chagas disease vectors. The desiccation dimension for *T. infestans*, *T. delpontei*, *T. dimidiata,* and *T. sordida* niches seems to extend to very dry areas. For *T. vitticeps*, xeric areas seem to limit the geographical range of their realized niche. The maximum VPD limits the western and southern distributions of *T. vitticeps*, *T. delpontei,* and *T. patagonica*. All species showed high tolerance to desiccation with survival times (35 °C-RH ~ 15%) ranging from 24 to 38 days, except for *T. dimidiata* (9 days), which can be explained by a higher water-loss rate, due to a higher cuticular permeability along with a higher critical water content. This approach indicates that most of these triatomine bugs could be exploiting the dryness dimension of their fundamental niche. Incorporating such species-specific traits in studies of distribution, range, and limits under scenarios of changing climate could enhance predictions of movement of disease-causing vectors into novel regions.

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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

2 # Using eco-physiological traits to understand the realized niche:
3 # the role of desiccation tolerance in Chagas disease vectors

4 **Gerardo J. de la Vega[1,2,3] · Pablo E. Schilman[1,2]**

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Introduction

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39 Finding an explanation for the distribution pattern of spe-
40 cies and understanding the factors that limit their geographic
41 range have long been central issues in ecology (Mac Arthur
42 1984). This knowledge is vital for making critical predic-
43 tions about climate change impacts on conservation, eco-
44 nomics, and human health issues (Tingley et al. 2014).
45 Species distributions are constrained by their physiological
46 tolerances expressed in their fundamental niche, the multi-
47 variate space whose axes comprise those parts of the envi-
48 ronment that influence the species' potential fitness (Hutch-
49 inson 1957). Moreover, species are further constrained to
50 their realized niche by biotic interactions (e.g., competition
51 and parasitism) and dispersal barriers. In biogeographical
52 terms, the realized niche includes not only the effects of

species interactions, but also the constraints of dispersal limitation, and the lack of contemporary environments corresponding to parts of the fundamental niche (Colwell and Rangel 2009). Understanding how species' distributions are governed by climate, and how they would react to climate change requires to investigate how species fill their potential niche, i.e., the fundamental niche in a given environment or geographic space. These concepts are used as metrics for understanding the extent to which intrinsic physiological and extrinsic abiotic constraints could explain species' distributional limits (Monahan 2009).

Temperature and desiccation are considered the most important abiotic factors for terrestrial life due to their effect on the physiology of organisms (Denny 2016). In spite of this, they cannot be easily measured along all multivariate axes from the fundamental niche. Relatively few environmental dimensions (e.g., temperature and water stress) and their physiological traits (e.g., thermal and desiccation tolerance) are also critical for the prediction of an organism's distribution under novel circumstances such as a species introduction/invasion or climate change (Kearney 2006; Araújo et al. 2013; Gouveia et al. 2014). In arid environments, insects are often at risk of desiccation given their high surface area-to-volume ratio (Edney 1977; Gibbs 2002). As a consequence, to survive, they have a highly restrictive water economy and physiological mechanisms to reduce water loss (Zachariassen 1996). There are at least three ways to modify or enhance desiccation tolerance and survival: (1) decrease water loss by reducing cuticular permeability and/or loss of water by gas exchange or excretion; (2) carry more body water (e.g., increase size); and (3) manage losing more water (lower Critical Water Content (CWC) or some combination of all of these traits changes (Benoit and Denlinger 2010; Edney 1977; Hadley 1984; Weldon et al. 2016). This desiccation resistance has a physiological cost that could be reduced by behavioral patterns (Chown and Nicolson 2004). Water balance plays an important role in determining energy budgets, activity patterns, survival, and population dynamics, henceforth, geographic distribution (Kleynhans and Terblanche 2011; Tee and Lee 2015). According to the desiccation adaptation hypothesis, the costs of desiccation resistance are balanced through its benefits, allowing the organisms to live in arid environments (Bujan et al. 2016). Insects from arid environments would have higher desiccation tolerance, which could be reflected in their distribution range limited by areas with high relative values of vapor pressure deficit (VPD) (e.g., hot and dry).

Vector-borne diseases account for more than 17% of all infectious diseases, causing more than 1 million deaths annually around the world (WHO 2002). Many of these vectors are bloodsucking insects, which ingest disease-producing microorganisms during a blood meal from an infected host (human or animal), and later inject it into a new host during their subsequent blood meal. Mosquitoes are the best known disease vector (e.g., Malaria, Dengue, Yellow fever, and Zika) (WHO 2002). Others include ticks, flies, sandflies, fleas, and triatomine bugs. Triatomines (Hemiptera: Reduviidae) are the Chagas disease vectors, one of the most important parasitemia in Americas (WHO 2002). Several studies have been carried out evaluating humidity preferences for triatomines (e.g., Roca and Lazzari 1994; Lorenzo and Lazzari 1999). The preference of *Triatoma infestans* has been evaluated in relative humidity gradients obtaining preferences to near zero percent humidity (Roca and Lazzari 1994). Another work, in trials with shelters demonstrated that they prefer low relative humidities, i.e., shelters with 20% over those with 80% RH (Lorenzo and Lazzari 1999). Due to its low rate of water loss, *Rhodnius prolixus* would be a species adapted to xeric environments (Benoit and Denlinger 2010), yet it has been proven that hatching of eggs occurs at times of day when humidity is at its maximum (Schilman et al. 2009) and that low humidity has deleterious effects on hatching success (Clark 1935; Schilman et al. 2009). This result has also been observed in other triatomines such as *Pastrongylus megistus* and *T. vitticeps* with low hatching values at low humidities (Pires et al. 2002; de Souza et al. 2010). In the latter, the authors also showed that its geographical distribution can be explained mainly by the wetter season (de Souza et al. 2010). The effect of moisture on triatomines is also observed in the vector control stages, since it has been suggested that a higher relative humidity favors control by entomopathogens (Luz et al. 2004). To understand spatial segregation or overlapped distributions of organisms, including disease vectors, species distribution models (SDM) are usually used. The distribution of a species can be modeled using either correlative models or more mechanistic approaches or a combination of both (Martin and Lefebvre 1995). The use of the physiological characteristics of a species and its tolerance limits in mechanistic models, and the correlations between the coordinates of the species and the environmental variables can generate a hybrid model with reasonable and better predictions than either a correlative or a mechanistic model alone (Buckley et al. 2010).

The main goal of this study was to explore whether incorporation of eco-physiological traits such as desiccation tolerance can improve our understanding of species distribution. To do this, we used seven species of triatomines, i.e., *Rhodnius prolixus*, *Triatoma dimidiata*, *T. infestans*, *T. vitticeps*, *T.sordida*, *T. delpontei,* and *T. patagonica*, selected according to their epidemiological relevance, distribution and phylogenetic relationship, and (hopefully) also covering a diversity of physiological strategies. These species have a different degree of epidemiological relevance in America with primary and secondary importance and a broad distribution from northern Mexico to Patagonia Argentina. In

addition, they belong to two different genera and different complexes and clades. In this way, we tried to understand how triatomines exploit their potential niche if their realized niche is closer to or further away from the fundamental niche in the dimension explored.

Materials and methods

Determining the realized niche

Using SDM, we modeled the realized niche for seven triatomines species distributed along Latin America: *Rhodnius prolixus*, *Triatoma dimidiata*, *T. infestans*, *T. vitticeps*, *T. sordida*, *T. delpontei, and T. patagonica*. Coordinates of presence used here were previously used by Fergnani et al. (2013), de la Vega et al. (2015), and de la Vega and Schilman (2017) (database can be found in: https://doi.org/10.6084/m9.figshare.5364268). The database consists of pseudo-presence from the estimated distribution range for the triatomines. We used random subsamples for our target group as an unbiased data set. A similar approach has been used in Richmond et al. (2010) and Fourcade et al. (2014). To eliminate a potential bias of clustered occurrences, the data sets were filtered, so that there was only one record per cell of 1 km^2 for each species (the same resolution as the bioclimatic variables). We used bioclimatic variables derived from the new version of WorldClim data set (http://worldclim.org/version2) to model the climate component of the realized ecological niche of each species. The new version of WorldClim data set has average monthly climate data for minimum, mean, and maximum temperatures and for precipitation for 1970–2000. The WorldClim data set also provides water vapor pressure (ea) which we used to generate a new bioclimatic variable, the maximum vapor pressure deficit from the driest month (called Bio20 from the 19 original bioclimatic variables). Although the new version of Worldclim does not have the same 19 bioclimatic variables as the previous version (http://worldclim.org/version1), we derived some of them using "raster" package (Hijmans and van Etten 2015) in R software (R Core Team 2015) [mean annual temperature (Bio1), maximum temperature of the warmest month (bio5), minimum temperature of the coldest month (bio6), and mean annual precipitation (bio12)].

Maximum vapor pressure deficit from the driest month (Bio20) was derived from water vapor pressure or actual vapor pressure (ea) and the values of saturation vapor pressure (es) to determine the vapor pressure deficit (VPD). The VPD is defined as the difference between the saturated vapor pressure (es) and the actual vapor pressure (ea) at a given temperature, briefly, the amount of water vapor lacking in the environment for the air to be saturated. A

modified formula of Mitchell et al. (2004) was used to generate the variables using the maximum temperature values (T_{max}):

$$\text{es} = 0.6107 \exp\left((17.38 \times T_{max})/239 + T_{max}\right)$$

$$\text{VPD} = \text{es} - \text{ea}.$$

Values from water vapor pressure in Kpa were converted to Torr (1 Torr ~ 0.133 kpa) for the VPD. After each month transformation, we determined the maximum vapor pressure deficit from the driest month at each grid cell.

The SDM was performed with the MaxEnt software, a correlative model that is based on the maximum-entropy approach for species habitat modeling. This program is a "niche-based model, thereby it represents an approximation of the species' realized niche, in the study area and environmental dimensions being considered" (Phillips et al. 2006). In addition, it is a modeling method that does not require points of "absences" that can generate habitat probabilities for the establishment of a species as a presence-only model (Graham and Hijmans 2006; Phillips et al. 2006). This correlative model was used with the bioclimatic variables created and selected by their ecological importance, while avoiding multi-collinearity across them, to determine the realized niche. The approach used was to calculate variance inflation factor (VIF), which estimates how much the variance of a regression coefficient is inflated due to multi-collinearity in the model, for all predictors and exclude the ones with VIF > 10 (Zuur et al. 2010). We used the default configuration of maxent function of the "dismo" package in the R software (Hijmans et al. 2015). We used tenfold cross-validation run type to select the average response of these ten replicates. In addition, we selected the Jackknife procedure to quantify the contribution of each bioclimatic variable for each model. In addition, we performed a MESS analysis (multivariate environmental similarity surface) and the limiting factor mapping technique to determine, which and where are the limiting factors that affect the distribution boundary of the species (Elith et al. 2010; Hill et al. 2012). This method generates a map, where, in each grid cell, each predictor variable is replaced by its mean value over the species' occurrences; if a change results in a greater probability of habitat favorable to the establishment of the species, the changed variable is considered as the limiting factor (see Elith et al. 2010; Hill et al. 2012 for more details).

The realized niche for each triatomine was defined by applying a threshold to transform modeled probabilities of occurrence (or indices of suitability) into binary predictions of species presence and absence. There are potentially many rules for setting thresholds (Nenzén and

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Araújo 2011); we selected the maximize sum of sensitivity and specificity thresholds as a method to avoid fixed threshold (Svenning et al. 2008), which has been shown to produce accurate predictions (Jiménez-Valverde and Lobo 2007).

Determining desiccation tolerance

To determine how these triatomines species could live in arid or xeric environments, we measured their desiccation resistance. For all assays, we used unfed 1 week fifth-instar nymphs of the seven species: *Rhodnius prolixus*, *Triatoma dimidiata*, *T. infestans*, *T. vitticeps*, *T. sordida*, *T. delpontei, and T. patagonica*. Insects were reared at 28 °C under a 12:12 light/dark photoperiod (light on 08:00 am). In another haematophagous insect and disease vector, the tsetse fly *Glossina* sp., a positive correlation was found between a water balance trait and climate, but only in pupae, not in the other stages (Kleynhans and Terblanche 2009). Differing from *Glossina* sp., triatomines are hemimetabolous insects, i.e., they develop through gradual changes with no pupal stage. Triatomine´s nymphs often resemble the adult stage with similar shape, and both are obligatory haematophagous, yet lacking wings and functional reproductive organs, and they live and complete their life cycle in the same shelter. Thus, we assume that inter-specific differences on tolerance to desiccation will be more significant than intra-specific differences, i.e., across stages, for limiting the species distribution. Variations of water content for hematophagous insects such as triatomines depend on the reproductive capacity (mature/immature stages) and starvation (Benoit and Denlinger 2010). Insects that do not ingest free water increase water content only when ingesting blood; thereafter, they have two stages of diuresis, one with a rapid water loss and a slower one (Benoit and Denlinger 2010). Therefore, using unfed 1 week fifth-instar insects, we assume a stable stage in the water-loss dynamics, mainly loosing water through the cuticula, and by gas exchange, but not by excretion or diuresis.

Survival and desiccation resistance of a species depends not only in its water-loss rate, but also on the amount of water that can be lost without adverse effects. Thus, in the present study, we measured and performed a detailed analysis of the water relations, i.e., total (TWC) and critical water content (CWC; the amount of water remaining when the insect becomes moribund), as well as water-loss rates (WLR), gross cuticular permeability (GCP) and survival times (ST) were also estimated for the seven species of triatomines. The TWC and CWC were determined by a gravimetric method. The WLR is the water loss through the cuticle plus the loss through the spiracles when the insect exchanges gases. All masses were measured to the nearest 0.1 mg using an analytical balance (AJ100; Mettler Toledo, Columbus, OH, USA).

Each individual was weighed prior to placing them into experimental containers (5 cm high × 2.5 cm diameter with perforated sides to allow air circulation) (live mass). Each experimental container was placed inside the drying chamber, where an airflow (ca. 50 ml min⁻¹) was passed through tubes containing Drierite to dehydrate the air before entering an experimental chamber and then exiting through the opposite end. This made possible to maintain a low relative humidity (RH) in the environment inside the dehydration chamber (RH ~ 15%). The dehydration chamber was placed in a temperature-controlled cabinet at 35 °C.

Insects were daily checked and those unable to right themselves after being overturned and perturbed were defined as moribund, and were weighed again (moribund mass), and finally after drying them at least 72 h, or to constant mass at 60 °C (dry mass) (Schilman et al. 2007). The mass loss rate was considered equivalent to water-loss rate (Edney 1977; Schilman et al. 2007). Mass loss (mg) was calculated by subtracting live mass (mg) from moribund mass (mg). Water-loss rate (in mg h⁻¹) was calculated by dividing mass loss (mg) by the time until the insect had the moribund mass measurements. The total and critical water content were expressed as a percentage of live body mass:

$$\text{TWC}\,(\%) = ((\text{LM} - \text{DM}) \times 100)/\text{LM},$$

where TWC (%) is the total water content expressed as a percentage of live body mass, LM is live mass (mg), and DM is dry mass (mg):

$$\text{CWC}\,(\%) = ((\text{MM} - \text{DM}) \times 100)/\text{LM},$$

where CWC (%) is the critical water content expressed as a percentage of live body mass, MM is moribund mass (mg), and DM is dry mass (mg). In addition, the survival time (ST) was the time (in days) until reaching the critical water content. This could be a useful measure of desiccation tolerance which directly relates to disease vectors through biting frequency and thus disease transmission probability (Kleynhans and Terblanche 2011; Rolandi and Schilman 2012). Gross Cuticular Permeability (GCP) (cuticular and respiratory water loss combined) was calculated by dividing total water-loss rate (mg h⁻¹) by the estimated surface area of the triatomine (cm²) and the water pressure saturation deficit (Torr). This calculation yields gross cuticular permeability in the classic units of μg cm⁻² h⁻¹ Torr⁻¹. The surface area of each triatomine was estimated using the equation proposed for *R. prolixus* by Rolandi et al. (2014)

$$S = 146.36 + 3.01 \times 10^{-3} \times \text{LM}^2,$$

where S measured in cm², and LM is the live mass of the insect (mg). The water vapor pressure deficit at 35 °C and 15% RH is ≈ 35.8 Torr.

Understanding the desiccation dimension of the realized niche with the desiccation tolerance

The simple ecological hypothesis proposed is that insect species would have high suitability values in areas, where the water vapor pressure deficit is low. That is, species with high critical water content would be limited by areas with high values of water vapor pressure deficit (e.g., hot and dry). The variable BIO 20 was selected to evaluate the realized niche with a physiological analysis. Values of BIO 20 were taken from 1000 randomly coordinates in the realized niche and related to the survival time (ST). Since BIO 20, units are Torr and ST days, the following procedure and handling with the raster package of the software R (R Core Team 2015) was performed:

$$WLR_{ij} = Bio20_{ij} \times GCP_s \times S_s,$$

$$ST_{ij} = (LM_s - MM_s)/WLR_{ij}.$$

From gross cuticular permeability (GCP_s) formula, a hypothetical water-loss rate of each grid cell ij was first obtained (WLR_{ij}): the maximum water vapor pressure deficit from the driest month ($Bio20_{ij}$) was multiplied by the surface (S_s) and the gross cuticular permeability (GCP_s) of species ($_s$). Then, the critical time for each cell ij was determined from the amount of water that the species can lose until moribund [live mass (LM) − moribund mass (MM)] divided by the water-loss rate of the cell ij (WLR_{ij}). The value of ST_{ij} will determine grid cells with different times until reaching the moribund mass relative to each species. According to the ecological hypothesis, we expect higher ST_{ij} in the realized niche than ST obtained in the laboratory.

After determining the temperature and humidity relationship by the water vapor pressure deficit (Bio 20) dimension of the realized niche and if desiccation tolerance could explain it, we also determined if there was a geographical pattern (latitudinal middle point of their realized niche) for parameters related to desiccation (WLR, GCP, CWC, and ST). In turn, regressions were done between the tolerance variables and the water vapor pressure deficit (Bio 20). It is also important to know how different are the extreme values in the realized niche, as well as the desiccation tolerance, allowing us to understand how these triatomines species exploit the humidity dimension of the fundamental niche. These ecological and geographical patterns would allow us to provide a novel contribution to the macroecological patterns, and also improve the understanding of the distributions and boundaries of the vectors in the continent.

To observe if the desiccation tolerances depend on the adaptations of the species to drier regions independent of their phylogenetic relationships, phylogenetic independent contrast (PICs) were performed (Felsenstein 1985). When a new ecological niche is available, species occupying a similar niche are the best candidates to invade the new niche. As a consequence, nearby species would be phenotypically similar to those which are occupied by equivalent niches for historical reasons, and are, therefore, subject to similar selective pressures (Felsenstein 1985; Losos 2008). Because inter-specific comparisons involve taking into account the phylogenetic relationship of the species (Felsenstein 1985), the relationship between physiological tolerances and the geographic or ecological gradient was evaluated with two types of analysis. A (non-realistic) analysis was performed assuming a "star"-type phylogeny, where all species diverge at the same time, and another analysis that included the most likely phylogenetic relationship of the used species. Phylogenetic independent contrasts were performed using the topology of the phylogenetic tree and the length of its branches. The phylogenetic tree was constructed using the maximum-likelihood method from aligned sequences of the 16S rDNA fragment for the seven species obtained from Hypsa et al. (2002) and the root was forced in the protruding node of *R. prolixus* with the package "caper" (Orme 2013) of R (R Core Team 2015).

The assumptions of normality and homogeneity of variance were evaluated for all analyses by graphical inspection of residuals and with the Shapiro–Wilk and Levene tests. When the assumptions were not satisfied, the generalized models (GLS) with *varIdent* function of the package "nlme" (Pinheiro et al. 2014) of R (R Core Team 2015) were used, to include the heteroscedasticity in the statistical model. The tables show the means with the standard deviation that were compared with an ANOVA test. The overall error was corrected by Bonferroni correction (seven analysis variables: $p < 0.007$).

Results

The realized niche and the dryness dimension

After pre-processing the variables, mean annual temperature (Bio 1) was excluded from all species models and maximum temperature from the warmest month (Bio5) for *T. patagonica* and *T. dimidiata* models because of their high VIF value. The goodness of fit of MaxEnt predictions was high showing an optimal performance (mean AUC values are summarized in Table 1). The minimum temperature of the coldest month (Bio6) appeared as the primary variable explaining the realized niche of these seven triatomines (Table 1). The relative contribution of minimum temperature of the coldest month for each insect was always more than 50% vs. less than 30% for the remaining variables. In addition, the importance of minimum temperature of the coldest month in each model

Table 1 Relative contribution for bioclimatic variables to the Maxent model for seven species of triatomine bugs

Bioclimatic variable	R. prolixus	T. vitticeps	T. delpontei	T. dimidiata	T. patagonica	T. sordida	T. infestans
Bio5 = max temperature of warmest month	6.8 (17.6)	8.6 (3.9)	2 (7.8)	–	–	1.3 (6.7)	10.8 (15.5)
Bio6 = min temperature of coldest month	73.3 (67.7)	56.4 (45.6)	48.1 (52)	72 (58.3)	45.9 (59.4)	50 (44.7)	60.6 (57.1)
Bio12 = annual precipitation	13.6 (6.3)	22.5 (8.1)	11 (35.9)	17.3 (17.5)	32 (18.7)	25.3 (18.2)	15.6 (18.8)
Bio20 = max vapor pressure deficit of driest month	6.4 (8.4)	12.5 (42.5)	38.9 (4.3)	10.7 (24.2)	22.1 (21.9)	23.3 (30.4)	13 (8.6)
AUC value (mean ± SD)	0.82 ± 0.01	0.96 ± 0.01	0.94 ± 0.03	0.71 ± 0.03	0.92 ± 0.01	0.82 ± 0.02	0.80 ± 0.01

Between parentheses is the relative contribution to the model but reevaluated by a permutation analysis. Area under the receiver operating characteristic curve (AUC) mean and standard deviation values are also shown

Bio1 Mean annual temperature, excluded in pre-processing analysis (VIF > 100), *Bio5* Max. Temperature of Warmest Month excluded in successive pre-processing analysis for *T. dimidiata* and *T. patagonica* models (VIF > 10)

is shown in the jackknife test (Online Resource 1). The suitability areas for the distribution of these triatomines are mapped in Fig. 1a. Such distributions seem to be more limited by the effect of the minimum temperature of the coldest month as shown in the limiting factors maps (green color in Fig. 1b). The dryness dimension of the realized niche, expressed as the maximum VPD from the driest month (Bio 20), seems to clearly constrain the distribution of *T. vitticeps*, and affects the western and southern distributions of *T. delpontei* and *T. patagonica* (yellow color in Fig. 1b). The response curves for Bio 20 show that the realized niche (black dotted line determines the realized niche threshold) for *T. dimidiata*, *T. sordida*, *T. delpontei,* and *T. infestans* models seems to show a higher probability of their presence in arid environments (VPD > 30 Torr) (Fig. 2).

The desiccation tolerance for triatomines

The results showed differences across species in their mass ($F_{6, 116} = 137.53$, $p < 0.0001$), ranging from 25 to 150 mg with low intra-specific mass variation. Although, total water content (TWC) was between 70 and 75% of the mass for all triatomines analyzed, the *posteriori* test revealed that there were no differences between *R. prolixus*, *T. infestans,* and *T. delpontei*, and neither between *T. dimidiata*, *T. sordida,* and *T. vitticeps* ($F_{6, 116} = 11.30$, $p < 0.0001$; Table 2). However, for critical water content (CWC), most species analyzed showed a range between 25 and 32% of their live mass except *T. dimidiata* which had a significantly higher CWC than the other species (48%) ($F_{6, 116} = 23.22$, $p < 0.0001$; Table 2). This value of CWC is also reflected in its shorter survival time (9 days), i.e., time to reach a critical state, lower than other species which had values between 24 and 38 days of survival ($F_{6, 116} = 56.76$, $p < 0.0001$; Table 2). Other parameters for assessing the desiccation tolerances, Water-Loss Rate (WLR) and Gross Cuticular Permeability (GCP), revealed that there were significant differences across species with higher values for *T. vitticeps* and *T. dimidiata* compared with the other species (Table 2)

(WLR: $F_{6, 116} = 57.83$, $p < 0.0001$; GCP: $F_{6, 116} = 45.66$, $p < 0.0001$).

Understanding the desiccation dimension of the realized niche with the desiccation tolerance

The ecological hypothesis here implies that species with high desiccation tolerance would be limited by areas with high relative values of water vapor pressure deficit (e.g., hot and dry). As explained in the methods section, we linked the extreme values of ambient dryness (Bio 20) with the physiological parameters (GCP, WLR, and S). Our results demonstrate that the realized niche for these triatomines species reaches zones close to the limits of their tolerances. As expected, no species inhabited regions with deleterious values of maximum VPD in the driest month (Fig. 3); they all have realized niche point values higher than their ST. On one hand, the realized niche of *T. dimidiata* is near the limits of its estimated ST or the time to reach the CWC (Fig. 3). In ecological terms, this seems to show that the realized niche is near (or tends towards) the limits of their fundamental niche expressed by the desiccation tolerance limits. On the other hand, *T. vitticeps* seem to show a higher potential niche, because the realized niche seems to be far from its desiccation tolerance limits. As depicted in Fig. 3, as a novel eco-physiological approach for insects, the realized niche for these bugs could be expanded the dryness dimension to their fundamental niche limits. The horizontal dashed line shows the limits of the fundamental niche, and most of the triatomines´ realized niches (grey line) are close to it.

We tested if desiccation tolerances depend on the adaptations to xeric environments for these species performing regression analysis with and without excluding the phylogenetic effects. We expected under the desiccation adaptation hypothesis an inverse relationship between physiological parameters and the mean value of Bio 20 for the realized niches. However, there was not a significant relationship between any of the desiccation tolerance parameters (GCP, WLR, CWC, and ST) and the mean Bio 20 value for the
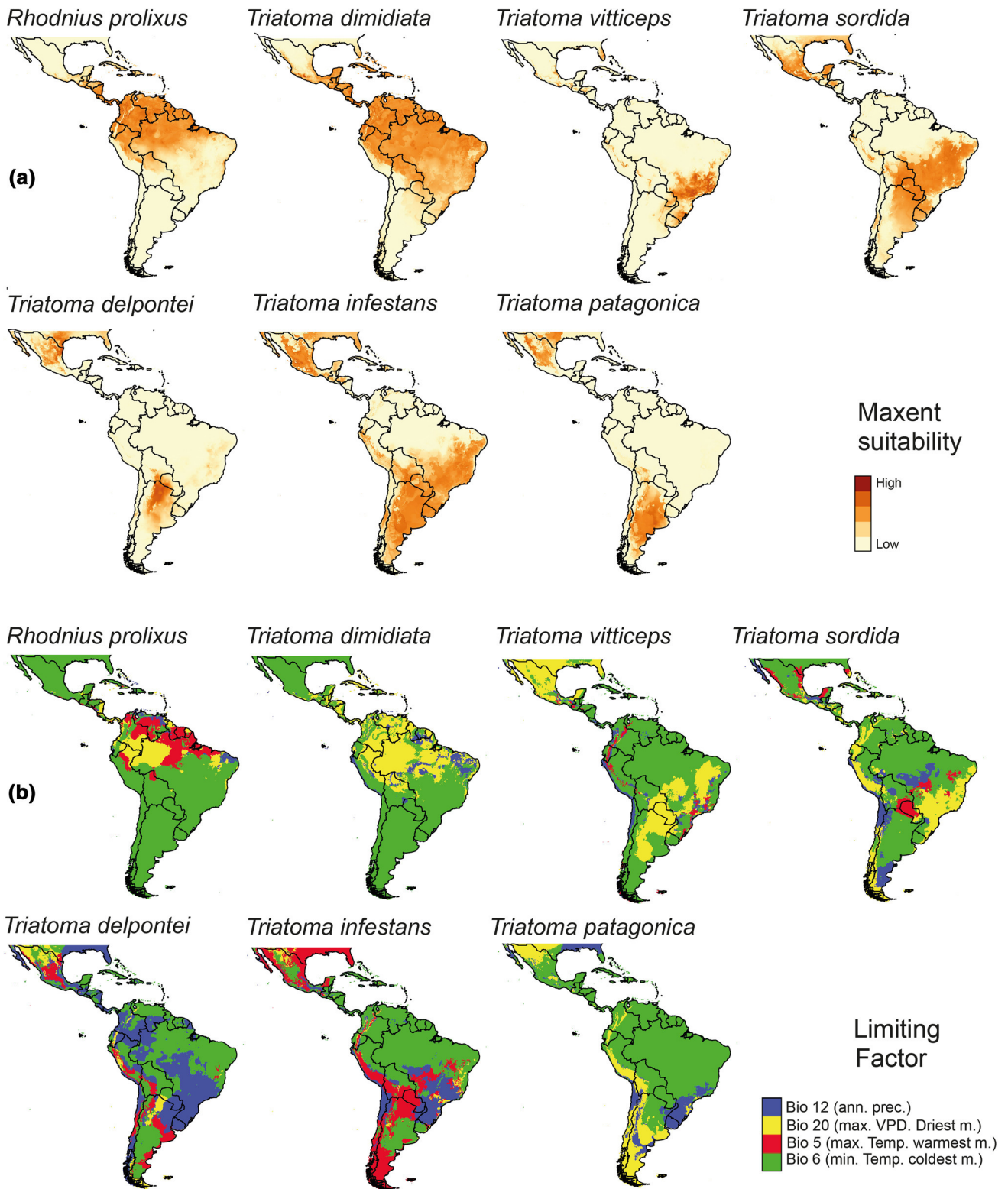
Fig. 1 Realized niche modeled by species distribution models (maxent) for seven triatomines and their limiting factor map. **a** Habitat suitability maps resulting from Maxent distribution modeling. **b** Limiting factor maps (relationship between each model performance and the predictor variables at each pixel; for details, see Elith et al. 2010 and Hill et al. 2012). *Bio5* max temperature of warmest month, *Bio6* min temperature of coldest month, *Bio12* annual precipitation, *Bio20* max vapor pressure deficit of driest month
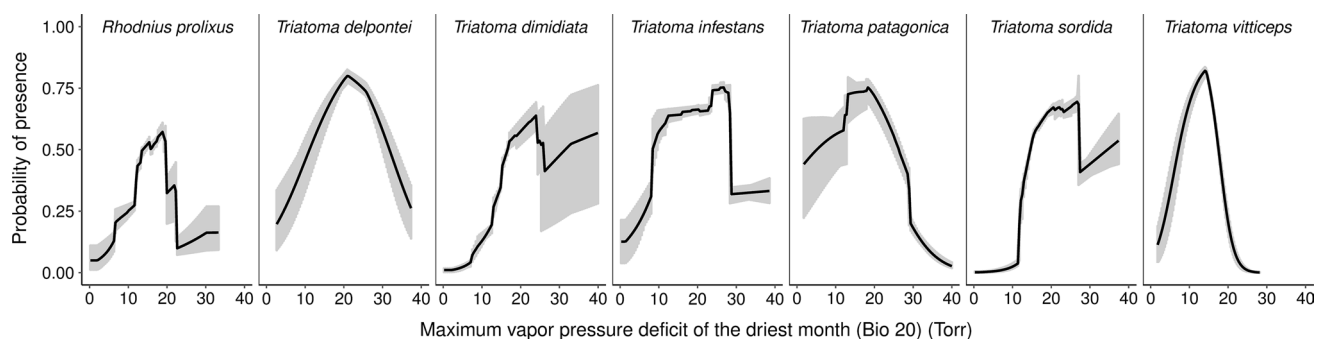
Fig. 2 Marginal response curves show how suitability changes as a function of variations in the Bio 20 (the maximum vapor pressure deficit of the driest month), and all other bioclimatic variables were at their mean sample value. Grey lines represent the ten replicates. Black dashed line represents the probability threshold to determine the realized niche

Table 2 Desiccation tolerance parameters for seven triatomines

	R. prolixus	T. vitticeps	T. delpontei	T. dimidiata	T. patagonica	T. sordida	T. infestans
Live mass (mg)	26.21 ± 6.02 a	146.42 ± 36.89 c	98.99 ± 15.01 b	123.03 ± 26.60 bc	41.33 ± 10.07 e	26.91 ± 6.46 a	76.08 ± 16.23 d
Moribund mass (mg)	13.77 ± 3.05	89.78 ± 25.57	55.10 ± 7.15	99.88 ± 23.01	22.17 ± 6.38	14.90 ± 3.55	42.99 ± 10.36
Dry mass (mg)	6.4 ± 1.4	46.53 ± 16.47	24.02 ± 4.96	41.70 ± 14.40	11.23 ± 3.21	8.08 ± 1.88	18.86 ± 6.47
Water-loss rate ($\mu g\ h^{-1}$)	23.68 ± 6.27 a	86.12 ± 28.41 b	52.38 ± 16.43 c	112.97 ± 38.05 b	22.71 ± 7.85 a	18.73 ± 4.49 a	46.49 ± 10.35 c
TWC (%)	75.05 ± 3.75 a	68.72 ± 5.69 bc	75.75 ± 3.30 a	66.96 ± 5.43 c	72.81 ± 4.21 ab	69.72 ± 3.55 bc	75.74 ± 3.86 A
CWC (%)	28.30 ± 6.71 a	30.22 ± 7.67 a	31.72 ± 5.02 a	48.07 ± 6.86 b	27.05 ± 9.03 a	25.42 ± 4.66 a	32.14 ± 4.10 A
ST (days)	23.75 ± 8.65 a	29.52 ± 12.58 ab	37.23 ± 10.51 b	9.17 ± 3.11 c	37.79 ± 16.02 ab	26.56 ± 16.02 ab	29.93 ± 6.40 ab
GCP ($\mu g\ h^{-1}$ $cm^{-2}\ Torr^{-1}$)	0.37 ± 0.1 a	0.97 ± 0.35 cd	0.70 ± 0.21 bd	1.37 ± 0.44 c	0.35 ± 0.12 a	0.30 ± 0.07 a	0.67 ± 0.14 b

Comparison of live body mass, total water content (TWC), critical water content (CWC), rate of water loss (WLR), gross cuticular permeability with area-independent rate of water loss ($\mu g\ h^{-1}\ cm^{-2}\ Torr^{-1}$), and time to reach critical water content or estimated survival time (ST)

Different letters show significant differences under Bonferroni correction ($p < 0.007$). Mean values are shown with standard deviation
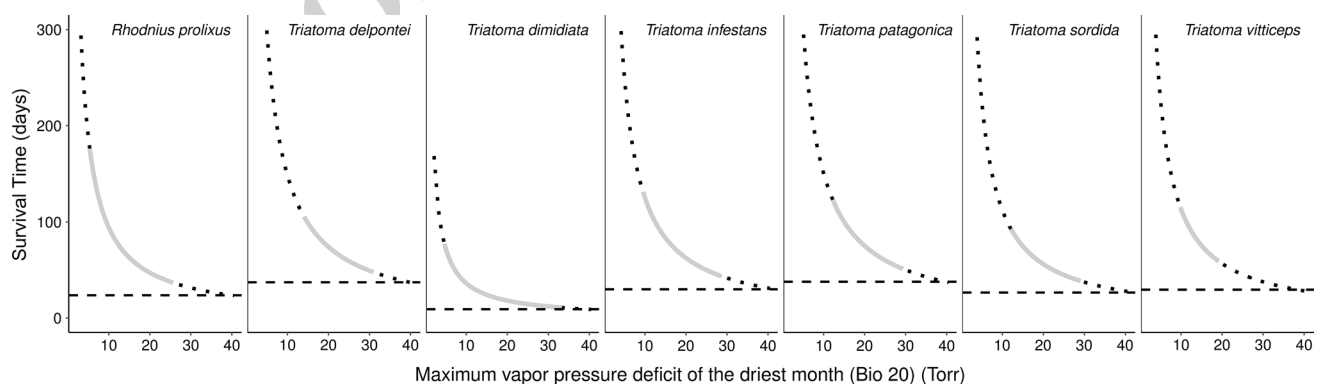

Fig. 3 Understanding the dryness dimension of the realized niche with the desiccation tolerance from seven triatomines. Plots show for each triatomines species the variation of the Time to reach to Critical Water Content (ST in days) by changing in the Maximum Vapor Pressure Deficit—an expression of the dryness of the realized niche- (Bio 20 in Torr units). See method for the variable transformation that linked Bio 20 to the time until reaching the moribund state. The black dashed line represents the experimental value of ST for each species. In addition, black dotted line represents the ST values for 1000 randomly coordinates outside the realized niche and black line represents the values inside the Realized Niche for each species

realized niche; neither in a more realistic analysis including the phylogenetic relation between species (Online Resource 2).

Discussion

Our study links the biogeographical level using a correlative model (SDM) with the physiological level measuring tolerance to desiccation in seven species of Triatominae, including the main vectors of Chagas disease. This approach is critical for predicting the future distributions of species, which is particularly worthy for epidemiological or medically important vectors, whose distribution may shift with a changing climate in the southern hemisphere. This also represents the first attempt to link the dryness dimension of the realized niche and physiological limitations such as desiccation tolerance for Chagas disease vectors. This eco-physiological approach using SDM and desiccation tolerance assays allows us to understand how they are exploiting their niche, and test the desiccation adaptation hypothesis, which could explain the distribution of these Chagas disease vectors.

The realized niche and its dryness dimension

The desiccation dimension of the realized niche for triatomines seems to extend to areas with high dryness (*T. infestans*, *T. delpontei*, *T. dimidiata,* and *T. sordida*), although for a few species (*R. prolixus* and *T. vitticeps*), xeric environments seem to limit the geographical distribution of their realized niche (Figs. 1, 2). The limiting factors maps can explain the regions, where the models predict a low probability of presence (Fig. 1b). In the Andean region, we can see the greatest effect of two variables, i.e., minimum temperature of the coldest month (Bio 6) and maximum water vapor pressure deficit for the driest month (Bio 20). The effect of low temperature due to altitude would be consistent with the effect of critical temperatures on insects as a physiological limit in their distribution (Carcavallo et al. 1999; de la Vega et al. 2015; de la Vega and Schilman 2017). The effect of the maximum water vapor pressure deficit can be clearly observed in *T. vitticeps*, *T. delpontei,* and *T. patagonica* to the west and south of their distributions. Although this variable does not have the greatest effect on the distribution model, it could be constraining their limits. In addition, the effect of maximum water vapor pressure deficit for the driest month (Bio 20) can be understood for *T. vitticeps* as a limiting factor towards the north of its distribution, where the Brazilian Catinga begins. This species is distributed from the Atlantic Forest to Cerrado biomes (Gurgel-Gonçalves et al. 2012), and the main abiotic factors that could explain its distribution are the mean annual precipitation and the

precipitation of the warmest quarter (De Souza et al. 2010). In addition, the SDM that determines the realized niche for these seven triatomines used the effect of cold temperatures to explain the distribution of species, as was previously shown by de la Vega and Schilman (2017). The richness of triatomines species could be mainly explained by environmental variables related to temperature and water-energy balance (Diniz-Filho et al. 2013). **AQ11**

The desiccation tolerance for triatomines

There were large differences between live mass for this triatomine bugs, ranging from 26 to 146 mg with low intraspecific mass variation, although total water content (TWC) was between 67 and 76% of their mass (Table 1). This result agrees with Hadley (1984), where the TWC of the arthropods ranges between 65 and 75% of their mass. Some physiological features may be modified by laboratory conditions, such as insect mass, although it is suggested that tolerance to water loss would not be influenced by lab conditions (Chown et al. 2011; Lyons et al. 2012). The high tolerance to desiccation is observed in the amount of water lost and the rate at which water was lost. The survival times (ST) for the different species were between 24 and 38 days, except for *T. dimidiata* that was significantly shorter (9 days). The difference could be explained in part due to a lower percentage of water that can be lost, or higher CWC (near 50% of the live mass) compared with 25–30% for the other species and for the higher WLR and GCP. In terms of rate of water lost (WLR), Benoit and Denlinger (2010) compare **AQ14** the WLR across different species of hematophagous females (expressed as percentage of weight loss per hour), and determined that hemipterans are fairly resistant to dehydration, with WLR lower than 0.8% h^{-1}. We also measured very low values of WLR, lower than 0.25% h^{-1} (between 0.03 and 0.21% h^{-1}), showing a greater resistance compared to other species. Female hematophagous arthropods from xeric or arid habitats are more resistant to desiccation than species from mesic or hygric regions (Benoit and Denlinger 2010). **AQ12 AQ13**

The CWC is also reflected in the number of days that the insects survived in the experiments (ST) and greater CWC determined a shorter ST ($F_{1, 121} = 48.18$, $p < 0.0001$, $R^2 = 0.28$). However, there is no linear relationship between the insect mass and ST ($F_{1, 121} = 0.003$, $p = 0.95$, $R^2 = 0.001$) as the larger size is a simple strategy for desiccation tolerance (Benoit and Denlinger 2010). However, there are other strategies for drying tolerance, a low WLR, or a low gross cuticular permeability (GCP) (Hadley 1984). *T. vitticeps* and *T. dimidiata* were the species with higher values of WLR and GCP (86–112 µg h^{-1} and 1–1.3 µg h^{-1} cm^{-2} $Torr^{-1}$), although these values are lower than other insects from mesic zones (Edney 1977; Hadley 1984). In triatomines, these parameters had only been measured in *R.*

prolixus males (Rolandi et al. 2014) and in fifth-instar (Wigglesworth 1945). The latter study was carried out measuring the percentage of weight lost in 24 h at 30 °C of fed nymphs reaching a GCP of 1.68 µg h^{-1} cm^{-1} Torr^{-1} with a mass of 146 mg (Wigglesworth 1945). Beyond the methodology, our results differ from the latter by the rapid increases in mass following a blood meal in *R. prolixus* nymphs (Coast 2009) (we work with a week old unfed 5th instar nymphs, mass = 26.21, GCP = 0.37 µg h^{-1} cm^{-1} Torr^{-1}). In addition, this variability can also be affected by other factors such as using flowing or static air during desiccation (Jurenka et al. 2007, or compare results found in Schilman et al. 2005 and 2007), acclimatization (Gibbs 2002), starvation (Rolandi et al. 2014), temperature and humidity (Kleynhans and Terblanche 2011), or insect sexual maturity (Benoit and Denlinger 2010).

Understanding the desiccation dimension of the realized niche with the desiccation tolerance

The ecological hypothesis here implies that the realized niche of desiccation sensitive species is limited to moist environments, i.e., with low VPD, while more desiccation resistant species could occupy more xeric environments, i.e., with high VPD. Under an assumption of no biotic interactions, the realized niche of the species would be expressed by the desiccation tolerance limits filling the fundamental niche. Most of the species tested had similar days of survival (ST) and CWC percentages (except for *T. dimidiata*), and their realized niche is in areas with medium-to-high values of dryness (Bio 20). These triatomines had lower CP and CWC than other species from more humid environments (Hadley 1984; Klok and Chown 1997), which allow them to survive many days (ST) under arid conditions, and few of them are considered from xeric ambient (Benoit and Denlinger 2010). As demonstrated in the results, these triatomines could have been full expanded their realized niche in the dryness dimension of the fundamental niche. In addition, *T. vitticeps* could be under-exploiting the desiccation dimension of the environment, and could expand its realized niche into drier areas. On the other hand, *T. dimidiata* inhabits areas where the dryness dimension of the environment could be constraining its realized niche. The preference of *T. infestans* for RH has been tested in the laboratory and under semi-natural conditions (Roca and Lazzari 1994; Lorenzo and Lazzari 1999), which could explain the high suitability for areas with high water vapor pressure deficits. In addition, the challenge of getting rid of excess water by diuresis after feeding by hematophagous insects could be enhanced in a dryer environment (Benoit and Denlinger 2010). Furthermore, higher temperature and lower relative humidity are climatic factors that decrease the development time from egg to adult of Chagas disease vectors, promoting a higher population density. Warm temperatures also speed up biochemical reactions, yielding a rise in activity, and growth rates, which in turn bring an increase in metabolic rate and nutrient transformation rate. As a consequence, it could be expected an increase on the frequency of biting with the concomitant boost in the transmission of infectious diseases (Rolandi and Schilman 2012) and an expansion of the geographic distribution (Curto et al. 1994; Carcavallo et al. 1999). Although our regression analysis did not show **AQ15** any relationship between the desiccation parameters tested and the dryness dimension for these triatomines, higher hierarchical levels including humid environment distributions could be taken into account to show any adaptations to xeric environments in triatomines. In addition, physiological adaptations to dry conditions could not be reflected as behavioral adaptations, such as changing microhabits in humid regions during the hottest time of the day (Lapinski and Tschapka 2014).

Desiccation resistance may also be constrained by other adaptations to warm habitats, such as thermo-tolerances, measured as critical thermal maximum (CT_{max}) (Bujan et al. 2016). Moreover, as temperature and VPD are often positively correlated, the same traits that favor desiccation resistance may also favor thermal tolerance. Variations in the geographic scale of the niche due to changing environmental conditions caused by climate change depend on species-specific traits. It has been predicted that there will be an increase in the frequency and severity of droughts due to global warming (IPCC 2014). Desiccation and temperature are two (related) primary environmental stressors that limit species distributions and could affect their niche in three ways: (1) reduce the niche size of species sensitive to both stressors along both axes (e.g., high CP and CWC, and low CT_{max}); (2) reduce the niche size along a single axis in species that are sensitive to just one of the two stressors (e.g., temperature, low CT_{max}, ULT); and (3) elicit negligible changes to the niche of species tolerant to both desiccation and temperature (very low CP and CWC, and high CT_{max}) (Bulleri et al. 2016). These traitomines bugs have shown upper critical thermal limits (CT_{max}) much higher than the maximum temperature of the warmest month that will not be affected by an increasing temperature of few degrees (Belliard 2015; de la Vega et al. 2015; de la Vega and Schilman 2017). In addition, the peri-domiciles some of these triatomines species inhabit do not buffer the environmental temperature changes or changes in humidity as well as at domiciles (Balsalobre 2016). Therefore, it would be expected that future realized niches and distributions of some of these triatomines could be constrained by their desiccation tolerance as the limits of the fundamental niche. However, this conclusion cannot be generalized to domiciliated species, which are usually the most important vectors (e.g., *T. infestans*); therefore, policy makers could be at high

risk of taking wrong decisions with their consequences to health issues.

Author contribution statement Conceived the idea and designed the experiments: PES and GJdlV. Experimental assay: GJdlV and PES. Data analysis: GJdlV. Led the writing of the manuscript: GJdlV. Contributed reagents/materials: PES.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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Dear Author

During the process of typesetting your article, the following queries have arisen. Please check your typeset proof carefully against the queries listed below and mark the necessary changes either directly on the proof/online grid or in the 'Author's response' area provided below

Query	Details Required	Author's Response
AQ1	Please confirm whether the change made in the title is OK.	
AQ2	Please check and confirm that the authors and their respective affiliations (Aff1, Aff2) have been correctly identified and amend if necessary.	
AQ3	Please confirm the inserted city name is correct and amend if necessary.	
AQ4	Colwell and Range, 2009 has been changed to Colwell and Rangel 2009 so that this citation matches the list.	
AQ5	WHO 2015 has been changed to WHO 2002 so that this citation matches the list.	
AQ6	Pires 2002 has been changed to Pires et al. 2002 so that this citation matches the list.	
AQ7	Martin and Lefevre, 1995 has been changed to Martin and Lefebvre 1995 so that this citation matches the list.	
AQ8	Zuur et al. 2009 has been changed to Zuur et al. 2010 so that this citation matches the list.	
AQ9	Felsentein 1985 has been changed to Felsenstein 1985 so that this citation matches the list.	
AQ10	Reference: Reference (Clark 1935, Luz et al. 2004, Losos 2008, Curto et al. 1994, Hypsa et al. 2002) was mentioned in the manuscript; however, this was not included in the reference list. As a rule, all mentioned references should be present in the reference list. Please provide the reference details to be inserted in the reference list.	
AQ11	Dinz-Filho et al. 2013 has been changed to Diniz-Filho et al. 2013 so that this citation matches the list.	
AQ12	Hadley (1994) has been changed to Hadley (1984) so that this citation matches the list.	
AQ13	Lyons et al. 2014 has been changed to Lyons et al. 2012 so that this citation matches the list.	
AQ14	Benoit and Delinger (2010) has been changed to Benoit and Denlinger (2010) so that this citation matches the list.	
AQ15	Carcavallo et al. 1998 has been changed to Carcavallo et al. 1999 so that this citation matches the list.	
AQ16	The following references are not cited in text: Chown (2001), Li et al. (2015).	
AQ17	Kindly check and provide page numbers for the reference Orme (2013), Pinheiro et al. (2014), WHO Expert Committee World Health Organization (2002).	