RESEARCH PAPER

Phylogenetic structure of geographical co-occurrence among New World Triatominae species, vectors of Chagas disease

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Abstract

Aim: The tropical niche conservatism (TNC) hypothesis is one of the most prominent evolutionary hypotheses that has been supported as an explanation for the diversity gradients of several animal taxa, mainly vertebrates. However, the validity of TNC for less-known taxa such as disease vectors is not clear. Here, we test predictions of TNC in driving the geographical co-occurrence among triatomine species, vector insects of Chagas disease. We aim to infer the relative effects of ecological and evolutionary processes in determining triatomine species richness at broad spatial scales.

Location: America.

Taxon: Triatominae (Hemiptera: Reduviidae).

Methods: We gathered distributional, phylogenetic and climatic information for 63 triatomine species. We apply the phylogenetic field (PF) framework based on the phylogenetic structure of species co-occurrences, considering their climatic preferences. We defined PFs of species by estimating the phylogenetic structure of species co-occurrence within a focal species' range. Likewise, climatic conditions within focal species' ranges were defined as their preferred climates. We applied a spatial-phylogenetic statistical framework to evaluate geographical variation of species' co-occurrence and tested the significance of PFs based on biogeographically informed null models.

Results: Phylogenetic fields of 17 out of 59 triatomine species showed a trend from overdispersed to clustered, coincident with tropical to subtropical–temperate climate. Triatomines co-occur with more closely related species in temperate areas and more distantly related species in tropical areas. Temperature seasonality was inversely related to the phylogenetic structure of co-occurrence within species ranges.

Main conclusions: Geographical co-occurrence among triatomine species revealed a tropical to subtropical–temperate gradient from overdispersed to clustered PFs and a correspondence between the type of climate in which these species are found and their PFs. Phylogenetic structure within triatomine ranges is explained by their evolutionary history. Our study provides a methodological framework to evaluate the New World triatomine geographical co-occurrence patterns under a phylogenetic

perspective and our results make an important contribution to the understanding of the broad-scale biodiversity patterns in Triatominae.

KEYWORDS

biodiversity, Chagas, geographical co-occurrence, historical processes, macroecology, niche conservatism, phylogenetic structure, Triatominae

1 | INTRODUCTION

Determining the causes behind the latitudinal diversity gradient (LDG), the tendency of species richness to increase from the poles to the tropics, is a fundamental goal of ecology and biogeography. Despite being the oldest and most ubiquitous diversity pattern (Hawkins & Porter, 2001), we still lack an overarching explanation for its origin and maintenance, with dozens of hypotheses having been proposed thus far (Fine, 2015). Nevertheless, these hypotheses can be broadly categorized into ecological and evolutionary hypotheses, of which the latter have gained more support recently (Fine, 2015; Mittelbach et al., 2007). Among the evolutionary explanations for the LDG, the Tropical Niche Conservatism (TNC) hypothesis—the tendency of species to retain their ancestral (tropical) climatic niches (Wiens & Donoghue, 2004)—has received ample support in the last decade or so (Buckley et al., 2010; Morales-Castilla, Davies, & Rodríguez, 2019). The TNC hypothesis predicts higher species richness in tropical compared to temperate environments, owing to the longer time that tropical lineages have had to accumulate species coupled with their constrained ability to colonize temperate regions as a result of niche conservatism (Wiens & Donoghue, 2004). Evidence for TNC has come from several lineages but mostly from well-known taxa (e.g. terrestrial vertebrates and vascular plants; Buckley et al., 2010; Hawkins et al., 2012; Kerkhoff, Moriarty, & Weiser, 2014), with only a few studies testing and supporting this hypothesis in complete lineages from the most diverse group of terrestrial animals: insects (swallowtail butterflies, Condamine, Sperling, Wahlberg, Rasplus, & Kergoat, 2012; ants, Economo, Narula, Friedman, Weiser, & Guénard, 2018). Still, these studies focus on relatively well-known insect taxa, raising the question about how representative are the patterns and their explanations for other insect taxa (Ballesteros-Mejía, Kitching, Jetz, & Beck, 2017) such as vectors of human diseases (Stephens et al., 2016).

Among the insect taxa that are vectors of human diseases, the triatomine bugs (Hemiptera: Reduviidae) are particularly amenable for describing and testing hypotheses about geographical patterns of insect biodiversity. Indeed, there is comprehensive information on their geographical distribution (Ceccarelli et al., 2018b) as well as their phylogenetic relationships (Justi, Galvão, & Schrago, 2016; Justi, Russo, Mallet, Obara, & Galvão, 2014). Many species of the Triatominae are considered to be potential vectors of the *Trypanosoma cruzi* parasite (Galvão & Justi, 2015), which causes Chagas disease, an illness that affects 6–8 million people in Latin America (World Health Organization (WHO), 2015). The subfamily Triatominae is composed of over 150 described species, mainly endemic to the New World, and divided into five tribes: Alberproseniini, Bolboderini, Cavernicolini, Rhodniini and Triatomini, with the latter two being the most diverse and epidemiologically relevant tribes (Justi & Galvão, 2017).

Triatomine species inhabit a variety of environments, from wild to domestic and peridomestic habitats (Galvão & Justi, 2015; Gaunt & Miles, 2000) in tropical, subtropical and temperate areas. Similar to many other taxa, triatomine species show an ubiquitous LDG but with a marked longitudinal diversity trend south of the Equator (increasing to the East), with higher species richness in dry areas of Central and Northeast Brazil, such as the Chaco, Cerrado and Caatinga biomes (Diniz-Filho, Ceccarelli, Hasperué, & Rabinovich, 2013; Fergnani, Ruggiero, Ceccarelli, Menu, & Rabinovich, 2013; Rodriguero & Gorla, 2004). The few studies evaluating the Triatominae LDG have favoured ecological explanations as its determinants. For example, Rodriguero and Gorla (2004) found a correlation between species richness and mean annual land surface temperature (used as a surrogate for available energy), supporting the argument that a positive richness-temperature relationship occurs at broad geographical scales. Similar results were obtained by Diniz-Filho et al. (2013), suggesting that most of the variation in species richness of triatomines could be explained by environmental variables that can be considered surrogates for climatic variability, ambient energy and water–energy balance. Accordingly, Fergnani et al. (2013) showed that triatomine species richness tends to increase in hot and dry regions of the Chaco, Cerrado and Caatinga biomes of South America characterized by high energy and low water availability, with stable high temperatures being the strongest predictor of triatomine richness. Regarding evolutionary explanations of triatomine diversity patterns, there is only one recent study that claimed that climatic niche conservatism may be responsible for triatomine diversity (Ibarra-Cerdeña, Zaldívar-Riverón, Peterson, Sanchez-Cordero, & Ramsey, 2014). This study, however, focused solely on species of one genus (*Triatoma*) distributed across North and Central America, thus neglecting a large part of triatomine species in the most diverse regions of the Americas.

Recent advances on the knowledge about triatomine biogeography (Ceccarelli et al., 2018b; Diniz-Filho et al., 2013) and evolution (Justi et al., 2014, 2016) set the stage for a comprehensive analysis of Triatominae biodiversity patterns under an evolutionary framework, considering their complete geographical distribution and species

richness. In fact, the ecological and evolutionary factors responsible for broad-scale patterns of species richness can be revealed by studying species geographical ranges and their overlap (Gotelli et al., 2009) and the phylogenetic structure of such overlap (Peixoto et al., 2017). A species-oriented approach that combines geographical distribution and phylogenetic information of species has been proposed to infer the drivers of species co-occurrence, and thus geographical patterns of species richness (Villalobos, Rangel, Alexandre, & Diniz-Filho, 2013). This approach is based on the concept of 'phylogenetic fields' (PF)—the phylogenetic structure of species co-occurrence within individual species' ranges—as a characteristic of species that allows assessing whether individual species co-occur with closely or distantly related species or with a random set of species.

Studies aiming to understand ecological and/or evolutionary processes as the underlying driver of insect species co-occurrence are very scarce, and usually focus on more diverse insect groups, such as butterflies, ants or beetles (i.e. Ballesteros-Mejia et al., 2017; Hawkins & Devries, 2009; Hortal et al., 2011; Jenkins et al., 2011). In this study, we aimed to understand the geographical co-occurrence of Triatominae species, an important group of disease vectors, with relatively understudied ecological and evolutionary patterns, by combining climatic (ecological) and phylogenetic (evolutionary) patterns. Under the joint effect of a tropical origin of the Triatominae subfamily (Justi et al., 2016) and the role of climatic niche conservatism in determining species richness regional patterns (Ibarra-Cerdeña et al., 2014), we expect the geographical co-occurrence and phylogenetic structure among New World Triatominae species to correspond with the particular climates where they occur. More specifically, triatomine species occurring in the ancestral tropical environments of the subfamily, characterized by low temperature seasonality and range, would show overdispersed PFs owing to their co-occurrence with both closely and distantly related species as a result of niche conservatism and the greater amount of time for species accumulation in their region of origin. In contrast, triatomine species occurring in temperate environments characterized by higher temperature seasonality and range would co-occur with closely related species, thus showing clustered PFs, as a result of the relatively recent colonization of this non-ancestral environment by derived and related lineages (Buckley et al., 2010; Stevens, 2006; Wiens & Donoghue, 2004).

2 | MATERIALS AND METHODS

2.1 | Triatomine occurrence data

We included all the Triatominae species for which molecular data were available, comprising a total of 63 species of the tribes Rhodniini and Triatomini (see Appendix S1). These species were included in the most comprehensive phylogeny of Triatominae reported to date (Justi et al., 2014). The taxa included in the analysis belong to nine genera (*Dipetalogaster*, *Eratyrus*, *Hermalentia*, *Mepraia*, *Panstrongylus*, *Paratriatoma*, *Psammolestes*, *Rhodnius* and *Triatoma*), representing approximately 40% of all described species of the Triatominae subfamily for the American continent.

Geographical distribution of the 63 triatomine species was obtained based on two approaches: (a) georeferenced occurrence locations and (b) polygons (range maps) based on those georeferenced occurrence locations. Occurrence locations (georeferenced points) were obtained from the triatomine occurrence database DataTri (Ceccarelli et al., 2018b). The range map polygons were constructed using the 'alphahull' R package (Pateiro-López & Rodríguez-Casal, 2010; R Core Team, 2019), implementing the α-convex hull method of a set of points in the plane for $\alpha > 0$. The concept of α-convex hull generalizes the definition of the convex hull of a set of points X in the Euclidean plane, being the smallest convex set that contains X (Edelsbrunner, Kirkpatrick, & Seidel, 1983).

Each type of geographical range (points or polygons) was overlaid by regular grids of 0.5° and 1° (longitude–latitude cells) resolution. These different resolutions were used to consider potential scale-dependency, and its interaction with different approaches used for building geographical ranges for large-scale biodiversity analysis (Hortal, 2008) and they are resolutions previously used in large-scale diversity analyses of several insects groups in general (i.e. Beck & Kitching, 2007; Narayan Shah, Tonkin, Haase, & Jähnig, 2015; Zeuss, Brandl, Brändle, Rahbek, & Brunzel, 2014) and of triatomines in particular (i.e. Diniz-Filho et al., 2013). In addition, the larger resolution (1°) will allow us to compare our results with previous Triatominae richness and distribution studies (Diniz-Filho et al., 2013; Ramsey et al., 2015; Rodriguero & Gorla, 2004). Although such resolutions may overestimate species geographical distribution at fine spatial scales, at larger spatial scales these resolutions are consistent with survey-based data (Hawkins, Rueda, & Rodríguez, 2008) and present a less biased representation of geographical distribution than occurrence records (Hurlbert & Jetz, 2007).

From these grids, we built four presence–absence matrices containing all species (rows) and sites/grid cells (columns), for each resolution and range type (points and polygons). The resulting matrices for points were a 63 × 148,302 species/cells matrix at 0.5° and a 63 × 66,717 species/cells matrix at 1° resolution. For polygons, a 63 × 490,564 species/cells matrix at 0.5° resolution and a 63 × 129,224 species/cells matrix at 1° resolution. Based on these matrices, species richness of each cell was defined by the number of triatomine species ranges overlapping that cell for polygons (considering a positive grid cell when at least part is covered by a species' range) and the number of unique occurrences of different species for points. In addition, we used the total number of triatomine species ranges (polygons) overlapping each cell to show the overall triatomine species richness pattern.

2.2 | Species-level co-occurrence: Diversity fields

The diversity field (DF) of a species (referred to as 'focal species') is defined as the number of species overlapping across its geographical range. Therefore, the DF of a given triatomine species can be

described as the species assemblage present throughout the focal species' range, reflecting its tendency to occur in regions with many or few other triatomine species. Depending on the species with which the focal species co-occurs (i.e. all species within a clade against specific lineages or ecological guilds), a focal species can co-occur with a larger or smaller number of species.

To describe the DF of each species, we generated a Species Richness Frequency Distribution (SRFD) that represents the richness variation across the focal species' range (included the focal species); and this SRFD can be interpreted as a function of species' co-occurrence (Villalobos & Arita, 2010). We calculated such SRFDs from the presence–absence matrices by gathering species richness values across each species-occupied cell. From these matrices, we also estimated the total number of co-occurring species (i.e. species richness) within each focal species range as well as the mean and skewness of its SRFD. Mean and skewness of an SRFD describe the within-range richness structure present over all sites occupied by a focal species, representing the average value and the asymmetry of species richness across its geographical range respectively (Villalobos & Arita, 2010).

2.3 | Phylogenetic reconstruction and divergence time estimates

Triatominae phylogeny was based on Justi et al. (2014, 2016), and included sequences for two new species (*Psammolestes coreodes* and *Triatoma patagonica*) from GenBank (see Appendix S1).

The phylogeny was reconstructed under a Bayesian framework, using BEAST 1.8 on the CIPRES Science Gateway (Miller, Pfeiffer, & Schwartz, 2010). Topology and divergence timing were estimated using GTR + G + I model, with the *Triatoma dominicana* fossil calibration on the same node as in Hwang and Weirauch (2012) and Justi et al. (2016). The prior was set as a normal distribution with a mean of 37 and an *SD* of 5. Root calibration, necessary for the accuracy of the estimation (Mello & Schrago, 2014), was set as a minimum of 50 Myr (Hwang & Weirauch, 2012). Analyses ran for 50×10^6 generations with tree sampling every 1,000 generations. Burn-in was set to 25%.

2.4 | Species-level phylogenetic structure: PFs

Triatomine phylogeny and the DF were used to estimate the PF of each triatomine species, thus considering the phylogenetic structure of species co-occurrence within individual species ranges. The PF of a species is defined by a single value characterizing the overall phylogenetic structure of all species contained within its range including itself (Villalobos et al., 2013).

To describe the PF, we used the Phylogenetic Species Variability (PSV) index. This index quantifies how phylogenetic relatedness decreases the variance of an hypothetical unselected trait shared by all species in the assemblage (Helmus, Bland, Williams, & Ives, 2007). This index informs about the degree of relatedness in the phylogenetic structure of an assemblage. PSV values vary between 0 (no variability, phylogenetic clustering) and 1 (maximum variability, phylogenetic overdispersion) as the maximum attainable value under a star phylogeny representing species' phylogenetic independence. The value of this index is not affected by species richness and abundance (Helmus et al., 2007). In this study, the index is represented by a 'sp' subscript (PSVsp) because the index was calculated within a focal species range instead of a single site, as is commonly done for local assemblages in community phylogenetics.

As the phylogenetic structure of a species assemblage depends on the clade under consideration (Hardy & Senterre, 2007), in this study, a species' PF considers all co-occurring species belonging to the Triatominae subfamily.

2.5 | Statistical analyses

Phylogenetic field estimates and statistical analyses were carried out in the R statistical language 3.5.1 (R Core Team, 2019), using the 'maptools' (Bivand & Lewin-Koh, 2018), 'letsR' (Vilela & Villalobos, 2015) and 'picante' (Kembel et al., 2010) R packages.

To test the null hypothesis that Triatominae PF patterns differ from those expected by chance (i.e. co-occurrence among species is the result of seemingly random assembly, regardless of their range's geographical location and their phylogenetic relationships), we compared the observed PFs of each species against a distribution of 1,000 randomly generated PF replicates. Additionally, for each model replicate, the null PF of each species is generated by randomly sampling, without replacement, the observed number of co-occurring species from the global phylogeny. With this procedure, the probability of sampling a species is proportional to its geographical range size, with large-ranged species being more likely to co-occur with other species. To help interpret the geographical position of these species, we mapped each triatomine species using their ranges' latitudinal midpoints obtained with the 'Polygon centroids' geometry tool of QGIS free software 2.18.26 (QGIS Development Team, 2018).

The PF of a species can be related to other species' attributes relevant to its co-occurrence patterns because it is considered as a species' property (Barnagaud et al., 2014; Villalobos, Olalla-Tárraga, Cianciaruso, Rangel, & Diniz-Filho, 2016). Thus, we regressed PSVsp values with total and mean species richness within ranges and with skewness of their SRFDs to assess whether there was a possible relationship between PFs and within-range species richness and structure. We also plotted, for each species, their PSVsp values against their ranges' latitudinal midpoints to explore for a possible geographical gradient in their PF.

To test whether a species' PF (dependent variable) is related to some 'preferred' climatic condition—as inferred from the climatic conditions of the area occupied by the species (independent variables)—we regressed the PF of each species (both for all species and

for only those with significant PSVsp) with two thermal variables, temperature seasonality (Bio4) and temperature annual range (Bio7) (i.e. temperature SD and amplitude respectively), and a variable related to water–energy balance, actual mean annual evapotranspiration (AET) known to influence triatomine species richness and distribution (Diniz-Filho et al., 2013). Thermal variables were taken from Worldclim 1.4 (www.worldclim.org; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and AET variable from the agroclimatic database of the Agromet Group of the United Nations Food and Agriculture Organization with the software New_LocClim 1.10 (Grieser, Gommes, & Bernardi, 2006). To account for all climatic variability, the variables were considered as the mean, median, minimum and maximum values over the geographical range of each focal species. To consider the phylogenetic non-independence of species in regressions, we used the phylogenetic generalized least squares (PGLS) method while estimating the phylogenetic signal of model residuals by means of the lambda parameter (Revell, 2010). All analyses were carried out in the R statistical language (R Core Team, 2019), using the 'ape' (Paradis, Claude, & Strimmer, 2004) and 'caper' (Orme et al., 2013) packages.

The R codes used to carry out spatial and phylogenetic estimates of the datasets and statistical analyses are available on GitHub (https://github.com/fabro/Triatominae_PhyloFields).

3 | RESULTS

We analysed whether there were statistically significant differences between the proportions of each species PF (clustered, overdispersed and random) results, obtained for each resolution (0.5° and 1°) and type of geographical range data (points and polygons) used. As all the analyses showed non-significant differences (see Appendix S2), we chose to describe only the results obtained from the analysis at 0.5° resolution with polygons as geographical range data.

3.1 | Geographical co-occurrence and triatomine phylogenetic structure

The overall species richness pattern (Figure 1) showed an LDG with a longitudinal trend south of the Equator, where the highest species richness accumulated in dry areas of the Chaco, Cerrado and Caatinga biomes as mentioned previously. Although we considered only 63 species in our analyses, the species richness pattern shown by this species set was practically the same as the pattern obtained when considering the most complete set of triatomine species with available geographical information at a continental scale (135 species; see Appendix S3). Accordingly, the patterns obtained with our species set were not geographically based in comparison with the current geographical knowledge about Triatominae species richness.

The total number of species that co-occur within each focal species' geographical range varied between 2 and 38 species. However, 75% of the species co-occurred with 7–12 other species

(see Appendix S3). The phylogenetic structure of species co-occurrence within each focal triatomine species' range resulted in PSVsp values between 0.474 and 1 (see Appendix S3). Only four species (*Dipetalogaster maxima*, *Mepraia spinolai*, *Triatoma bruneri* and *Triatoma flavida*) had PSVsp = 1. These are species co-occurring with only one or two other species within their geographical range, and thus are not amenable for comparison between observed and null values, nor to estimate their phylogenetic structure.

3.2 | Null models and geographical position of phylogenetic structure

Comparison between observed PSVsp values and the null model showed that only 28% of the focal species analysed (17 species out of 59) presented statistically significant values. More specifically, the PF pattern results showed that 8% of the species had overdispersed fields, 20% had clustered fields, whereas 64% had random phylogenetic structure (i.e. did not exhibit any clear phylogenetic structure different from those expected by chance; see Appendix S3). For the remaining 8% of the species, the PF could not be calculated because they co-occurred with only one or two species within their geographical range.

The analysis of the relationships between phylogenetic structure and co-occurrence patterns showed a trend from overdispersed to clustered PF coincident with the tropical to subtropical–temperate climatic gradient (Figure 2). Species with clustered PF co-occurred with more phylogenetically related species and had their latitudinal midpoints in subtropical–temperate areas, whereas species with overdispersed PF co-occurred with more phylogenetically distant species and had latitudinal midpoints inside the tropical zone (see Appendix S3).

3.3 | Triatomine PF versus DF

Phylogenetic fields showed significant relationships with other attributes of species' ranges. The relationship between PSVsp and total species richness within the range of each focal species (the number of species that are distributed within the focal species range) was negative ($r = -.39$, $p ≤ .05$, Figure 3). Species that showed a significant PSVsp related to an overdispersed phylogenetic structure co-occurred with between nine to 20 other triatomine species. Most species that had significant PSVsp related to a clustered phylogenetic structure co-occurred within their ranges with between 5 and 16 other species; and only three species (*Panstrongylus megistus*, *Triatoma sordida* and *Triatoma infestans*) co-occurred with more than 29 species (Figure 3). Furthermore, the relationship between PSVsp and SRFD mean values (the average number of species within each cell throughout the focal species' range) was also negative ($r = -.5$, $p ≤ .05$, Figure 4). Finally, there was a positive ($r = .26$, $p ≤ .05$, Figure 5) relationship between the SRFD skewness and the phylogenetic structure (PSVsp) of co-occurrence. Thus, triatomine species with overdispersed PF co-occurred with relatively few species in most of the sites where they are distributed (SRFD
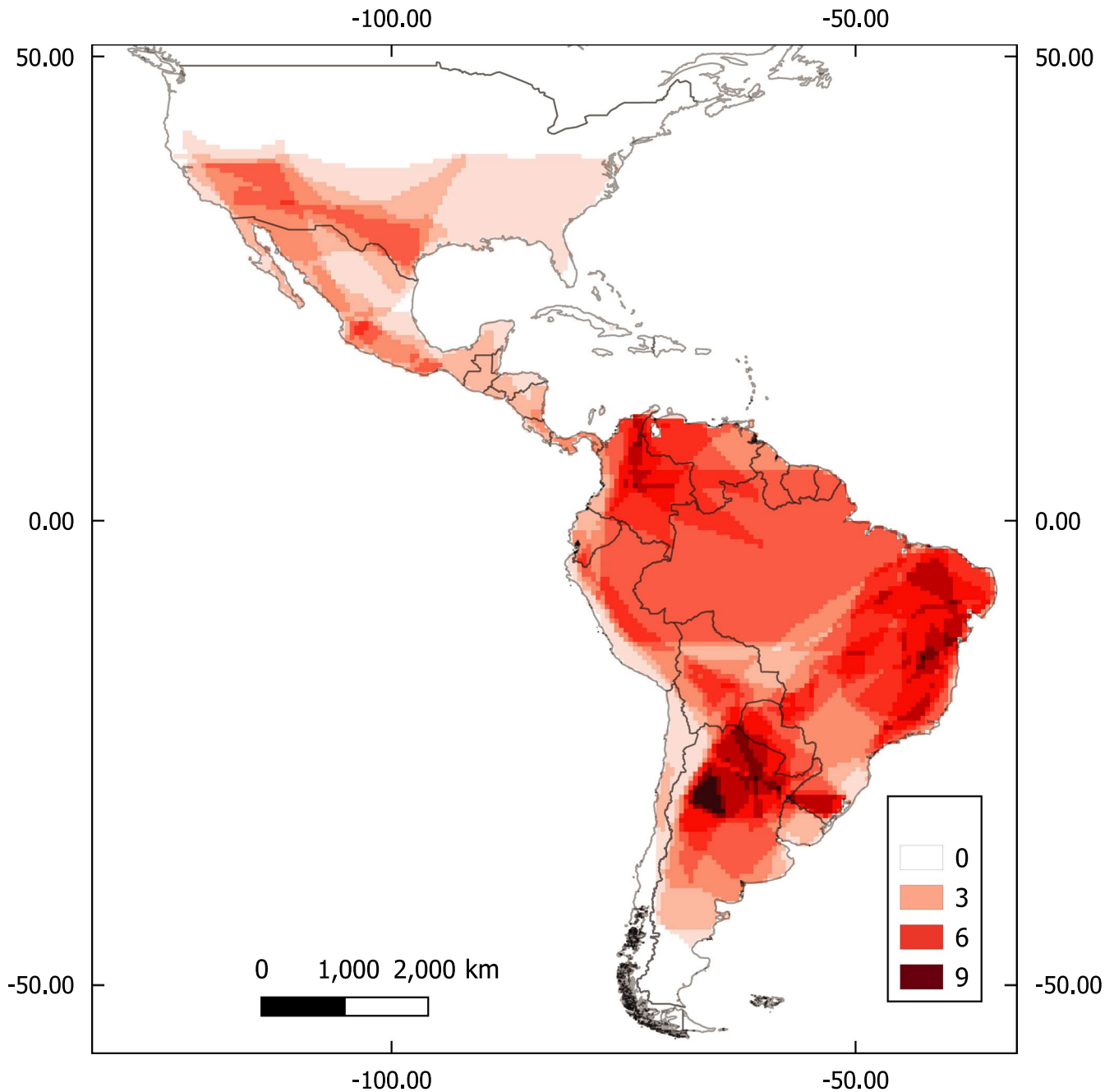
FIGURE 1 Overall Triatomine species richness pattern. Scaled colour ramp expresses the total number of species co-occurring in each 0.5° cell

positively skewed), whereas triatomine species with clustered PF co-occur with many species in most of the sites where they are distributed (SRFD negatively skewed).

3.4 | Triatomine PFs and climatic variables

The relationship between temperature seasonality (Bio4) and PF of those species with significant PSVsp, estimated by PGLS was found to be negative and statistically significant in the regression only when using the maximum values as descriptor across focal species' distributions

(PSVsp ~ Bio4max + Bio7max + AETmax). That is, lower temperature seasonality values matched with high PSVsp values (tendency of species with overdispersed PF in tropical areas) and higher temperature seasonality values matched with lower PSVsp values (tendency of species with clustered PF in subtropical/temperate areas; Table 1). Whereas the relationships between climatic variables and PF of all species showed statistically non-significant relationships. The statistically significant regressions of those species with significant PSVsp yielded an ML value of λ not significantly different from 0 (Table 1). The values of the dependent and independent variables for each triatomine species used in the PGLS regressions are shown in Appendix S4.
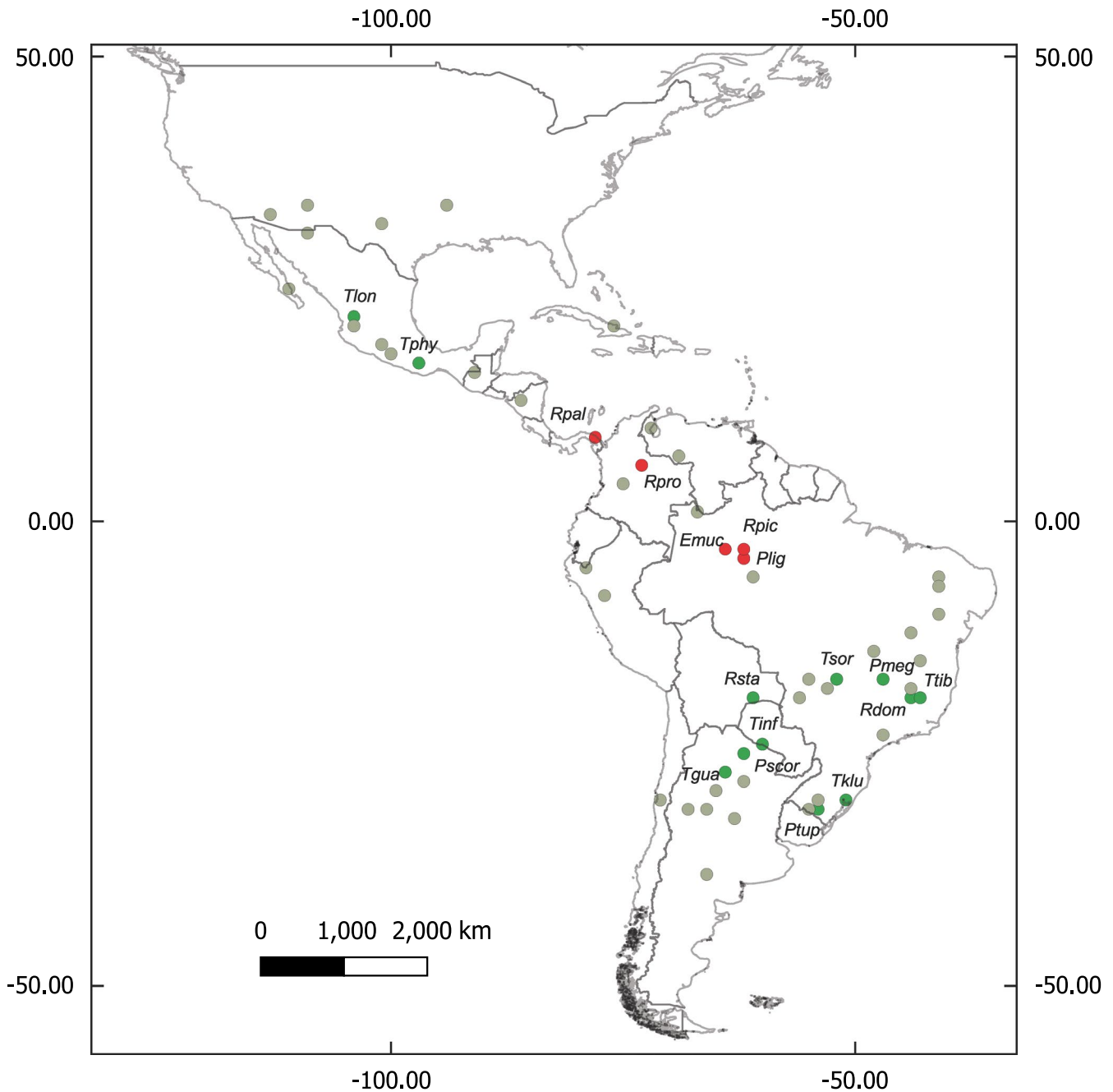
FIGURE 2 Geographical representation of significant phylogenetic field (PSVsp values) of each focal triatomine species. Circles represent the latitudinal midpoints of each species' geographical range. Red and green circles represent species with overdispersed and clustered phylogenetic structures, respectively, whereas grey circles represent those with random phylogenetic structures. *Tlon*: *Triatoma longipennis*; *Tphy*: *Triatoma phyllosoma*; *Rpal*: *Rhodnius pallescens*; *Rpro*: *Rhodnius prolixus*; *Emuc*: *Eratyrus mucronatus*; *Rpic*: *Rhodnius pictipes*; *Plig*: *Panstrongylus lignarius*; *Tsor*: *Triatoma sordida*; *Pmeg*: *Panstrongylus megistus*; *Ttib*: *Triatoma tibiamauculata*; *Rsta*: *Rhodnius stali*; *Rdom*: *Rhodnius domesticus*; *Tinf*: *Triatoma infestans*; *Pscor*: *Psmmolestes coreodes*; *Tgua*: *Triatoma guasayana*; *Ptup*: *Panstrongylus tupynambai*; *Tklu*: *Triatoma klugi*

4 | DISCUSSION

Triatominae diversification dates back to around 32 Ma (24–38 Ma; Hwang & Weirauch, 2012; Justi et al., 2016), with a northern South American origin of the group proposed by Justi et al. (2016). Based on its current species richness pattern (Diniz-Filho et al., 2013; Rodriguero & Gorla, 2004) and the application of the PF approach (Villalobos et al.,

2013), we were able to obtain a species-oriented perspective to test hypotheses on geographical patterns of triatomine co-occurrence.

We were able to support our expectation that the co-occurrence among triatomines could be the result of climatic niche conservatism. As expected, under the TNC hypothesis, triatomine co-occurrence showed a tropical to subtropical–temperate gradient from overdispersed to clustered PF and a correspondence between
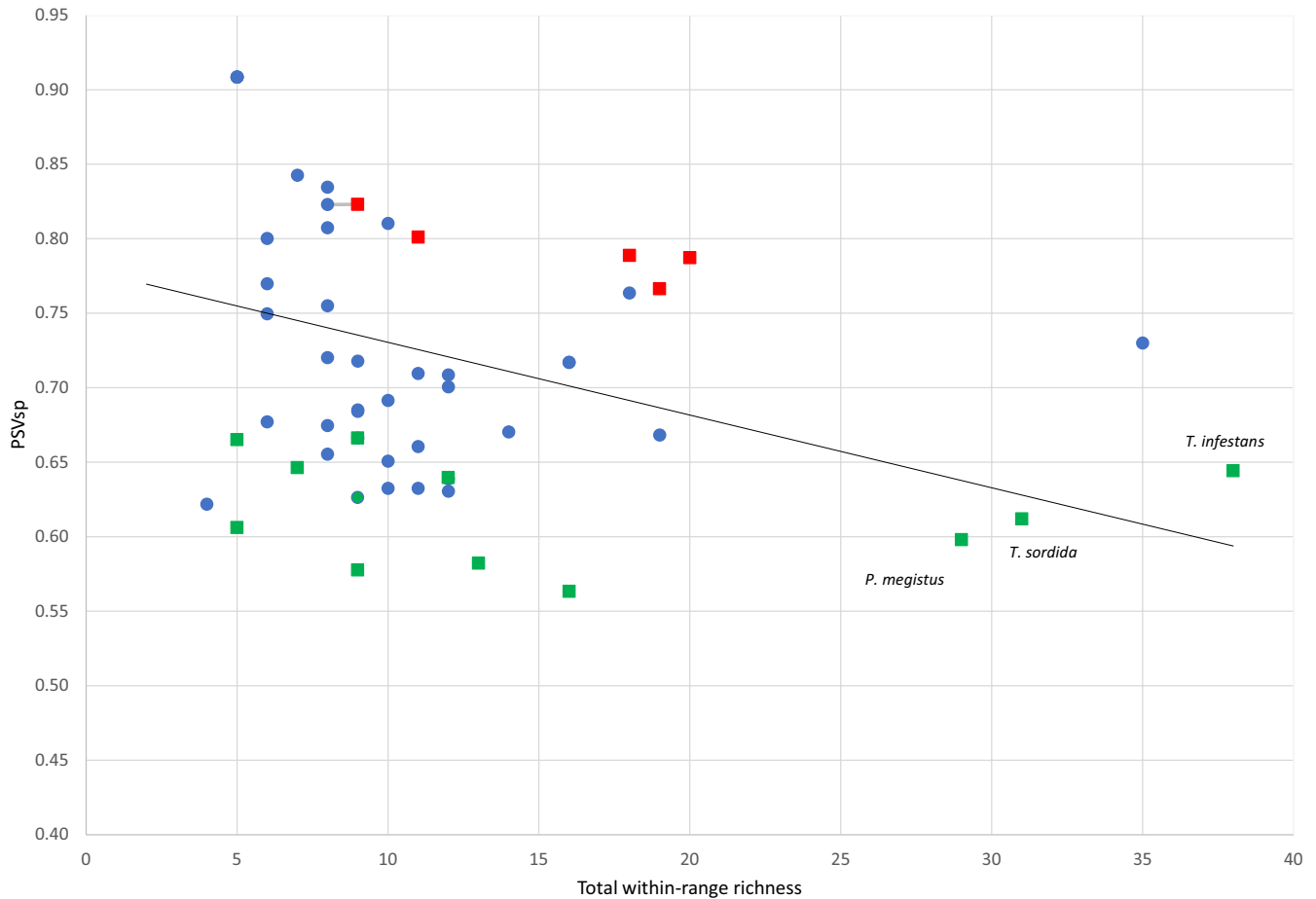
FIGURE 3 Statistical relationship between phylogenetic field (represented by PSVsp) and diversity field (as total within-range richness) for triatomine species. Squares represent significant clustered (green) and overdispersed (red) phylogenetic fields from null model comparisons. Blue points represent those species that have phylogenetic fields that cannot be distinguished from randomness. Line represents the fitted least squares regression for all data points

the type of climate in which these species are found and their PF. In tropical areas with higher richness, triatomines co-occur with both closely and distantly related species, thus showing overdispersed PF. Conversely, TNC would predict lower species richness in temperate areas where a relatively low number of species have been able to colonize (Hawkins, Diniz-Filho, Jaramillo, & Soeller, 2006; Wiens & Donoghue, 2004) and such species may share similar niche preferences favouring the colonization of those regions characterized by different conditions than the regions around the centre of origin. Accordingly, triatomine species in those areas co-occur with more closely related species, presenting clustered PF. However, only the Northern temperate areas present lower species richness than in the tropical areas, whereas south of the Equator there is a longitudinal diversity trend with higher species richness in dry areas of the Chaco, Cerrado and Caatinga biomes, like the tropical species richness. Furthermore, these dry areas of highest species richness are within the geographical ranges of several triatomine species of epidemiological importance, such as *T. infestans*, *T. sordida* and *P. megistus* that, in turn, co-occur with the largest number of species within their geographical range while presenting clustered PF (Figure 3).

Our analyses also revealed that the tropical to subtropical–temperate pattern from overdispersed to clustered PF of species is supported by the evolutionary history of Triatominae, that is, a northern South American origin, as proposed by Justi et al. (2016). Although there are no previous works in triatomines with an approach comparable to the one applied in this study, the results conform well with those obtained for other taxonomic groups. For example, for birds, the Eurasian, Central Asian and Nearctic species had the most clustered fields, while species with the most overdispersed fields occurred in tropical areas, especially in Africa and South America (Barnagaud et al., 2014). It has been suggested that triatomine species distributed in southern South America diverged more recently than the equatorial and North American species. Indeed, the southern South American triatomine species are phylogenetically more closely related than their northern relatives, with an evolutionary history of rapid and high diversification (Justi & Galvão, 2017; Justi et al., 2016) related to several climatic and ecological changes occurring as a consequence of the Andean uplift (Hoorn, Guerrero, Sarmiento, & Lorente, 1995; Hoorn et al., 2010) that could have given rise to isolated populations in the diagonal dry corridor as, for example, the extant *Triatoma klugi* in the Pampean Province, *T. infestans* in the Chacoan Province or *T. sordida* and *Triatoma*
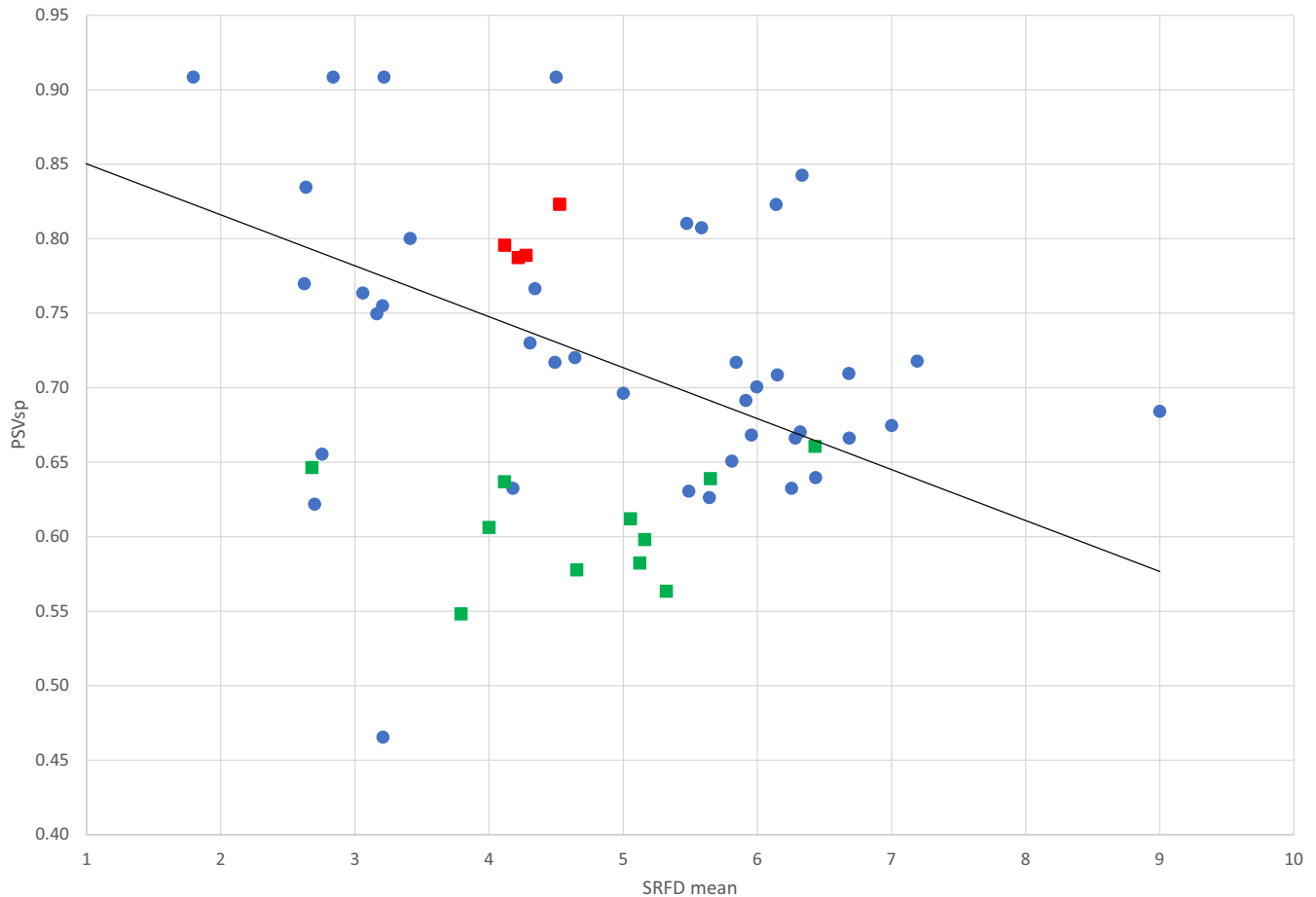
FIGURE 4 Statistical relationship between phylogenetic field (represented by PSVsp) and diversity field (as SRFDs' mean) for triatomine species. Squares represent significant clustered (green) and overdispersed (red) phylogenetic fields from null model comparisons. Blue points represent those species that have phylogenetic fields that cannot be distinguished from randomness. Line represents the fitted least squares regression for all data points

guasayana in the Cerrado Provinces (Provinces as in Morrone, 2014). Such historical processes could explain the main clustered phylogenetic structures of colonizer species co-occurrence in the southern part of the Americas.

Another potential explanation for clustered PF of subtropical–temperate triatomines is that the southern South American species are phylogenetically close, share environmental preferences (i.e. niche conservatism; Wiens & Graham, 2005) and thus also their geographical distributions (Barnagaud et al., 2014; Villalobos et al., 2013) adding support to the assumption that they may share their niche as the result of historical processes. Indeed, a previous study on North and Central American triatomines showed that the climatic niches of sister species are significantly more similar than expected under their background environments (Ibarra-Cerdeña et al., 2014).

The species of the Rhodniini tribe occur from Central America to northern Argentina. The clustered phylogenetic structure resulting from our analysis and the phylogenetic relationship with the co-occurring species *Rhodnius domesticus*, *Rhodnius stali* and *P. coreodes* could also be explained by the geological changes that occurred in South America. As discussed in Justi et al. (2016), the

Pebas system (Hoorn et al., 2010), as a vicariant event, would have separated the pictipes group from the prolixus group (Schofield & Galvão, 2009). *Rhodnius stali*, one of the species of the pictipes group, had its ancestor isolated in the areas designated as the Chacoan subregion (Morrone, 2014), and reached its current geographical distribution co-occurring with *Triatoma* species. Another possible vicariant event analysed in Justi et al. (2016) was the Acre system (Hoorn et al., 2010), that would explain the possible separation of *R. domesticus* from other members of the prolixus group. The ancestor of *R. domesticus* must have been isolated in Southern South America (current Parana Dominion, as defined by Morrone, 2014), also reaching its current geographical distribution co-occurring with species of the Triatomini tribe. *Psammolestes coreodes*, the southernmost representative species of the Rhodniini tribe, has been recorded in the open, semi-arid woodlands and savannahs of Argentina and Brazil (Abad-Franch et al., 2009), co-occurring with *Triatoma*, *Panstrongylus* and *Rhodnius* species, and Abad-Franch and Monteiro (2007) considered *Psammolestes* as a trans-Amazonian vicariant which arose as an individual lineage in association with ancestral furnariid bird species with a specialized trait adapted to exploit bird nest habitats.
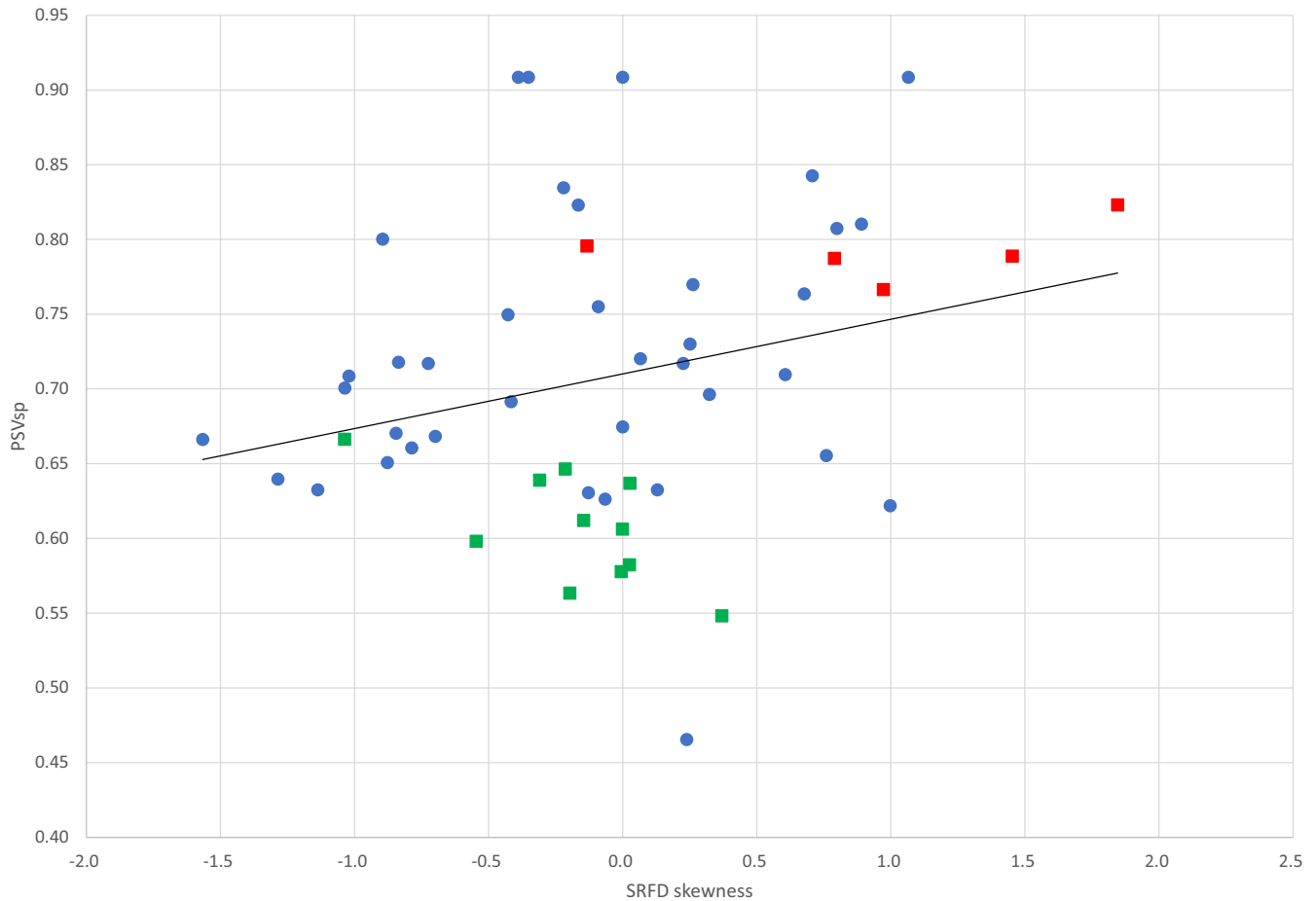
FIGURE 5 Statistical relationship between phylogenetic fields (represented by PSVsp) and diversity fields (as SRFDs' skewness) for triatomine species. Squares represent statistically significant clustered (green) and overdispersed (red) phylogenetic fields from null model comparisons. Blue points represent those species that have phylogenetic fields that cannot be distinguished from randomness. Line represents the fitted least squares regression for all data points

Most of the triatomine species analysed did not show a significative phylogenetic structure. A potential explanation for such a pattern could be related to processes related to range size variation (Borregaard, Gotelli, & Rahbek, 2012; Pigot, Phillimore, Owens, & Orme, 2010) with those species with more dynamic ranges co-occurring with a mixture of both closely and distantly related species and thus showing no clear pattern of phylogenetic structure. The tropical origin of the subfamily (Justi et al., 2016) and the diversification within the same geographical domain could also explain the non-significant patterns, allowing incumbent and colonizer species to occur at the same regions and co-occur with closely and distantly related species, producing random PF.

The temperature seasonality used in our analysis was significantly related to the phylogenetic structure of co-occurrence within focal species and the most important explanatory variable. Triatomines with overdispersed PF occurred in tropical areas (low temperature seasonality), whereas triatomine species with clustered PF tended to occur in temperate/cold areas (higher temperature seasonality). Thus, we could not reject the hypothesis of a relationship between the phylogenetic structure of co-occurrence and species' climatic preferences. Interestingly, this climatic

variable seems to play an important role as environmental driver in triatomines not only in their phylogenetic structures but also in the species richness patterns, and in the individual species' geographical distributions (Diniz-Filho et al., 2013; Ibarra-Cerdeña et al., 2014; Mendes Pereira et al., 2013).

Even though our analyses did not include all species of the Triatominae subfamily, we do not expect our findings would be altered by adding the missing Triatominae species, mainly because the species richness pattern of our studied species is the same as the one shown by all triatomine species with available geographical information at a continental scale (Ceccarelli et al., 2018b), and particularly because the missing species belong to tribes with relatively small number of species (Alberproseniini [2 sp.], Bolboderini [13 sp.] and Cavernicolini [2 sp.]) or to the other two tribes (Rhodniini [8 sp.] and Triatomini [+50 sp.]) that are species well represented in our analysis. The species not included in our analysis are rare and difficult to sample, and we had to limit ourselves to all the species represented in the most complete and resolved phylogeny available to date (Justi et al., 2014). Furthermore, South American species sampling is nearly complete regarding known diversity, and diversification is so recent that any inclusion of species would probably not affect the results.

TABLE 1 PGLS regression between American triatomine species' phylogenetic fields (PSVsp) and climatic variables (temperature seasonality (Bio4), annual range (Bio7) and actual annual evapotranspiration (AET) considered as the mean, median, minimum and maximum values over the geographical range of each focal species). Species with significant PSVsp refer to species with clustered and overdispersed phylogenetic structure. In all cases, the results are from data analysed at 0.5° resolution. The maximum likelihood value of lambda is shown as ML λ

	All species (0.5° grain)			Species with significant PSVsp (0.5° grain)		
	Regression coefficient	ML λ	Adjusted r^2	Regression coefficient	ML λ	Adjusted r^2
PSVsp ~ climatic variables mean values						
Bio4mean	0.01199299[a]	0.679	−.04355[a]	−0.049085[a]	0	.4472*
Bio7mean	0.00041526[a]			0.020830[a]		
AETmean	0.01160798[a]			0.038430[a]		
PSVsp ~ climatic variables median values						
Bio4median	0.033311[a]	0.667	−.03437[a]	−0.03572[a]	0	.4503*
Bio7median	−0.023718[a]			0.014227[a]		
AETmedian	0.010024[a]			0.046318[a]		
PSVsp ~ climatic variables min values						
Bio4min	−0.011059[a]	0.588	−.03673[a]	−0.016468[a]	0	.1868[a]
Bio7min	0.015836[a]			−0.037156[a]		
AETmin	−0.010465[a]			0.0142470[a]		
PSVsp ~ climatic variables max values						
Bio4max	−0.0199217[a]	0.607	−.03584[a]	−0.070861*	0	.5614**
Bio7max	0.0283304[a]			0.032036[a]		
AETmax	0.0064468[a]			0.028709[a]		

The results of the regression test are denoted by superscripts: [a]Not significant, *$p < .05$; **$p < .01$.

Phylogenetic relationships of insect vectors of parasitic diseases are important for understanding the evolution of epidemiologically relevant traits, and may be useful in vector control, particularly because many domiciliary vector species are under reasonable population control, and new sylvatic species are becoming more important in *T. cruzi* transmission, as is the case in Argentina (Ceballos et al., 2011), Bolivia (Noireau, Cortez, Monteiro, Jansen, & Torrico, 2005), Brazil (Gurgel-Gonçalves, Galvão, Costa, & Peterson, 2012) and Ecuador (Suarez-Davalos, Dangles, Villacis, & Grijalva, 2010). Several species of the Triatominii and Rhodnini tribes, belonging to species complexes or groups of great epidemiological importance for Chagas disease in North and South America, were included in our analysis and resulted in significant PSVsp values in the PF analysis (i.e. *E. mucronatus*, *P. megistus*, *T. infestans*, *T. guasayana*, *T. sordida*, *T. longipennis*, *T. phyllosoma*, *R. prolixus*). Additionally, most of these species co-occur with the largest number of species within their respective geographical ranges, and are important vectors of Chagas disease, with habitat distributions that go beyond sylvatic areas (i.e. domiciles and peri-domiciles), and are subjected to passive dispersion, both by people and other mammals and birds (Gourbière, Dorn, Tripet, & Dumonteil, 2012). Furthermore, the above-mentioned species might exhibit higher phenotypic plasticity regarding different climatic conditions and be more susceptible to infections because they live in more fragmented areas in contact with more small mammal species that generally carry higher rates of infection (Vaz, D'Andrea, & Jansen, 2007).

Finally, we believe that our study is a valuable and important contribution to the knowledge of macroecological patterns in insects. Our study provides a conceptual and methodological framework to evaluate geographical coexistence patterns under a phylogenetic perspective. We demonstrate the usefulness of the PF approach to integrate species' distributional, phylogenetic and climatic information for linking evolutionary and ecological approaches to understand biodiversity geographical patterns of an important group of organisms, the New World triatomine, as vectors of Chagas disease. More importantly, our triatomine PF results reveal the actual evolutionary information contained in the phylogeny resulting from geographical coexistence among the species analysed, determining the large-scale biodiversity patterns of the group. We suggest that the results presented here might be important to integrate it to the scarce existent phylogenetic information to a more comprehensive understanding of triatomine broad-scale biodiversity patterns and we are confident that this approach will contribute to a wider ecological, evolutionary and taxonomic interpretation of the processes that shaped present-day triatomine geographical distribution.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interests.

DATA AVAILABILITY STATEMENT

The data of triatomine species geographical distributions that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.c.3946936 (Ceccarelli et al., 2018a).

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BIOSKETCH

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