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Vector species richness predicts local mortality rates from Chagas disease

Guilherme Gonzaga da Silva [a,b], Vinicius Marques Lopez [a,c], Ana Carolina Vilarinho [b,f], Felipe H. Datto-Liberato [a,c], Carlo José Freire Oliveira [d], Robert Poulin [e], Rhainer Guillermo-Ferreira [a,b,c,d,*]

[a] Lestes Laboratory, Center of Entomology and Experimental Biology, Federal University of Triangulo Mineiro – UFTM, Uberaba, MG, Brazil
[b] Federal University of Sao Carlos – UFSCar, São Carlos, SP, Brazil
[c] Graduate Program in Entomology, University of Sao Paulo – USP, Ribeirão Preto, SP, Brazil
[d] Graduate Program in Tropical Medicine and Infectiology, Department of Natural and Biological Sciences, Federal University of Triangulo Mineiro – UFTM, Uberaba, MG, Brazil
[e] Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand
[f] Health Sciences Institute, Federal University of Triangulo Mineiro – UFTM, Uberaba, MG, Brazil

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ABSTRACT

Vector species richness may drive the prevalence of vector-borne diseases by influencing pathogen transmission rates. The dilution effect hypothesis predicts that higher biodiversity reduces disease prevalence, but with inconclusive evidence. In contrast, the amplification effect hypothesis suggests that higher vector diversity may result in greater disease transmission by increasing and diversifying the transmission pathways. The relationship between vector diversity and pathogen transmission remains unclear and requires further study. Chagas disease is a vector-borne disease most prevalent in Brazil and transmitted by multiple species of insect vectors of the subfamily Triatominae, yet the drivers of spatial variation in its impact on human populations remain unresolved. We tested whether triatomine species richness, latitude, bioclimatic variables, human host population density, and socioeconomic variables predict Chagas disease mortality rates across over 5000 spatial grid cells covering all of Brazil. Results show that species richness of triatomine vectors is a good predictor of mortality rates caused by Chagas disease, which supports the amplification effect hypothesis. Vector richness and the impact of Chagas disease may also be driven by latitudinal components of climate and human socioeconomic factors. We provide evidence that vector diversity is a strong predictor of disease prevalence and give support to the amplification effect hypothesis.

1. Introduction

Vector-borne diseases are a major public health concern, as they can have severe consequences for human well-being. The transmission of pathogens may be influenced by both evolutionary and ecological drivers, making it crucial to understand the role of biodiversity in the emergence and spread of these diseases, some of which are classified as neglected tropical diseases (Ostfeld and Keesing, 2000; Keesing et al., 2010). Studies have shown that biodiversity within ecological communities plays a significant role in the transmission of vector-borne diseases (Kocher et al., 2022). Hence, the presence of multiple host and vector species within these communities can have both direct and indirect effects on disease prevalence. Therefore, the conservation and management of biodiversity can play a key role in reducing the burden of vector-borne diseases (Ostfeld and Keesing, 2000).

Past reviews have argued that biodiversity reduces disease prevalence, via a hypothesis sometimes called the 'dilution effect' (DEH; e.g., Dobson et al., 2006; Ostfeld and Keesing, 2012; Civitello et al., 2015). Although there is increasing support for the DEH (Civitello et al., 2015), its predictions remain inconclusive as there is evidence of no such effect in some host-pathogen communities (Huang et al., 2016; Ferraguti et al., 2021). The amplification effect hypothesis (AEH), on the other hand, posits that increased biodiversity can result in a heightened risk of disease transmission (Keesing et al., 2006). It assumes that species-rich communities correlate with parasite-rich communities (Kamiya et al., 2014a). Specifically, the diversity of host communities upstream can contribute to the diversity of parasite communities in downstream host populations (Hechinger and Lafferty, 2005), which may be

* Corresponding author at: Center of Entomology and Experimental Biology, Federal University of Triangulo Mineiro – UFTM, Av. Tutumas, 490, 38061500 Uberaba, MG, Brazil.
E-mail address: rhainer.ferreira@uftm.edu.br (R. Guillermo-Ferreira).

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particularly relevant for vector-borne diseases where vectors act as upstream sources of infection for downstream hosts.

These two competing hypotheses (DEH and AEH) provide a valuable perspective on how changes in biodiversity may impact the transmission, maintenance, and prevalence of disease within ecosystems. Therefore, to fully comprehend the impact of biodiversity and disturbance on disease transmission, it is essential to examine the consistency and strength of the relationship between hosts and pathogens in the context of the opposite predictions made by the dilution and amplification hypotheses. One key component of biodiversity is species richness. Thus, to gain a deeper understanding of the relationship between vector diversity, disease transmission and host mortality rates, it is important to examine the factors that influence variation in vector richness among different regions.

Species richness can be positively associated with the incidence of vector-borne diseases (Johnson et al., 2015). In this context, host density across all suitable species can have a significant impact on parasite persistence, with higher host densities often leading to higher parasite diversity (Kamiya et al., 2014b). Furthermore, latitudinal and bioclimatic gradients can also affect vector diversity, as they are often linked to higher net primary productivity. Studies have shown that these gradients can be strong predictors of biodiversity, with a higher parasite and vector diversity found in regions with higher productivity. For example, latitude and climate can positively correlate with parasite and vector diversity (Lafferty, 2009). Hence, understanding these factors can help to identify areas of higher disease transmission risk and the potential impact of biodiversity conservation on transmission and mortality rates.

Most research has focused on the effects of host diversity on pathogen transmission, whereas vector diversity has seldom been examined (Johnson et al., 2013; Roche et al., 2013). Vector diversity is supposed to increase disease risk (Brooks and Zhang, 2010; Roche et al., 2013; Takimoto et al., 2022), nevertheless, some theoretical models suggest otherwise in certain conditions (Roche and Guégan, 2011). Due to species interactions within ecological communities, amplification and dilution effects may alter pathogen transmission depending on the ecological context (Keesing et al., 2006). For instance, species interactions (e.g., with predators, hosts, parasites, and competitors) can potentially hamper or facilitate pathogen transmission. In the case of parasites and vectors, the effects of vector species richness on disease prevalence and host death rates are still obscure. Some research suggests that decreasing vector species richness may consistently reduce pathogen transmission, while a greater vector species richness would amplify it (Roche and Guégan, 2011; Roche et al., 2013).

Chagas disease is a parasitic infection caused by the protozoan *Trypanosoma cruzi*. The primary mode of transmission is the bite and contact with faeces of infected triatomine vectors, also known as "kissing bugs". However, but still related to the presence of vectors, the disease may also be transmitted through oral (food-borne) transmission, blood transfusion, organ transplant and congenital transmission (https://www.who.int/news-room/fact-sheets/detail/chagas-disease-(american-trypanosomiasis)). The disease is most prevalent in Latin America and can have severe consequences including death (Martinez et al., 2019). Chagas disease has been documented to have occurred in Latin America for a minimum of 9000 years (Araújo et al., 2009). In recent times, significant shifts in human populations, particularly the transition from rural to urban settings during the last century, have led to a transformation of the disease's transmission cycle from a predominantly sylvatic state to an urbanized one. This shift is primarily facilitated by vectors that have adapted to human-modified environments (Colussi et al., 2022).

The development of resistance among these vectors to insecticides has compromised the efficacy of vector control measures, necessitating a greater emphasis on investigating the ecological dynamics of Chagas disease cycles. It is crucial to focus research efforts on comprehending the ecological aspects pertaining to reservoirs, hosts, and vectors (Flores-Ferrer et al., 2018). Notably, studies have indicated possible effects of reservoir and vector diversity on disease prevalence (Gottdenker et al., 2012; Méndez-Cardona et al., 2022). Additionally, deforestation, leading to a loss of habitat and host diversity, may contribute to an increased frequency of human-vector interactions in both rural and urban fringe areas.

Chagas disease prevalence and higher mortality rates are likely linked to endemic areas of triatomines (Martins-Melo et al., 2021). In Latin America, the vectors of *T. cruzi* belong to different species of the genera *Triatoma*, *Rhodnius* and *Panstrongylus* (Coura, 2014; Mendes et al., 2016). In recent years, the threat of Chagas disease has increased as previously unknown biodiversity of triatomine vectors has been discovered (Costa et al., 2021), and new species have emerged as vectors in areas where the traditional main vector has been controlled (Cantillo-Barraza et al., 2022). Moreover, recent increases in food-borne transmission of the disease are alarming and are probably influenced by vector richness and abundance (Coura, 2014). Therefore, it is important to understand how vector species richness can directly or indirectly contribute to the transmission of Chagas disease to reduce the burden of the disease on specific populations where there is a higher risk of infection.

Here, we tested whether mortality rates due to Chagas disease could be predicted by Triatominae species richness. Furthermore, we analysed the relationship between triatomine species richness and human population density (host density), socioeconomic predictors, bioclimatic variables, and latitude. We expected that kissing bug richness would be more predictive of mortality than socioeconomic predictors (Gross domestic product, (GDP) per capita).

2. Material and methods

2.1. Data sources

Occurrence data for mortality due to Chagas disease in humans were obtained from the DATASUS surveillance system (datasus.saude.gov.br), which is maintained by the Brazilian Health Ministry and Brazilian Unified Health System (SUS). This system maintains a nationwide data repository on several causes of morbidity and mortality, and their respective frequencies by year and city. We retrieved data on the number of deaths by Chagas disease for each city in the country in 2018, 2019, and 2020. Data for 2021 and 2022 were not completely available at the time of the study. We chose to use data for mortality instead of hospital admission rates because Chagas is a silent disease, and the number of deaths stands out over the number of admissions. Hence, we considered mortality a better predictor of pathogen prevalence and transmission. The Brazilian Institute of Geography and Statistics (IBGE, ibge.gov.br) was used to retrieve the geographic coordinates for each city with a respective unique code that matches those of SUS, which facilitated cross-checking the datasets. Centroids of each city were recorded to a spatial resolution of 50 km^2 for further analysis. Human population density, human development index (HDI) and GDP per capita were also obtained for each city from the IBGE database.

Finally, occurrence data for all species of Triatominae kissing bugs were extracted from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org). We retrieved data for each species in the three genera that may transmit Chagas disease to humans in Brazil, namely *Triatoma* Laporte, 1832, *Panstrongylus* Berg, 1879 and *Rhodnius* Stål, 1859. There were 42,178 coordinates

for *Triatoma* spp., 9,810 for *Panstrongylus* and 7,344 results for *Rhodnius* spp. Records for the genus only without species designation were excluded from analyses. Minimal convex polygons were created for each species, which were rendered to compute Triatominae species richness in a grid with 50 × 50 km cells. Hence, each cell had a value for species richness, considering the overall distribution of each species in the Neotropics. All computations were performed using the software QGis 3.24.1 (QGIS 2023, https://qgis.org/).

2.2. Statistical analyses

To address whether vector species richness predicts mortality rates, we built Generalized Estimating Equations Models (GEE). This method was chosen to account for spatial autocorrelation in the analysis (Dormann et al., 2007). We built the models with linear log distribution, considering the number of deaths per 1,000 inhabitants as our dependent variable and (i) vector species richness, and the covariate confounding variables, (ii) GDP per capita, (iii) HDI, (iv) human host population density, and (v) bioclimatic variables as predictors. These covariate variables were included to consider potential effects of alternative hypotheses that would assume climate, latitude, host density and human conditions are priority when addressing insect vector distribution.

The bioclimatic variables used were annual mean temperature (bio1) and annual mean precipitation (bio12); they were obtained from the WorldClim database (https://www.worldclim.org/) (Fick and Hijmans, 2017). Grids of 50 × 50 km were created using the QGIS software, and each variable was computed as the mean value for each grid. A specific grid ID number was used as a random subject factor in the analysis. Two GEE models were built, one treating only the richness of the two most speciose genera, *Rhodnius* and *Triatoma*, separately, and one considering the total vector species richness.

To address whether bioclimatic factors or host density influenced vector species richness, we built other GEE models using the same approach as described above. In these models, we considered vector species richness as our dependent variable, and (i) annual mean temperature (Bio1), (ii) annual mean precipitation (Bio12), (iii) human population density, and (iv) latitude as covariate predictors. The specific grid ID number was again used as a random subject factor in GEE analysis. Four GEE models were built, one treating the richness of each triatomine genus separately and one considering total vector species richness. All statistical analyses were performed using SPSS software (version 26.0).

In these analyses, latitude, temperature, and HDI were highly correlated. Hence, to avoid the effects of collinearity in our analyses, these variables were reduced to one Principal Component Analysis (PCA) axis in the analysis (76.44 % variance; component contribution: latitude = 0.938, HDI = 0.842, temperature = -0.839).

We also built other models by using an alternate method to control for spatial autocorrelation. We used the same variable configurations as described above, however, the GPS coordinates of each city were used to build a spatial correlation matrix that was used to control for spatial autocorrelation, instead of grid identity. For this, we built Generalized Linear Mixed Models (GLMM) with linear distribution using the *glmmTMB* package (Brooks et al., 2017) in the R environment v.4.2.2 (R Core Team, 2016, https://www.r-project.org/). Raw data is available at https://zenodo.org/record/7800041.

3. Results

Our study considered 5570 grid cells covering the full area of Brazil, each representing one data point in the analyses. Across these cells, mortality due to Chagas disease ranged from 0 to nearly 0.7 deaths per 1,000 inhabitants and human host population density varied across several orders of magnitude, whereas total Triatominae (vector) species richness ranged from two to 27 species.

The results show that Triatominae species richness and host population density can clearly predict mortality rates due to Chagas disease, but not GDP per capita (Table 1, Fig. 1). The two predictors had opposite effects: Triatominae species richness was positively related to mortality rates, whereas host population size was negatively related to mortality rates. The results of the GLMMs performed as an alternative analytical approach were essentially identical (see Supplementary Table S1). Our results also suggest that Triatominae species richness is mostly influenced by bioclimatic and latitudinal gradients but not by human population density (Table 2, Fig. 2). Again, the results of the GLMMs were very similar; all effects were in the same direction, although significance sometimes differed between the two analytical approaches (see Supplementary Table S2).

4. Discussion

Vector-borne diseases remain a major cause of illness and mortality worldwide, especially in tropical areas. Yet there remain unanswered questions regarding the factors driving spatial variation in their prevalence and impact. Two competing hypotheses, the DEH and the AEH, make contrasting predictions regarding the role of local diversity as a determinant of transmission rates (Keesing et al., 2006, 2010; Ostfeld and Keesing, 2012; Civitello et al., 2015). Here, we provide evidence that the latter hypothesis, AEH, applies to Chagas disease, an important source of mortality in Latin America. In this context, Chagas disease deserves special attention since it is characterized by more than 100 species of triatomines with potential vector capacity. In the specific case of Brazil, more than 60 vector species have already been identified. Understanding the relationship between disease dispersion and ecoepidemiology, and the richness of these vectors, provides important new information and a foundation for new approaches to fighting the disease.

Our results show that species richness is a predictor of mortality rates due to Chagas disease (i.e., a surrogate of pathogen transmission rates), supporting the AEH. However, latitude, climate, and HDI also showed a positive relationship with the annual number of deaths, whereas the human host population density was negatively related to the number of deaths. When addressing the predictors of triatomine richness, latitude and mean annual temperature were the main predictors of vector richness overall and separately for the three genera. Moreover, for *Triatoma* only, precipitation showed a negative relationship with species richness. Considering that the results show that intermediate latitudes had higher mortality rates and vector species richness, the relationship between Chagas disease and HDI and human population density may be driven by a latitudinal component of human socioeconomic factors in Brazil. It is known that populations in the most arid and warmest climates are among the most underdeveloped (Sathler, 2021), which correspond to the regions with higher triatomine species richness in Brazil. Nevertheless, because mortality rates were higher at intermediate values of latitude, temperature and HDI, one might suggest that vector richness and mortality are more related to the vectors' climatic niche. If HDI was a strong predictor of mortality and vector richness, we would expect higher values of both at extreme low values of HDI. The fact that mortality rates decrease with population density may be due to both an intraspecific dilution effect, better control and monitoring of different forms of transmission, and better health-related development and availability of medical care in larger cities.

Table 1
Results for Generalized Estimating Equations Models testing for the relationship between mortality rates by Chagas disease (per year per 1,000 inhabitants) and Triatominae (vector) species richness, population density, Gross domestic product (GDP)per capita as well as the combined effect of latitude, annual temperature, precipitation, and human development index (HDI). Latitude/temperature/HDI show high collinearity and were analysed as a Principal Component Analysis (PCA) axis. Results of the analysis treating the richness of the genera *Rhodnius* and *Triatoma* separately are shown, as well as those of the analysis considering total vector species richness. The significant results are shown in bold.

			95 % Wald-CI			
	β	Estimate	Inferior	Superior	Wald X^2	*P*
Rhodnius richness	0.009	0.002	0.006	0.012	29.857	**<0.001**
Triatoma richness	0.006	0.001	0.004	0.008	36.487	**<0.001**
Host population density	−0.011	0.002	−0.015	−0.006	21.605	**<0.001**
GDP per capita	0.004	0.003	−0.004	0.011	0.943	0.315
Latitude/temperature/HDI	0.013	0.003	0.007	0.019	19.353	**<0.001**
Precipitation	<0.001	<0.001	<0.001	<0.001	0.009	0.922
Total richness	0.006	0.001	0.004	0.007	74.13	**<0.001**
Host population density	−0.011	0.002	−0.015	−0.006	21.693	**<0.001**
GDP per capita	0.004	0.004	−0.004	0.012	0.790	0.374
Latitude/temperature/HDI	0.012	0.002	0.007	0.016	22.787	**<0.001**
Precipitation	<0.001	<0.001	<0.001	<0.001	0.287	0.592

CI, confidence interval.

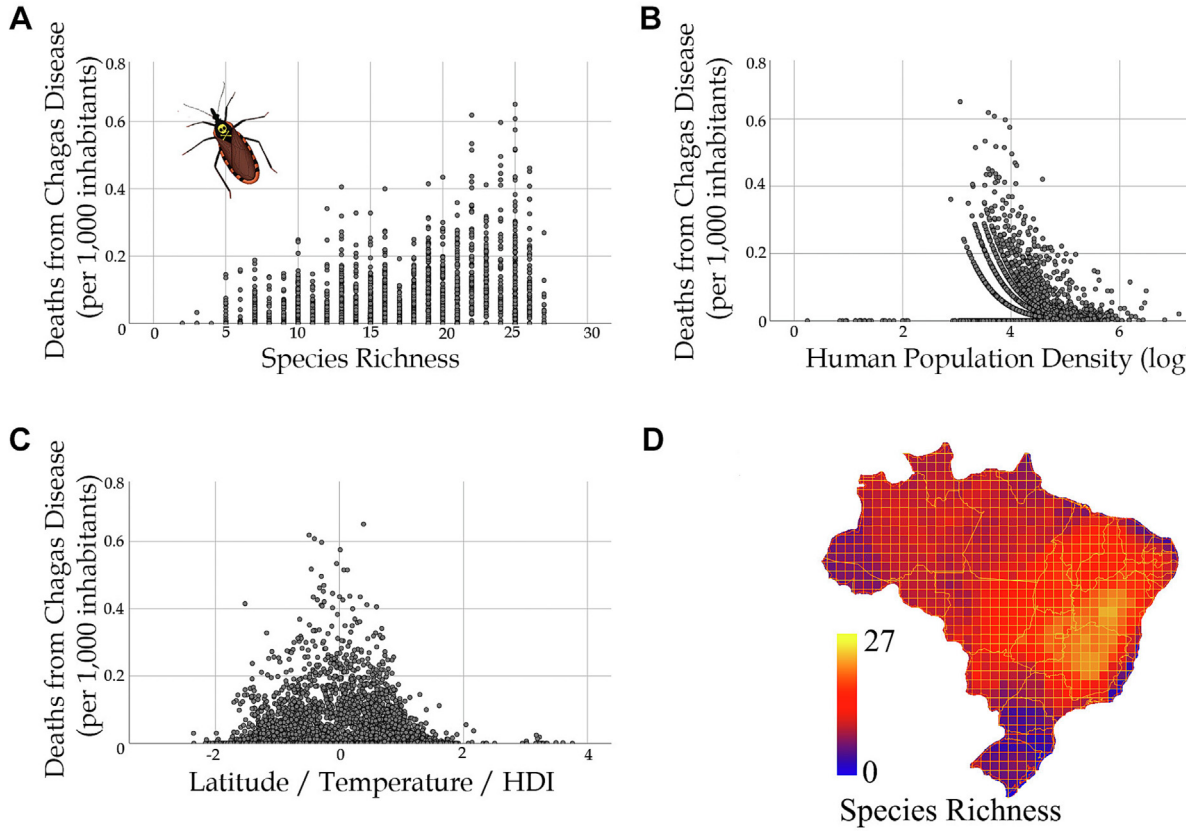

Fig. 1. The number of deaths due to Chagas disease registered in Brazil during the years 2018, 2019, and 2020, and its relationship with Triatominae species richness (A), human host population density (B), latitude, mean annual temperature, and human development index (HDI; C). Central-eastern regions in Brazil show a higher Triatominae species richness (D). Each point in A-C corresponds to one city or one 50 km × 50 km cell.

Several studies have addressed the relationship between biodiversity and host-parasite dynamics; however, few studies have examined how vector diversity affects the spread of vector-borne diseases (Takimoto et al., 2022). A higher vector species richness may provide additional pathogen transmission routes and generate amplifying effects. A model (Roche et al., 2013) suggests that, by increasing vector species richness, it is possible to enhance pathogen transmission due to a greater overall abundance of vectors. Furthermore, increasing vector species richness may change transmission rates due to multiple ecological and behavioural processes that may drive either dilution or amplification effects (Takimoto et al., 2022). Diversity among vectors in terms of blood feeding behaviour, host preference, habitat occupancy, aggregation behavior and movement may all determine the contact rate between vectors and susceptible hosts, hence leading to differences and variability in pathogen transmission dynamics.

Other studies have shown that vector richness may increase disease prevalence. For instance, mosquito richness may influence the prevalence of West Nile virus in wild birds (la Puente et al., 2018). On the other hand, recent evidence shows that mosquito

Table 2
Results for Generalized Estimating Equations Models testing for the relationship between Triatominae species richness and: (i) mean annual temperature (Bio1)/latitude/human development index (HDI), (ii) mean annual precipitation (Bio12), (iii) human host population density. Latitude/temperature/HDI show high collinearity and were analysed as a Principal Component Analysis (PCA) axis. Results of the analyses treating the richness of each genus separately are shown, as well as those of the analysis considering total vector species richness. The significant results are shown in bold.

			95 % Wald-CI			
	β	Estimate	Inferior	Superior	Wald X^2	*P*
Rhodnius						
Precipitation	0.000	0.000	0.000	0.000	0.091	0.763
Latitude/temperature/HDI	−1.35	0.0935	−1.531	−1.164	207.6	**<0.001**
Host population	0.105	0.0984	−0.088	0.297	1.130	0.288
Triatoma						
Precipitation	−0.003	0.000	−0.003	−0.002	120.407	**<0.001**
Latitude/temperature/HDI	−0.327	0.1166	−0.556	−0.099	7.888	**0.005**
Host population	0.194	0.1295	−0.060	0.448	2.244	0.134
Panstrongylus						
Precipitation	0.000	0.000	0.000	0.000	1.263	0.261
Latitude/temperature/HDI	−0.465	0.0831	−0.628	−0.302	31.341	**<0.001**
Host population	0.109	0.0853	−0.059	0.276	1.622	0.203
Total richness						
Precipitation	−0.002	0.000	−0.003	−0.002	26.18	**<0.001**
Latitude/temperature/HDI	−2.14	0.250	−2.63	−1.65	73.29	**<0.001**
Host population	0.407	0.277	−0.137	0.951	2.151	0.142

CI, confidence interval.

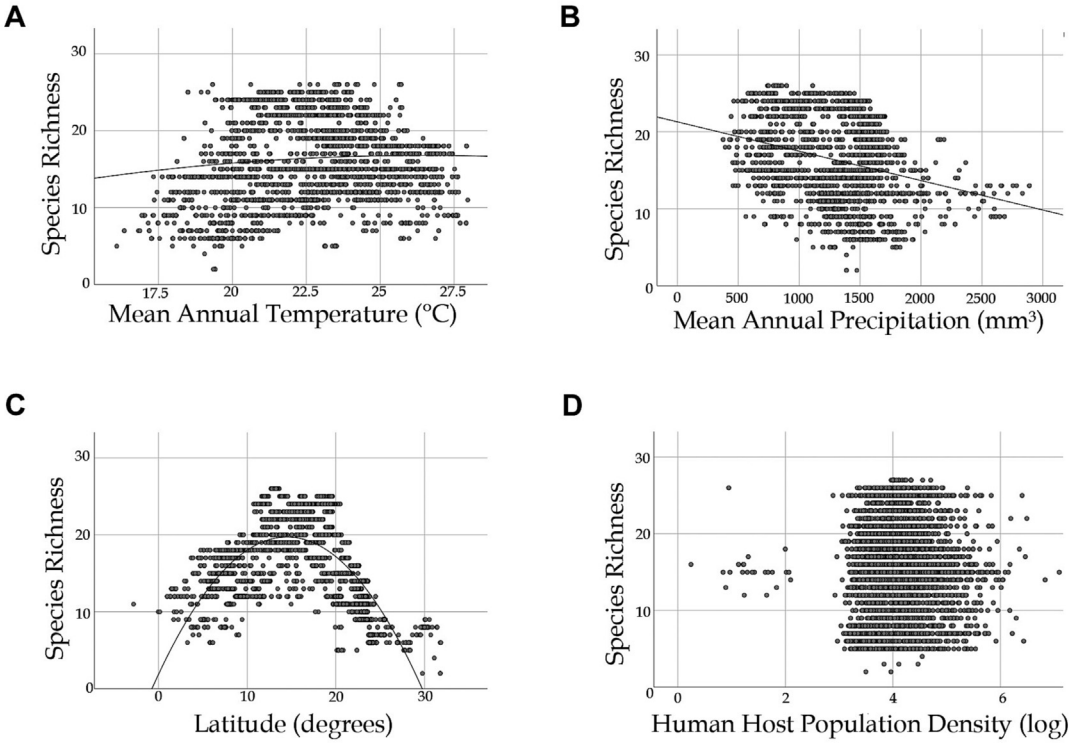

Fig. 2. Triatominae species richness in Brazil and its relationship with mean annual temperature (A), mean annual precipitation (B), latitude (C) and human host population density (D). Each point in A-D corresponds to one city or one 50 km × 50 km cell.

vector richness had no relationship with prevalence of pathogens, but vertebrate host richness did (Ferraguti et al., 2021). Thus, in line with some earlier studies on vector-borne diseases but in contrast with others, our results indicate that triatominae species richness has a clear positive relationship with death rates caused by Chagas disease in Brazil.

There is also compelling evidence indicating that reservoir richness can either amplify or dilute pathogen transmission (Roiz et al., 2019). However, the available evidence regarding Chagas disease is currently limited. For example, Dumonteil et al. (2018) did not observe any association between *Trypanosoma* diversity, a possible indicator of disease risk, and reservoir species diversity. In sylvatic environments, wild reservoir species typically exhibit higher diversity and lower infection rates compared with synanthropic/domestic animals and humans (Lilioso et al., 2020). Moreover, recent findings indicate that urban environments may

promote the infection by a greater number of trypanosomatid parasites in humans and dogs compared with wild reservoir species (Castillo-Castañeda et al., 2022).

In a study focusing on mammalian host diversity, researchers did not find a correlation between disease risk and host diversity (Oda et al., 2014). However, they did find a positive relationship between the number of infected triatomines and the densities of infected rodent species (Oda et al., 2014). The prevalence of parasites and vectors may exhibit an inverse correlation with host and reservoir diversity, which are ultimately influenced by anthropogenic environmental degradation, urbanization, and forest fragmentation (Ogrzewalska et al., 2011).

The risk of infection depends on the population and spatial dynamics of vectors, reservoirs, and hosts, particularly in wildlife environments. Consequently, infection rates are directly influenced by the extent and characteristics of interactions between humans and animals (including domesticated, synanthropic, and wildlife species). Therefore, it is crucial to comprehend the impacts of anthropogenic changes and land use patterns on such ecological dynamics to effectively assess disease risk (Morand and Lajaunie, 2021; Plowright et al., 2021). In the case of Chagas disease, the increasing deforestation of natural environments and the complex interaction network between trypanosomatid parasites, triatomine kissing bugs (15 genera) (Urdaneta-Morales et al., 2014), and hosts (more than 130 recognized species) (Georgieva et al., 2017) make the study of this case an enigmatic and challenging endeavor within a One Health approach (Essack, 2018).

One must also consider that the determinants of the risk of Chagas disease transmission are highly complex, mainly because most deaths occur in the chronic phase - often decades after the infections. Hence, human movement (e.g. rural exodus) can affect the data that were used here. Nevertheless, the fact that the number of deaths by Chagas disease may be higher in vector rich and endemic regions may suggest this effect is negligible. Human movement to the warm and arid areas that are most favorable to Triatomines (areas with higher mortality rates due to the disease) were rather small in the last century, compared with the large urban and colder areas in the south and southeastern regions of Brazil. Indeed, the exodus was contrary in Brazil – from the warm northern and northeastern regions to the south.

In summary, we demonstrate a clear positive relationship between local species richness of vectors, and annual death rates caused by Chagas disease, a major vector-borne disease afflicting human populations in Latin America. This result takes into account spatial autocorrelation across regions, as well as variations in climatic and socioeconomic factors. Our findings provide support for an amplification effect, whereby the more vector species that co-occur in an area, the greater the possible transmission pathways toward human hosts – including oral transmission. We also provide insights into the modeling of vector biodiversity and the associated infection risk. Such macroecological studies are establishing a robust framework that enhances the accuracy of predicting global patterns of infectious disease distribution and emergence (Stephens et al., 2016). In addition to contributing to the diversity-disease debate in ecological epidemiology, our results reveal key determinants of spatial variation in disease impacts, laying a foundation for the development of national-level policies for the control of Chagas disease. Future studies should address the role of reservoir diversity and land use changes in Chagas disease.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2023.10.002.

References

Araújo, A., Jansen, A.M., Reinhard, K., Ferreira, L.F., 2009. Paleoparasitology of Chagas disease: a review. Mem. Inst. Oswaldo Cruz 104, 9–16. https://doi.org/10.1590/S0074-02762009000900004.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9 (2), 378–400. https://doi.org/10.32614/RJ-2017-066.

Brooks, C.P., Zhang, H., 2010. A null model of community disassembly effects on vector-borne disease risk. J. Theoret. Biol. 264 (3), 866–873. https://doi.org/10.1016/j.jtbi.2010.03.016.

Cantillo-Barraza, O., Zuluaga, S., Medina, M., Triana-Chávez, O., 2022. New *Trypanosoma cruzi* transmission scenarios in the department of Boyacá, Colombia after the interruption of transmission by *Rhodnius prolixus*. Act. Biol. 44 (44), 43–44.

Castillo-Castañeda, A.C., Patiño, L.H., Zuñiga, M.F., Cantillo-Barraza, O., Ayala, M.S., Segura, M., Ramírez, J.D., 2022. An overview of the trypanosomatid (Kinetoplastida: Trypanosomatidae) parasites infecting several mammal species in Colombia. Parasit. Vectors 15 (1), 1–13. https://doi.org/10.1186/s13071-022-05595-y.

Civitello, D.J., Cohen, J., Fatima, H., Halstead, N.T., Liriano, J., McMahon, T.A., Rohr, J. R., 2015. Biodiversity inhibits parasites: broad evidence for the dilution effect. Proc. Nat. Acad. Sci. 112 (28), 8667–8671. https://doi.org/10.1073/pnas.1506279112.

Colussi, C., Stafuza, M., Nepote, M., Mendicino, D., 2022. Seroprevalence of Chagas disease in urban and rural indigenous populations of the south of Gran Chaco. Rev. Soc. Bras. Med. Trop. 55, e0479–e2021. https://doi.org/10.1590/0037-8682-0479-2021.

Costa, J., Dale, C., Galvão, C., Almeida, C.E., Dujardin, J.P., 2021. Do the new triatomine species pose new challenges or strategies for monitoring Chagas disease? An overview from 1979–2021. Mem. Inst. Oswaldo Cruz 116, e210015.

Coura, J.R., 2014. The main sceneries of Chagas disease transmission. The vectors, blood and oral transmissions-A comprehensive review. Mem. Inst. Oswaldo Cruz 110, 277–282. https://doi.org/10.1590/0074-0276140362.

Dobson, A., Cattadori, I., Holt, R.D., Ostfeld, R.S., Keesing, F., Krichbaum, K., Hudson, P.J., 2006. Sacred cows and sympathetic squirrels: the importance of biological diversity to human health. PLoS Med. 3 (6), e231.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30 (5), 609–628. https://doi.org/10.1111/j.2007.0906-7590.05171.x.

Dumonteil, E., Ramirez-Sierra, M.J., Pérez-Carrillo, S., Teh-Poot, C., Herrera, C., Gourbière, S., Waleckx, E., 2018. Detailed ecological associations of triatomines revealed by metabarcoding and next-generation sequencing: implications for triatomine behavior and *Trypanosoma cruzi* transmission cycles. Sci. Rep. 8 (1), 4140. https://doi.org/10.1038/s41598-018-22455-x.

Essack, S.Y., 2018. Environment: the neglected components of the One Health triad. Lancet Planet. Health 2, e238–e239. https://doi.org/10.1016/S2542-5196(18)30124-4.

Ferraguti, M., la Puente, J., Jiménez-Clavero, M.Á., Llorente, F., Roiz, D., Ruiz, S., Figuerola, J., 2021. A field test of the dilution effect hypothesis in four avian multi-host pathogens. PLoS Pathog. 17, (6). e1009637. https://doi.org/10.1371/journal.ppat.1009637.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37 (12), 4302–4315. https://doi.org/10.1002/joc.5086.

Georgieva, A.Y., Gordon, E.R., Weirauch, C., 2017. Sylvatic host associations of Triatominae and implications for Chagas disease reservoirs: a review and new host records based on archival specimens. PeerJ 5, e3826. https://doi.org/10.7717/peerj.3826.

Gottdenker, N.L., Chaves, L.F., Calzada, J.E., Saldaña, A., Carroll, C.R., 2012. Host life history strategy, species diversity, and habitat influence *Trypanosoma cruzi* vector infection in changing landscapes. PLoS Negl. Trop. Dis. 6 (11), e1884. https://doi.org/10.1371/journal.pntd.0001884.

Hechinger, R.F., Lafferty, K.D., 2005. Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. Proc. Royal Soc. B-Biol. Sci. 272 (1567), 1059–1066. https://doi.org/10.1098/rspb.2005.3070.

Huang, Z.Y.X., Van Langevelde, F., Estrada-Peña, A., Suzán, G., De Boer, W.F., 2016. The diversity–disease relationship: evidence for and criticisms of the dilution effect. Parasitology 143 (9), 1075–1086. https://doi.org/10.1017/S0031182016000536.

Johnson, P.T., Preston, D.L., Hoverman, J.T., LaFonte, B.E., 2013. Host and parasite diversity jointly control disease risk in complex communities. Proc. Nat. Acad. Sci. 110 (42), 16916–16921. https://doi.org/10.1073/pnas.1310557110.

Johnson, P.T., Ostfeld, R.S., Keesing, F., 2015. Frontiers in research on biodiversity and disease. Ecol. Lett. 18 (10), 1119–1133. https://doi.org/10.1111/ele.12479.
Kamiya, T., O'Dwyer, K., Nakagawa, S., Poulin, R., 2014a. Host diversity drives parasite diversity: meta-analytical insights into patterns and causal mechanisms. Ecography 37 (7), 689–697. https://doi.org/10.1111/j.1600-0587.2013.00571.x.
Kamiya, T., O'Dwyer, K., Nakagawa, S., Poulin, R., 2014b. What determines species richness of parasitic organisms? A meta-analytical review across animal, plant and fungal hosts. Biol. Rev. 89 (1), 123–134. https://doi.org/10.1111/brv.12046.
Keesing, F., Holt, R.D., Ostfeld, R.S., 2006. Effects of species diversity on disease risk. Ecol. Lett. 9 (4), 485–498. https://doi.org/10.1111/j.1461-0248.2006.00885.x.
Keesing, F., Belden, L.K., Daszak, P., Dobson, A., Harvell, C.D., Holt, R.D., Ostfeld, R.S., 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature 468 (7324), 647–652. https://doi.org/10.1038/nature09575.
Kocher, A., Cornuault, J., Gantier, J.-C., Manzi, S., Chavy, A., Girod, R., Murienne, J., 2022. Biodiversity and vector-borne diseases: Host dilution and vector amplification occur simultaneously for Amazonian leishmaniases. Mol. Ecol. 32 (8), 1817–1831. https://doi.org/10.1111/mec.16341.
la Puente, J., Ferraguti, M., Ruiz, S., Roiz, D., Llorente, F., Pérez-Ramírez, E., Figuerola, J., 2018. Mosquito community influences West Nile virus seroprevalence in wild birds: implications for the risk of spillover into human populations. Sci. Rep. 8 (1), 2599. https://doi.org/10.1038/s41598-018-20825-z.
Lafferty, K.D., 2009. The ecology of climate change and infectious diseases. Ecology 90 (4), 888–900. https://doi.org/10.1890/08-0079.1.
Lilioso, M., Reigada, C., Pires-Silva, D., Fontes, F.V.H., Limeira, C., Monsalve-Lara, J., Almeida, C.E., 2020. Dynamics of food sources, ecotypic distribution and *Trypanosoma cruzi* infection in *Triatoma brasiliensis* from the northeast of Brazil. PLoS Negl. Trop. Dis. 14 (9), e0008735. https://doi.org/10.1371/journal.pntd.0008735.
Martinez, F., Perna, E., Perrone, S.V., Liprandi, A.S., 2019. Chagas disease and heart failure: an expanding issue worldwide. Eur. Cardiol. Rev. 14 (2), 82 10.15420/ecr.2018.30.2.
Martins-Melo, F.R., Castro, M.C., Werneck, G.L., 2021. Levels and trends in Chagas disease-related mortality in Brazil, 2000–2019. Acta Trop. 220,. https://doi.org/10.1016/j.actatropica.2021.105948 105948.
Mendes, M.T., Carvalho-Costa, T.M., da Silva, M.V., Anhê, A.C.B.M., Guimarães, R.M., da Costa, T.A., Oliveira, C.J.F., 2016. Effect of the saliva from different triatomine species on the biology and immunity of TLR-4 ligand and *Trypanosoma cruzi*-stimulated dendritic cells. Parasit. Vectors 9 (1), 1–14. https://doi.org/10.1186/s13071-016-1890-x.
Méndez-Cardona, S., Ortiz, M.I., Carrasquilla, M.C., Fuya, P., Guhl, F., González, C., 2022. Altitudinal distribution and species richness of triatomines (Hemiptera: Reduviidae) in Colombia. Paras. Vectors 15 (1), 450. https://doi.org/10.1186/s13071-022-05574-3.
Morand, S., Lajaunie, C., 2021. Outbreaks of Vector-Borne and Zoonotic Diseases Are Associated With Changes in Forest Cover and Oil Palm Expansion at Global Scale. Front Vet Sci 8,. 661063. https://doi.org/10.3389/fvets.2021.661063.
Oda, E., Solari, A., Botto-Mahan, C., 2014. Effects of mammal host diversity and density on the infection level of *Trypanosoma cruzi* in sylvatic kissing bugs. Med. Vet. Ent. 28 (4), 384–390. https://doi.org/10.1111/mve.12064.
Ogrzewalska, M., Uezu, A., Jenkins, C.N., Labruna, M.B., 2011. Effect of forest fragmentation on tick infestations of birds and tick infection rates by *Rickettsia* in the Atlantic Forest of Brazil. EcoHealth 8, 320–331. https://doi.org/10.1007/s10393-011-0726-6.
Ostfeld, R.S., Keesing, F., 2000. Biodiversity series: the function of biodiversity in the ecology of vector-borne zoonotic diseases. Can. J. Zool. 78 (12), 2061–2078. https://doi.org/10.1139/z00-172.
Ostfeld, R.S., Keesing, F., 2012. Effects of host diversity on infectious disease. Annu. Rev. Ecol. Evol. Syst. 43, 157–182. https://doi.org/10.1146/annurev-ecolsys-102710-145022.
Plowright, R.K., Reaser, J.K., Locke, H., Woodley, S.J., Patz, J.A., Becker, D.J., Tabor, G. M., 2021. Land use-induced spillover: a call to action to safeguard environmental, animal, and human health. Lancet Planet. Health 5 (4), e237–e245. https://doi.org/10.1016/S2542-5196(21)00031-0.
Roche, B., Guégan, J.-F., 2011. Ecosystem dynamics, biological diversity and emerging infectious diseases. C. R. Biol. 334 (5–6), 385–392.
Roche, B., Rohani, P., Dobson, A.P., Guegan, J.-F., 2013. The Impact of Community Organization on Vector-Borne Pathogens. Am. Nat. 181 (1), 1–11. https://doi.org/10.1016/j.crvi.2011.02.008.
Roiz, D., Vázquez, A., Ruiz, S., Tenorio, A., Soriguer, R., Figuerola, J., 2019. Evidence that passerine birds act as amplifying hosts for usutu virus circulation. Ecohealth 16, 734–742. https://doi.org/10.1086/668591.
Sathler, D., 2021. Understanding human development, poverty and water scarcity patterns in the Brazilian Semi-arid through cluster analysis. Envir. Sci. Policy 125, 167–178. https://doi.org/10.1016/j.envsci.2021.09.004.
Stephens, P.R., Altizer, S., Smith, K.F., Alonso Aguirre, A., Brown, J.H., Budischak, S.A., Byers, J.E., Dallas, T.A., Jonathan Davies, T., Drake, J.M., Ezenwa, V.O., Farrell, M.J., Gittleman, J.L., Han, B.A., Huang, S., Hutchinson, R.A., Johnson, P., Nunn, C.L., Onstad, D., Poulin, R., 2016. The macroecology of infectious diseases: a new perspective on global-scale drivers of pathogen distributions and impacts. Ecol. Lett. https://doi.org/10.1111/ele.12644.
Takimoto, G., Shirakawa, H., Sato, T., 2022. The Relationship between Vector Species Richness and the Risk of Vector-Borne Infectious Diseases. Am. Nat. 200 (3), 330–344. https://doi.org/10.1086/720403.
Urdaneta-Morales, S., 2014. Chagas' disease: An emergent urban zoonosis. The caracas valley (Venezuela) as an epidemiological model. Front. Public Health 2, 265. https://doi.org/10.3389/fpubh.2014.00265.