

UNIVERSIDADE FEDERAL DE SÃO CARLOS
CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

Padrões Ecogeográficos da interação parasita-hospedeiro: uma abordagem EcoHealth

Guilherme Gonzaga da Silva

São Carlos - SP

2023

UNIVERSIDADE FEDERAL DE SÃO CARLOS
CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

Padrões Ecogeográficos da interação parasita-hospedeiro: uma abordagem EcoHealth

Orientador: Rhainer Guillermo Nascimento Ferreira

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais, da Universidade Federal de São Carlos, como parte das exigências para obtenção do título de Doutor em Ciências, área de concentração em Ecologia e Recursos Naturais.

São Carlos - SP

2023



UNIVERSIDADE FEDERAL DE SÃO CARLOS

Centro de Ciências Biológicas e da Saúde
Programa de Pós-Graduação em Ecologia e Recursos Naturais

Folha de Aprovação

Defesa de Tese de Doutorado do candidato Guilherme Gonzaga da Silva, realizada em 26/09/2023.

Comissão Julgadora:

Prof. Dr. Rhainer Guillermo Nascimento Ferreira (UFSCar)

Prof. Dr. Leandro Juen (UFPA)

Prof. Dr. Paulo de Marco Júnior (UFG)

Prof. Dr. Fabio de Oliveira Roque (UFMS)

Prof. Dr. Carlo José Freire de Oliveira (UFTM)

O Relatório de Defesa assinado pelos membros da Comissão Julgadora encontra-se arquivado junto ao Programa de Pós-Graduação em Ecologia e Recursos Naturais.

Agradecimentos

À minha família pelo suporte de sempre, em particular ao meu pai José Gonzaga que mesmo não estando presente fisicamente, continua presente em memória, sendo a maior referência e incentivo para a minha formação. E também ao meu vô Aurindo pelo carinho de sempre.

Ao meu orientador Prof. Dr. Rhainer, por ter aceitado me orientar mesmo após eu cair de paraquedas no laboratório e, principalmente, por ter continuado a me orientar no doutorado. Obrigado pelos conhecimentos transmitidos, pelas partidas de RPG e pelas oportunidades de ida ao campo. Estendo os agradecimentos também à sua esposa, Carol. Sigo eternamente grato a ambos por me ajudarem enormemente no que foi provavelmente o momento mais desafiador dessa trajetória, quando precisei me afastar das atividades acadêmicas para iniciar tratamento de saúde, que foi iniciado prontamente graças a vocês.

Cabe aqui agradecer também ao pessoal da área de saúde da UFSCar e à toda a equipe de saúde do Hospital Universitário da UFSCar, que me acolheu durante meu tratamento e que continua me acompanhando.

Aos amigos que fiz no laboratório, em particular ao Rodrigo, Vini e Datto. Obrigado pela companhia, pelo apoio, pela ajuda com os trabalhos, pelas conversas e risadas.

Aos amigos e colegas que fiz enquanto estive em São Carlos e que ajudaram a tornar a jornada mais leve. São muitas pessoas que conheci e aprendi um pouco com cada uma. Grato pela troca com todos vocês.

À todos os colaboradores dos trabalhos que compõe essa tese e que se dispuseram a compartilhar dados e conhecimentos para tornar estes trabalhos possíveis, em particular ao Prof. Dr. Robert Poulin pela inestimável contribuição.

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001.

RESUMO

Um dos padrões biogeográficos mais reconhecíveis é o padrão latitudinal de biodiversidade. Dele derivam diversos outros padrões que têm sido estudados há décadas. As interações entre os organismos também estão sujeitas a estes padrões. De particular interesse se encontram os organismos parasitas, uma vez que muitos destes organismos atuam como vetores de patógenos de interesse médico e veterinário. A estreita dependência de parasitas para com seus hospedeiros gera particularidades na forma como estes organismos respondem às variações dos diferentes fatores bióticos e abióticos. A elucidação destes elementos pode subsidiar abordagens interdisciplinares inovadoras como a ecossáude, que busca integrar saúde humana, animal e do meio-ambiente. Desse modo, a presente tese teve como objetivo explorar os fatores bioclimáticos em escala macro e o papel de dinâmicas de distribuição populacional e diversidade de hospedeiros e vetores nas interações parasita-hospedeiro. Os resultados adicionaram evidências do papel dos gradientes abióticos sobre os parasitas em uma escala mais ampla, e indicam que diferentes modos de vida podem levar a diferentes respostas a estes fatores. Também foi demonstrado que a biodiversidade de hospedeiros influencia a transmissão de patógenos em sistemas envolvendo vetores. No entanto, a inclusão de múltiplos sistemas parasita-hospedeiro pode dificultar o estudo dessas interações devido à complexidade subjacente das dinâmicas populacionais.

Palavras-chave: parasitismo, gradientes ecológicos, saúde pública, medicina tropical, biodiversidade

ABSTRACT

One of the most recognizable biogeographic patterns is the latitudinal gradient of biodiversity. From it, several other patterns have been derived and studied for decades. The interactions among organisms are also subject to these patterns. Of particular interest are the parasitic organisms, since many of these organisms act as vectors of pathogens of medical and veterinary interest. The close dependence of parasites on their hosts generates particularities in the way these organisms respond to variations in different biotic and abiotic factors. The elucidation of these elements can subsidize innovative interdisciplinary approaches such as ecohealth, which seeks to integrate human, animal, and environmental health. Thus, the present thesis aimed to explore the bioclimatic factors at macroscale and the role of population distribution dynamics and diversity of hosts and vectors in host-parasite interactions. The results added evidence of the role of abiotic gradients on parasites at a broader scale and indicate that different modes of parasitic lifestyles can lead to different responses to these factors. It was also demonstrated that host biodiversity influences the transmission of pathogens in systems involving vectors. However, the inclusion of multiple host-parasite systems can hinder the study of these interactions due to the underlying complexity of population dynamics.

Keywords: parasitism, ecological gradients, public health, tropical medicine, biodiversity

ÍNDICE

INTRODUÇÃO GERAL	8
Referências	11
CAPÍTULO 1 - Do Latitudinal and bioclimatic gradients drive parasitism in Odonata?	16
Abstract.....	16
1. Introduction.....	17
2. Materials and Methods.....	20
2.1. <i>Data compilation.....</i>	<i>20</i>
2.2. <i>Tree construction.....</i>	<i>21</i>
2.3. <i>Latitude and bioclimatic variables.....</i>	<i>21</i>
2.4. <i>Phylogenetic models with repeated measures</i>	<i>22</i>
2.5. <i>Phylogenetic signal estimates</i>	<i>23</i>
3. Results	23
3.1. <i>Phylogenetic models with repeated measurements</i>	<i>23</i>
3.2. <i>Phylogenetic signal estimates</i>	<i>24</i>
4. Discussion	24
Acknowledgements	26
Appendix A. Supplementary data	26
References.....	27
CAPÍTULO 2 - Effects of ecological marginality on the abundance of fleas on small mammals across Eurasia.....	39
Abstract.....	39
1. Introduction.....	39
2. Materials and Methods.....	41
2.1. <i>Data compilation.....</i>	<i>41</i>
2.2. <i>Outlying mean index (OMI) analysis and spatial measures</i>	<i>42</i>
2.3. <i>Marginality and spatial analysis.....</i>	<i>43</i>
3. Results	43
3.1. <i>Marginality and spatial analysis.....</i>	<i>43</i>
4. Discussion	44
References.....	46
CAPÍTULO 3 - Vector species richness predicts local mortality rates by Chagas disease	58
Abstract.....	58

1. Introduction.....	59
2. Material and Methods	62
2.1. <i>Data sources</i>	62
2.2. <i>Statistical Analyses</i>	62
3. Results	64
4. Discussion	64
Acknowledgements	67
References	67
CONCLUSÕES GERAIS	77

INTRODUÇÃO GERAL

Talvez a característica que mais salta aos olhos quando analisamos a vida na Terra é a sua incrível diversidade. Essa diversidade intriga a comunidade científica de várias maneiras intrigantes. Em primeiro lugar, ela suscita perguntas fundamentais, como: quantas espécies habitam nosso planeta? E, igualmente intrigante, por que a biodiversidade apresenta variações tão dramáticas em diferentes partes da Terra? Além disso, no âmbito dos ecossistemas, a evolução e coexistência de inúmeras espécies, bem como suas interações com o ambiente abiótico, levantam questões complexas. Como essas diferentes espécies se adaptam e compartilham recursos dentro de um ecossistema com recursos finitos? Quais são os fatores que influenciam a distribuição geográfica de espécies específicas e a formação de gradientes de biodiversidade? E como as mudanças ambientais, como a degradação do habitat e as alterações climáticas, afetam as interações entre as espécies e a saúde de todos os atores envolvidos? Apesar dos avanços recentes na pesquisa, essas questões continuam a desafiar os cientistas, demonstrando a complexidade e a fascinação da biodiversidade em nosso mundo.

Essas intrincadas e complexas relações entre a biodiversidade e o ambiente costumam ser manifestadas em tendências macroecológicas ou, como são conhecidas, padrões ecogeográficos. Padrões ecogeográficos refletem a prevalência de características e distribuição de espécies em resposta a uma série de fatores ambientais, geográficos e ecológicos. Uma série de fatores influencia esses padrões, incluindo o clima, a disponibilidade de recursos, a topografia, as interações entre as espécies e até mesmo eventos históricos. Por exemplo, o aumento da diversidade biológica dos polos em direção ao equador é tido como um dos padrões mais fundamentais da Ecogeografia, se tornando o padrão mais reconhecível da Ecologia (Gaston & Blackburn, 1999, 2000; Willig et al., 2003). Esse padrão é reconhecido há pelo menos dois séculos (Dobzhansky, 1950) e reflete como a biodiversidade se distribui e responde a condições ambientais variáveis como recurso alimentares, temperatura, umidade, barreiras geográficas e interações intra e interespecíficas ao redor do mundo. Portanto, essas tendências ecogeográficas capturam as nuances da distribuição e da adaptação das espécies em resposta a um caleidoscópio de fatores ambientais e ecológicos.

Embora a Ecogeografia tenha tradicionalmente se concentrado em traços fenotípicos, como tamanho corporal e coloração (e.g., Salewski & Watt, 2017; Lopez et al., 2021), recentemente tem havido um aumento significativo de esforços no sentido de compreender uma

variedade de outras características, incluindo aquelas de natureza funcional, genética, ecológica e fisiológica (Schemske et al., 2009; Dallas et al., 2018; Poulin, 2021). Esse aspecto multidisciplinar pode permitir novas abordagens na investigação dos padrões de distribuição das espécies, considerando a complexidade de suas interações ecológicas e seus diferentes hábitos de vida (Baiser et al., 2019; Lopes et al., 2019; Vintsek et al., 2022).

Nesse contexto, organismos de hábito parasita, devido à sua estreita interdependência com os hospedeiros e ao seu estilo de vida único, emergem como um sistema particularmente intrigante para a exploração das relações envolvendo os padrões ecogeográficos (Kamiya et al., 2014b). Os parasitas desempenham um papel notável nos ecossistemas, já que até metade de todas as espécies animais adotou essa estratégia de vida (Poulin & Morand, 2000). Esses organismos também atuam como elo entre comunidades, conectando redes alimentares, contribuindo para a estabilidade dos ecossistemas e influenciando a estrutura de múltiplos níveis de biodiversidade por meio de complexos ciclos de vida que envolvem transmissão trófica (Lafferty et al., 2006). Além disso, eles demonstram uma notável sensibilidade às pequenas variações ambientais e frequentemente desempenham um papel significativo como agentes de doenças, afetando tanto seres humanos quanto a vida selvagem. Essa interdependência entre sociedades humanas e seu ecossistema adjacente tem sido o foco de estudo de abordagens interdisciplinares como a *ecossaúde* (*ecohealth*). Tais abordagens holísticas buscam a colaboração interdisciplinar para a conservação da saúde humana, da saúde animal e do meio-ambiente (Zinsstag, 2012; Mi et al., 2016; Vanhove et al., 2020).

A importância dessas abordagens tem se evidenciado diante de crescentes episódios epidêmicos e pandêmicos envolvendo patógenos que saltaram de populações de animais não-humanos para humanos, sejam intermediados por vetores ou não (Vanhove et al., 2021; Wang et al., 2023). Intervenções inovadoras baseadas em *ecossaúde* já se mostraram bem-sucedidas como, por exemplo, no controle da transmissão de patógenos como o causador da doença de Chagas através do manejo dos insetos vetores da doença (Pereira et al., 2022). Portanto, ao incorporar a ecologia e a geografia na análise das interações parasita-hospedeiro, abrimos uma janela fascinante que nos impulsiona a buscar respostas mais profundas sobre a diversidade da vida e os processos ecológicos e evolutivos que moldaram os sistemas naturais e encontrar métodos inovadores para manejar o impacto desses organismos na saúde humana.

Parasitas podem ser utilizados como modelos, uma vez que são organismos que respondem diferencialmente a padrões ecológicos e geográficos, considerando seus limites fisiológicos, além de sua dependência da biologia e distribuição do hospedeiro para sobreviver

(Akinyi et al., 2019; Nunn & Dokey, 2006; Poulin et al., 2011). Em linhas gerais, para explicar os padrões ecogeográficos das interações parasita-hospedeiro, algumas hipóteses foram propostas. Dentre elas, pode-se citar: (i) Gradiente de Diversidade Latitudinal; (ii) centro de abundância; (iii) efeito de diluição/amplificação.

O gradiente de diversidade latitudinal prevê tendências no aumento na riqueza de espécies em direção às regiões tropicais, com uma diminuição gradual em direção aos polos. Isso se apoia na premissa das regiões tropicais serem mais favoráveis à diversidade de espécies devido ao clima quente e estável, bem como à constante disponibilidade de recursos. Uma outra hipótese ecogeográfica sugere que as densidades de indivíduos atingem o máximo no centro da faixa de distribuição de uma espécie e diminuem em direção às bordas (i.e., hipótese do centro de abundância) (Brown et al., 1995; Sagarin & Gaines, 2002). Isso significa que as populações no centro experimentam condições ideais, enquanto as das bordas enfrentam condições menos favoráveis (Eckert et al., 2008; Gaston, 2003; Pulliam, 1988). Assim, populações marginais seriam mais suscetíveis a estresses ambientais, predadores e parasitas infecções por parasitas (Gaston, 2003).

Por fim, duas hipóteses se destacam no contexto das interações entre biodiversidade e doenças. A primeira é a hipótese do "efeito de diluição de patógenos", que sugere que o aumento da biodiversidade reduz a prevalência de doenças. Isso ocorre porque comunidades mais ricas em espécies atuam como um amortecedor, diminuindo a propagação de patógenos (Dobson et al., 2006; Ostfeld & Keesing, 2012; Civitello et al., 2015). Por outro lado, a hipótese do "efeito de amplificação" propõe que o aumento da biodiversidade pode, na verdade, aumentar o risco de transmissão de doenças (Keesing et al., 2006). Essa ideia se baseia na correlação entre comunidades ricas em espécies e a presença de muitos parasitas. Portanto, compreender as vias de transmissão e o papel da biodiversidade no surgimento e disseminação de doenças é fundamental, especialmente diante do impacto significativo da atividade humana sobre a biodiversidade (Ostfeld & Keesing, 2000; Keesing et al., 2010; Ogrzewalska et al., 2011).

Nesse contexto, esta tese teve como objetivo explorar os fatores climáticos em larga escala, bem como as dinâmicas de distribuição populacional, a diversidade de hospedeiros e vetores nas complexas interações entre parasitas e hospedeiros. Os objetivos específicos da tese foram divididos em capítulos, onde se busca testar as hipóteses elencadas acima:

Capítulo 1 – Do latitudinal and bioclimatic gradients drive parasitismo in Odonata?:

Determinar se há relação entre latitude e prevalência de ácaros aquáticos e gregarinas que parasitam odonatos.

Capítulo 2 – Effects of ecological marginality on the abundance of fleas on small mammals

across Eurasia: Determinar se há um preditor geográfico ou climático para a abundância de pulgas que parasitam pequenos mamíferos na região da Eurásia.

Capítulo 3 – Vector species richness predicts local mortality rates by Chagas disease:

Testar se a taxa de mortalidade pela doença de Chagas pode ser predita pela riqueza de espécies de seus vetores Triatominae, e como essa riqueza se relaciona com fatores socioeconômicos e bioclimáticos.

Referências

- Akinyi, M. Y., Jansen, D., Habig, B., Gesquiere, L. R., Alberts, S. C. & Archie, E. A. (2019). Costs and drivers of helminth parasite infection in wild female baboons. *Journal of Animal Ecology* 88(7), 1029–1043. <https://doi.org/10.1111/1365-2656.12994>
- Baiser, B., Gravel, D., Cirtwill, A. R., Dunne, J. A., Fahimipour, A. K., Gilarranz, L. J., Grochow, J. A., Li, D., Martinez, N. D., McGrew, A., Poisot, T., Romanuk, T. N., Stouffer, D. B., Trotta, L. B., Valdovinos, F. S., Williams, R. J., Wood S. A. & Yeakel, J. D. (2019). Ecogeographical rules and the macroecology of food webs. *Global Ecology and Biogeography* 28(9), 1204-1218. <https://doi.org/10.1111/geb.12925>
- Brown, J., Mehlman, W., & Stevens, G. (1995). Spatial variation on abundance. *Ecology* 76(7), 2028–2043.
- 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. *Proceedures of the National Academy of Sciences* 112(28), 8667–8671. <https://doi.org/10.1073/pnas.1506279112>

- Dallas, T., Gehman, A. L. M., Aguirre, A. A., Budischak, S. A., Drake, J. M., Farrell, M. J., Ghai, R., Huang, S. & Morales-Castilla, I. (2019). Contrasting latitudinal gradients of body size in helminth parasites and their hosts. *Global Ecology and Biogeography* 28(6), 804–813. <https://doi.org/10.1111/geb.12894>
- 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 Medicine* 3(6), e231. <https://doi.org/10.1371/journal.pmed.0030231>
- Dobzhansky, T. (1950). Evolution in the Tropics. *American Scientist* 38(2), 208–221.
- Eckert, C., Samis, K. & Loughheed, S. (2008). Genetic variation across species' geographical ranges: the central – marginal hypothesis and beyond. *Molecular Ecology* 17, 1170–1188. <https://doi.org/10.1111/j.1365-294X.2007.03659.x>
- Gaston, K. J. (2003). The Structure and Dynamics of Geographic Ranges. *Evolutionary Ecology* 266.
- Gaston, K. J. & Blackburn, T. M. (1999). A Critique for Macroecology. *Oikos* 84(3), 353. <https://doi.org/10.2307/3546417>
- Gaston, K. J., & Blackburn, T. M. (2000). *Pattern and Process in Macroecology*. Blackwell Publishing.
- 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-analysis across animal, plant and fungal hosts. *Biological Reviews* 89, 123–134. <https://doi.org/10.1111/brv.12046>.
- 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>
- Keesing, F., Holt, R. D. & Ostfeld, R. S., (2006). Effects of species diversity on disease risk. *Ecology Letters* 9(4), 485–498. <https://doi.org/10.1111/j.1461-0248.2006.00885.x>

- Lafferty, K. D., Dobson, A. P. & Kuris, A. M. (2006). Parasites dominate food web links. *Proceedings of the National Academy of Sciences* 103(30), 11211-11216.
<https://doi.org/10.1073/pnas.060475510>
- Lopez, V.M., Tonetto, A.F., Leite, R.C. & Guillermo, R. (2019). Effects of Abiotic Factors and Ecogeographic Patterns on the Ecology, Distribution, and Behavior of Aquatic Insects. In: Del-Claro, K., Guillermo, R. (eds) *Aquatic Insects*. Springer, Cham.
https://doi.org/10.1007/978-3-030-16327-3_4
- Lopez, V. M., Tosta, T. A. A., da Silva, G. G., Bartholomay, P. R., Williams, K. A. & Guillermo-Ferreira, R. (2021). Color lightness of velvet ants (Hymenoptera: Mutillidae) follows an environmental gradient. *Journal of Thermal Biology* 100, 103030.
<https://doi.org/10.1016/j.jtherbio.2021.103030>
- Mi, E., Mi, E. & Jeggo, M. (2016). Where to now for one health and ecohealth? *EcoHealth* 13(1), 12-17. <https://doi.org/10.1007/s10393-016-1112-1>
- Nunn, C. L. & Dokey, A. T. W. (2006). Ranging patterns and parasitism in primates. *Biology Letters* 2(3), 351–354. <https://doi.org/10.1098/rsbl.2006.0485>
- Ostfeld, R. S. & Keesing, F. (2000). Biodiversity series: the function of biodiversity in the ecology of vector-borne zoonotic diseases. *Canadian Journal of Zoology* 78(12), 2061–2078. <https://doi.org/10.1139/z00-172>
- Ostfeld, R. S. & Keesing, F. (2012). Effects of host diversity on infectious disease. *Annual Review of Ecology, Evolution, and Systematics* 43, 157–182.
<https://doi.org/10.1146/annurev-ecolsys-102710-145022>
- Pereira, F. M., Penados, D., Dorn, P. L., Alcántara, B., Monroy, M. C. (2022) The long-term impact of an Ecohealth intervention: Entomological data suggest the interruption of Chagas disease transmission in southeastern Guatemala. *Acta Tropica* 235, 106655.
<https://doi.org/10.1016/j.actatropica.2022.106655>
- Poulin, R. (2021). Functional biogeography of parasite traits: hypotheses and evidence. *Philosophical Transactions of the Royal Society B* 376(1837), 20200365.
- Poulin, R. & Morand, S. (2000). The diversity of parasites. *The quarterly review of biology* 75(3), 277-293.

- Poulin, R., Krasnov, B. R., Mouillot, D. & Thieltges, D. W. (2011). The comparative ecology and biogeography of parasites. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366(1576), 2379–2390. <https://doi.org/10.1098/rstb.2011.0048>
- Pulliam, R. (1988). Sources, sinks, and population regulation. *The American Naturalist* 132(5), 652–661.
- Sagarin, R. D. & Gaines, S. D. (2002). The “abundant centre” distribution: To what extent is it a biogeographical rule? *Ecology Letters* 5(1), 137–147. <https://doi.org/10.1046/j.1461-0248.2002.00297.x>
- Salewski, V. & Watt, C. (2017). Bergmann's rule: a biophysiological rule examined in birds. *Oikos* 126(2). <https://doi.org/10.1111/oik.03698>
- Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M., & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annual review of ecology, evolution, and systematics* 40, 245-269. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173430>
- Vanhove, M. P. M., Hugé, J., Bisthoven, L. J., Keune, H., Laudisoit, A., Thys, S., Verheyen, E. & Antoine-Moussiaux, N. (2020) EcoHealth reframing of disease monitoring. *Science* 370(6518), 773-773. <https://doi.org/10.1126/science.abe8239>
- Vanhove, M. P. M., Thys, S., Decaestecker, E., Antoine-Moussiaux, N., De Man, J., Hugé, J., Keune, H., Sterckx, A. & Bisthoven, L. J. (2021). Global change increases zoonotic risk, COVID-19 changes risk perceptions: a plea for urban nature connectedness. *Cities & Health* 5(sup1), s131-s139. <https://doi.org/10.1080/23748834.2020.1805282>
- Vintsek, L., Klichowska, E., Nowak, A. & Nobis, M. (2022). Genetic differentiation, demographic history and distribution models of high alpine endemic vicariants outline the response of species to predicted climate changes in a Central Asian biodiversity hotspot. *Ecological Indicators* 144, 109419. <https://doi.org/10.1016/j.ecolind.2022.109419>
- Wang, Y., Zhao, S., Wei, Y., Li, K., Jiang, X., Li, C., Ren, C., Yin, S., Ran, J., Han, L., Zee, B. C. & Chong, K. C. (2023). Impact of climate change on dengue fever epidemics in South and Southeast Asian settings: A modelling study. *Infectious Disease Modelling* 8(3), 645-655. <https://doi.org/10.1016/j.idm.2023.05.008>

- Willig, M. R., Kaufman, D. M. & Stevens, R. D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual review of ecology, evolution, and systematics* 34(1), 273-309. <https://doi.org/10.1146/annurev.ecolsys.34.012103.144032>
- Zinsstag, J. (2012). Convergence of ecohealth and one health. *EcoHealth* 9(4), 371-373. <https://doi.org/10.1007/s10393-013-0812-z>

CAPÍTULO 1 - Do Latitudinal and bioclimatic gradients drive parasitism in Odonata?

Abstract

Prevalence of parasites in wild animals may follow ecogeographic patterns, under the influence of climatic factors and macroecological features. One of the largest scale biological patterns on Earth is the latitudinal diversity gradient; however, latitudinal gradients may also exist regarding the frequency of interspecific interactions such as the prevalence of parasitism in host populations. Dragonflies and damselflies (order Odonata) are hosts of a wide range of ecto- and endoparasites, interactions that can be affected by environmental factors that shape their occurrence and distribution, such as climatic variation, ultraviolet radiation and vegetation structure. Here, we retrieved data from the literature on parasites of Odonata, represented by 90 populations infected by ectoparasites (water mites) and 117 populations infected by endoparasites (intestinal gregarines). To test whether there is a latitudinal and bioclimatic gradient in the prevalence of water mites and gregarines parasitizing Odonata, we applied Bayesian phylogenetic comparative models. We found that prevalence of ectoparasites was partially associated with latitude, showing the opposite pattern from our expectations – prevalence was reduced at lower latitudes. Prevalence of endoparasites was not affected by latitude. While prevalence of water mites was also positively associated with vegetation biomass and climatic stability, we found no evidence of the effect of bioclimatic variables on the prevalence of gregarines. Our study suggests that infection by ectoparasites of dragonflies and damselflies is driven by latitudinal and bioclimatic variables. We add evidence of the role of global-scale biological patterns in shaping biodiversity, suggesting that parasitic organisms may prove reliable sources of information about climate change and its impact on ecological interactions.

1. Introduction

Recent advances in the study of host–parasite interactions have unraveled spatial and environmental gradients (Stephens et al., 2016). Parasites are notable elements of ecosystems, since up to half of all animal species evolved such a lifestyle (Poulin and Morand, 2000). These organisms act as connectors between communities by linking food webs, providing stability to ecosystems, and structuring multiple levels of biodiversity through their use of trophic transmission during complex life cycles (Lafferty et al., 2006). A large number of studies addressed how environmental factors may determine the presence or absence of parasites in free-living organisms and their diversity and prevalence in natural populations (Kamiya et al., 2014; Morand, 2015; Clark, 2018).

A myriad of factors may affect parasitism (Amaral et al., 2017), including climatic and other macroecological patterns (Fecchio et al., 2020). One of the largest scale biological patterns on Earth is the latitudinal diversity gradient (LDG). Over the past decades, it has been shown that species diversity increases from the poles towards the tropics and the equator (Pianka, 1966; Rohde, 1992; Willig et al., 2003; Jablonski et al., 2017). Although several hypotheses have been proposed to explain this pattern, most remain inconclusive (see Pontarp et al., 2019) for an extensive review of these hypotheses). For instance, most hypotheses deal with rates of diversification and biogeographic rules that shape diversity (Mittelbach et al., 2007); the increasing diversity as a function of productivity, since high resource availability potentially supports a wider set of lineages (Janzen, 1970; Connell, 1971); or the decreasing diversity with environmental temperature which mediates biological processes (Allen et al., 2002; Brown et al., 2004).

Studies on coevolutionary processes and interspecific interactions have helped address some of these hypotheses that attempt to unravel the main selective forces driving the evolution of LDG patterns (Schemske et al., 2009). For instance, host–parasite interactions have become good models to test for the mechanisms behind LDG patterns – diversity of parasites per host tends to be higher towards the tropics, including for protozoan parasites of birds (Svensson-Coelho et al., 2014), helminths of cricetid rodents (Preisser, 2019) and ectoparasites of marine fish (Rohde and Heap, 1998). Similarly, early predictions suggested that there should also be a higher prevalence of parasites in the tropics, due to the more stable environment and stronger coevolution between parasites and hosts (Janzen, 1970; Connell, 1971). Recent evidence supports these claims for blood parasites, showing that their prevalence increases with lower latitudes in birds (Merino et al., 2008) and parasite loads tend to be higher in tropical

populations of lizards (Salkeld et al. 2008, but see Cuevas et al., 2020). This tendency may be related to the increasing abundance and diversity of vectors and/or the response of parasite reproduction and transmission rates to climate at lower latitudes, and a way to test this hypothesis would be a comparison of parasitism rates in the same host species across a latitudinal range (Schemske et al., 2009).

Although LDG patterns may also affect parasite occurrence and prevalence, these organisms seem to be affected differentially by latitudinal variations due to their dependence on host biology and distribution, since parasites depend on their hosts for survival (Kamiya et al., 2014). Evidence in support of the LDG pattern was found for ectoparasites (e.g., Krasnov et al., 2007), however, several other studies have shown that diverse factors affect parasite diversity (Kamiya et al., 2014; Clark, 2018; Eriksson et al., 2020; Fecchio et al., 2020), which may explain why endoparasites respond differently compared with ectoparasites, and tend not to follow latitudinal gradients (Poulin, 1995). Therefore, here we focused on addressing the hypothesis that parasite prevalence exhibits a latitudinal gradient, with higher infection rates at lower latitudes due to climatic stability (Janzen, 1970; Connell, 1971). Moreover, we addressed whether this pattern is observable only for ectoparasites, but not for endoparasites, which may suffer less direct effects of environmental temperature and humidity (Poulin, 1995).

For this, we tested whether there is a latitudinal and bioclimatic gradient in the prevalence of water mites and gregarines parasitizing dragonflies and damselflies (order Odonata). We hypothesized that the prevalence of water mites and gregarines across distinct host populations would respond differently to latitudinal gradients: (i) prevalence of water mites should increase towards lower latitudes and warmer climates, since water mite distribution and abundance are highly dependent on host availability (Pozojević et al., 2018), which is higher at lower latitudes and warmer climates (Kalkman et al., 2008); (ii) prevalence of gregarines should show no response to climatic/latitudinal gradients, since gregarines are endoparasites with trophic transmission from insect prey (Åbro, 1976), a transmission mode unlikely to be affected by climate. We test these hypotheses with a comparative approach, accounting for the influence of host phylogeny, using a global dataset compiled from published results extracted from the literature.

Dragonflies and damselflies, similar to many other aquatic insects, are ubiquitously parasitized by a diversity of ecto- and endoparasites (Mendes et al., 2019). For instance, biting midges *Forcipomyia* spp. (Diptera: Ceratopogonidae) are ectoparasites that feed on the haemolymph by piercing the odonate host on the wings or thorax (Wildermuth and Martens, 2007; Guillermo-Ferreira and Vilela, 2013; Cordero-Rivera et al., 2019). Water mites

Arrenurus spp. (Acari: Hydrachnidia) adopt a similar strategy. Mite larvae attach to the insect host thorax or abdomen to feed on digested tissue and haemolymph (Rolff and Martens, 1997). Gregarines (Apicomplexa: Eugregarinorida) also have high prevalence in some odonate groups. These are endoparasites that infect the gut of arthropods and, in some cases, an individual odonate may be parasitized by a horde of these parasites (Ilvonen et al., 2018), while there may be a negative covariance between gregarines and water mites in other cases (Kaunisto et al., 2018). It is noteworthy that most studies on odonate parasites were carried out in temperate regions, resulting in gaps in knowledge for most regions, mainly the tropics.

Dragonfly and damselfly hosts – and consequently their parasites – are affected by several environmental features that shape their distribution, mainly climate (Hassall and Thompson, 2008), solar radiation (De Marco et al., 2015), and vegetation structure (Guillermo-Ferreira and Del-Claro, 2011a; da Silva Monteiro Júnior et al., 2013). Latitude is a convenient proxy for environmental factors, however testing for the direct effect of these factors themselves allows us to better understand why various ecto- and endoparasites may respond differently to latitude. For instance, water mites are expected to be affected by environmental factors in such a way that temperature may affect egg hatching (Zawal et al., 2018a) and the degree of melanization of mite feeding tubes by the host immunological system (Robb and Forbes, 2005). Moreover, mite distribution may be related to warmer riparian springs (Więcek et al., 2013), specific vegetation characteristics (Cyr and Downing, 1988) and flood regimes (Zawal et al., 2018b). Similarly, insect susceptibility to gregarine parasites may also be reduced by high temperatures (Åbro, 1976; Jancarova et al., 2016) and humidity (Clopton and Janovy, 1993). Host occurrence and distribution in the habitat may also affect parasite prevalence. Hence, bioclimatic factors and vegetation biomass surrogates, such as net primary productivity and plant height, are usually considered good predictors of odonate richness and spatial patterns (Rodrigues et al., 2016; Brasil et al., 2019). Vegetation provides resources for odonates, such as substrates for larval emergence (Tavares et al., 2017) and reproduction sites and perches for adults (Guillermo-Ferreira and Del-Claro, 2011a, 2011b), which may constrain their occurrence, distribution and abundance (as well as prey availability) (Hykel et al., 2020) at sites where parasite incidence/transmission is facilitated (Zawal and Buczyński, 2013; Hupało et al., 2014).

2. Materials and Methods

2.1. Data compilation

To determine whether there is a relationship between latitude and prevalence of water mites and gregarines parasitizing Odonata, we built models based on data retrieved from the literature. Studies were obtained by extensively searching for articles containing the keywords “odonata” or “damselfl*” or “dragonfl*” and “parasit*” and “latitud*” or “prevalen*” or “water mite” or “gregarin*”. We searched the academic database Web of Science, with some articles retrieved by other means such as cited references or additional searches of studies indexed in Google Scholar. For inclusion in the dataset, studies had to report not only data on prevalence of parasites in dragonflies or damselflies, but also information on the site of sampling (allowing latitude to be obtained), the number of sampled host individuals, and the species identity of the sampled hosts. Several studies had to be excluded due to missing information; for example, some studies did not report essential data such as geographic coordinates or species identification, the latter necessary to conduct phylogenetic analysis. Our initial search retrieved 111 articles on parasitism by water mites and/or gregarines, of which 71 were omitted due to lacking species identification, bioclimatic variables or geographic coordinates. We extracted data for prevalence, host species identity, sampling effort (number of collected individuals) and coordinates of the sampling locality from the remaining articles ($n = 40$) to build a matrix comprising all available data for these parasitic interactions. When populations were sampled repeatedly within the same year, we used mean values of prevalence, and if the sampling occurred in different years, we used separate annual values as repeated measures. We then considered as valid entries only those in which parasite prevalence was higher than zero. We had to exclude species that did not appear in the Odonata supertree we used in the Phylogenetic Comparative Models and sites where there were missing data for some environmental envelopes. After this further pruning of the data in the matrix, we ended up with information for 28 different species of Odonata parasitized by water mites and 32 species parasitized by gregarines retrieved from 27 articles, considering that there were multiple valid data entries for the same host species. A dataset with the data included in the analysis and tables with the lists of full-text articles used and those that were excluded following the literature review are provided as Supplementary Tables S1–S4, as well as a PRISMA (Moher et al., 2009) flow chart (Supplementary Fig. S1). The geographic distribution of sampling localities included in the data set is shown in Fig. 1. All entries retained in the data set are from the Northern

Hemisphere. Histograms of frequency of samples as a function of latitude are provided as Supplementary Figs. S2 and S3.

2.2. Tree construction

The phylogenetic trees used in this study were obtained from the Odonata Super Tree available through the Odonate Phenotypic DataBase (OPDB) Project (Waller and Svensson, 2017). At the time of the analysis, this supertree consisted of 809 species of Odonata, with node distances based on molecular data from GenBank and calibrated with fossil data. To manipulate the tree, we used the software R, version 3.5.3 (R Core Team, 2019. R: A language and environment for statistical computing.) with the “ape” package (Paradis and Schliep, 2019). We cut out from the final trees the species that did not feature in the dataset. This procedure was necessary since the analysis requires a perfect match of species names in the dataset and at the “tips” of the tree. In the process, using the 28 host species in the tree for water mite parasitism, and the 32 species in the tree for gregarine parasitism from our final data matrix, we built a secondary tree containing only species that matched those in the matrix and that were included in the supertree, while maintaining the original node distances. We also tested the tree for ultrametricity and checked if it was fully bifurcated, as required by phylogenetic comparative methods (Garamszegi, 2014), using “ape” R package functions. The resultant trees are available at <https://doi.org/10.17632/d7ttdszxyw.1>.

2.3. Latitude and bioclimatic variables

Our predictors initially consisted of 24 variables including bioclimatic and vegetation-related variables. The bioclimatic predictors were extracted from the WorldClim database (Hijmans, 2005; O’Donnell and Ignizio, 2012) for each of the sampled locations (see <https://www.worldclim.org/data/bioclim.html> for the description of each bioclimatic variable). We also used other continuous variables such as latitude, and annual mean UV-B radiation (measured as spectral surface UV-B irradiance and erythemal dose product at 15 arc-minute resolution, available at <https://www.ufz.de/gluv/index.php/en=32367>, Beckmann et al., 2014), plant height (crown-area-weighted mean height estimates derived from Geoscience Laser Altimeter System (GLAS) shots of approximately 70/230 meters of resolution, available at https://daac.ornl.gov/cgi-bin/dsviewer.pl/ds_id=1271, Healey, S.P., Hernandez, M.W., Edwards, D.P., Lefsky, M.A., Freeman, E., Patterson, P.L., Lindquist, E.J., 2015. CMS: GLAS

LiDAR-derived Global Estimates of Forest Canopy Height, 2004–2008. ORNL DAAC. <https://doi.org/10.3334/ORNLDAAC/1271>), and global patterns of Net Primary Production (NPP); obtained through a terrestrial carbon model applied to the global normalized difference vegetation index (NDVI) derived from the Advanced Very High Resolution Radiometer (AVHRR) Global Inventory Modelling and Mapping Studies (GIMMS), available in a grid of 0.25×0.25 degrees of resolution in a pattern of millions of grams of carbon per grid cell at <https://sedac.ciesin.columbia.edu/data/set/hanpp-net-primary-productivity>, Imhoff and Bounoua, 2006).

We used a principal component analysis (PCA) to reduce the BioClim variables to be used in future analysis due to high collinearity between the 19 climatic envelopes, UV-B and latitude. These PCA analyses, run separately for water mites and gregarines, resulted in three major axes for each parasite (considering a minimum cumulative axis contribution threshold of 85%). We extracted the scores for each axis and used them as predictor variables in our analyses. Since riparian vegetation is considered a predictor of odonate hosts, we considered the predictors NPP and plant height in our models as proxies for plant biomass, besides PCA scores.

2.4. Phylogenetic models with repeated measures

We built phylogenetic generalized linear models using the package “MCMCglmm” (Hadfield, 2010), which is capable of handling phylogenetic information in multilevel models and used Markov chain Monte Carlo (MCMC) sampling to obtain values from posterior distributions. We modelled water mite prevalence and gregarine prevalence in populations of Odonata (90 samples for water mites and 117 samples for gregarine parasitism). For each model, predictor variables included standardized (to a mean of zero and standard deviation of one) species means and within species predictors. Our predictors consisted of the bioclimatic and environmental variables represented as PCA scores (see above) that may encompass potential drivers of the relationships between parasite prevalence variation, sample size and plant biomass proxies (NPP and plant height). We built one model for each parasite group, using host species and study ID as random effects. We ran four chains for each model in MCMCglmm using the *MCMCglmm()* function with ‘gaussian’ family and default priors. Each chain consisted of 200,000 iterations with a burn-in period of 100,000, thinned every 100 steps,

for a total of 4,000 samples. The code was adapted from another study that used a similar approach (Barrow et al., 2019). Predictor variables were rescaled before analyses (range: 0–1).

2.5. *Phylogenetic signal estimates*

Phylogenetic signal was estimated from the superior distributions of the models, similar to the phylogenetic heritability described by Lynch (1991). Similar to heritability in quantitative genetics, we can estimate the phylogenetic signal in parasite prevalence as the proportion of the total variance that is attributed to phylogenetic variance. We estimated the phylogenetic signal using the models where species, sample size and study ID were used as random effects. In the package “MCMCglmm”, the mean and the 95% highest posterior density (HPD) of the phylogenetic signal (k) is computed for each MCMC chain by dividing the phylogenetic variance–covariance (VCV) matrix by the sum of the phylogenetic, species and residual VCV matrices (Hadfield and Nakagawa, 2010).

3. Results

Across 90 populations of 28 host species (27 Zygoptera, one Anisoptera), prevalence of water mites ranged from 1.6% to 100% (mean = 44%). Among the 117 populations of 32 host species (29 Zygoptera, three Anisoptera), prevalence of gregarines ranged from 1.1% to 100% (mean = 45.2%). Mean prevalence per region is shown in Fig. 2.

The PCAs showed a strong relationship between latitude and bioclimatic variables and UV-B (Table 1). The PCA for water mites resulted in three major axes, with 45–69–87% cumulative variance explained. The PCA for gregarines also resulted in three axes with 40–73–86% cumulative variance explained.

3.1. *Phylogenetic models with repeated measurements*

The model built for water mite prevalence in Odonata with species and study ID as random effects indicates a negative effect of the third axis of the PCA and a positive effect of NPP (Fig. 3A). Results also suggest a positive effect of latitude and a negative effect of UV-B on the prevalence of these parasites (captured by the third axis of the PCA). The third axis of the PCA also showed a strong relationship with Bio2 (diurnal temperature amplitude) and Bio7

(annual temperature amplitude). For gregarines, latitude, climate and vegetation had no association with prevalence (Fig. 3B).

3.2. Phylogenetic signal estimates

The phylogenetic signal was stronger in the model built for prevalence of gregarines ($\lambda = 0.35$, 95% confidence interval (CI) = 0.08–0.68) in Odonata than in the model for water mite prevalence ($\lambda = 0.37$, 95% CI = 0.08–0.74).

4. Discussion

Our results suggest an association between latitudinal and bioclimatic variations with the prevalence of parasitism in odonate populations. Results showed that the third axis of the PCA analysis was responsible for explaining the geographic variation in the prevalence of water mites parasitizing dragonflies and damselflies. However, no pattern was found for gregarines. Hence, we found that the prevalence of ectoparasites, but not endoparasites, increases with increasing latitude, opposite to our initial hypothesis. Furthermore, climatic variables mostly affected parasitism by water mites, especially NPP and Mean Temperature Diurnal Range (Bio2, which had higher relationship with the third axis of the PCA). Nevertheless, considering that this PCA axis only explained 18% of the variance, the effect of latitude and temperature may not be substantial. The strength of the phylogenetic signals detected by our models did not indicate a major influence of host phylogeny on prevalence. The phylogenetic signal index we used varies from 0 to 1, with $\lambda = 1$ representing a strong signal and $\lambda = 0$ representing the absence of any phylogenetic signal (Garamszegi, 2014).

The biodiversity of most free-living organisms responds positively to the latitudinal gradient, i.e., it increases toward the tropics, however, the diversity of parasites may respond differently (Kamiya et al., 2014). While there is evidence that parasite richness and diversity are not driven by latitudinal variation (Kamiya et al., 2014; Clark, 2018), and even present an inverse tendency to increase with latitude in some cases (Fecchio et al., 2020), parasite prevalence has been shown to respond more consistently to latitudinal gradients, with prevalence of many parasites increasing towards the equator (Merino et al., 2008; Cuevas et al., 2020; Fecchio et al., 2020). Our results suggest that the prevalence of water mites increases towards higher latitudes, which is the inverse pattern of the predictions by Janzen (1970) and

Connell (1971) that higher parasitic loads should be expected at lower latitudes due to climatic stability. These results go against the general rule for latitudinal gradients that expects an increase in species interactions toward the equator (Schemske et al., 2009; Cuevas et al., 2020; Fecchio et al., 2020). The pattern found in our study may be a consequence of host biology and occurrence, both of which also follow a latitudinal gradient (Møller, 1998; Raffel et al., 2008; Salkeld et al., 2008; Pearson and Boyero, 2009), but may also show that endoparasites of insects exhibit similar prevalences regardless of environmental conditions.

Factors other than the latitudinal gradient may also influence parasitism, such as host-related determinants – behavior, taxonomic group and body size (Morand, 2015) and other climatic variables (Guernier et al., 2004). Here, some of the climatic or environmental factors considered showed an effect on prevalence of water mites, especially Net Primary Production. The observable effect of NPP (an indicator of vegetation density and plant biomass) may suggest that forested environments influence the prevalence of water mites in odonate hosts. Considering that conservation areas may exhibit a higher host richness and abundance, reduced prevalence may be an outcome of a dilution effect due to higher host availability. The prevalence of gregarines showed no response towards lower latitudes, nor did it show a relationship with any bioclimatic dimension. These results are contrary to those found for other endoparasites, such as haematozoans of birds and lizards (Merino et al., 2008; Salkeld et al., 2008). These studies highlight the role of climate, especially temperature, in determining prevalence and other ecological processes that influence parasite biodiversity. In our study, gregarine prevalence might have been influenced by host dependence, since endoparasites are in a relatively stable environment inside their hosts (Rohde and Heap, 1998).

Higher parasite prevalence may be related to host activity patterns that could be driven by temperature seasonality and could shape host exposure to parasites (Salkeld et al., 2008). Indeed, since mites and gregarines show seasonal patterns, the period when sampling occurs may also influence estimates of prevalence of parasites, especially in temperate regions (Forbes et al., 2012; Mlynarek et al., 2015). The results obtained here also suggest a role of climatic stability and seasonality on water mite prevalence. For instance, water mite prevalence was lower in sites where diurnal and annual temperature amplitude were higher (Bio2 and Bio7, respectively), probably affecting the stability of mite and host populations. Another explanation could be the effect of temperature variation across seasons on immunity parameters of the hosts (Raffel et al., 2008). A role of temperature in immunity was observed for odonates, in which higher temperatures may cause an increase in immune response and resistance to *Arrenurus*

water mites (Robb and Forbes, 2005). Hence, higher latitudes may result in higher prevalence due to lower host resistance to water mites. Nevertheless, more evidence is needed to identify macroecological factors driving parasitism in insects, since most available data are related to vertebrate hosts (Morand, 2015; Stephens et al., 2016) and the available data regarding arthropod hosts is limited by sampling effort bias (Kamiya et al., 2014) or restricted to higher latitudes in the case of the Odonata database studied here. The limitation of this database is mostly biased by the sampling gaps in tropical regions, mainly in the southern hemisphere. All collection sites were located in the Northern Hemisphere, and the samples were obtained across a time span of several decades (see dataset in Supplementary Tables S1–S4). Nevertheless, the collection sites cover a broad latitudinal range, and any year-to-year variation in local bioclimatic conditions is likely insignificant compared with large scale geographic variation.

In conclusion, only the prevalence of water mites parasitizing Odonata responds to latitudinal and bioclimatic gradients, tending to be highest at lower latitudes. Our study adds evidence that supports the notion that endoparasites remain unaffected inside their hosts. The role of bioclimatic variables in determining prevalence indicates that parasitic organisms may prove reliable sources of information about climate change and its impact on ecological interactions.

Acknowledgements

GGs thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES, Brazil for a scholarship grant (Proc. 88882.426416/2019-01). RG thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Brazil for a productivity grant (Proc. 307836/2019-3), and the São Paulo Research Foundation – FAPESP, Brazil for ongoing support (Proc. 2019/20130-2).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ijpara.2020.11.008>.

References

- Åbro, A., 1976. The mode of gregarine infection in Zygoptera (Odonata). *Zool. Scr.* 5, 265–275. <https://doi.org/10.1111/j.1463-6409.1976.tb00708.x>.
- Allen, A.P., Brown, J.H., Gillooly, J.F., 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* 297, 1545–1548. <https://doi.org/10.1126/science.1072380>.
- Amaral, H.L.daC., Bergmann, F.B., dos Santos, P.R.S., Silveira, T., Krüger, R.F., 2017. How do seasonality and host traits influence the distribution patterns of parasites on juveniles and adults of *Columba livia*? *Acta Trop.* 176, 305–310. <https://doi.org/10.1016/j.actatropica.2017.08.023>.
- Barrow, L.N., McNew, S.M., Mitchell, N., Galen, S.C., Lutz, H.L., Skeen, H., Valqui, T., Weckstein, J.D., Witt, C.C., 2019. Deeply conserved susceptibility in a multi-host, multi-parasite system. *Ecol. Lett.* 22, 987–998. <https://doi.org/10.1111/ele.13263>.
- Beckmann, M., Václavík, T., Manceur, A.M., Šprtová, L., von Wehrden, H., Welk, E., Cord, A.F., 2014. glUV: A global UV-B radiation data set for macroecological studies. *Methods Ecol. Evol.* 5, 372–383. <https://doi.org/10.1111/2041-210X.12168>.
- Brasil, L.S., Silverio, D.V., Cabette, H.S.R., Batista, J.D., Vieira, T.B., Dias-Silva, K., Oliveira-Junior, J.M.B., Carvalho, F.G., Calvão, L.B., Macedo, M.N., Juen, L., 2019. Net primary productivity and seasonality of temperature and precipitation are predictors of the species richness of the Damselflies in the Amazon. *Basic Appl. Ecol.* 35, 45–53. <https://doi.org/10.1016/j.baae.2019.01.001>.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789. <https://doi.org/10.1890/03-9000>.
- Clark, N.J., 2018. Phylogenetic uniqueness, not latitude, explains the diversity of avian blood parasite communities worldwide. *Glob. Ecol. Biogeogr.* 27, 744–755. <https://doi.org/10.1111/geb.12741>.
- Clopton, R.E., Janovy, J., 1993. Developmental niche structure in the gregarine assemblage parasitizing *Tenebrio molitor*. *J. Parasitol.* 79, 701. <https://doi.org/10.2307/3283608>.

- Connell, J.H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Den Boer, P.J., Gradwell, G.R. (Eds.), *Dynamics of Populations*. PUDOC, Wageningen, pp. 298–312.
- Cordero-Rivera, A., Barreiro, A.R., Otero, M.C., 2019. *Forcipomyia paludis* (Diptera: Ceratopogonidae) in the Iberian Peninsula, with notes on its behaviour parasitizing odonates. *Boletín la SEA*, 243–250.
- Cuevas, E., Vianna, J.A., Botero-Delgado, E., Doussang, D., González-Acuña, D., Barroso, O., Rozzi, R., Vásquez, R.A., Quirici, V., 2020. Latitudinal gradients of haemosporidian parasites: Prevalence, diversity and drivers of infection in the Thorn-tailed Rayadito (*Aphrastura spinicauda*). *Int. J. Parasitol. Parasites Wildl.* 11, 1–11. <https://doi.org/10.1016/j.ijppaw.2019.11.002>.
- Cyr, H., Downing, J.A., 1988. Empirical relationships of phytomacrofaunal abundance of plant biomass and macrophyte bed characteristics. *Can. J. Fish. Aquat. Sci.* 45, 976–984. <https://doi.org/10.1139/f88-120>.
- da Silva Monteiro Júnior, C., Couceiro, S.R.M., Hamada, N., Juen, L., 2013. Effect of vegetation removal for road building on richness and composition of Odonata communities in Amazonia, Brazil. *Int. J. Odonatol.* 16, 135–144. <https://doi.org/10.1080/13887890.2013.764798>.
- De Marco, P., Batista, J.D., Cabette, H.S.R., 2015. Community assembly of adult odonates in tropical streams: An ecophysiological hypothesis. *PLoS One* 10. <https://doi.org/10.1371/journal.pone.0123023>.
- Eriksson, A., Doherty, J.F., Fischer, E., Gracioli, G., Poulin, R., 2020. Hosts and environment overshadow spatial distance as drivers of bat fly species composition in the Neotropics. *J. Biogeogr.* 47, 736–747. <https://doi.org/10.1111/jbi.13757>.
- Fecchio, A., Bell, J.A., Bosholn, M., Vaughan, J.A., Tkach, V.V., Lutz, H.L., Cueto, V.R., Gorosito, C.A., González-Acuña, D., Stromlund, C., Kvasager, D., Comiche, K.J.M., Kirchgatter, K., Pinho, J.B., Berv, J., Anciães, M., Fontana, C.S., Zyskowski, K., Sampaio, S., Dispoto, J.H., Galen, S.C., Weckstein, J.D., Clark, N.J., 2020. An inverse latitudinal gradient in infection probability and phylogenetic diversity for *Leucocytozoon* blood parasites in New World birds. *J. Anim. Ecol.* 89, 423–435. <https://doi.org/10.1111/1365-2656.13117>.

- Forbes, M.R., Mlynarek, J.J., Allison, J., Hecker, K.R., 2012. Seasonality of gregarine parasitism in the damselfly, *Nehalennia irene*: Understanding unimodal patterns. *Parasitol. Res.* 110, 245–250. <https://doi.org/10.1007/s00436-011-2478-1>.
- Garamszegi, L.Z., 2014. Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice. Springer, Berlin. Guernier, V., Hochberg, M.E., Guégan, J.F., 2004. Ecology drives the worldwide distribution of human diseases. *PLoS Biol.* 2, 740–746. <https://doi.org/10.1371/journal.pbio.0020141>.
- Guillermo-Ferreira, R., Del-Claro, K., 2011a. Oviposition site selection in *Oxyagrion microstigma* Selys, 1876 (Odonata: Coenagrionidae) is related to aquatic vegetation structure. *Int. J. Odonatol.* 14, 275–279. <https://doi.org/10.1080/13887890.2011.621109>.
- Guillermo-Ferreira, R., Del-Claro, K., 2011b. Resource defense polygyny by *Hetaerina rosea* Selys (Odonata: Calopterygidae): Influence of age and wing pigmentation. *Neotrop. Entomol.* 40, 78–84. <https://doi.org/10.1590/S1519-566X2011000100011>.
- Guillermo-Ferreira, R., Vilela, D.S., 2013. New records of *Forcipomyia (Pterobosca) incubans* (Diptera: Ceratopogonidae) parasitizing wings of Odonata in Brazil. *Biota Neotrop.* 13, 360–362. <https://doi.org/10.1590/S1676-06032013000100037>.
- Hadfield, J.D., 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* 33, 1–22.
- Hadfield, J.D., Nakagawa, S., 2010. General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multitrait models for continuous and categorical characters. *J. Evol. Biol.* 23, 494–508. <https://doi.org/10.1111/j.1420-9101.2009.01915.x>.
- Hassall, C., Thompson, D.J., 2008. The effects of environmental warming on odonata: A review. *Int. J. Odonatol.* 11, 131–153. <https://doi.org/10.1080/13887890.2008.9748319>.
- Hijmans, R.J., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol. A J. R. Meteorol. Soc.* 25, 1965–1978. <https://doi.org/10.1002/joc.1276>.
- Hupało, K., Rachalewski, M., Rachalewska, D., Tończyk, G., 2014. Gregarine parasitism in two damselfly hosts: Comparison between species, sexes, and sites (Odonata: Calopterygidae). *Odonatologica* 43, 199–211.

- Hykel, M., Růžičková, J., Dolný, A., 2020. Perch selection in *Sympetrum* species (Odonata: Libellulidae): importance of vegetation structure and composition. *Ecol. Entomol.* 45, 90–96. <https://doi.org/10.1111/een.12778>.
- Ilvonen, J.J., Kaunisto, K.M., Suhonen, J., 2018. Odonates, gregarines and water mites: why are the same host species infected by both parasites? *Ecol. Entomol.* 43, 591–600. <https://doi.org/10.1111/een.12634>.
- Imhoff, M.L., Bounoua, L., 2006. Exploring global patterns of net primary production carbon supply and demand using satellite observations and statistical data. *J. Geophys. Res. Atmos.* 111, 1–8. <https://doi.org/10.1029/2006JD007377>.
- Jablonski, D., Huang, S., Roy, K., Valentine, J.W., 2017. Shaping the latitudinal diversity gradient: New perspectives from a synthesis of paleobiology and biogeography. *Am. Nat.* 189, 1–12. <https://doi.org/10.1086/689739>.
- Jancarova, M., Hlavacova, J., Votypka, J., Volf, P., 2016. An increase of larval rearing temperature does not affect the susceptibility of *Phlebotomus sergenti* to *Leishmania tropica* but effectively eliminates the gregarine *Psychodiella sergenti*. *Parasit. Vectors* 9, 553. <https://doi.org/10.1186/s13071-016-1841-6>.
- Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104, 501–528. <https://doi.org/10.1086/282687>.
- Kalkman, V.J., Clausnitzer, V., Dijkstra, K.D.B., Orr, A.G., Paulson, D.R., Van Tol, J., 2008. Global diversity of dragonflies (Odonata) in freshwater. *Hydrobiologia* 595, 351–363. <https://doi.org/10.1007/s10750-007-9029-x>.
- Kamiya, T., O’Dwyer, K., Nakagawa, S., Poulin, R., 2014. What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biol. Rev.* 89, 123–134. <https://doi.org/10.1111/brv.12046>.
- Kaunisto, K.M., Morrill, A., Forbes, M.R., 2018. Negative covariance between water mite and gregarine parasitism for adult dragonflies, *Leucorrhinia intacta* (Hagen): an age-related pattern? *Parasitol. Res.* 117, 3909–3915. <https://doi.org/10.1007/s00436-018-6100-7>.
- Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S., Poulin, R., 2007. Geographical variation in the “bottom-up” control of diversity: Fleas and their small mammalian hosts. *Glob. Ecol. Biogeogr.* 16, 179–186. <https://doi.org/10.1111/j.1466-8238.2006.00273.x>.

- Lafferty, K.D., Dobson, A.P., Kuris, A.M., 2006. Parasites dominate food web links. *Proc. Natl. Acad. Sci. U.S.A.* 103, 11211–11216. <https://doi.org/10.1073/pnas.0604755103>.
- Lynch, M., 1991. Methods for the analysis of comparative data in evolutionary biology. *Evolution* 45, 1065–1080. <https://doi.org/10.1111/j.1558-5646.1991.tb04375.x>.
- Mendes, G.C., da Silva, G.G., Ricioli, L.S., Guillermo, R., 2019. The biotic environment: multiple interactions in an aquatic world. In: Del-Claro, K., Guillermo, R. (Eds.), *Aquatic Insects*. Springer International Publishing, New York, pp. 95–116. https://doi.org/10.1007/978-3-030-16327-3_5.
- Merino, S., Moreno, J., Vásquez, R.A., Martínez, J., Sánchez-Monsálvez, I., Estades, C. F., Ippi, S., Sabat, P., Rozzi, R., McGehee, S., 2008. Haematozoa in forest birds from southern Chile: Latitudinal gradients in prevalence and parasite lineage richness. *Austral Ecol.* 33, 329–340. <https://doi.org/10.1111/j.1442-9993.2008.01820.x>.
- Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H.A., McCain, C.M., McCune, A.R., McDade, L.A., McPeck, M.A., Near, T.J., Price, T.D., Ricklefs, R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, J.M., Turelli, M., 2007. Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecol. Lett.* 10, 315–331. <https://doi.org/10.1111/j.1461-0248.2007.01020.x>.
- Mlynarek, J.J., Knee, W., Forbes, M.R., 2015. Host phenology, geographic range size and regional occurrence explain interspecific variation in damselfly-water mite associations. *Ecography (Cop.)* 38, 670–680. <https://doi.org/10.1111/ecog.00997>.
- Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G., 2009. Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *PLoS Med* 6,. <https://doi.org/10.1371/journal.pmed1000097> e1000097.
- Møller, A.P., 1998. Evidence of larger impact of parasites on hosts in the tropics: investment in immune function within and outside the tropics. *Oikos* 82, 265. <https://doi.org/10.2307/3546966>.
- Morand, S., 2015. (macro-) Evolutionary ecology of parasite diversity: From determinants of parasite species richness to host diversification. *Int. J. Parasitol. Parasites Wildl.* 4, 80–87. <https://doi.org/10.1016/j.ijppaw.2015.01.001>.

- O'Donnell, M.S., Ignizio, D.A., 2012. Bioclimatic predictors for supporting ecological applications in the conterminous United States. *US Geol. Surv. Data Ser.* 691, 1–10.
- Paradis, E., Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35, 526–528. <https://doi.org/10.1093/bioinformatics/bty633>.
- Pearson, R.G., Boyero, L., 2009. Gradients in regional diversity of freshwater taxa. *J. N. Am. Benthol. Soc.* 28, 504–514. <https://doi.org/10.1899/08-118.1>.
- Pianka, E.R., 1966. Latitudinal gradients in species diversity: a review of concepts. *Am. Nat.* 100, 33–46. <https://doi.org/10.1086/282398>.
- Pontarp, M., Bunnefeld, L., Cabral, J.S., Etienne, R.S., Fritz, S.A., Gillespie, R., Graham, C.H., Hagen, O., Hartig, F., Huang, S., Jansson, R., Maliet, O., Münkemüller, T., Pellissier, L., Rangel, T.F., Storch, D., Wiegand, T., Hurlbert, A.H., 2019. The latitudinal diversity gradient: novel understanding through mechanistic ecoevolutionary models. *Trends Ecol. Evol.* 34, 211–223. <https://doi.org/10.1016/j.tree.2018.11.009>.
- Poulin, R., 1995. Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecol. Monogr.* 65, 283–302. <https://doi.org/10.2307/2937061>.
- Poulin, R., Morand, S., 2000. The diversity of parasites. *Q. Rev. Biol.* 75, 277–293. <https://doi.org/10.1086/393500>.
- Pozojević, I., Brigić, A., Gottstein, S., 2018. Water mite (Acari: Hydrachnidia) diversity and distribution in undisturbed Dinaric karst springs. *Exp. Appl. Acarol.* <https://doi.org/10.1007/s10493-018-0294-3>.
- Preisser, W., 2019. Latitudinal gradients of parasite richness: a review and new insights from helminths of cricetid rodents. *Ecography (Cop.)* 42, 1315–1330. <https://doi.org/10.1111/ecog.04254>.
- Raffel, T.R., Martin, L.B., Rohr, J.R., 2008. Parasites as predators: unifying natural enemy ecology. *Trends Ecol. Evol.* 23, 610–618. <https://doi.org/10.1016/j.tree.2008.06.015>.
- Robb, T., Forbes, M.R., 2005. On understanding seasonal increases in damselfly defence and resistance against ectoparasitic mites. *Ecol. Entomol.* 30, 334–341. <https://doi.org/10.1111/j.0307-6946.2005.00689.x>.

- Rodrigues, M.E., de Oliveira Roque, F., Quintero, J.M.O., de Castro Pena, J.C., de Sousa, D.C., De Marco Junior, P., 2016. Nonlinear responses in damselfly community along a gradient of habitat loss in a savanna landscape. *Biol. Conserv.* 194, 113–120. <https://doi.org/10.1016/j.biocon.2015.12.001>.
- Rohde, K., 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65, 514–527 <https://www.doi.org/10.2307/3545569>.
- Rohde, K., Heap, M., 1998. Latitudinal differences in species and community richness and in community structure of metazoan endo- and ectoparasites of marine teleost fish. *Int. J. Parasitol.* 28, 461–474. [https://doi.org/10.1016/S0020-7519\(97\)00209-9](https://doi.org/10.1016/S0020-7519(97)00209-9).
- Rolff, J., Martens, A., 1997. Completing the life cycle: Detachment of an aquatic parasite (*Arrenurus cuspidator*, Hydrachnellae) from an aerial host (*Coenagrion puella*, Odonata). *Can. J. Zool.* 75, 655–659. <https://doi.org/10.1139/z97-084>.
- Salkeld, D.J., Trivedi, M., Schwarzkopf, L., 2008. Parasite loads are higher in the tropics: temperate to tropical variation in a single host-parasite system. *Ecography (Cop.)* 31, 538–544. <https://doi.org/10.1111/j.0906-7590.2008.05414.x>.
- Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M., Roy, K., 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Evol. Syst.* 40, 245–269. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173430>.
- 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., Park, A., Vazquez-Prokopec, G.M., Schmidt, J.P., Poulin, R., 2016. The macroecology of infectious diseases: a new perspective on global-scale drivers of pathogen distributions and impacts. *Ecol. Lett.* 19, 1159–1171. <https://doi.org/10.1111/ele.12644>.
- Svensson-Coelho, M., Ellis, V.A., Loiselle, B.A., Loiselle, J.G., Ricklefs, R.E., 2014. Reciprocal specialization in multihost malaria parasite communities of birds: A temperate-tropical comparison. *Am. Nat.* 184, 624–635. <https://doi.org/10.1086/678126>.
- Tavares, R.I.S., Mandelli, A.M., Mazão, G.R., Guillermo-Ferreira, R., 2017. The relationship between habitat complexity and emergence time in damselflies. *Limnologia* 65, 1–3. <https://doi.org/10.1016/j.limno.2017.04.009>.

- Waller, J.T., Svensson, E.I., 2017. Body size evolution in an old insect order: No evidence for Cope's Rule in spite of fitness benefits of large size. *Evolution* (N. Y.) 71, 2178–2193. <https://doi.org/10.1111/evo.13302>.
- Więcek, M., Martin, P., Gąbka, M., 2013. Distribution patterns and environmental correlates of water mites (Hydrachnidia, Acari) in peatland microhabitats. *Exp. Appl. Acarol.* 61, 147–160. <https://doi.org/10.1007/s10493-013-9692-8>.
- Wildermuth, H., Martens, A., 2007. The feeding action of *Forcipomyia paludism* (Diptera: Ceratopogonidae), a parasite of Odonata imagines. *Int. J. Odonatol.* 10, 249–255. <https://doi.org/10.1080/13887890.2007.9748302>.
- Willig, M.R., Kaufman, D.M., Stevens, R.D., 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* 34, 273–309. <https://doi.org/10.1146/annurev.ecolsys.34.012103.144032>.
- Zawal, A., Bańkowska, A., Nowak, A., 2018a. Influence of temperature and light–dark cycle on hatching of *Eylais extendens*. *Exp. Appl. Acarol.* 74, 283–289. <https://doi.org/10.1007/s10493-018-0238-y>.
- Zawal, A., Buczyński, P., 2013. Parasitism of Odonata by *Arrenurus* (Acari: Hydrachnidia) larvae in the Lake Świdwie, nature reserve (NW Poland). *Acta Parasitol.* 58, 486–495. <https://doi.org/10.2478/s11686-013-0162-6>.
- Zawal, A., Stryjecki, R., Buczyńska, E., Buczyński, P., Pakulnicka, J., Bańkowska, A., Czernicki, T., Janusz, K., Szlauer-Łukaszewska, A., Pešić, V., 2018b. Water mites (Acari, Hydrachnidia) of riparian springs in a small lowland river valley: what are the key factors for species distribution? *PeerJ* 6. <https://doi.org/10.7717/peerj.4797> e4797.

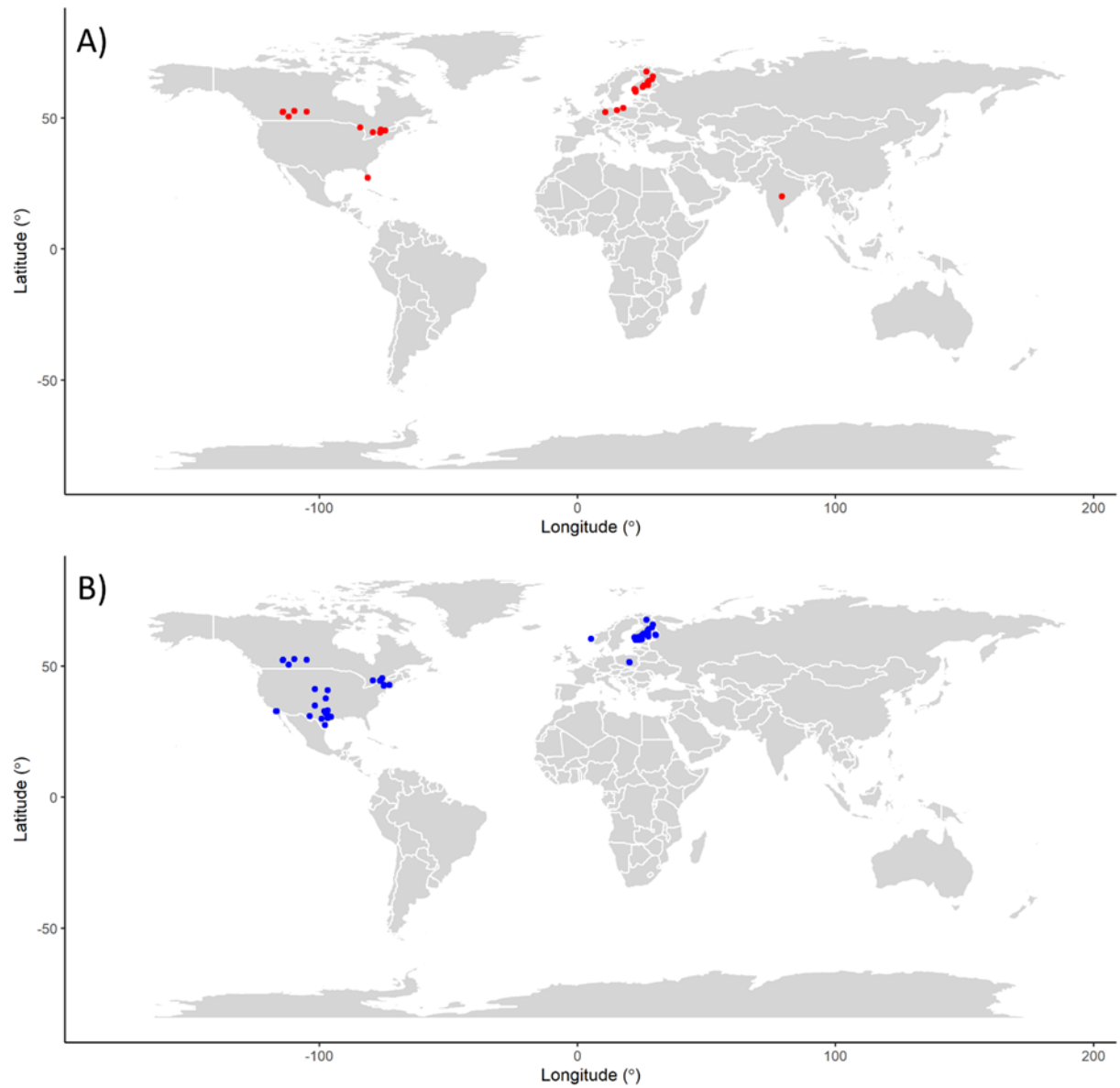
Figures

Figure 1. Locations of the host-parasite samples retrieved from the literature and included in the dataset on parasitized Odonata, representing occurrences of water mites (A) and gregarines (B).

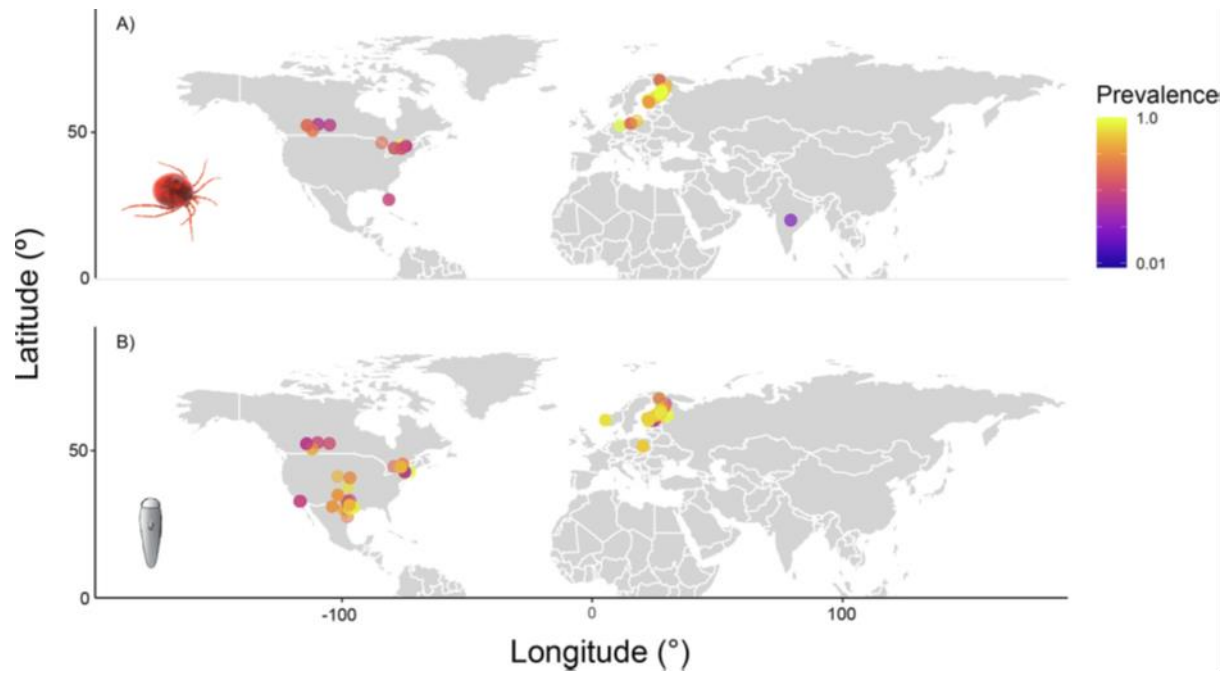


Figure 2. The distribution of prevalence of water mites (A) and gregarines (B) in populations of Odonata across studies in the Northern Hemisphere. The heat scale bar represents the gradient of prevalence, from low (close to 0.01) to maximum (1.0). Note: when more than one population was sampled from the same location, the mean prevalence was computed across samples for illustrative purposes only.

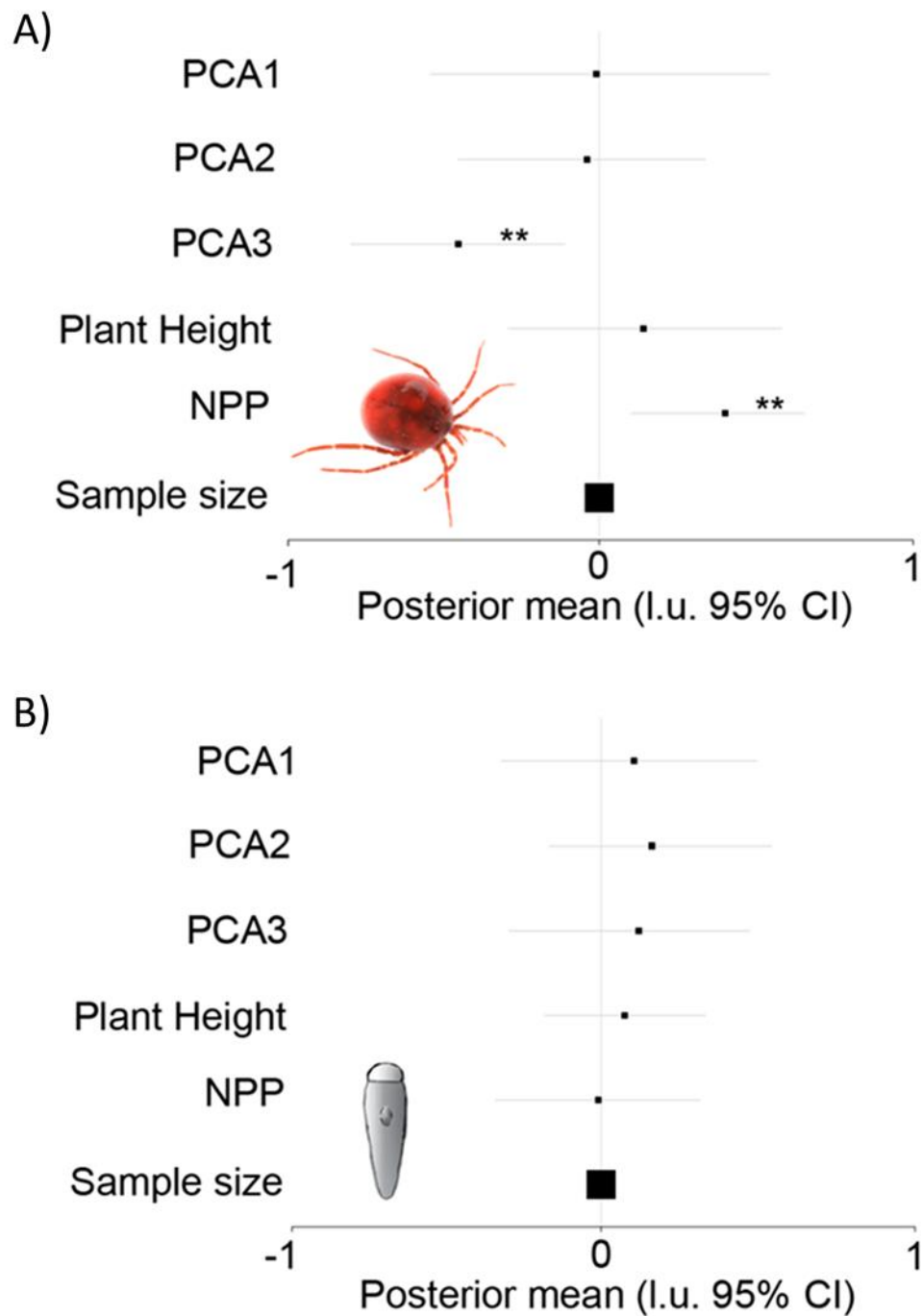


Figure 3. Forest plot for the results of the Generalised Linear Mixed Models using Markov chain Monte Carlo built with prevalence of water mites (A) and gregarines (B) as response variables and host species and study ID as random effects, showing posterior mean estimates and lower and upper (l.u.) 95% credible intervals of predictors. Significance values of pMCMC: ** <math><0.01</math>.

Tables

Table 1. Parameters describing the bioclimatic variables, UV-B radiation and latitude of sampled sites. The correlations of these parameters are shown on the first axis of the principal component analysis. The scores of the three axes were used in further analyses as predictor variables.

Variables	Water mites			Gregarines		
	PCA1	PCA2	PCA3	PCA1	PCA2	PCA3
Bio1	0.935	-0.119	-0.131	0.981	-0.046	0.084
Bio2	0.383	0.249	0.828	0.566	-0.697	0.336
Bio3	0.750	-0.384	0.334	0.903	-0.276	-0.074
Bio4	-0.543	0.746	0.344	-0.615	-0.467	0.604
Bio5	0.867	0.184	0.365	0.823	-0.422	0.357
Bio6	0.630	-0.419	-0.637	0.836	0.317	-0.246
Bio7	-0.251	0.688	0.658	-0.238	-0.733	0.618
Bio8	0.248	-0.373	0.308	0.354	-0.358	-0.259
Bio9	0.486	-0.686	-0.354	0.838	0.155	-0.377
Bio10	0.925	0.136	0.165	0.881	-0.268	0.327
Bio11	0.793	-0.436	-0.395	0.954	0.142	-0.156
Bio12	0.805	0.442	-0.275	0.283	0.918	0.213
Bio13	0.846	-0.251	0.197	0.468	0.771	-0.106
Bio14	0.432	0.809	-0.384	-0.047	0.838	0.458
Bio15	-0.025	-0.779	0.593	0.099	-0.533	-0.730
Bio16	0.885	-0.116	0.169	0.353	0.820	-0.084
Bio17	0.426	0.800	-0.406	0.093	0.865	0.448
Bio18	0.724	0.174	0.102	-0.206	0.630	0.281
Bio19	0.378	0.720	-0.559	0.195	0.872	0.105
UV-B	0.841	0.259	0.415	-0.848	0.267	-0.380
Latitude	-0.861	-0.309	-0.342	0.863	-0.357	0.325

CAPÍTULO 2 - Effects of ecological marginality on the abundance of fleas on small mammals across Eurasia

Abstract

A general biogeographic rule postulates a center of abundance distribution for organisms and states that abundance reaches its maximum at the center of the distribution range of a given species and decreases towards the edges of this range. Patterns of spatial variation in parasitism are closely related to host spatial patterns. Density and aggregation of hosts, for example, are well known predictors of richness and abundance of parasites. Therefore, parasitism diversity is driven by multiple factors, including host-related and environmental-related predictors. Considering this, we hypothesized that mean abundance of parasites would be higher towards the limits of the occurrence area of hosts. We used marginality measures (i.e., the distance between mean habitat conditions used by species and mean habitat conditions of the sampling area) and Bayesian linear mixed models to test whether there is a geographic or climatic predictor of abundance of parasites using a database describing fleas parasitizing small mammals across Eurasia. We found that mean abundance of fleas in the host populations was not influenced by any variables we tested. Our study demonstrates the complexity of elements affecting multiple host-parasite systems on larger scales. These findings suggest that research on the topic may benefit from fewer confounding effects of population dynamics and may help understand what factors drive parasite abundance and its variation from the center to the marginal areas of host distribution ranges.

1. Introduction

A general biogeographic rule postulates a “center of abundance” distribution for organisms, and states that abundance (i.e., densities of individuals) reaches its maximum at the center of the distribution range of a given species and decreases towards the edges of this range, which lies along the species’ niche (Brown et al., 1995; Sagarin & Gaines, 2002). When considering niche as a N-dimensional hypervolume able to sustain a population (Hutchinson, 1957), it is possible to infer that a species’ center of occurrence will mostly overlap its environmental niche (Maguire, 1973). These patterns imply that populations that live at the center of their range experience optimal conditions, in contrast to populations along the margins

of the range that are exposed to suboptimal conditions (Eckert et al., 2008; Gaston, 2003; Pulliam, 1988). Thus, this “centrality/marginality hypothesis” should be reflected in general aspects of the organisms, such as morphology, genetics and physiology (Eckert et al., 2008; Pironon et al., 2015). Due to the occupation of a less suitable environment, marginal populations may face more abiotic and biotic stressors, and thus, they may also be more susceptible to natural enemies, such as predators and parasite infections (Gaston, 2003).

Parasites are vectors of a wide variety of pathogenic organisms of veterinary and medical importance (Kiffner et al., 2011; Ramos et al., 2020). Ticks (Ixodida), for example, transmit more infectious organisms than any other hematophagous arthropods, being the second-most important vector of veterinary concern worldwide, behind only mosquitoes (Nicholson et al., 2018). Fleas are also important vectors of pathogens, mostly known as plague (*Yersinia pestis* bacteria) vectors from rodents to humans (G. Beran, 1994; Bosio et al., 2020). Rodents are cosmopolitan animals, with some species having lived near human agglomerations from the earliest stages of civilization to modern cities (Anglely et al., 2018; Pearce-Duvet, 2006). Some species, such as *Rattus norvegicus* (Berkenhout, 1979), have adapted to urban environments and become pests in most cities worldwide (Anglely et al., 2018; Raymond et al., 2018; Uria et al., 2013). Rodents in general are natural hosts for a large set of pathogens able to infect humans (Mills & Childs, 1998; Vandamme, 2015), highlighting the epidemiological importance of understanding the dynamics that mediate these interactions between hosts, parasites and pathogens (Colwell et al., 2011; Pfäffle et al., 2013). Recent studies have revealed many environmental and spatial factors as drivers of host-parasite interactions (da Silva et al., 2021; Dallas et al., 2018; Stephens et al., 2016).

Patterns of spatial variation in parasitism are closely related to host spatial patterns (Akinyi et al., 2019; Nunn & Dokey, 2006; Poulin et al., 2011). Density and aggregation of hosts, for example, are well known predictors of richness and abundance of parasites (Kiffner et al., 2011; Medina & Langmore, 2019). Considering that higher host abundance is expected at the center of the species’ distributional range (Martínez-Meyer et al., 2013), the impact of density of host individuals on parasitism across the host range could be assessed through sampling, however sampling effort could influence parasites sampling and be a confounding variable in comparative studies relating parasite diversity and home range of hosts (Guégan & Kennedy, 1996; Walther et al., 1995). Therefore, parasitism diversity is driven by multiple factors, including host-related and environmental-related predictors (Maestri et al., 2020).

Among the environmental factors that affect parasitism, some bioclimatic drivers influence various parasitological parameters, such as diversity of species and intensity of infestation (Amaral et al., 2017; da Silva et al., 2021; Oakgrove et al., 2014). For example, frequency of avian blood-borne parasites co-infections is driven by temperature, precipitation and tree cover (Oakgrove et al., 2014). Ectoparasites such as ticks and fleas, in turn, may respond differently. Prevalence of water mites in Odonata hosts respond positively to vegetation biomass and climatic stability, with a tendency to decrease towards lower latitudes (da Silva et al., 2021). The influence of environmental variables has also been demonstrated in hard ticks parasitizing medium-sized mammals, where seasonality was the most important predictor for presence of larvae and nymphs of ticks (Lamattina et al., 2018). Environmental gradients also have an effect on the turnover of flea species parasitizing rodent hosts (Maestri et al., 2017). The variation of community structure and composition of species across sites is also influenced by such environmental elements, with different components of diversity responding to different environmental gradients on a spatial scale (Maestri et al., 2020; Krasnov et al., 2008). Although there is evidence supporting common patterns of spatial distribution for wild populations of many animals (Albery et al., 2022), little is known about the factors that drive these patterns, with even less known about the factors shaping the distribution of the parasites of these species (Albery et al., 2022; Byers et al., 2019).

Therefore, we used marginality measures and Bayesian linear mixed-models to test whether there is a geographic or climatic predictor of abundance of fleas parasitizing small mammals across Eurasia. We hypothesized that mean abundance of parasites would be higher towards the limits of the occurrence area of hosts. Therefore, we expected that abundance would increase as marginality increases.

2. Materials and Methods

2.1. Data compilation

To determine whether host ecological niche or spatial distribution influence parasitism in small mammalian hosts, we used a database of fleas' occurrence in rodents and shrews sampled across Europe and Asia provided by Professor Boris Krasnov. The data was gathered through regional surveys across regions of different sizes of which areas estimations were used in the analysis. The database consisted initially of 143 species of small mammals, with abundance data per flea species per hosts sampled per region. The geographic centroid and area

(in square kilometers) of the regions of sampling were also available. We excluded those host species with cosmopolitan distribution, those with less than ten individuals sampled and those occurring in less than 8 regions. After this filtering, we obtained a list of 20 species comprising of sampling number and region of occurrence. We also calculated mean abundance and diversity of fleas per species at each region of occurrence. We search the GBIF database for occurrence data of these 20 species and filtered the data for valid occurrences (GBIF.org, 13 November 2020, GBIF Occurrence Download <https://doi.org/10.15468/dl.cumw7a>). The analysis was performed using R, version 4.1.0 (R Core Team, 2019. R: A language and environment for statistical computing). After this process, with obtained valid data for 16 host species which were included in our final analysis.

2.2. *Outlying mean index (OMI) analysis and spatial measures*

To perform the OMI analysis, we used the subniche package (Karasiewicz et al., 2017). The OMI analysis (Dolédec et al., 2000) offers a measure of species marginality, that is, the distance between mean habitat conditions used by species and mean habitat conditions of the sampling area. For this analysis, we extracted the mean values of the bioclimatic variables from the WorldClim database (Hijmans, 2005; O'Donnell & Ignizio, 2012) for each region, using their centroids and approximated diameters (in meters) to calculate the area from which the parameters would be extracted. The diameters were approximated by applying a simple geometric formula ($A=\pi r^2$) to the area information. This procedure was necessary because the algorithm through which we extracted bioclimatic data uses circular areas and centroid coordinates as input (Hijmans, 2022). The first step of the OMI analysis consists in performing a PCA on the database of environmental data. We used the data for each sampled population of each species per region. The standardized environmental table obtained through the PCA was then used to perform the OMI analysis. The niche parameters were then obtained (Dolédec et al., 2000). We measured diversity of fleas using the Shannon index, calculated with the vegan package (Oksanen, 2010). Marginality results are presented in Appendix Table 1, with marginality calculated per species in Appendix Table 2. To perform the spatial measures, we used valid occurrence data from GBIF to calculate the centroids of the host species spatial distribution. Then, we measured the distance in kilometers between the centroids of the region where the mammalian species were sampled to the centroids of the area of distribution for each species. We also included sampling effort as a predictor, since the number of hosts examined

varied among the species surveyed and there is evidence for influence of sampling effort on parasite richness (Walther et al., 1995).

2.3. Marginality and spatial analysis

We built Bayesian linear mixed-models using the package “MCMCglmm” (Hadfield, 2010), which is capable of handling information in multivariate models using Markov chain Monte Carlo techniques. For each model, we modelled the mean abundance of fleas in all samples of small mammalians populations. We also included the host species identity and the regions of sampling as random effect variables. Our predictors consisted of distance (in kilometers) for each sample to the centroid of the area of occurrence of the hosts species, number of host individuals sampled per locality, latitude of the centroid of host occurrence, marginality measures (OMI) and the Shannon index for diversity of fleas. We use natural log transformation to account for nonlinearity in the response variable “mean abundance”. The MCMCglmm models were calculated using standard parameters and compared using deviance information criterion (DIC) (Spiegelhalter et al., 2002).

3. Results

3.1. Marginality and spatial analysis

The OMI analysis showed marginality indices ranging from 2.768 to 138.775 to one sample of the following species. The lowest values of marginality were observed in *Apodemus uralensis* (Pallas, 1811), *Microtus agrestis* (Linnaeus, 1761), *Microtus arvalis* (Pallas, 1779), *Sorex araneus* Linnaeus, 1758 and *Sorex caecutiens* Laxmann, 1788 occurring in the Middle Ural region. The highest values for marginality were found in *M. agrestis* (Linnaeus, 1761), *Neomys fodiens* (Pennant, 1771), *S. araneus* Linnaeus, 1758 and *Sorex minutus* Linnaeus, 1766 occurring in Scotland.

The best fitted model included only marginality, Shannon index and latitude as predictive variables. This model revealed that the mean abundance of fleas in the host populations was not influenced by any of the variables we tested (Table 1). We provide the forest plot for these results (Figure 1). We also provide the dispersion graphs of the log-transformed mean abundance as function to marginality (Figure 2), Shannon index (Figure 3) and latitude (Figure 4), since these were the variables included in the best fitted model. Models

which included sampling effort and distance predictors had poorer fitting using DIC. The values for a model composed of all the variables initially included in the analysis are presented in the Appendix Table 3.

4. Discussion

The hypothesis that there exists a “center of abundance” distribution for organisms describes an important biogeographical pattern. It proposes that abundance (i.e., densities of individuals) reaches its maximum at the center of the distribution range of a given species and decreases towards the edges of this range, where niche conditions become marginal (Brown et al., 1995; Sagarin & Gaines, 2002). Suboptimal niche conditions may also be associated with greater susceptibility to natural enemies, such as parasite infections. Here, we tested this idea using fleas parasitic on Eurasian small mammals. We found that local mean abundance of fleas was not influenced by marginality of the host range, host diversity (Shannon index) or latitude. We hypothesized that mean abundance of parasites would be higher towards the limits of the geographical range of hosts, however the results show that mean abundance was not influenced by marginality. Our results did not show any correlation between the number of hosts sampled and abundance of fleas. We also did not find any influence of factors such as latitude or distance between hosts sampling area and area of occurrence on abundance of fleas.

According to the “central-marginal hypothesis”, populations living at the edges of their area of occurrence experience suboptimal conditions and, therefore, have lower genetic variation, lower reproductive success and lower resistance to pathogens and parasites than populations living at the center of their ranges (Eckert et al., 2008). As environmental conditions gradients begin to reach the tolerance limits of organisms, they tend to scatter in small populations, with increasing geographic and genetic distance between them, at the margins of their range (Eckert et al., 2008; Sexton et al., 2009). These environmental conditions are drivers of host patterns of distributions, and thus, indirectly also of their parasites (Krasnov, 2008). Parasites such as fleas, that spend most of their lives away from the host bodies, are more sensitive to variations in environmental conditions, while still to some degree dependent of host responses to the environment (Krasnov, 2008). The turnover of flea species among different sites in the Mongolia region, for example, was shown to be influenced mostly by air temperature, followed by the turnover of their rodent hosts (Maestri et al., 2017). However, there is recent evidence against this relationship between center-marginal gradients of

environmental conditions and species geographic patterns (Dallas & Hastings, 2018), even on a genetic level (Ntuli et al., 2020). In a study of bats from south Asia, researchers did not find any relation between distance from niche centroids and higher abundance or genetic diversity, however they found a negative correlation between genetic diversity and human constructions (Chaiyes et al., 2020). These finding may indicate that other factors than only environmental variables act as predictors of the geographic distribution of species, with abundance and genetic diversity varying according to a set of local variables (Dallas & Hastings, 2018). Thus, the lack of relationship between latitude and abundance of fleas in our data may result from such local-dependent variables, that may be more influential on the host-parasite system we studied.

We found that sampling effort does not affect mean abundance of fleas. A basic premise in most models that try to describe host-parasite dynamics is that parasite transmission is a function of host density (Hopkins et al., 2020). In fact, sampling effort could be considered a proxy for density of hosts (Guégan & Kennedy, 1996; Walther et al., 1995). This relation between parasitism and host density is also found for other groups. Lower densities of fruit fly hosts, for example, could confer a refuge effect from parasitoids (Okuyama, 2016). The contrary was observed for birds, where avian brood parasitism is more intense in populations living in low-density colonies or occupying smaller breeding territory ranges (Medina & Langmore, 2019). Nevertheless, there is evidence that for some cases, flea prevalence and abundance could be better predicted by host home ranges than host densities (Krasnov, 2008). This effect of home ranges is also found in other animals, such as lizards, where the number of ticks collected per individual host is positively correlated with home range of the hosts (Wieczorek et al., 2020). The distance between the centre of the host range and the actual area of sampling did not influence abundance of fleas on rodents in our study.

In carnivore mammals the live within social groups, however, there was evidence for a negative relationship between parasitism and population density (Albery et al., 2020). These findings indicate a major role of active behaviors of spatial organization of hosts in selecting spaces with low risk of parasitism (Albery et al., 2020). Black-tailed prairie dogs also change their behavior when faced with flea parasitism (Eads et al., 2017). In a study with urban brown rats *R. norvegicus* (Berkenhout, 1979) sampled across sites in New York City, researchers found a diverse community of parasites, with more similarities in composition of species in sites nearer one from another (Anglely et al., 2018). These findings may be a consequence of the territorial behavior and small home range of these animals (Himsworth et al., 2014). Rodents are very social animals, able to detect and respond to parasitic infestation in

conspecifics (Kavaliers et al., 2020). Thus, they are able to actively react to parasitic infestation and decrease the effect of population density on abundance of fleas. This may indicate that other sets of variables not included among our predictors are affecting parasitism in the host-parasite systems we sampled.

In conclusion, neither of the variables we tested had an influence on the mean abundance of fleas of small mammalian hosts. Our study demonstrates the complexity of elements affecting multiple host-parasite systems on larger scales. Future research on the topic adopting local approaches may benefit from fewer confounding effects of population dynamics and, thus, may help understand what factors drive parasite abundance and how it may vary from the center to the marginal areas of host distribution ranges.

References

- Akinyi, M. Y., Jansen, D., Habig, B., Gesquiere, L. R., Alberts, S. C., & Archie, E. A. (2019). Costs and drivers of helminth parasite infection in wild female baboons. *Journal of Animal Ecology*, 88(7), 1029–1043. <https://doi.org/10.1111/1365-2656.12994>
- Albery, G. F., Newman, C., Ross, J. B., MacDonald, D. W., Bansal, S., & Buesching, C. (2020). Negative density-dependent parasitism in a group-living carnivore. *Proceedings of the Royal Society B: Biological Sciences*, 287(1941), 20202655. <https://doi.org/10.1098/rspb.2020.2655>
- Albery, G. F., Sweeny, A. R., Becker, D. J., & Bansal, S. (2022). Fine-scale spatial patterns of wildlife disease are common and understudied. *Functional Ecology*, 36(1), 214–225. <https://doi.org/10.1111/1365-2435.13942>
- Amaral, H. L. da C., Bergmann, F. B., dos Santos, P. R. S., Silveira, T., & Krüger, R. F. (2017). How do seasonality and host traits influence the distribution patterns of parasites on juveniles and adults of *Columba livia*? *Acta Tropica*, 176(September 2016), 305–310. <https://doi.org/10.1016/j.actatropica.2017.08.023>
- Angley, L. P., Combs, M., Firth, C., Frye, M. J., Lipkin, I., Richardson, J. L., & Munshi-South, J. (2018). Spatial variation in the parasite communities and genomic structure of urban rats in New York City. *Zoonoses and Public Health*, 65(1), e113–e123. <https://doi.org/10.1111/zph.12418>

- Beran, G. (1994). Handbook of ZOOZOSES (G. W. Beran, J. H. Steele, A. S. Benenson, M. Torten, D. W. Dreesen, M. Ristic, & A. C. Pier (eds.); Second Edition. CRC Press. <https://doi.org/10.1201/9781003006107>
- Bosio, C. F., Jarrett, C. O., Scott, D. P., Fintzi, J., & Hinnebusch, B. J. (2020). Comparison of the transmission efficiency and plague progression dynamics associated with two mechanisms by which fleas transmit *Yersinia pestis*. *PLoS Pathogens*, 16(12), 1–19. <https://doi.org/10.1371/journal.ppat.1009092>
- Brown, J., Mehlman, W., & Stevens, G. (1995). Spatial variation on abundance. *Ecology*, 76(7), 2028–2043.
- Byers, J. E., Schmidt, J. P., Pappalardo, P., Haas, S. E., & Stephens, P. R. (2019). What factors explain the geographical range of mammalian parasites? *Proceedings of the Royal Society B: Biological Sciences*, 286(1903). <https://doi.org/10.1098/rspb.2019.0673>
- Chaiyes, A., Escobar, L. E., Willcox, E. V., Duengkae, P., Suksavate, W., Watcharaanantapong, P., Pongpattananurak, N., Wacharapluesadee, S., & Hemachudha, T. (2020). An assessment of the niche centroid hypothesis: *Pteropus lylei* (Chiroptera). *Ecosphere*, 11(5). <https://doi.org/10.1002/ecs2.3134>
- Colwell, D. D., Dantas-Torres, F., & Otranto, D. (2011). Vector-borne parasitic zoonoses: Emerging scenarios and new perspectives. *Veterinary Parasitology*, 182(1), 14–21. <https://doi.org/10.1016/j.vetpar.2011.07.012>
- da Silva, G. G., Poulin, R., & Guillermo-Ferreira, R. (2021). Do latitudinal and bioclimatic gradients drive parasitism in Odonata? *International Journal for Parasitology*, 51(6), 463–470. <https://doi.org/10.1016/j.ijpara.2020.11.008>
- Dallas, T. A., Aguirre, A. A., Budischak, S., Carlson, C., Ezenwa, V., Han, B., Huang, S., & Stephens, P. R. (2018). Gauging support for macroecological patterns in helminth parasites. *Global Ecology and Biogeography*, 27(12), 1437–1447. <https://doi.org/10.1111/geb.12819>
- Dallas, T. A., & Hastings, A. (2018). Habitat suitability estimated by niche models is largely unrelated to species abundance. *Global Ecology and Biogeography*, 27(12), 1448–1456. <https://doi.org/10.1111/geb.12820>

- Dolédec, S., Chessel, D., & Gimaret-Carpentier, C. (2000). Niche separation in community ecology: A new method. *Ecology*, 81(10), 2914–2927.
- Eads, D. A., Biggins, D. E., & Eads, S. L. (2017). Grooming behaviors of black-tailed prairie dogs are influenced by flea parasitism, conspecifics, and proximity to refuge. *Ethology*, 123(12), 924–932. <https://doi.org/10.1111/eth.12690>
- Eckert, C., Samis, K., & Loughheed, S. (2008). Genetic variation across species' geographical ranges : the central – marginal hypothesis and beyond. *Molecular Ecology*, 17, 1170–1188. <https://doi.org/10.1111/j.1365-294X.2007.03659.x>
- Gaston, K. J. (2003). The Structure and Dynamics of Geographic Ranges. *Evolutionary Ecology*, 266.
- Guégan, J. F., & Kennedy, C. R. (1996). Parasite richness/sampling effort/host range: The fancy three-piece jigsaw puzzle. *Parasitology Today*, 12(9), 367–369. [https://doi.org/10.1016/0169-4758\(96\)10054-5](https://doi.org/10.1016/0169-4758(96)10054-5)
- Hadfield, J. D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R package. *Journal of Statistical Software*, 33(2), 1–22. <https://www.jstatsoft.org/v33/i02/>
- Hijmans, R. J. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965–1978.
- Hijmans, R. J. (2022). raster: Geographic Data Analysis and Modelling. <https://cran.r-project.org/package=raster>
- Himsworth, C. G., Jardine, C. M., Parsons, K. L., Feng, A. Y. T., & Patrick, D. M. (2014). The characteristics of wild rat (*Rattus* spp.) populations from an inner-city neighborhood with a focus on factors critical to the understanding of rat-associated zoonoses. *PLoS ONE*, 9(3). <https://doi.org/10.1371/journal.pone.0091654>
- Hopkins, S. R., Fleming-Davies, A. E., Belden, L. K., & Wojdak, J. M. (2020). Systematic review of modelling assumptions and empirical evidence: Does parasite transmission increase nonlinearly with host density? *Methods in Ecology and Evolution*, 11(4), 476–486. <https://doi.org/10.1111/2041-210X.13361>
- Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22(0), 415–427. <https://doi.org/10.1101/sqb.1957.022.01.039>

- Karasiewicz, S., Dolédec, S., & Lefebvre, S. (2017). Within outlying mean indexes: Refining the OMI analysis for the realized niche decomposition. *PeerJ*, 2017(5), 1–17. <https://doi.org/10.7717/peerj.3364>
- Kavaliers, M., Ossenkopp, K., & Choleris, E. (2020). Pathogens, odors, and disgust in rodents. *Neuroscience and Biobehavioral Reviews*, 119(September), 281–293. <https://doi.org/10.1016/j.neubiorev.2020.09.037>
- Kiffner, C., Vor, T., Hagedorn, P., Niedrig, M., & Rühle, F. (2011). Factors affecting patterns of tick parasitism on forest rodents in tick-borne encephalitis risk areas, Germany. *Parasitology Research*, 108(2), 323–335. <https://doi.org/10.1007/s00436-010-2065-x>
- Krasnov, B. R. (2008). *Functional and Evolutionary Ecology of Fleas*. In Cambridge University Press. Cambridge University Press. <https://doi.org/10.1017/CBO9780511542688>
- Krasnov, B. R., Shenbrot, G. I., Khokhlova, I. S., Vinarski, M., Korralo-Vinarskaya, N., & Poulin, R. (2008). Geographical patterns of abundance: testing expectations of the ‘abundance optimum’ model in two taxa of ectoparasitic arthropods. *Journal of Biogeography*, 35(12), 2187–2194. <https://doi.org/10.1111/j.1365-2699.2008.01978.x>
- Lamattina, D., Costa, S. A., Arrabal, J. P., Venzal, J. M., Guglielmone, A. A., & Nava, S. (2018). Factors associated with hard tick (Acari: Ixodidae) parasitism in medium-sized mammals in the Atlantic Rainforest region of Argentina. *Ticks and Tick-Borne Diseases*, 9(6), 1451–1458. <https://doi.org/10.1016/j.ttbdis.2018.06.009>
- Maestri, R., Shenbrot, G. I., & Krasnov, B. R. (2017). Parasite beta diversity, host beta diversity and environment: application of two approaches to reveal patterns of flea species turnover in Mongolia. *Journal of Biogeography*, 44(8), 1880–1890. <https://doi.org/10.1111/jbi.13025>
- Maestri, R., Shenbrot, G. I., Warburton, E. M., Khokhlova, I. S., & Krasnov, B. R. (2020). Contrasting responses of beta diversity components to environmental and host-associated factors in insect ectoparasites. *Ecological Entomology*, 45(3), 594–605. <https://doi.org/10.1111/een.12834>
- Maguire, B. (1973). Niche Response Structure and the Analytical Potentials of Its Relationship to the Habitat. *The American Naturalist*, 107(954), 213–246. <https://doi.org/10.1086/282827>

- Martínez-Meyer, E., Díaz-Porras, D., Peterson, A. T., & Yáñez-Arenas, C. (2013). Ecological niche structure and rangewide abundance patterns of species. *Biology Letters*, 9(1). <https://doi.org/10.1098/rsbl.2012.0637>
- Medina, I., & Langmore, N. E. (2019). Host density predicts the probability of parasitism by avian brood parasites. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374(1769). <https://doi.org/10.1098/rstb.2018.0204>
- Mills, J. N., & Childs, J. E. (1998). Ecologic studies of rodent reservoirs: Their relevance for human health. *Emerging Infectious Diseases*, 4(4), 529–537. <https://doi.org/10.3201/eid0404.980403>
- Nicholson, W. L., Sonenshine, D. E., Noden, B. H., & Brown, R. N. (2018). Ticks (Ixodida). In *Medical and Veterinary Entomology* (Issue 2002). Elsevier Inc. <https://doi.org/10.1016/B978-0-12-814043-7.00027-3>
- Ntuli, N. N., Nicastro, K. R., Zardi, G. I., Assis, J., McQuaid, C. D., & Teske, P. R. (2020). Rejection of the genetic implications of the “Abundant Centre Hypothesis” in marine mussels. *Scientific Reports*, 10(1), 1–12. <https://doi.org/10.1038/s41598-020-57474-0>
- Nunn, C. L., & Dokey, A. T. W. (2006). Ranging patterns and parasitism in primates. *Biology Letters*, 2(3), 351–354. <https://doi.org/10.1098/rsbl.2006.0485>
- O'Donnell, M. S., & Ignizio, D. A. (2012). Bioclimatic predictors for supporting ecological applications in the conterminous United States. *US Geological Survey Data Series*, 691(10), 1–10.
- Oakgrove, K. S., Harrigan, R. J., Loiseau, C., Guers, S., Seppi, B., & Sehgal, R. N. M. (2014). Distribution, diversity and drivers of blood-borne parasite co-infections in Alaskan bird populations. *International Journal for Parasitology*, 44(10), 717–727. <https://doi.org/10.1016/j.ijpara.2014.04.011>
- Oksanen, J. (2010). Vegan: ecological diversity. *Diversity*, 1(6), 1–14. <https://doi.org/10.1029/2006JF000545>
- Okuyama, T. (2016). Parasitoid aggregation and interference in host–parasitoid dynamics. *Ecological Entomology*, 41(4), 473–479. <https://doi.org/10.1111/een.12320>
- Pearce-Duvel, J. M. C. (2006). The origin of human pathogens: Evaluating the role of agriculture and domestic animals in the evolution of human disease. *Biological Reviews*

of the *Cambridge Philosophical Society*, 81(3), 369–382.
<https://doi.org/10.1017/S1464793106007020>

Pfäffle, M., Littwin, N., Muders, S. V., & Petney, T. N. (2013). The ecology of tick-borne diseases. *International Journal for Parasitology*, 43(12–13), 1059–1077.
<https://doi.org/10.1016/j.ijpara.2013.06.009>

Pironon, S., Villellas, J., Morris, W. F., Doak, D. F., & García, M. B. (2015). Do geographic, climatic or historical ranges differentiate the performance of central versus peripheral populations? *Global Ecology and Biogeography*, 24(6), 611–620.
<https://doi.org/10.1111/geb.12263>

Poulin, R., Krasnov, B. R., Mouillot, D., & Thieltges, D. W. (2011). The comparative ecology and biogeography of parasites. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1576), 2379–2390. <https://doi.org/10.1098/rstb.2011.0048>

Pulliam, R. (1988). Sources, sinks, and population regulation. *The American Naturalist*, 132(5), 652–661.

Ramos, V. N., Lemos, F. G., Azevedo, F. C., Arrais, R. C., Lima, C. F. M., Candeias, I. Z., Martins, M. M., Sandrin, A. C. L. G., Siqueira, S. M., & Szabó, M. P. J. (2020). Wild carnivores, domestic dogs and ticks: Shared parasitism in the Brazilian Cerrado. *Parasitology*, 147(6), 689–698. <https://doi.org/10.1017/S0031182020000335>

Raymond, L., Byers, K. A., & Himsworth, C. G. (2018). Beyond zoonosis: The mental health impacts of rat exposure on inner-city residents. *Journal of Environmental Health*, 81(4), 8–13. <https://www.jstor.org/stable/26530743>

Sagarin, R. D., & Gaines, S. D. (2002). The “abundant centre” distribution: To what extent is it a biogeographical rule? *Ecology Letters*, 5(1), 137–147. <https://doi.org/10.1046/j.1461-0248.2002.00297.x>

Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). *Evolution and Ecology of Species Range Limits*. <https://doi.org/10.1146/annurev.ecolsys.110308.120317>

Spiegelhalter, D. J., Best, N. G., Carlin, B. P., & Van Der Linde, A. (2002). Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society. Series b: Statistical Methodology*, 64(4), 583–639.

- 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. *Ecology Letters*, 19(9), 1159–1171. <https://doi.org/10.1111/ele.12644>
- Uria, I. T., Mateu Mahiques, J., & Mughini Gras, L. (2013). Temporal distribution and weather correlates of Norway rat (*rattus norvegicus*) infestations in the city of Madrid, Spain. *EcoHealth*, 10(2), 137–144. <https://doi.org/10.1007/s10393-013-0829-3>
- Vandamme, T. F. (2015). Rodent models for human diseases. *European Journal of Pharmacology*, 759, 84–89. <https://doi.org/10.1016/j.ejphar.2015.03.046>
- Walther, B. A., Cotgreave, P., Price, R. D., Gregory, R. D., & Clayton, D. H. (1995). Sampling Effort and Parasite Species Richness. *Parasitology Today*, 11(8), 306–310. [https://doi.org/10.1016/0169-4758\(95\)80047-6](https://doi.org/10.1016/0169-4758(95)80047-6)
- Wieczorek, M., Rektor, R., Najbar, B., & Morelli, F. (2020). Tick parasitism is associated with home range area in the sand lizard, *Lacerta agilis*. *Amphibia Reptilia*, 41(4), 479–488. <https://doi.org/10.1163/15685381-bja10018>

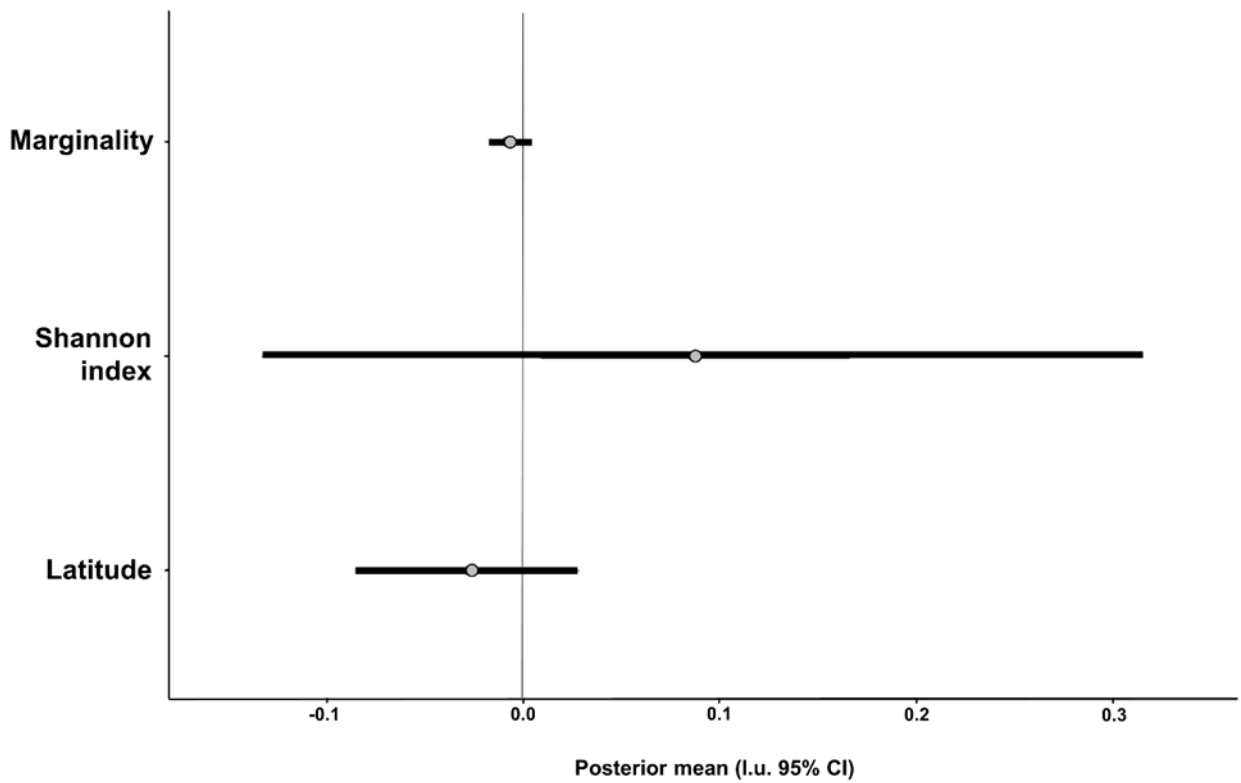
Figures

Figure 1. Forest plot for the results of the Generalized Linear Mixed Models using Markov chain Monte Carlo built with log-transformed mean abundance of fleas of small mammals as response variables and host species and regions of sampling as random effects. Posterior mean estimates with lower and upper (l.u.) 95% credible intervals of predictors are presented. Significance values of pMCMC: <0.01.

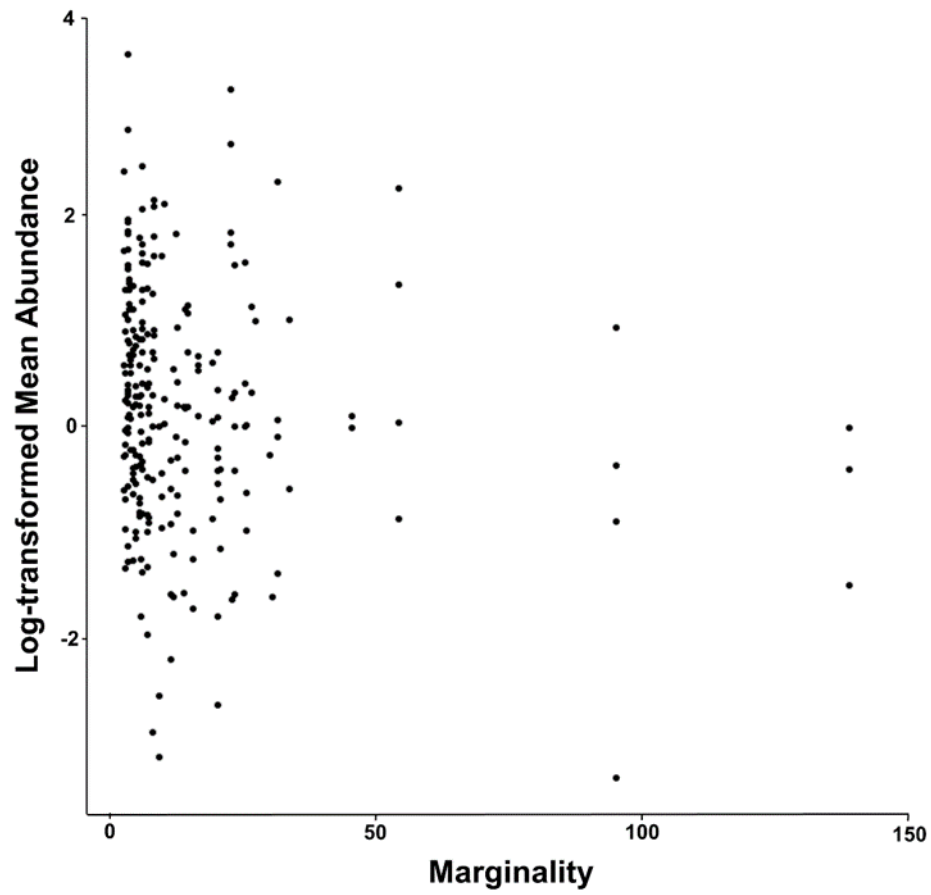


Figure 2. Dispersion graph showing the log-transformed mean abundance of flea species on small mammal hosts as a function of habitat marginality (i.e. difference between local climate conditions and the mean conditions across the species range), among 16 small mammal species occurring in Eurasia.

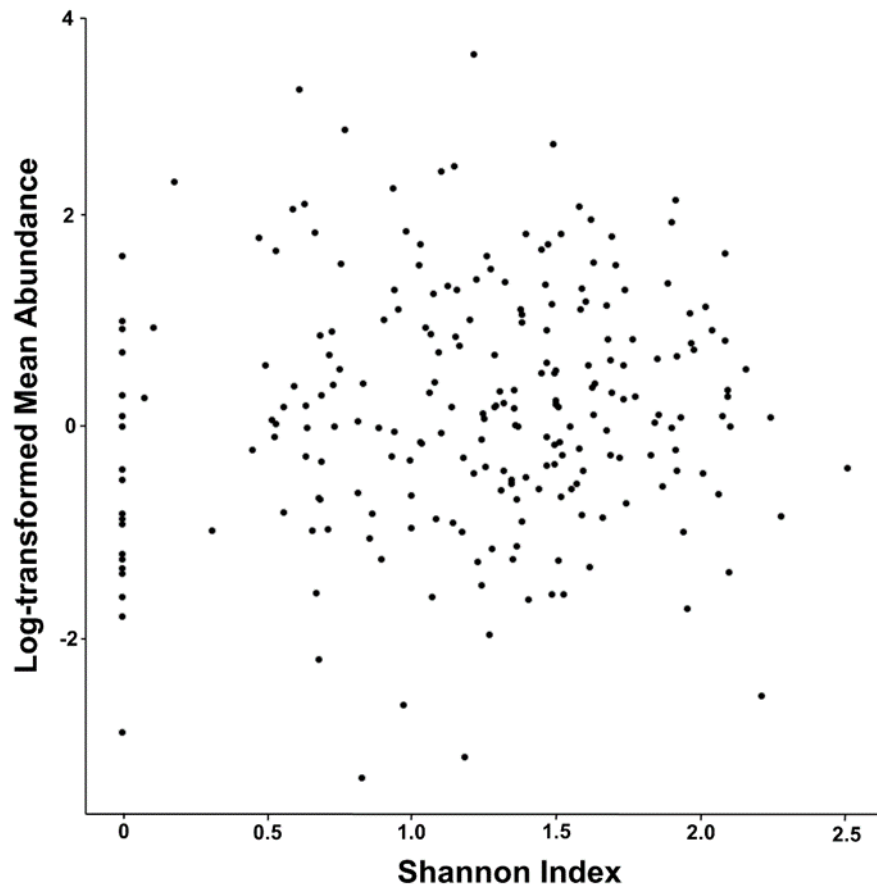


Figure 3. Dispersion graph showing the log-transformed mean abundance of flea species on small mammal hosts as a function of Shannon index as a measure of diversity of fleas, among 16 small mammals occurring in Eurasia. Models including sampling effort were discarded based on DIC criteria.

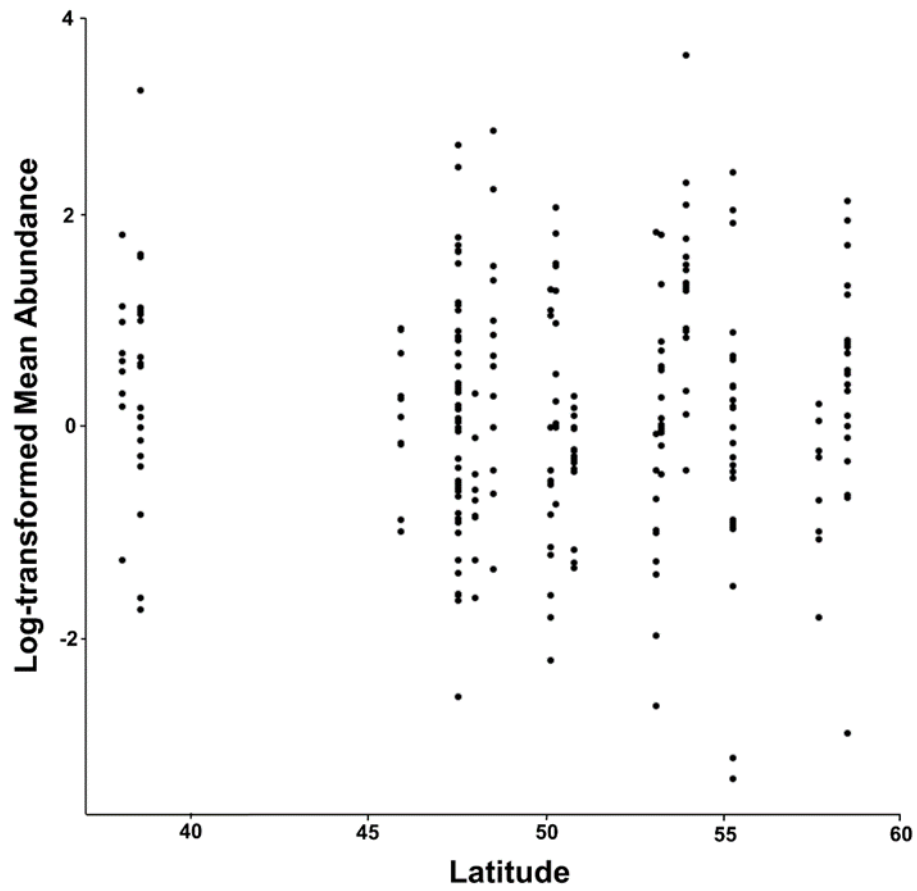


Figure 4. Dispersion graph showing the log-transformed mean abundance of flea species on small mammal hosts as a function of latitude of the centroid of the host occurrence, among 16 small mammals occurring in Eurasia.

Tables

Table 1. Results for the best fitted model (DIC = 621.81), log-transformed mean abundance ~ marginality + Shannon index + latitude, where mean abundance is number of fleas recovered per number of sampled hosts per region, marginality corresponds to the measures of the Outlying Mean Index and latitude is taken from the centroid of the geographical range of the host species. The posterior means, lower and upper credible intervals (95%) are also presented. Neither of the tested variables affect mean abundance, according to pMCMC (<0.05).

Variable	Posterior Mean	Lower CI (95%)	Upper CI (95%)	pMCMC
Marginality	-0.0074	-0.0172	0.0013	0.11
Shannon Index	0.0836	-0.1293	0.3171	0.46
Latitude	-0.0277	-0.0817	0.0919	0.33

CAPÍTULO 3 - Vector species richness predicts local mortality rates by Chagas disease

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 Triatominae insect vectors, 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 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 & 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 et al., 2013; Roche and Guégan, 2011).

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 (WHO, 2020). 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 (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 km² for further analysis. Human population density, human development index 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, 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* species, 9,810 for *Panstrongylus* and 7,344 results for *Rhodnius* species. 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).

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) human development index (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 vectors distribution.

The bioclimatic variables used were Mean Annual Temperature (bio1) and Mean Annual 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 the 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 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 (Magnusson et al., 2016) in the R environment v.4.2.2 (R Core Team, 2016). Raw data is available at <https://zenodo.org/record/7800041>.

3. Results

Our study considered 5570 grid cells covering all of Brazil's area, 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, human host population density varied across several orders of magnitude, whereas total Triatominae (vector) species richness ranged from 2 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, Figure 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, Figure 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 remains unanswered questions regarding the factors driving spatial variation in their prevalence and impact. Two competing hypotheses, the dilution effect hypothesis (DEH) and the amplification effect hypothesis (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 a hundred 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 amplification effect hypothesis. 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.

Several studies have addressed the relationship between biodiversity and parasite-host 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 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 to 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 to 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).

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 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 also 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.

Acknowledgements

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. RGF thanks CNPq for a productivity grant (312847/2022-0).

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, 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.

- 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>
- 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, e0479-2021. <https://doi.org/10.1590/0037-8682-0479-2021>
- WHO. (2020). *Chagas disease (also known as American trypanosomiasis)*. [https://www.who.int/news-room/fact-sheets/detail/chagas-disease-\(american-trypanosomiasis\)](https://www.who.int/news-room/fact-sheets/detail/chagas-disease-(american-trypanosomiasis))
- 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>
- 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. <https://doi.org/10.1590/0074-02760210015>
- 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., and Hudson, P. J., 2006. Sacred cows and sympathetic squirrels: the importance of biological diversity to human health. *PLoS Med.* 3(6), e231. <https://doi.org/10.1371/journal.pmed.0030231>
- Dormann, C. F., McPherson, J. M., Araújo, M. B., Bivand, R., Bolliger, J., Carl, G., and 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](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., 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>
- 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>

- 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., Muriene, 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>
- Magnusson, A., Skaug, H., A. N.-R. P. V., & 2017, un, 2016. Package 'glmmTMB'. *Cran.Microsoft.Com.* <https://cran.microsoft.com/snapshot/2021-09-26/web/packages/glmmTMB/glmmTMB.pdf>

- 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.
<https://doi.org/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, 105948.
<https://doi.org/10.1016/j.actatropica.2021.105948>
- 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](https://doi.org/10.1016/S2542-5196(21)00031-0)
- QGIS, 2023. <https://qgis.org/>
- R Core Team, 2016. *R: A Language and Environment for Statistical Computing*.
<https://www.r-project.org/>
- 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.crv.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>

Figures

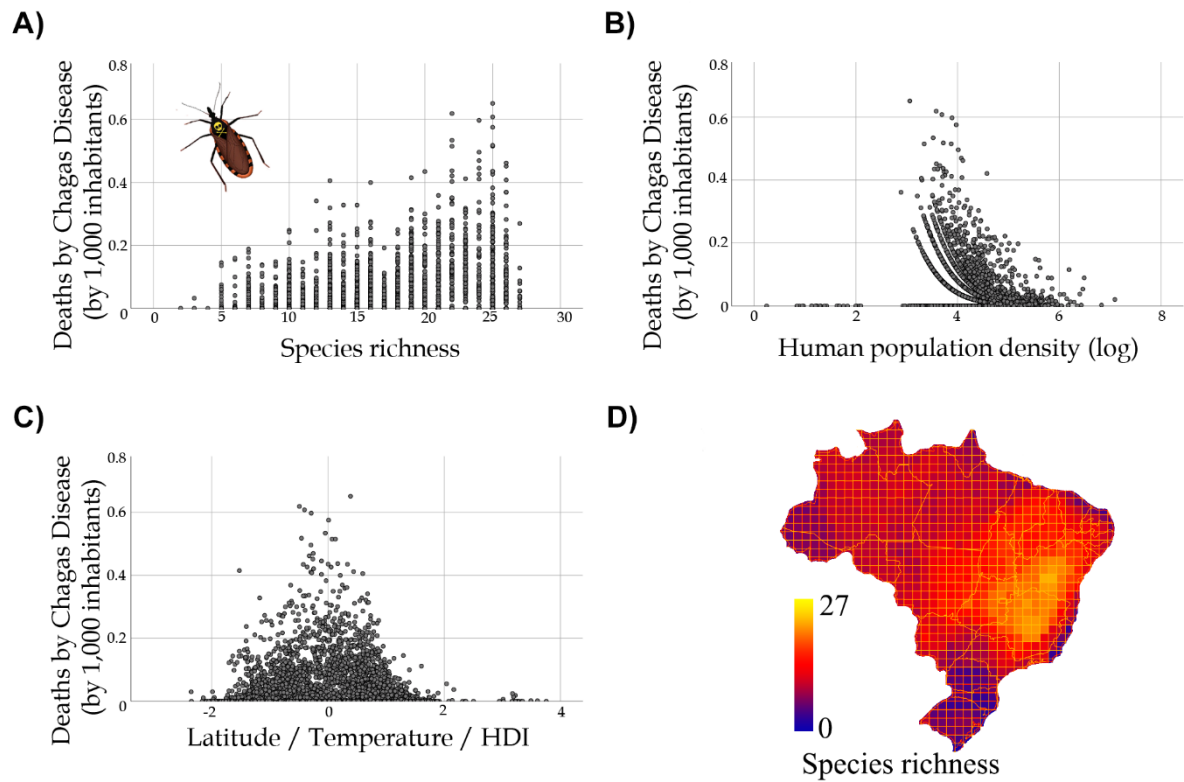


Figure 1. The number of deaths due to Chagas disease registered in Brazil during the years 2018, 2019, and 2020 and its relationship with Triatominae species richness (A), human host population density (B), latitude, mean annual temperature, and Human Development index (C). Central-eastern regions in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

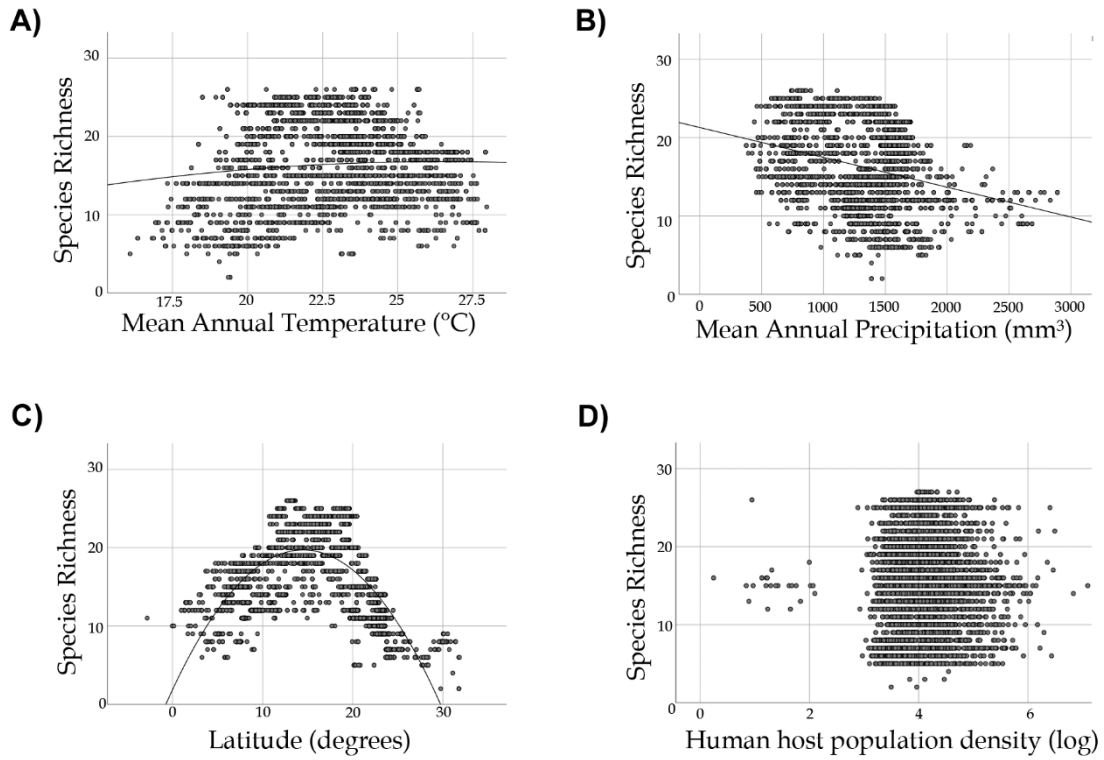


Figure 2. Triatominae species richness in Brazil and its relationship with Mean Annual Temperature (A), Mean Annual Precipitation (B), Latitude (C) and Human host population density (D). Each point in A-D corresponds to one city or one 50 km × 50 km cell.

Tables

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, 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 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.

	β	Estimate	95% Wald-CI		Wald X^2	p
			Inferior	Superior		
<i>Rhodnius</i> richness	.009	.002	.006	.012	29.857	<.001
<i>Triatoma</i> richness	.006	.001	.004	.008	36.487	<.001
Host Population density	-.011	.002	-.015	-.006	21.605	<.001
GDP per capita	.004	.003	-.004	.011	.943	.315
Latitude/Temperature/HDI	.013	.003	.007	.019	19.353	<.001
Precipitation	<.001	<.001	<.001	<.001	.009	.922
Total richness	.006	.001	.004	.007	74.13	<.001
Host Population density	-.011	.002	-.015	-.006	21.693	<.001
GDP per capita	.004	.004	-.004	.012	.790	.374
Latitude/Temperature/HDI	.012	.002	.007	.016	22.787	<.001
Precipitation	<.001	<.001	<.001	<.001	.287	.592

Table 2. Results for Generalized Estimating Equations Models testing for the relationship between Triatominae species richness and: (i) Mean Annual Temperature (Bio1)/Latitude/HDI, (ii) Mean Annual Precipitation (Bio12), (iii) Human host population density. Latitude/Temperature/HDI show high collinearity and were analysed as a 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.

	β	Estimate	95% Wald-CI		Wald X^2	p
			Inferior	Superior		
<i>Rhodnius</i>						
Precipitation	.000	.000	.000	.000	.091	.763
Latitude/Temperature/HDI	-1.35	.0935	-1.531	-1.164	207.6	<.001
Host population	.105	.0984	-.088	.297	1.130	.288
<i>Triatoma</i>						
Precipitation	-.003	.000	-.003	-.002	120.407	<.001
Latitude/Temperature/HDI	-.327	.1166	-.556	-.099	7.888	.005
Host population	.194	.1295	-.060	.448	2.244	.134
<i>Panstrongylus</i>						
Precipitation	.000	.000	.000	.000	1.263	.261
Latitude/Temperature/HDI	-.465	.0831	-.628	-.302	31.341	<.001
Host population	.109	.0853	-.059	.276	1.622	.203
Total richness						
Precipitation	-.002	.000	-.003	-.002	26.18	<.001
Latitude/Temperature/HDI	-2.14	.25	-2.63	-1.65	73.29	<.001
Host population	.407	.277	-.137	.951	2.151	.142

CONCLUSÕES GERAIS

Nossos resultados adicionam evidências ao papel dos gradientes latitudinais e bioclimáticos sobre os parasitas em uma escala mais ampla, e indicam que as interações parasita-hospedeiro estão sujeitas às variações climáticas. Nossas descobertas indicam que endoparasitas podem evitar a maior parte da influência direta do clima externo, enquanto os ectoparasitas estariam mais suscetíveis às variações ambientais. No entanto, essas interações podem permanecer elusivas em múltiplos sistemas parasita-hospedeiro, devido à complexidade subjacente da dinâmica populacional dos hospedeiros. O impacto dessas dinâmicas foi sugerido em nossa pesquisa pela falta de qualquer influência da distribuição da população de hospedeiros em sua área de vida sobre a abundância média de parasitas. A elucidação dessas dinâmicas é de particular interesse para a saúde pública, pois contribui para a compreensão dos aspectos ecológicos da transmissão de patógenos e podem subsidiar estudos interdisciplinares como abordagens de ecossistema para a conservação de saúde humana, animal e do meio-ambiente. Nossa observação de que a mortalidade por patógenos transmitidos por vetores está positivamente correlacionada com a riqueza local de vetores também contribui com evidências sobre o papel da biodiversidade na epidemiologia e sua relevância para políticas de saúde pública. Futuras pesquisas sobre interações parasita-hospedeiro devem considerar a complexidade das dinâmicas populacionais e devem se beneficiar ao considerarem também a cada vez mais indissociável influência da atividade humana sobre os gradientes ambientais e seu impacto nessas interações.