UNIVERSIDADE FEDERAL RURAL DE PERNAMBUCO

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PROGRAMA DE PÓS-GRADUAÇÃO EM ETNOBIOLOGIA E
CONSERVAÇÃO DA NATUREZA

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Macroecologia de parasitos: como espaço, clima e hospedeiros determinam a diversidade de helmintos em amplas escalas espaciais

Recife-PE

2021

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Tese submetida ao Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza (UFRPE, UEPB, UFRPE, UPE) como parte dos requisitos para obtenção do título de doutor.

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Macroecologia de parasitos: como espaço, clima e hospedeiros determinam a diversidade de helmintos em amplas escalas espaciais

Tese defendida e aprovada em: 05/07/2021

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2021

Epígrafe

"É como nas grandes histórias, Sr. Frodo, as que realmente importaram. Cheias de escuridão e perigo, e às vezes você não quer saber o fim. Porque como o final poderia ser feliz? Como o mundo poderia voltar ao modo como era quando tantas coisas ruins haviam acontecido? [...] As pessoas nessas histórias tiveram muitas chances de voltar atrás, só que não o fizeram. Eles continuaram, porque estavam segurando em algo. [...] O bem que há neste mundo, Sr. Frodo, pelo qual vale a pena lutar."

(Sam Gamgee)
O Senhor dos Anéis: As Duas Torres por J. R. R. Tolkien

Agradecimentos

Ao Deus e Pai de Jesus Cristo, a quem devo a minha vida e todo o bem que me tem acontecido. Também à minha família querida, minha base e meu auxílio. Agradeço aos meus pais Isabel e Paulo por sempre terem alimentado o amor à natureza em mim desde a infância, cada um do seu jeito. Quando criança as pessoas me perguntavam o que eu gostaria de ser quando crescesse, e me lembro de responder que queria ser cientista e trabalhar com animais. Creio que estou finalmente chegando lá. Obrigado, mãe, por sempre me comprar vários livros e documentários sobre bichos, os quais eu gosto tanto e tenho guardado com carinho até hoje. Obrigado por me considerar um biólogo desde criança e comprar microscópios de brinquedo pra eu ficar olhando formigas e casca de cebola. Obrigado, pai, pelas escapadas que a gente dava pro meio do mato em Aldeia pra ficar admirando a paisagem e comendo frutas do pé. Saudades dos nossos passeios. Também agradeço às minhas irmãs Lais e Débora por me aguentarem, apesar de eu ser bem chato. Obrigado por terem orgulho de mim e vibrarem com minhas vitórias. Amo vocês! Também meu muito obrigado à minha namorada, Poli. Obrigado por estar sempre comigo, por toda amizade, companheirismo e amor. Também obrigado pela paciência e por entender meus sumiços quando eu preciso focar no trabalho. Caminhar ao seu lado tem sido um privilégio enorme! Eu nem consigo expressar o quanto vocês todos me mantêm andando.

Aos que conviveram comigo no Laboratório de Síntese Ecológica e Conservação da Biodiversidade (ECOFUN) desde que eu cheguei. Obrigado ao meu orientador Thiago Gonçalves-Souza por me aceitar quando eu o procurei há quatro anos e meio sem saber de quase nada. Obrigado por investir tempo, confiança, energia e paciência na minha formação. Obrigado ao meu coorientador Robert Poulin por ter aceitado ajudar na orientação da minha tese e por ter me recebido no seu laboratório durante o doutorado sanduíche. Obrigado também aos meus queridos amigos do lab. A amizade e paciência de vocês foi crucial para o meu crescimento como pesquisador e ser humano. Obrigado Arthur, Cássio, Gabi, Gabriel, Ingrid, Paulo, Pedro, Reginaldo e Theo. Vocês são os melhores! Um agradecimento especial também ao meu amigo Leonardo Chaves. Obrigado por todos os conselhos, pelo apoio e pelo suporte. Sua amizade é muito estimada por mim.

À Universidade Federal Rural de Pernambuco e ao Programa de Pós-Graduação em Etnobiologia e Conservação por todo apoio estrutural e logístico.

Sumário

Resumo

Um dos objetivos da macroecologia e da biogeografia como empreendimentos científicos é entender os princípios que governam a diversidade biológica independentemente do grupo ou sistema estudados. Em particular, estudar o que determina a diversidade alfa e beta de parasitos em amplas escalas espaciais apresenta alguns desafios significativos. Esses organismos vivem em estreita associação com seus hospedeiros, o que adiciona um nível de complexidade que, se ignorado, pode resultar em conclusões precipitadas. Por exemplo, o clima e a riqueza de hospedeiros são importantes preditores da diversidade alfa de parasitos na escala macroecológica, mas seus efeitos são tipicamente tratados separadamente, apesar da possibilidade de interações. Adicionalmente, a maioria dos estudos com diversidade beta em larga escala são com ectoparasitos de mamíferos ou foram realizados na região do Paleártico, o que apresenta oportunidades para investigar novas regiões e grupos de hospedeiros a fim de avançar na generalidade da teoria macroecológica para parasitos. Além disso, até onde sabemos, nenhum estudo em grande escala foi conduzido para investigar como os preditores da diversidade beta de parasitos variam com a escala. Portanto, com base em um novo banco de dados de helmintos parasitas de anfíbios, utilizamos modelos de equações estruturais para investigar os efeitos diretos e indiretos do clima e da riqueza de hospedeiros sobre a diversidade alfa de parasitos em escala global. Adicionalmente, usamos modelos generalizados de dissimilaridade para investigar como os papéis relativos do clima, diversidade de hospedeiros e distância espacial sobre a diversidade beta de parasitos varia com a escala espacial (global vs. regional) e região zoogeográfica (Neártico vs. Neotropical). Também investigamos se a seleção de subconjuntos taxonômicos distintos do hospedeiro (famílias) influencia as tendências gerais na diversidade beta de parasitos. Em primeiro lugar, descobrimos que o clima afeta a riqueza global de parasitas tanto direta quanto indiretamente por meio da riqueza de hospedeiros. Essa descoberta é importante no contexto de co-extinções em cascata causadas pelas mudanças climáticas e enfatiza a importância do uso de abordagens analíticas que permitem a avaliação de relações indiretas entre preditores. Em relação à diversidade beta, encontramos que a distância espacial é o principal preditor da substituição de espécies em escala global e que sua importância relativa em relação ao clima diminui com a escala espacial. Similarmente, demonstramos que a importância relativa dos preditores estudados varia com a região zoogeográfica. Curiosamente, encontramos resultados contrastantes ao comparar diferentes famílias de hospedeiros coletadas na mesma região. Diferenças biológicas entre os hospedeiros podem resultar em pressões divergentes para a colonização e persistência dos parasitos, o que

pode justificar uma investigação mais aprofundada. A principal mensagem desta descoberta pode ser a importância de incluir a história de vida do hospedeiro em estudos de diversidade beta de parasitos em escala macroecológica. Tais contingências são uma oportunidade para uma exploração mais aprofundada, pois têm implicações importantes para a busca de preditores universais da diversidade. Nosso estudo é uma nova contribuição importante para a macroecologia de parasitos, integrando preditores da diversidade alfa e investigando o papel da escala espacial, biorregião e subconjunto taxonômico do hospedeiro na substituição de espécies de parasitos no espaço geográfico. Até onde sabemos, este é o primeiro estudo com parasitos a utilizar essas abordagens em escala tão ampla.

Palavras-chave: macroecologia; clima; espaço; diversidade de parasitos; anfíbios

Abstract

One of the goals of macroecology and biogeography as scientific endeavours is to discover general principles that govern biological diversity regardless of biological group or the studied system. In particular, studying parasite alpha and beta diversity at broad spatial scales presents some significant challenges. These organisms live in close association with their hosts, which adds a level of complexity that if ignored can result in wrong conclusions. For instance, climate and host richness are important drivers of parasite alpha diversity at the macroecological scale, but their effects are typically treated separately, despite the possibility of interactions. In relation to beta diversity, most large-scale studies have either focused on mammalian ectoparasites or on the Palearctic realm, which presents opportunities to investigate novel realms and host groups in order to advance the generality of parasite macroecological theory. Furthermore, to the best of our knowledge, no large-scale study has been conducted to investigate how the drivers of parasite beta diversity vary with scale. Based on a novel dataset of helminth parasites of amphibians, we used structural equation modelling to investigate the direct and indirect effects of climate and host richness as drivers of parasite alpha diversity at the global scale. Furthermore, we used generalized dissimilarity modelling to investigate how the relative roles of climate, host diversity, and spatial distance as drivers of parasite beta diversity vary with spatial scale (global vs regional) and zoogeographical realm (Nearctic vs Neotropical). Additionally, we investigated whether selecting distinct host taxonomic subsets (families) influences general trends in parasite beta diversity. First, we found that climate affects global parasite richness both directly and indirectly via host richness. These findings are important in the context of cascade co-extinctions caused by climate change, and they emphasize the importance of using analytical approaches that allow for the evaluation of indirect relationships among predictors. In relation to parasite beta diversity, we found that spatial distance is the strongest predictor of parasite turnover at the global scale and that its relative importance in relation to climate decreases at the regional scale. In addition, we demonstrated that the relative importance of our predictors varies with the zoogeographical realm. Interestingly, we found contrasting results when comparing different host families collected in the same realm. Given that biological differences between hosts can result in diverging pressures for parasite colonization and persistence, this may warrant further investigation. The take-home message from this discovery could be the importance of including host life-history specifically in parasite beta diversity studies at the macroecological level. Such contingencies are an opportunity for further exploration, as they have important implications

for the search for universal drivers of parasite diversity at large scales. Our study is an important new contribution to parasite macroecology, integrating predictors of parasite alpha diversity and investigating the role of spatial scale, bioregion, and host taxonomic subset on parasite species turnover across geographic space. To the best of our knowledge, this is the first study on parasites to take these approaches on such a large scale.

1. Introdução Geral

1.1. Objetivos e Questionamentos

A presente tese teve como objetivo entender os fatores que determinam a diversidade e composição de espécies de helmintos em amplas escalas espaciais. Especificamente, buscamos entender (**1**) quais são os efeitos diretos e indiretos do clima e da diversidade de hospedeiros sobre os padrões globais da diversidade alfa de parasitos, e (**2**) como o efeito relativo do clima, a diversidade de hospedeiros e a distância geográfica variam com a escala espacial (regional e global), o grupo de parasitos (nematódeos e trematódeos) e a região zoogeográfica (Neártico e Neotropical). Do ponto de vista teórico, grande parte da teoria ecológica foi construída na perspectiva dos organismos de vida-livre. Sendo assim, a consideração de como organismos parasitas respondem aos mesmos preditores pode lançar uma nova luz sobre a generalidade das explicações presentes na literatura atual. Do ponto de vista prático, entender o que determina a diversidade alfa e beta de parasitos pode ter implicações importantes para a conservação. Por exemplo, a riqueza de parasitos pode ser utilizada como uma medida da pressão de parasitismo. Portanto, entender como diferentes variáveis estão relacionadas a um aumento na riqueza de parasitos nos ajuda a entender como estas mesmas variáveis estão ligadas a um aumento na pressão a que uma espécie de hospedeiro está sujeita. Adicionalmente, entender o que determina a diversidade beta de parasitos ajuda a elucidar o que limita a distribuição geográfica de patógenos.

1.2. Estratégias de Pesquisa

Por meio de uma revisão sistemática da literatura que incluiu 250 artigos e mais de 170 localidades, construímos um banco de dados global inédito de helmintos parasitas de anfíbios. Para o primeiro artigo, utilizamos uma combinação de modelos lineares generalizados mistos (GLMMs) e modelos de equação estruturais (piecewiseSEM) para entender quais eram os efeitos diretos e indiretos do clima (sazonalidade da precipitação, precipitação anual e sazonalidade da temperatura) e riqueza de hospedeiros na riqueza global de helmintos parasitas. Uma vantagem dos modelos mistos é a possibilidade de controlar certas fontes de dependência nos dados através da inclusão de fatores aleatórios. Por sua vez, através da abordagem de modelos de equações estruturais é possível considerar múltiplas variáveis e suas interações, levando em consideração tanto seus efeitos diretos como os indiretos sobre a variável resposta. Para o segundo artigo, utilizamos modelos generalizados de dissimilaridade (GDMs). Os

GDMs são extensões do método de regressão de matrizes, sendo um método bastante flexível que permite considerar a não-linearidade da taxa de substituição de espécies em relação aos gradientes investigados.

1.3.Estrutura da Tese

A tese possui dois artigos correspondendo aos objetivos descritos acima. O primeiro artigo já se encontra publicado no periódico *Global Ecology and Biogeography* (doi: 10.1111/geb.13213) e está focado na diversidade alfa de parasitos em escala global (objetivo 1). Até onde temos conhecimento, esse artigo trouxe uma abordagem única no estudo da riqueza de parasitos em amplas escalas, integrando os principais preditores (climáticos e bióticos) e, além disso, considerando tanto efeitos diretos (clima → parasita) quanto indiretos (clima → hospedeiro → parasita). O segundo artigo está aceito na *Philosophical Transactions of the Royal Society B: Biological Sciences.* Neste artigo, focamos na diversidade beta nas escalas global e biogeográfica para investigar a importância relativa de processos ligados à dispersão e ao nicho na determinação da composição de helmintos em anuros (objetivo 2). Em especial, testamos se existem preditores gerais da diversidade beta de parasitos independentes da escala e parcela de hospedeiros estudados.

2. Fundamentação Teórica

2.1. Ecologia em amplas escalas

Um dos principais objetivos da ecologia enquanto ciência é entender quais fatores determinam a diversidade biológica. No entanto, este é um termo multidimensional, cuja decomposição em diferentes componentes é fundamental para que se torne operacional. Robert Whittaker, por exemplo, propôs que a diversidade biológica poderia ser expressa em três dimensões: alfa, beta e gama (WHITTAKER, 1960; 1972). A diversidade alfa (ou riqueza de espécies) corresponde ao número de espécies encontradas em um local. A diversidade beta está relacionada às diferenças nas identidades das espécies (i.e., diferenças na composição e riqueza de espécies) entre localidades, sendo o elo entre a diversidade local (alfa) e a regional (gama) (ANDERSON, 2011; WHITTAKER, 1960; 1972). Enquanto o foco na diversidade alfa está em quais processos afetam o número de espécies encontradas nas localidades, o foco na diversidade beta se relaciona a entender que fatores definem a identidade das comunidades locais. Ambas as ênfases são igualmente importantes, tendo em vista que apresentam perspectivas

complementares acerca de quais fatores determinam a diversidade biológica (ver MOUSING *et al.*, 2016).

Na busca por explicar os fatores que determinam os padrões históricos e atuais de diversidade, os ecólogos por muito tempo estiveram focados em processos ecológicos que ocorriam em maior intensidade em pequenas escalas, tais como competição, predação e condições abióticas locais (RICKLEFS, 1987). Tal abordagem local (ou "tradicional") foi o berço para diversos avanços teóricos importantes da ecologia (e.g., CONNEL, 1961; PAINE, 1966; MACARTHUR e LEVINS, 1967). No entanto, as comunidades locais também são resultado de processos regionais, como eventos históricos, barreiras geográficas e gradientes climáticos (RICKLEFS, 2004). Portanto, a integração de processos locais com processos que ocorriam em escalas temporais e espaciais maiores foi um passo importante para o avanço da teoria ecológica para além das contingências locais (ver RICKLEFS, 1987; RICKLEFS, 2004). Nesse ínterim, a abordagem macroecológica oferece uma perspectiva ampla e integra processos em diferentes escalas na busca por explicar padrões gerais (BROWN, 1995).

Embora a macroecologia enquanto disciplina tenha sido formalizada no final do século XX (BROWN e MAURER, 1989; BROWN, 2005), padrões considerados macroecológicos estão presentes na literatura científica desde o período dos primeiros naturalistas. Por exemplo, o gradiente latitudinal da diversidade, o qual descreve o aumento da riqueza de espécies em locais de menor latitude, é conhecido desde o século XIX (HUMBOLDT, 1828). Desde então, dezenas de mecanismos ecológicos, históricos e evolutivos que combinam processos locais e regionais foram propostos a fim de explicar o que determina a variação espacial na diversidade alfa (PIANKA, 1966; ROHDE, 1992; WILLING, 2003; MITTELBACH *et al.,* 2007). De forma simples, a diversidade local é o resultado do balanço entre processos ecológicos, históricos e evolutivos que adicionam e removem espécies ao longo do tempo (FINE, 2015). No entanto, esse balanço vai depender de uma série de fatores, dentre os quais aqueles relacionados ao clima atual e histórico ocupam um lugar de destaque em várias hipóteses.

2.2. Padrões e processos em amplas escalas espaciais

Existe uma forte relação entre a variação espacial na riqueza de espécies e variáveis climáticas, especialmente temperatura e disponibilidade de água (HAWKINS *et al.*, 2003). A produtividade, taxa de especiação e tolerância fisiológica compõem três das principais hipóteses climáticas sugeridas na ecologia (WILLING *et al.* 2003; CURRIE *et al.,* 2004). A

explicação mais comum para a relação entre a produtividade e a riqueza é que regiões mais produtivas suportam populações viáveis para uma maior quantidade de espécies (BROWN, 2014). Embora a relação positiva entre a produtividade e a riqueza em amplas escalas seja comum (e.g., GILLMAN *et al.* 2015), o suporte para a explicação usual permanece inconclusivo (CURRIE *et al.,* 2004; STORCH *et al.,* 2018). Em relação à taxa de especiação, a hipótese da "velocidade evolutiva" afirma que a temperatura tem um efeito cinético positivo na diversificação, especialmente via altas taxas metabólicas e tempos geracionais menores (ROHDE, 1992). Apesar de algumas lacunas, há suporte consistente para essa hipótese (GILLMAN e WRIGHT, 2015). Por fim, de acordo com a hipótese da tolerância fisiológica, a riqueza é determinada pela quantidade de espécies que podem tolerar as condições abióticas locais (CURRIE *et al.,* 2004). O principal mecanismo tem relação com como climas amenos permitem o surgimento de uma gama maior de estratégias funcionais, o que também encontra suporte na literatura (SPASOJEVIC *et al.* 2014).

Assim como a diversidade alfa varia no espaço, a diversidade beta também é espacialmente heterogênea. Um dos padrões mais conhecidos é a diminuição da proporção de espécies compartilhadas (ou aumento da substituição) entre localidades com maior distância espacial ou ambiental. Esse padrão pode ser explicado tanto por processos baseados no nicho das espécies, como por processos relacionados à dispersão (SOININEN *et al.* 2007). Primeiramente, mudanças na diversidade beta podem estar relacionadas à resposta das espécies às características ambientais. Na síntese ecológica atual, esses processos baseados nas diferenças do nicho são conhecidos como "seleção" (VELLEND, 2016) ou "alocação de espécies" (LEIBOLD e CHASE, 2018). Segundo, as diferenças na composição entre localidades podem ter relação com a capacidade dispersiva das espécies ou pela existência de barreiras à dispersão. A influência da dispersão na composição pode ser observada pela maior diversidade beta em espécies com pouca capacidade de dispersão (QIAN, 2009). É certo que nenhum mecanismo poderia isoladamente explicar as variações observadas nas diversidades alfa e beta, por isso são necessários estudos que integrem diferentes preditores e suas interações (e.g., RODRIGUES et al. 2017). Tal abordagem é vantajosa, tendo em vista que leva em consideração as interações encontradas na natureza, evitando dualismos irreais entre hipóteses distintas.

2.3. Parasitos e seus efeitos

O parasitismo pode ser definido como um tipo de interação simbiótica interespecífica onde um dos indivíduos (o parasito) é beneficiado em detrimento de outro indivíduo (o hospedeiro). Parasitos passam ao menos parte do seu ciclo de vida em associação com seus hospedeiros, de onde obtém os nutrientes necessários para sua sobrevivência e reprodução. Os parasitos são um grupo extremamente diverso de organismos com representantes em praticamente todos os ramos da árvore da vida (POULIN e MORAND, 2004). Uma das formais mais comuns de categorizar esses organismos é dividindo-os em micro- e macroparasitos. Os microparasitos como bactérias, fungos e protistas, são caracterizados por um tamanho reduzido (normalmente microscópicos), tempos geracionais marcadamente menores que o de seus hospedeiros, capacidade de reprodução assexuada em seus hospedeiros e por normalmente induzirem uma resposta imune forte (GOATER *et al*. 2014). Os macroparasitos são os artrópodes (ácaros, carrapatos, pulgas, copépodos etc.) e os helmintos (trematódeos, cestódeos, nematódeos, acantocéfalos etc.), ambos caracterizados por serem geralmente visíveis a olho nu, apresentarem tempos geracionais próximos aos dos seus hospedeiros, gerarem uma resposta imunológica de intensidade baixa a média e por sua patogenicidade associada ao número de indivíduos (GOATER *et al*. 2014). O parasitismo é considerado por alguns como sendo a estratégia de consumo mais frequente na natureza (LAFFERTY *et al*. 2008), podendo afetar a dinâmica populacional dos hospedeiros, a estruturação das comunidades, a competição interespecífica e fluxo energético (ver HATCHER *et al*. 2006*;* HUDSON *et al*. 2006).

Apesar dos parasitos serem componentes fundamentais dos ecossistemas e poderem ter efeitos positivos sobre outras espécies da comunidade local (ver HATCHER *et al*. 2006; HUDSON *et al*. 2006; BUCK, 2019), não podemos negar que seus efeitos negativos sobre os hospedeiros levantam preocupações relacionadas à conservação, sobretudo de grupos que já estão sob frequente pressão negativa. Por exemplo, dentre os vertebrados, os anfíbios estão entre os animais mais susceptíveis à extinção por seu pequeno tamanho corporal, baixa capacidade de dispersão e baixa tolerância à perda de água e a mudanças na temperatura (WELLS, 2007). Junto a isso, diversas espécies de parasitos estão sendo responsáveis pelo declínio de populações de anfíbios ao redor do planeta. O parasitismo pode envolver mudanças comportamentais, fisiológicas e morfológicas nos hospedeiros, algumas das quais têm efeitos deletérios marcantes. Por exemplo, alterações fisiológicas causadas pelo fungo *Batracochytrium dendrobatidis* são responsáveis pelo declínio e extinção local de anfíbios em

várias localidades (OLSON *et al.*, 2013). Outro exemplo marcante é o trematódeo *Ribeiroia ondatrae*, cuja infecção está associada a uma série de deformidades em anfíbios, tais como ausência e má-formação de membros (JOHNSON *et al.* 2002). Os anfíbios expostos a esses trematódeos durante a fase de girino apresentam uma alta taxa de mortalidade (JOHNSON *et al.* 1999).

Os anfíbios são hospedeiros para várias espécies de parasitos, mas a maior parte da atenção tem sido direcionada aos microparasitos como o *B. dendrobatidis*. No entanto, assim como no caso da *R. ondatrae,* helmintos podem ter efeitos deletérios significativos sobre os anfíbios que precisam ser melhor explorados (KORPIVNIKAR *et al.* 2012). Embora algumas espécies como as citadas sejam mais marcantes, a diversidade de parasitos é uma medida discreta, porém importante da pressão de parasitismo (BORDES e MORAND, 2009). Elucidar o que determina a diversidade de parasitos tem aplicações práticas para entender o que determina o número de espécies que um hospedeiro tem e o que limita a distribuição geográfica de patógenos como os supracitados. Durante muito tempo, os parasitos foram deixados de lado nas investigações ecológicas, mas as últimas décadas viram o surgimento de um interesse renovado pela aplicação da teoria ecológica para entender a diversidade de parasitos (POULIN e MORAND, 2004). Entretanto, muitas questões permanecem em aberto, especialmente relacionadas ao que determina a diversidade de parasitos em amplas escalas espaciais e a aplicabilidade da teoria desenvolvida para organismos de vida livre.

2.4. O estudo da diversidade de parasitos em amplas escalas espaciais

A maior parte da teoria ecológica foi construída com base em organismos de vida-livre. No entanto, simbiontes como parasitas podem apresentar padrões distintos em relação aos preditores conhecidos, sobretudo pela associação íntima com seus hospedeiros. Em comparação à macroecologia de organismos de vida-livre, ainda há espaço para muito avanço na macroecologia de parasitos. Quanto à diversidade alfa, a maior parte dos estudos em ampla escala está focada em entender a resposta da riqueza de parasitos à latitude ou variáveis relacionadas aos hospedeiros (POULIN, 2014; MORAND, 2015). Adicionalmente, os estudos que não usam latitude tendem a utilizar abordagens que avaliam o efeito das variáveis de forma isolada (e.g., GUERNIER et al., 2004). Contudo, sabemos que existem variáveis relacionadas aos hospedeiros, tais como riqueza, as quais também variam em função de gradientes climáticos. Ignorar essa interação pode incorrer num entendimento equivocado do que determina os padrões de diversidade de parasitos. Adicionalmente, alguns estudos utilizam

métodos de ordenação para agrupar as variáveis climáticas (PREISSER, 2019). Tanto o uso dessas técnicas como da latitude como preditor acabam por mascarar as relações de causa-efeito entre o clima e os padrões de diversidade observados (ver HAWKINS e DINIZ-FILHO, 2004). Sendo assim, é importante que ao estudarmos como a riqueza global de parasitos varia, levemos em consideração as variáveis climáticas em si, assim como as interações entre as variáveis, adotando abordagens analíticas que nos permitam medir as interações entre os diferentes preditores (e.g., BELMAKER e JETZ, 2015; RODRIGUES et al. 2017).

Em relação à diversidade beta de parasitos, a maior parte dos estudos em ampla escala estudam os efeitos relativos da distância geográfica, composição de hospedeiros e gradientes climáticos na taxa de substituição (*turnover*) das espécies (BERKHOUT *et al.,* 2020; ERICKSSON *et al.*, 2020). Embora os parasitos passem grande parte do seu ciclo em associação com os hospedeiros, a maioria dos macroparasitos (e.g., helmintos e artrópodes) possui estágios larvais de vida-livre ou depositam ovos no ambiente (GOATER *et al.* 2014). Nesses estágios, estão sujeitos aos mesmos processos relacionados à influência do clima que os organismos de vida-livre. Portanto, o clima pode ter uma influência direta sobre a composição de parasitos selecionando as espécies que são capazes de suportar as condições climáticas locais (MAESTRI *et al.,* 2017). Em relação aos hospedeiros, estes são tanto a fonte última de recursos para os parasitos como a sua fonte de dispersão. Portanto, a diversidade de parasitos acompanha a de hospedeiros num paralelo com a relação consumidor-recurso para predadores e presas (KAMIYA *et al.* 2014; JOHNSON *et al.,* 2016). Quanto ao espaço geográfico, este é normalmente utilizado como *proxy* da limitação de dispersão (ERICKSSON *et al.*, 2020). Os estudos com diversidade beta de parasitos estão normalmente enviesados para as regiões mais frias do planeta e para alguns grupos de hospedeiros como aves e mamíferos (KRASNOV *et al.,* 2012; MAESTRI *et al.,* 2017; ERICKSSON *et al.*, 2020). A fim de que a teoria macroecológica para os parasitos seja o mais ampla possível, é necessário que estudemos novos grupos de hospedeiros e regiões.

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3. Artigo 1: Integrating climate and host richness as drivers of global parasite diversity

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Running title: drivers of global parasite diversity

Biosketch

Paulo Mateus Martins is currently a PhD candidate at the Universidade Federal Rural de Pernambuco (UFRPE), Brazil. With a particular (not exclusive) emphasis on macroparasites and amphibians, he engages in ecological puzzles concerning the mechanisms responsible for biodiversity patterns at different scales. This paper is part of his PhD, which focus on what drives distinct dimensions of parasite diversity at broad spatial scales.

Author contributions

Paulo Mateus Martins: Conceptualization, Methodology, Formal Analysis, Investigation, Data Curation, Writing – Original Draft. **Robert Poulin:** Conceptualization, Methodology, Writing – Review and Editing. **Thiago Gonçalves Souza:** Conceptualization, Methodology, Formal Analysis, Writing – Review and Editing, Supervision.

Abstract

Aim: Climate and host richness are essential drivers of global gradients in parasite diversity, and the few existing studies on parasites have mostly investigated their effects separately. The advantages of combining these factors into a single analytical framework include unravelling the relative roles of abiotic and biotic drivers of parasite diversity. We compiled a dataset of helminths of amphibians to investigate the direct and indirect effects of temperature seasonality, annual precipitation, precipitation seasonality and host richness as drivers of parasite diversity at the global scale. Our analyses focus not only on the least studied group of vertebrates regarding macroecology of parasite diversity, but also the host group most sensitive to climatic conditions, especially temperature seasonality and water availability.

Location: Global

Time period: 1955-2017.

Major taxa studied: Helminth parasites of amphibians.

Methods: We used piecewise structural equation modelling on a global dataset of helminths of amphibians, comprising 613 populations of 319 anuran species and 94 populations of 43 salamander species from ten zoogeographical realms.

Results: We found that precipitation seasonality and host richness both affect parasite diversity positively, but the latter presented a stronger effect. Additionally, we found that both temperature seasonality and total precipitation indirectly affected parasite richness through their respective negative and positive effects on host richness.

Main Conclusions: Future studies on global gradients in parasite diversity should include both direct and indirect effects of climatic factors as drivers of parasite diversity. Integrating multiple predictors into a single statistical framework that measures both direct and indirect effects increases our theoretical understanding of the relative importance and interactions among different diversity drivers at the macroecological scale. The indirect effects of temperature seasonality and total precipitation on parasite diversity are an interesting new insight brought by our study, with implications for future studies dealing with host-parasite coextinctions due to climate change.

Keywords: amphibians, climate, helminths, host diversity, temperature, parasite diversity, piecewiseSEM, precipitation

Introduction

Understanding why biological diversity is distributed unevenly across Earth's ecosystems persists as an essential goal in macroecology and biogeography. Despite many unresolved issues, one common ground is that no single factor can account for biodiversity gradients; therefore, studies considering multiple explanations promote a greater understanding of how different mechanisms determine species diversity at the macroecological scale (Belmaker & Jetz, 2015; Rodrigues, Olalla-Tárraga, Iverson, Akre, & Diniz-Filho, 2017). For broad geographical patterns, most studies rely on the effects that area, time, productivity, biotic interactions, mean temperature and climate stability have on the balance between species appearing and their exclusion over evolutionary time (reviewed in Fine, 2015). However, these studies are biased toward certain taxonomic groups (e.g., birds and mammals) or geographical areas (e.g., temperate zone) (Beck et al., 2012). Surprisingly, whether these major diversity drivers also affect symbiont and particularly parasite diversity remains largely unexplored (Stephens et al., 2016).

There is usually a strong correlation between species richness and climatic components leading to various hypotheses of how climate affects species diversity (Currie et al., 2004; Field et al., 2009). However, macroecological studies on parasite diversity are primarily focused on host-related drivers and latitudinal gradients (Poulin, 2014; Morand, 2015; but see Guernier et al., 2004; Preisser, 2019). Most studies found a positive association between host and parasite diversity regardless of both host and parasite taxa (Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014a). This relationship is considered analogous to the role of habitat heterogeneity for free-living organisms where high diversity is generated by high turnover (Johnson et al., 2016), or to the bottom-up control of diversity where species diversity at higher trophic levels is constrained by diversity at the lower level (Krasnov, Shenbrot, Khokhlova, & Poulin, 2007). In relation to latitudinal gradients, there is considerable heterogeneity in the relationship between parasite diversity and latitude, with some studies supporting it and others not. When latitudinal effects are detected, there seems to be a weak but positive association between latitude and parasite richness at least for metazoan parasites (see meta-analysis by Kamiya et al., 2014a).

Temperature and precipitation belong to the core of some prominent climate-based explanations, but how they affect parasite diversity remains largely unexplored (but see Guernier et al., 2004; Preisser, 2019). For instance, according to the climate stability hypothesis, the absence of marked climatic extremes has a positive effect on net speciation rates by

lowering extinction rates and promoting specialization (Fine, 2015; McKenna & Farrell, 2006). However, evolutionary processes such as speciation require hundreds of thousands of years to occur. Especially at short temporal scales (e.g., thousands of years), precipitation and temperature are more likely to affect diversity by influencing species persistence due to physiological constraints that limit species ranges (but see Araújo et al. 2008). In this context, ectotherms such as amphibians seem to be notably limited by tolerance to low temperatures and extremes (Wells, 2007).

Even though the broad-scale drivers of diversity such as climate stability and water availability are correlated with latitude, using the actual variables instead of latitude as a proxy represents a superior approach for linking biodiversity patterns to mechanisms (Hawkins & Diniz-Filho, 2004). Additionally, host-related drivers such as local richness may interact with climatic factors as drivers of parasite diversity (Rohde, 1999). To disentangle the respective roles and interactions of climate and host-related factors, it is desirable to have geographically widespread groups of hosts and parasites and include both direct and indirect effects of climate through an important host-related attribute that itself responds to climatic gradients. Host richness is an adequate candidate for this host-related factor due to its consistent relationship with parasite diversity (Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014b) and responsiveness to climate.

Identifying the drivers of diversity gradients has often been guided by human interest over the future of biodiversity and the urge to establish its status (Gaston, 2000). Some estimates suggest that parasitic organisms, notably parasitic worms (helminths) and arthropods, constitute 30 to 50% of the animal tree of life (see Poulin, 2014). Therefore, investigating what drives parasite diversity represents a major step towards understanding what affects a substantial portion of existing species. Additionally, parasite diversity is a potentially good measure of parasite pressure on hosts, being related to key factors such as host diversification, energetic demands and body condition (reviewed in Bordes & Morand, 2009).

Using the major broad-scale drivers of diversity and considering their interactions with important host-related factors is a promising approach to explore what determines parasite diversity at the macroecological scale. By using a novel global dataset on helminths of amphibians, we used structural equation modelling to investigate the direct and indirect effects of temperature seasonality, precipitation seasonality, total precipitation and host richness as drivers of parasite alpha diversity. We highlight that, to our knowledge, no previous study on

global parasite diversity has used amphibians as models, therefore our study besides bringing a new approach to the study of parasite diversity at broad spatial scales, explores an unprecedented group of hosts. We chose our climatic variables based on key climatic conditions required for both amphibian and helminth reproduction and survival (Goater, Goater, & Esch., 2014; Wells, 2007).

Given that both climate and host richness are essential drivers of parasite diversity through space and time, we might expect that global changes might affect parasites in two different ways. Future projections forecast (i) an increase in climate instability (i.e., extreme values of temperature, precipitation and drought: Fischer & Knutti, 2015) and (ii) an increase in the loss of amphibians worldwide (Nowakowski, Frishkoff, Thompson, Smith, & Todd, 2018) which, consequently, could have a strong negative effect on parasite diversity (see e.g., Carlson et al., 2017). Additionally, although most studies on negative impacts of amphibian parasites are focused on microparasites such as the chytrid fungus, helminths can cause substantial damage to their host (see Koprivnikar et al., 2012 and references therein). Therefore, our study could help predicting the conditions under which amphibians may face higher helminth parasite pressure.

Regarding the direction of the effects, our predictions are: (i) annual precipitation has a positive effect on host and parasite richness; (ii) temperature and precipitation seasonality affect negatively both host and parasite richness; and (iii) host richness has a positive effect on parasite richness. A great novelty in our approach is that it considers whether climate affects parasite diversity indirectly by influencing host richness. We particularly emphasize the importance of our predictor variables as major biological drivers of amphibian diversity due to their ectothermic metabolism, permeable skin and reproductive mode tied to water availability in most species.

Methods

Database

We compiled a comprehensive dataset on helminths parasitising amphibians by conducting a systematic search of the literature published between 1970 and 2018 in the Google Scholar (scholar.google.com) and Web of Science (isiknowledge.com) databases. To find published references, we combined the keywords "Helminth* OR Parasite*" with scientific and common names of different orders of amphibians: AND "Amphibia* OR Anura* OR Frog*

OR Toad* OR Caudata* OR Urodela* OR Salamander* OR Newt* OR Gymnophiona OR Caecilian*". To be included in our dataset, we considered the following inclusion criteria: (i) focus on the whole helminth community, (ii) specify the sampling locality (ideally with geographic coordinates), and (iii) provide the number of analysed hosts (minimum of five hosts). We disregarded studies describing new helminth species or focusing only on particular parasite groups. We also excluded surveys combining data from different localities separated from each other by more than 100 km, and studies that did not report host sample size. We removed hosts that were collected out of their native ranges to control for potential confounding variables associated with this condition. A list of the data sources is given in Appendix 1 – Data Sources. We updated host scientific names and taxonomic classification according to the Amphibian Species of the World 6.0 online database (https://amphibiansoftheworld.amnh.org/).

We restricted our analysis to helminths found in the lumen of the gut, lungs and urinary bladder for the following reasons: (i) in contrast to other organs and structures, most studies in our database surveyed the parasites in these organs; (ii) most parasites are identified down to the species level, (iii) most parasites have amphibians as their final hosts, which strengthens the associations between parasite diversity and factors related to amphibians. When not reported in the original papers, the site of infection of each helminth species was obtained from the literature. The full dataset is available at https://doi.org/10.5061/dryad.4mw6m907s.

Predictor variables

We obtained temperature seasonality (standard deviation *100), precipitation seasonality (coefficient of variation), annual precipitation and host richness for each locality to test their effects on parasite diversity, here defined as the number of parasite species per host population. We chose these climatic variables based on our model organisms. As ectotherms, amphibians are particularly sensitive to temperature fluctuations and have little control over water loss. Additionally, most amphibians require standing water or moist habitats to reproduce (Wells, 2007). Similarly, we expect helminths to be sensitive to these conditions during their environmental stages (see Pietrock & Marcogliese, 2003). Therefore, these variables may be explicitly linked to physiological tolerance for both groups of organisms. At first, we also included mean annual temperature in the model, but it was strongly correlated to temperature seasonality ($r= -0.86$, $p < 0.05$). Thus, we kept temperature seasonality in the final model because it had a much stronger effect on amphibian richness in our model.

The climatic variables were acquired from WorldClim version 2 based on data from 1970 to 2000 (Fick & Hijmans, 2017). Host richness was generated for each locality by combining primary geographical range data for different amphibian species. All amphibian diversity maps were acquired from the Mapping the World's Biodiversity initiative (BiodiversityMapping.org) (see Jenkins et al., 2013; Pimm et al., 2014 for details). Local host richness was then computed as the number of host species whose distributions overlapped the sampled locality. All rasters containing the data were standardized for a spatial resolution of ten minutes (~340 km²). We created grids of one squared degree per cell and calculated a mean coordinate for all populations sharing the same grid for extracting the predictor and dependent variables. Populations from the same species within the same grid were combined.

Data analysis

We fitted a Piecewise Structural Equation Model (piecewiseSEM; Lefcheck, 2016) to test the direct and indirect effects of temperature seasonality, precipitation seasonality, annual precipitation and host diversity as drivers of parasite diversity. One of the main advantages of SEM models is that they allow evaluating networks of direct and indirect effects among variables. Our Piecewise SEM model encompasses two underlying structured equations that represent (i) the effects of temperature seasonality, precipitation seasonality and annual precipitation on host richness, and (ii) the effects of the same climate variables and host richness on parasite richness. Both were fitted using Linear Mixed Models (LMMs). The main advantage of mixed models is the possibility of including the hierarchical structure of the data as a random factor. For both models, the random structure is represented by the zoogeographical realms that were categorized following Holt et al. (2013). Additionally, we included the amphibian taxonomic hierarchy (i.e., family, genus and species) as an additional random factor in the model (ii) to account for the possible dependence of parasite richness on some species-level host characteristics. Predictor climatic variables were standardised, and both host and parasite diversity were log +1 transformed to fit the model assumptions. We ran the Moran's I test for spatial autocorrelation in both models and found no spatial autocorrelation for model (ii). Given that model (i) showed spatial autocorrelation, we included the spatial autocorrelation structure directly in the mixed model. The final models were:

(i) lme (log_host_richness, temperature_seasonality + total_precipitation + precipitation_seasonality, random=~1|realm, corSpatial (form = ~longitude + latitude), data=dat)

(ii) lmer (log_helminth_richness~log_host_richness + temperature_seasonality + total_precipitation + precipitation_seasonality + (1|realm), offset = log(sampling_effort), data=dat)

We found five helminth groups infecting amphibians: acanthocephalans, cestodes, monogeneans, nematodes and trematodes. Due to limitations in the number of records for some groups and the overall low parasite richness in amphibians (see Appendix S2), we did not run separate models for each parasite group. Regarding hosts, we ran separate piecewise SEM models for anurans (frogs and toads) and salamanders, as these represented a major phylogenetic split in our dataset and may respond differently to our climatic variables. We checked for multicollinearity by calculating the variance inflation factor (VIF) for each predictor variable (Quinn & Keough, 2002). There was no indication of multicollinearity in any of our models (all VIF values < 3). The models were fitted by using the "lme4" (Bates, Mächler, Bolker, & Walker, 2015), "nlme" (Pinheiro, Bates, Debroy, & Sarkar, 2020) and "piecewiseSEM" (Lefcheck, 2016) packages in the environment R (R Core Team, 2020).

Results

We obtained 424 references, among which 241 were used to compile our data base after considering the inclusion criteria (see Appendix 1 – Data Sources) The final dataset (available at: https://doi.org/10.5061/dryad.4mw6m907s) comprises the richness of endohelminths (trematodes, cestodes, nematodes and acanthocephalans) parasitising 613 populations (495 after combining populations sharing the same grid) of 319 anuran species, and 94 populations (77 after combining populations sharing the same grid) of 43 salamander species collected from 1955 to 2017; no helminth community survey was available for any caecilian species. We collected data from 29 families of anurans and five families of salamanders. For anurans, most investigated species belong to the Ranidae, Hylidae and Bufonidae families (see Appendix S3), while for salamanders most species belong to the Plethodontidae, Salamandridae and Ambystomatidae families (see Appendix S4).

We obtained data from ten zoogeographical realms for anurans and five zoogeographical realms for salamanders (Figure 1). All predictor variables displayed a wider range of values for anurans than for salamanders (Table 1). Mean parasite richness was 3.9 (range: 1 to 21) helminth species for frogs and 3.1 (range: 1 to 10) for salamanders. For both amphibian orders, nematodes were the most common parasites followed, in that order, by trematodes and cestodes (see Appendix S2).

Overall, the model for anuran helminths explained 46% of parasite diversity (R^2_{Cond} = 0.46), among which 10% is attributed to precipitation seasonality and host diversity alone (R^2_{Marg} = 0.10). Temperature seasonality and total precipitation explained 43% of anuran diversity (R^2_{Marg} = 0.43). The model for salamanders did not uncover any effect of climate or host diversity on parasite diversity; therefore, below we focus on the results of the anuran models.

Regarding direct effects, anuran diversity (standardized β = 0.406, $p < 0.05$) and precipitation seasonality (standardized β = 0.266, $p < 0.05$) had a positive effect on helminth richness (Figure 2). Temperature seasonality (standardized β = -0.589, $p < 0.05$) and total precipitation (standardized β = 0.279, $p < 0.05$) had a negative effect on host richness, which resulted in a respective negative and positive indirect effect on parasite diversity mediated by host diversity (see Figure 2).

Discussion

Based on a comprehensive novel dataset of helminths parasitizing amphibians, we showed that both climate and host diversity affect parasite diversity at the global scale in a complex manner that include direct and indirect relationships. Host diversity is one of the main drivers of parasite diversity, and the responsiveness of amphibian richness to temperature seasonality and annual precipitation reveals that these climatic factors affect amphibian helminth diversity indirectly. Additionally, we found that precipitation seasonality affected parasite richness positively and independently of host diversity, which is probably explained by the reproductive synchrony of different amphibian species imposed by seasonal environments. The negative indirect effect of temperature seasonality on parasite richness has important implications for biodiversity conservation, given that increasing temperature seasonality due to climate change may cause cascading extinctions of amphibians and their parasites. Additionally, our results indicate that amphibian populations inhabiting more seasonal areas face more parasite pressure, given the positive association between precipitation seasonality and helminth richness. Our study also highlights the importance of analytical and theoretical frameworks that encompass multiple predictors and paths in the same model. Besides allowing simultaneous consideration of multiple explanations, it is possible to evaluate direct and indirect effects of distinct predictors.

The positive effect of host diversity on parasite diversity is in accordance with most previous findings (see meta-analysis by Kamiya et al., 2014b). In fact, host diversity is a strong predictor of parasite diversity regardless of taxa or spatial scale (Kamiya et al., 2014b; but see

Johnson et al., 2016 for discussion on scale). Johnson et al. (2016) found that this positive association between host and parasite richness is mainly explained by an increase in parasite beta diversity, resembling the influence of habitat heterogeneity for free-living organisms. Additionally, the spatial co-occurrence of multiple host species (high local host diversity) that are phylogenetically related can promote host-switching by parasites (Pedersen & Davies, 2009; Poulin, 2010). Thus, each host species may begin with its own unique set of parasite species but then exchanges occur among them, thereby increasing the average parasite richness among host species in that locality.

In addition, climate is a strong correlate of species diversity for free-living organisms, especially at large grains and extents (Field et al., 2009). Previous studies on parasites have also emphasized the prominence of climate as an important global predictor of parasite diversity (Dunn, Davies, Harris, & Gavin, 2010; Guernier et al., 2004; Preisser, 2019). Some proposed explanations for how climate affects species diversity are related for instance to climatic effects on the speed of evolutionary processes, the amount of available energy and to species tolerances (see Currie et al., 2004). Especially at short temporal scales such as our study (1955-2018), the climatic effects we have found are more likely to be associated with the actual species tolerance to contemporary climatic conditions, although we should not underestimate the importance of historical factors (see Mittelbach et al., 2007; Araújo et al., 2015).

The model for anurans revealed a positive effect of precipitation seasonality on helminth richness (Figure 2). We interpret this positive outcome based on the particularities of anuran reproduction. Interspecific parasite transmission requires different host species to have direct or indirect contact, giving parasites the opportunity to infect new host species, therefore increasing intraspecific parasite richness (Poulin & Morand, 2004). Most amphibians rely on standing water or wet environments to reproduce and can stay inactive when wet conditions are not available. Especially in arid environments, most amphibian species rely on standing water to reproduce (Wells, 2007). For such sites, a high precipitation seasonality may indicate that environmental requirements for anuran reproduction is available only during a short period of the year, and local species may share the same reproductive sites at the same time, increasing the possibility for host-switching.

The importance of temperature and water-related variables as determinants of amphibian diversity is in accordance with other findings (Qian, Wang, Wang, & Li, 2007; Rodríguez, Belmontes, & Hawkins, 2005). The strong negative effect of temperature

seasonality on anuran richness (Figure 2) is expected and may indicate that mechanisms related to physiological tolerance to temperature variation are in play. Species inhabiting high seasonal regions are liable to face extreme climatic fluctuations along the year. This is hypothesized to affect probabilities of extinction, especially for organisms with low dispersal abilities (see Fine, 2015 and references therein). When extended to the past geological history of the planet, this reasoning is at the core of why tropical environments preserve more lineages and hold a high species diversity (see McKenna & Farrell, 2006). Most amphibians rely on standing water to reproduce and have little or no control over water loss (Wells, 2007). These characteristics of amphibian biology may explain their sensitivity to water availability and the positive effect of annual precipitation on amphibian richness.

Helminths did not respond directly to temperature seasonality and annual precipitation, but these variables indirectly affected helminth diversity mediated by host richness (Figure 2). This result has important implications for biodiversity conservation. Parasite diversity declines with biodiversity loss and hosts differ in their extinction susceptibility (Lafferty, 2012). Among vertebrates, amphibians are the most vulnerable group of hosts. This is due to the specific water requirements for reproduction and survival along with low tolerance to temperature extremes (see Wells, 2007). Along with their low dispersal abilities, these aspects of amphibian biology make them especially susceptible to changes in the temperature and water regimes as a result of climate change (Foden et al., 2013). In fact, some amphibians face local extinction due to severe droughts due to recruitment failure (e.g., Scheele et al., 2012). Therefore, certain parasites of amphibians are likely to go extinct as their definitive hosts' diversity decreases. This coextinction and loss of interacting and dependent species is a special concern of biological conservation (see Colwell et al., 2012).

The model for salamanders did not detect any effect of climate or host richness on parasite richness. We can think of two possible reasons for this absence of effect. First, this could be explained by the smaller variation in both parasite and host richness among localities, as well as by the much smaller geographical extent of salamander data when compared to that of anurans (Figure 1; Table 1). Additionally, maybe the general taxonomic composition of their helminth fauna is different, and therefore may be driven by other factors.

In a broad dataset as the one we used, there are some shortcomings we need to consider while interpreting the results. First, there is a noticeable temporal spread in the years in which the hosts were collected (1955 – 2017). In a recent paper, Tessarolo et al. (2017) discussed the

temporal degradation of biodiversity data, which is inevitable due to the dynamic essence of natural systems. Old records therefore may present a "picture" of a state that no longer exists. For instance, some sampling sites may have gone through dramatic changes in land use. Second, it was not possible to control for potential confounding variables such as host sex and age given that most authors did not mention these in the original papers. Third, the means for the climatic variables are based on a narrower temporal scale than the dataset (1970 – 2000 for climatic variables against 1955 - 2017; Fick & Hijmans, 2017). However, none of these factors are likely to generate the significant effects we uncovered; they would be more likely to generate noise rather than bias the results in one particular direction.

Conclusion

We found that integrating climate factors and host diversity brings new insights on how different mechanisms jointly influence parasite diversity at the global scale. Recent surveys have highlighted the advantages of bringing ecological theory into parasite studies (Johnson et al., 2016; Stephens et al., 2016), along with a growing interest in identifying drivers of parasite diversity at multiple scales (Morand, 2015; Poulin, 2014). Here, we showed that both precipitation and temperature are in play for determining parasite richness through direct and indirect effects mediated by host diversity. When studying parasite diversity, future studies should consider indirect effects associated with how hosts respond to environmental variables and the indirect impact this can have on parasite diversity. Additionally, for broad-scale studies on parasites, we argue that studies should focus on the climatic gradient and host factors instead of latitude as a proxy (Hawkins & Diniz-Filho, 2004), especially when dealing with complex patterns such as interactions among species (see Romero et al., 2018), while also considering the direct and indirect relationship among distinct predictor variables. This understanding, which is relevant for dealing with future coextinctions due to climate change, would have been lost if we had ignored the interactions between climate and host diversity.

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Data Availability

The complete raw dataset is available at: https://doi.org/10.5061/dryad.4mw6m907s. A complete list of data sources for parasite richness can be found in the Appendix 1 – Data Sources. Amphibian diversity was acquired from Jenkins, Pimm and Joppa (2013) and Pimm et al. (2014) (available at https://biodiversitymapping.org/wordpress/index.php/amphibians/). Climatic data was downloaded from Fick and Hijmas (2017) (http://www.worldclim.org/version2).

Artigo 1: Tabela e Figuras

Table 1. Ranges of the raw climatic predictor variables and host richness associated with each host group.

Host Group	Temperature Seasonality (SD*100)	Annual Precipitation (mm)	Precipitation Seasonality (Coefficient of Variation)	Host Richness
Anurans	18.73 – 1,409.49	74 – 5,463	9.78 – 162.6	1 - 120
Salamanders	54.99 – 1,098.29	480 – 2,674	11 – 94.72	1-25
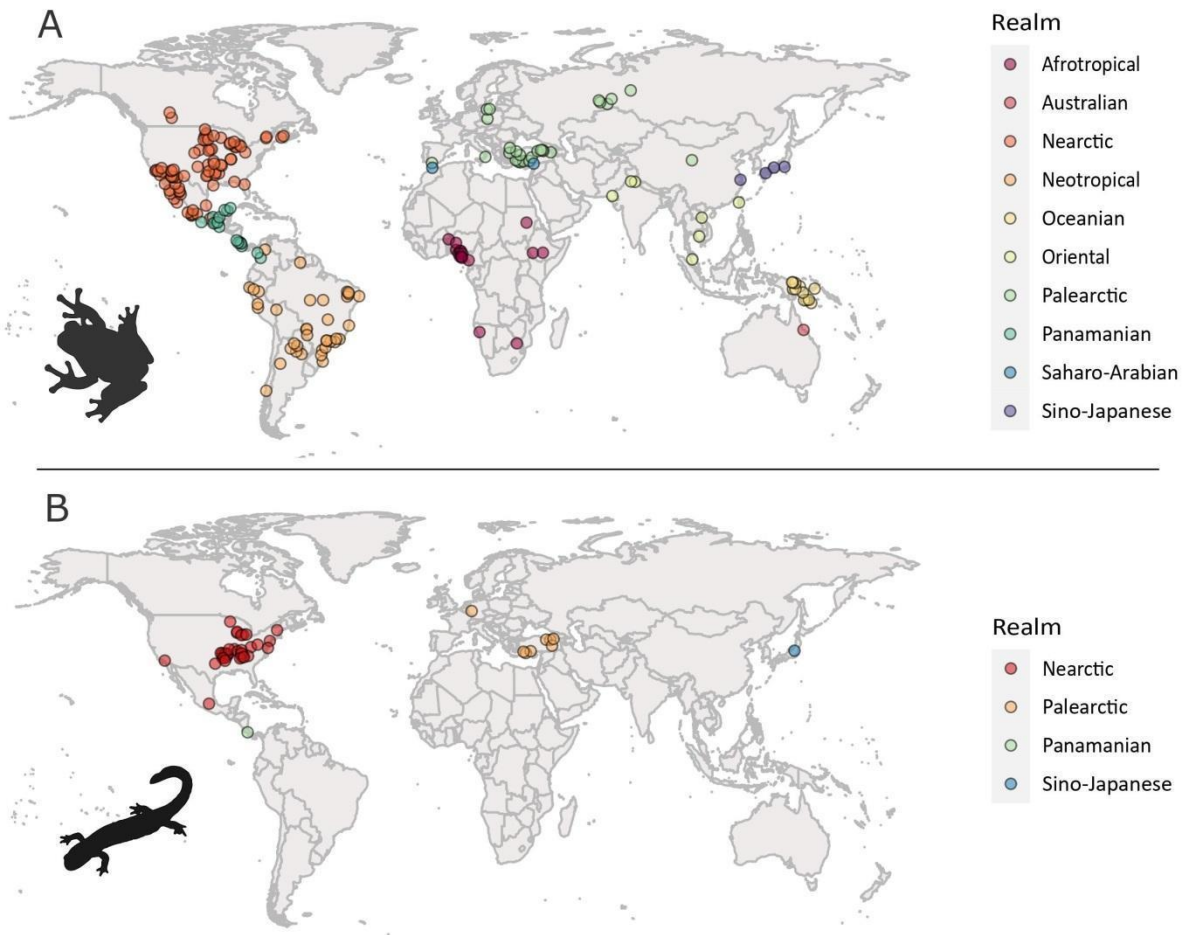
Figure 1. Spatial spread and zoogeographical realms of localities in which the anurans (1a) and salamanders (1b) were collected in the original studies that compose our final database.
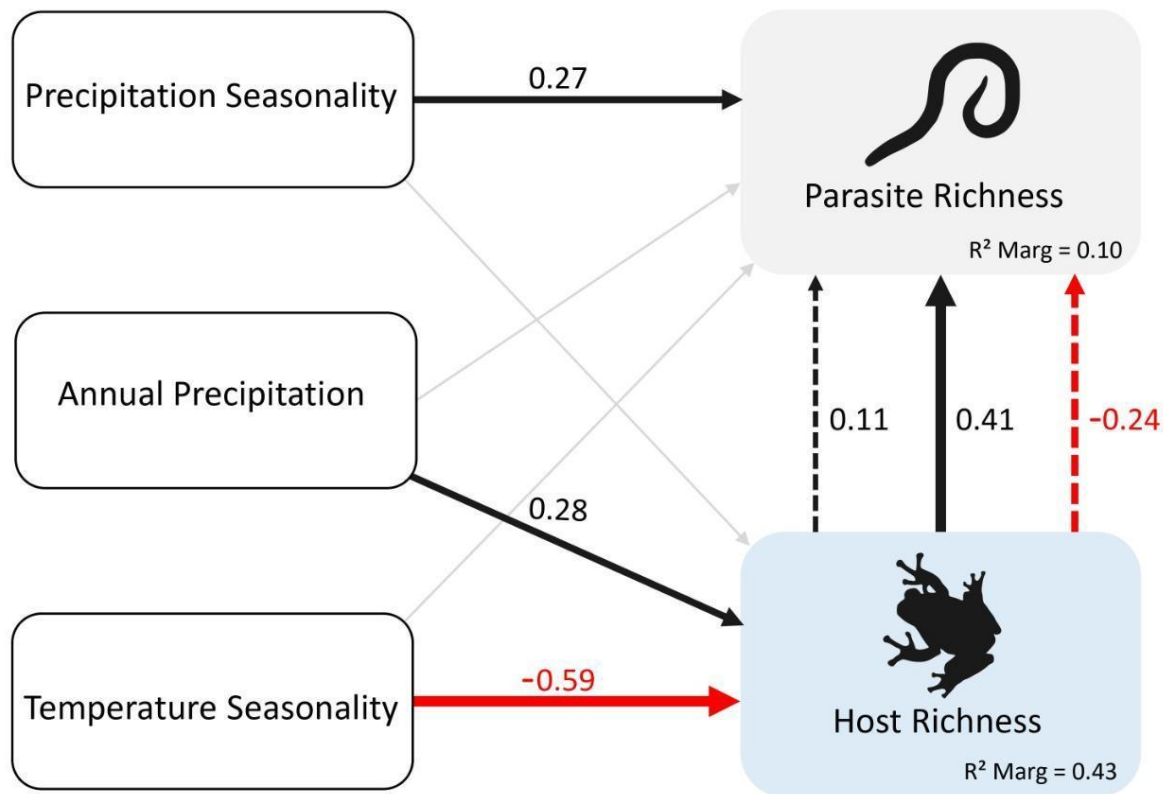
Figure 2. Piecewise structural equation model exploring the relationships among temperature seasonality, precipitation seasonality, total precipitation, host diversity and parasite diversity. Arrows show unidirectional relationships among variables. Black arrows designate positive effects, and red arrows negative relationships. Grey arrows denote non-significant paths ($p >$ 0.05) and arrows with dotted lines represent the indirect effects. Numbers next to arrows represent the standardized regression coefficients which are also expressed in the thickness of arrows. The indirect standardized coefficients were obtained by multiplying the coefficients of significant paths.

Artigo 1: Material Suplementar

Supporting Information Appendix S1. Data Sources.

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Supporting Information Appendix S2. Number of records, mean richness, and ranges for different parasite subsets per host group.

Parasite subset	Number of Records	Mean richness (Min-Máx)
Anurans		
All helminths	2,052	3.92 (1-21)
Nematoda	1,414	2.81 (1-14)
Trematoda	421	1.85 (1-7)
Cestoda	131	1.07 (1-2)
Acanthocephala	54	1.04 (1-2)
Monogenea	32	1.07 (1-2)
Salamanders		
All helminths	251	3.06 (1-10)
Nematoda	163	2.23 (1-7)
Trematoda	52	1.33 (1-3)
Cestoda	28	1.12 (1-2)
Acanthocephala	4	1
Monogenea	3	1
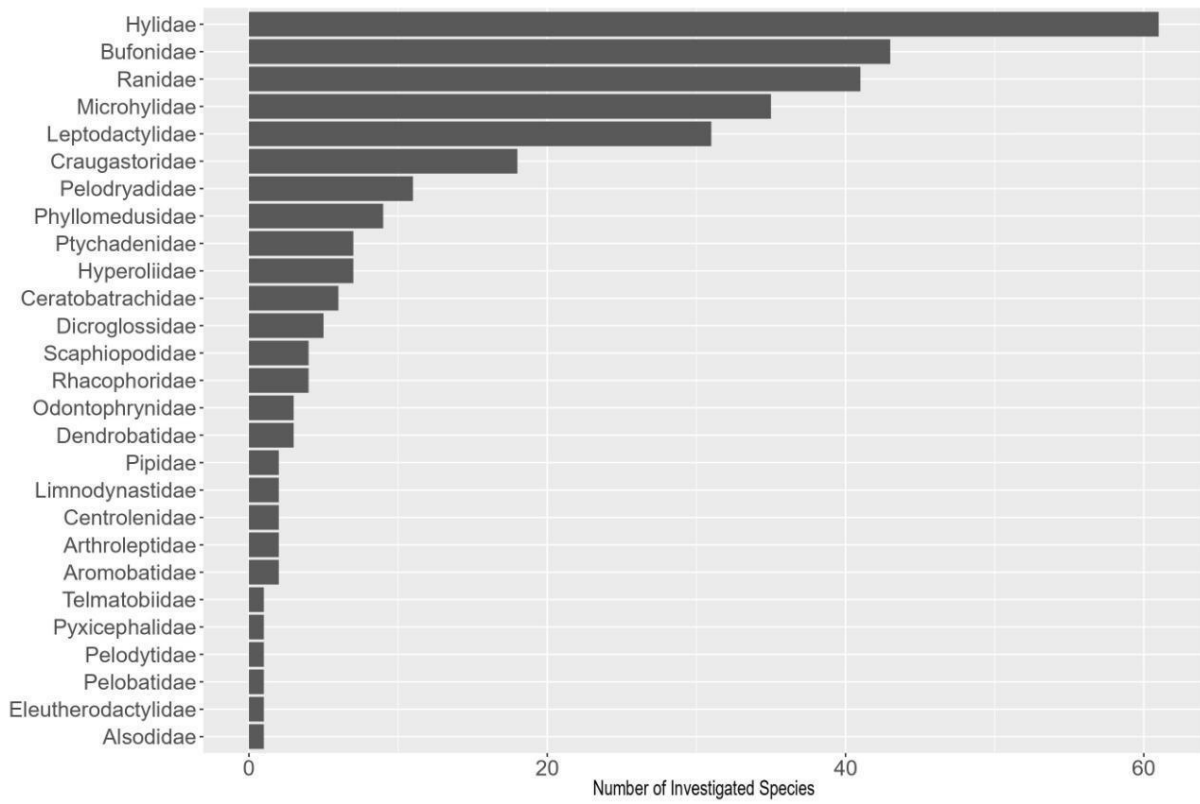
Supporting Information Appendix S3. Number of investigated species per anuran family.
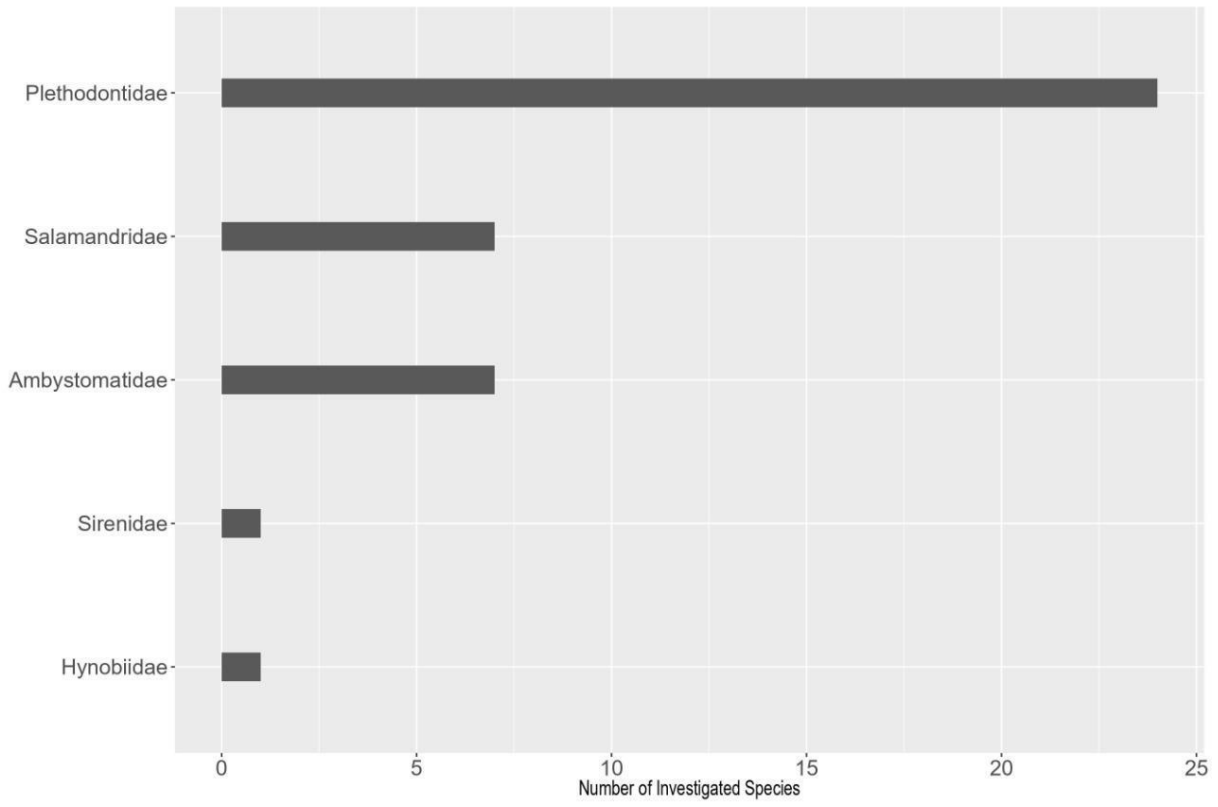
Supporting Information Appendix S4. Number of investigated species per salamander family.

4. Artigo 2: Broad scale drivers of parasite beta diversity among anuran hosts depend on scale, realm and parasite group

(Artigo aceito para a publicação no periódico *Philosophical Transactions of the Royal Society B: Biological Sciences*)

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Abstract

A robust understanding of what drives parasite beta diversity is an essential step towards explaining what limits pathogens' geographical spread. We used a novel global dataset (latitude -39.8 to 61.05 and longitude - 117.84 to 151.49) on helminths of anurans to investigate how the relative roles of climate, host composition and spatial distance to parasite beta diversity vary with spatial scale (global, Nearctic and Neotropical), parasite group (nematodes and trematodes) and host taxonomic subset (family). We found that spatial distance is the most important driver of parasite beta diversity at the global scale. Additionally, we showed that the relative effects of climate concerning distance increase at the regional scale when compared to the global scale and that trematodes are generally more responsive to climate than nematodes. Unlike previous studies done at the regional scale, we did not find an effect of host composition on parasite beta diversity. Our study presents a new contribution to parasite macroecological theory, evidencing spatial and taxonomic contingencies of parasite beta-diversity patterns, which are related to the zoogeographical realm and host taxonomic subset, respectively.

Introduction

Understanding how biotic and abiotic processes drive the spatial variation of biodiversity is still an important goal of biogeography and macroecology. For years, biodiversity studies were primarily focused on what drives the number of species found at the local scale, or alpha diversity [1]. However, during the last decades there has been a renewed interest in the variation in species composition among sites, or beta diversity [2]. Beta diversity acts as a link between local (alpha) and regional (gamma) diversities [2–4], making its study crucial to determine what drives diversity at broad scales. In beta diversity studies, species turnover refers to the replacement of species among sites due to environmental, geographical, and historical differences [5,6].

The usual approach for studying species turnover includes measuring the rate at which species composition changes across space [7,8]. In general, compositional similarity among sites tends to decrease (or dissimilarity tends to increase) with spatial distance. The proposed explanations for such distance-decay relationships include deterministic responses of species to biotic and abiotic conditions (i.e., niche-based processes) and spatial processes that influence the ability of organisms to find suitable environments, such as dispersal ability and its interaction with habitat configuration and history [8,9]. In the study of parasite turnover, niche-based processes are inferred from the effects of host-related and environmental variables, while geographical distance is generally used as a proxy for spatial processes such as dispersal limitation.

Current evidence suggests that parasite turnover at broad scales is mostly affected by host diversity and climate, with a minor effect of spatial distance [10–14]. Since many parasites release larvae and eggs into the environment, climate has an impact on parasite survival, emergence, and infectivity during these stages [15,16]. Furthermore, hosts are the ultimate resources for parasites, so parasite diversity often tracks host diversity in a parallel with the consumer-resource relationship for free-living organisms [17]. As a result, the available studies indicate that at large scales, parasite geographical distribution is primarily constrained by niche-based processes mediated by environmental variation and host composition.

Despite some exceptions [18], most large-scale studies on parasite beta diversity are either focused on ectoparasites, mammals, or cold regions (particularly the Palearctic), most likely due to data availability. However, the observed patterns and identified drivers of parasite diversity are likely to change in response to all those factors. [10], for example, found that host

composition explained a greater proportion of beta diversity in parasites infecting fish than parasites infecting mammals and birds, and proposed that differences in dispersal capacity between hosts could explain this variation. Similarly, even when collected from the same host group, different parasite groups may respond differently or to varying degrees to the same variables [10]. Probably because parasite groups with different life cycles may respond to environmental variables in different ways.

Additionally, our understanding of how these drivers vary among zoogeographic realms and spatial scales remains limited. First, each realm represents a distinct combination of past historical events and species pool [19], which may result in region-specific species-environment relationships [20]. For instance, the range of temperature is exceptionally high in northern zoogeographical realms. Thus, because most species have a low tolerance to this condition, temperature (especially extremes) tend to be the critical at limiting species' geographical spread in cold regions [21]. Based on the evidence that region- or system-specific relationships may affect the general findings, our ability to make broad statements about what governs parasite beta diversity at broad spatial scales is limited. As a result, assessing novel groups of hosts and parasites, as well as distinct realms, is critical for advancing parasite macroecological theory.

Regarding spatial scale, we know of no study investigating how parasite beta diversity drivers vary with spatial scale. However, the current synthesis in community ecology recognizes that biodiversity patterns result from a combination of niche and neutral processes whose relative importance varies with scale [22,23]. The importance of niche-based processes is evidenced by the observed associations between species composition and environmental conditions such as climate, even after controlling for spatial distance [21,24,25]. In contrast, the neutral theory [26] predicts that dispersal limitation increases with spatial distance, resulting in an increase in species dissimilarity regardless of environmental differences [23,27,28]. For some organisms, niche-based processes are stronger at smaller spatial scales, while dispersal tends to be limiting at larger scales. For example, [29] observed that at the biogeographical scale, geographical distance explained the most variation in arthropod composition, whereas microhabitat variation was more important at the metacommunity scale, but see [30]. This framework has currently advanced to a more predictive theory where both spatial and taxonomic scales represent useful information to explain broad-scale biodiversity patterns.

Based on a novel global (latitude ranging from -39.8 to 61.05 and longitude ranging from - 117.84 to 151.49) dataset on helminths of anurans, we investigate how including different taxonomic and spatial scales improves our understanding of the relative importance of climate, host composition and spatial distance as drivers of helminth beta diversity in anuran hosts. Our main question addresses how the relative roles of these factors as drivers of helminth turnover vary in relation to (i) spatial scale (global and regional), (ii) realm (Nearctic and Neotropical), and (iii) parasite group (nematodes and trematodes). We predict that (i) niche-based processes (here represented by a combination of climate and hot composition) will be more critical than dispersal limitation (here represented by spatial distance) at the realm scale (Nearctic and Neotropical), (ii) climatic extremes will be more important in the Nearctic than in the Neotropical realm, and (iii) trematodes will be more responsive to climate than nematodes because they are more sensitive and mostly rely on free-living aquatic infective stages, and (iv) host composition will be a strong determinant of parasite beta-diversity at all scales. Additionally, we investigated how selecting different host taxonomic subset (all anurans, Bufonidae, Hylidae and Ranidae) affect the general trends.

Methods

Host-parasite dataset

We updated a global dataset on helminths parasitising anurans used for a previous study [31] through a systematic review of the literature published between 1970 and 2020 in the Google Scholar (scholar.google.com) and Web of Science (isiknowledge.com) databases. As for the first study, we combined the keywords "Helminth* OR Parasite*" and keywords associated with different anuran groups: "Amphibia* OR Anura* OR Frog* OR Toad*. To be included in the final dataset, studies had to be surveys of parasites within a given amphibian population or community, and they had to: (i) provide a list of parasite taxa found in the hosts sampled, (ii) specify the number of analysed hosts, and (iii) specify the sampling location. We removed surveys describing new parasite species or focused on only a subset of the helminth community. We also excluded studies that combined parasite data from localities separated by more than 100 km. We opted to keep only hosts collected within their native ranges to avoid possible confounding factors connected with introduction to new areas.

We limited our analysis to nematodes and trematodes detected in the lumen of the gastrointestinal tract based on the following reasoning: (i) all compiled studies analysed the gut for parasites, (ii) it avoids generating artificial differences in parasite species composition based

on surveys of different infection sites, and (iii) most gut helminths are identified down to the species level. When not reported in the original papers, the infection site of each helminth species was obtained from the literature. Hosts and parasites had their scientific names updated following, respectively, the Amphibian Species of the World 6.0 [32] and the GBIF Backbone Taxonomy [33] datasets. For studies without coordinates, we used Google Maps (maps.google.com) to obtain approximate latitudes and longitudes of the sampling localities provided by the authors.

Spatial units and predictor variables

We used hierarchical clustering to group sampling sites that were distant from each other by less than 100 km. Clusters were created using the agglomeration method Unweighted Pair Group Method with Arithmetic Mean (UPGMA). We opted for this method instead of grouping by random grids to avoid arbitrarily splitting nearby localities that likely belong to the same community. We used these clusters as grouping variables and obtained the coordinates of the centroid of each cluster of localities. Then, we used those coordinates to obtain the climatic variables for each cluster. To test parasite responses to climate, we first chose variables that measured temperature and precipitation extremes. These were the maximum temperature of the warmest month, the minimum temperature of the coldest month, the precipitation of the wettest month, and the precipitation of the driest month. Furthermore, we used variables measuring temperature and precipitation variability that were uncorrelated with the first four. These were mean diurnal range (mean of monthly (max temp - min temp)) and precipitation seasonality (coefficient of variation). Global rasters for these variables were obtained from WorldClim version 2 [34] with a spatial resolution of 10 minutes (~340 km²). All climatic variables were standardised and checked for collinearity.

To assess the effect of host assemblage on parasite beta diversity, we used a dissimilarity matrix of host composition. To get host composition per site, we first downloaded the amphibian distribution polygons provided by the International Union for Conservation of Nature [35]. We considered that an anuran species occurred in a given locality when its respective polygon overlapped that site's coordinates. We ended up with a list of anuran species for each locality after the removal of duplicate entries having the clusters as grouping variables. We then generated host dissimilarity matrices using the Jaccard index. Throughout this paper, spatial distance (in km) is used as a proxy for dispersal limitation [14].

Dealing with uneven sampling effort

For parasite studies, sampling sites can have at least three critical dimensions of sampling effort: the number of analyzed host individuals, the number of analyzed host species, and which host species were analyzed. If not appropriately treated, differences in these dimensions can produce undesirable artefacts that could lead to incorrect conclusions regarding diversity drivers. As a way of dealing with this issue, we took the following approach. First, given that recorded parasite richness of a host population increases with the number of analyzed hosts, we only included host populations that had at least five surveyed individuals. Second, during the model fitting process, we gave a proportionally higher weight to locations with a higher number of individual hosts sampled. We set the "weightType" to "custom" in the "formatsitepair" function, which is the function that generates the site-pair table required for fitting a Generalized Dissimilarity Model within the "gdm" package [36].

Finally, we recognize that pairwise dissimilarity in parasite diversity can be high when disparate groups of hosts are analyzed. Given that host-parasite relationships tend toward specificity, such comparison would cause an apparent turnover in parasite species induced by sampling phylogenetically disparate host species rather than other biological processes. To see if comparing different host species affected dissimilarity in the overall dataset, we ran separate nematode analyses for the Bufonidae, Ranidae, and Hylidae families in the Nearctic realm. We chose those families because each appears in at least 15 data points in our dataset.

Data analysis

To investigate the effects of climate, host compositional dissimilarity and geographic distance on nematode and trematode turnover, we adopted the generalized dissimilarity modelling (GDM) approach. GDM was originally formulated as a non-linear extension of the matrix regression procedure that accommodates two types of nonlinearity that are common in ecological datasets: (i) the curvilinear relationship between environmental distance and compositional dissimilarity, and (ii) the non-stationarity in rates of species turnover along environmental gradients [37]. The nonlinearity is accommodated in GDM models by a flexible function that measures the turnover along a gradient based on splitting the response in *I-splines*, which function as partial regressions [37]. The maximum height of each plotted I-spline represents the total amount of turnover in relation to a given gradient, while all other predictors are kept constant, resulting in partial regression fits that demonstrate the importance of each predictor's effect on species turnover [11,37]. Higher coefficients express higher rates of compositional change along a given gradient [11,37].

We ran separate GDM to different spatial subsets of our dataset to investigate whether the relative roles of our predictors vary from the regional to the global scale and among distinct parasite groups. We restricted the regional analysis to the Nearctic and Neotropical realms, given that they were the best-sampled realms. This restriction to the best-sampled regions is an attempt to mitigate the effects of high variability due to uneven sampling and geographical coverage, which is especially severe in regions with fewer data points. To investigate whether the relative roles of our predictors also vary with the parasite group, we ran different GDMs at each scale with varying subsets of the parasite data. We ended up with nine GDMs: global (nematodes and trematodes), Nearctic (nematodes and trematodes), and Neotropical (nematodes and trematodes) [plus the separate analyses on Bufonidae, Hylidae and Ranidae]. We also ran the main analyses after removing parasites that only occurred in one cluster (i.e., singletons) to check whether our results were disproportionately influenced by rare species (see Table S1 in Supplementary Material).

The response matrix for all GDMs was a dissimilarity matrix of helminths per cluster based on the Raup-Crick index, whereas the predictors were the spatial distance between clusters, and pairwise dissimilarity matrices of host composition and climate. Variable and model significance, as well as variable importance, were calculated by the matrix permutation method using the "gdm.VarImp" function [36]. The importance of each variable is calculated by contrasting the percent change in deviation explained by the full model to the percent change in deviation explained by a model fit with that variable permuted [36]. Non-significant variables were removed, and GDM models calculated. We ran the GDM models using the "gdm" package [36] in the R environment [38]. The default of three I-splines was used to calculate the models [11,14].

We performed a k-fold cross-validation procedure for each model to evaluate the performance of our models in predicting parasite turnover. This method randomly divides the observations into k sets (or folds) of roughly equal size [39]. The first fold is used as a validation set, and the method is then applied to the remaining k-1 sets [39]. Following that, the mean squared error on the observations in the held-out fold is calculated [39]. This method is repeated k times, with each validation set containing a unique set of observations and estimates of error, which are then averaged to evaluate model performance [39]. We performed the cross-validation with the "sgdm" package's n-fold cross-validation procedure using the default of ten folds [40].

Results

The full dataset contains 162 clusters with 134 species of nematodes and 96 clusters with 69 species of trematodes, covering 330 host populations of 205 anuran species from 26 families occurring in sites spread in all continents (Figure 1). Throughout this paper, the strength of effect of a variable relates to the sum of its corresponding fitted I-spline coefficients (partial regressions), which measures the rate of parasite turnover in response to our predictors. We show the sum of the coefficients in Table 1, while the fitted curves for each model are presented in the Supplementary Material (Figures S1-S9). Sample sizes and number of host and parasite species for all data subsets are found in Table S2 in the supplementary material. Mean and ranges for climactic predictors are shown in Table S3. The results of the cross-validation procedure indicate a good overall model performance, with root mean square errors (RMSE) mostly below 0.32 (Table 1). Across all spatial data subsets (global, Nearctic, and Neotropical), pairwise parasite dissimilarity was exceptionally high (see Figure S10 in the Supplementary Material). Similar patterns are found in the separate subsets of Bufonidae, Hylidae and Ranidae (see Figure S11 in the Supplementary Material).

At the global scale, spatial distance followed by the minimum temperature of the coldest month and host composition explained approximately 32% of nematode turnover (Table 1). In comparison, the first two variables explained around 38% of trematode turnover (Table 1). In the Nearctic models, the minimum temperature of the coldest month followed by mean diurnal temperature range and spatial distance explained around 15% of nematode turnover and around 26% of trematode turnover, although the effect of spatial distance was negligible for the latter (Table 1). In the Neotropical realm, spatial distance and mean diurnal temperature range explained around 12% of nematode turnover (Table 1). For neotropical trematodes, spatial distance and precipitation of the wettest month explained around 23% of parasite turnover, although the latter variable's effect was only marginally significant (p=0.06) (Table 1).

In the Nearctic, the fitted I-splines curves showing the turnover rate along the minimum temperature of the coldest month's gradient indicates a clear threshold point where the turnover rate is higher for both parasite groups. Nearctic trematode turnover barely responded to the gradient until approximately minus eleven degrees (Figures S3). Similarly, the turnover rate for Nearctic nematodes is higher for values above roughly zero degrees (Figure S4). In contrast to the results in the Nearctic, the primary turnover thresholds for Neotropical parasites are mainly

related to spatial distance, though trematode turnover appears to accelerate at higher precipitation of wettest month values (Figures S4 and S5).

(i) How do the drivers of parasite turnover vary with spatial scale?

We found evidence confirming our hypothesis that the importance of spatial distance (a proxy for dispersal limitation) on parasite beta diversity decreases from global to regional (realm) scales. While spatial distance was critical at the global scale, its relative importance and strength in relation to climate diminishes at the regional level, especially in the Nearctic models (Table 1, Figure 2). For example, at the global scale, spatial distance was around 8.6 times a stronger predictor of nematode turnover than the minimum temperature of the warmest month. In contrast, this climatic variable was approximately 3.7 times a stronger predictor of Nearctic nematode turnover than spatial distance (Table 1).

(ii) How do the drivers of parasite turnover vary between realms?

We discovered that the key climatic variables, as well as their relative importance and strength, differ between zoogeographical realms (Table 1, Figure 2). More specifically, mean diurnal temperature range and minimum temperature of the coldest month were critical for Nearctic nematodes while only mean temperature diurnal range affected Neotropical nematodes (Table 1, Figure 2). Likewise, Nearctic trematodes responded to minimum temperature of the coldest month while tropical trematodes responded marginally ($p = 0.06$) to precipitation of the wettest month (Table 1, Figure 2). Therefore, we confirmed our hypothesis that temperature extremes are more important in the Nearctic than in the Neotropics.

(iii) How do the drivers of parasite turnover vary in relation to helminth group?

We found evidence that climatic differences are more critical for trematodes than for nematodes at the global and Nearctic scales. Notably, this is evidenced both in terms of strength of effect (Table 1) and variable importance (Figure 2). At the global scale, the effect of spatial distance on the nematode model was approximately 8.6 times stronger than the effect of minimum temperature, whereas the effect of spatial distance on trematodes was only approximately 1.8 times stronger than the effect of the same climatic variable (Table 1). Similar results were found in the Nearctic realm, where minimum temperature was around 3.7 times stronger than spatial distance for nematodes, while spatial distance was negligible for Nearctic trematodes (Table 1). At the Neotropical scale, we found a different result in terms of strength of effect. Proportionally, spatial distance was slightly stronger for neotropical trematodes than

neotropical nematodes (Table 1). Variable importance, on the other hand, exhibits the same general pattern as the other models (Figure 2).

Furthermore, we discovered evidence that the two groups respond to different climatic variables or to varying degrees when the variables are the same (Table 1, Figure 2). For instance, in the Nearctic, nematodes responded to spatial distance, minimum temperature of the coldest month and mean temperature diurnal range, whereas trematodes did not respond to the latter variable (Table 1, Figure 2). These differences are even more pronounced in the Neotropics, where nematodes responded to mean diurnal temperature range while trematodes responded (marginally, $p = 0.06$) to maximum precipitation of the wettest month (Table 1, Figure 2).

(iv)   Did host composition affect parasite beta diversity?

Surprisingly, we only detected an effect of host composition on parasite turnover in the global nematode model (Table 1). However, such effect was both weaker and less important than climate and spatial distance (Table 1, Figure 2).

(v)   Does selecting different host subsets affect general trends in parasite turnover?

We found different trends when we compared Ranidae, Bufonidae, and Hylidae hosts in the Nearctic bioregion (Table 1, Figure 3). Spatial distance was the only important predictor of nematode turnover in Bufonids, whereas spatial distance and precipitation of the wettest month influenced nematode turnover in Hylidae (Table 1, Figure 3). Nematode turnover in Ranidae was only influenced by mean diurnal temperature range (Table 1, Figure 3). These results were also different from the Nearctic nematode model when all hosts are considered (Table 1, Figure 2).

Discussion

Although most macroecological studies have investigated processes affecting the global distribution of free-living organisms on earth, to our knowledge, the processes underlying parasite beta diversity have never been investigated at the global scale. We studied for the first time how spatial scale can be used to tease apart the drivers of parasite beta-diversity from regional (zoogeographical realm) to global extents. Overall, spatial distance is a major driver of helminth turnover in anuran hosts. Additionally, we found five primary patterns: (i) For both parasite groups, the effects of climate on parasite beta diversity increase from the global to the regional scale. (ii) There is a spatially dependent effect of climate on beta diversity linked to the realms. Specifically, minimal temperature of the coldest month is dominant in the Nearctic,

while neotropical nematodes and trematodes responded to mean diurnal temperature range and precipitation of the wettest month, respectively. (iii) Nematodes and trematodes show distinct trends in their response to climate and spatial distance. More specifically, trematodes are generally more sensitive to climatic conditions while nematodes are more spatially structured. Additionally, the most important variables differed between parasite groups, especially in the neotropics. (iv) Overall, host turnover was not an important predictor of parasite turnover. (v) We found that drivers of parasite beta diversity vary with host taxonomic subset, even when analysing lower hierarchies such as host families.

The few existing broad-scale studies investigating the effects of climate, spatial distance and host composition on parasite beta diversity reveal some general trends in parasite beta diversity at the macroecological scale. For instance, [14] studied bat flies across the Neotropical realm (from Mexico to Brazil) and found that host composition and temperature seasonality are the main drivers of parasite beta diversity. Similarly, in another study at the regional scale (about 2,500 km in Mongolia), [11] demonstrated air temperature and host beta diversity as the best predictors of rodent flea turnover. The other existing studies such as [10,12,13] show high heterogeneity in investigated hosts, parasites, realms and scale (grain and extent). However, these studies point parasite beta diversity to be mainly affected by either host composition, climate, or a combination of both, with a negligible effect of spatial distance. Conversely, we found a major role of spatial distance as a driver of anuran parasite turnover at both the global and Neotropical scales. Although it should be interpreted with caution, the prominence of spatial distance in these models indicates that dispersal-based processes may be a major determinant of anuran helminth beta diversity.

Parasites rely on hosts to disperse, and there is evidence that spatial connectivity among host assemblages is an essential driver of parasite similarity [18]. As a result, spatial distance can be even more influential in host-parasite systems where both parasites and hosts are dispersal limited. Indeed, due to the nature of the helminth life cycle, these parasites rely on hosts for dispersing, and amphibians are recognized for their poor dispersal abilities. For instance, [41] found spatial turnover to be around four times higher for amphibians than birds, which is consistent with amphibians having many small ranged species. Besides being dispersal limited, previous studies argued that habitat specialization is a relevant factor determining small range sizes from amphibians compared with birds and mammals [7]. As a result, the marked differences in composition between sites and regions may be explained by the fact that poor dispersers may have higher speciation rates (as gene flow decreases) [42].

We found evidence for increasing the importance of niche-based processes from the global to the regional scale. This result is expected and follows the observed increase in niche-based processes at proportionally smaller scales, e.g., [29], but see [30]. However, we accept that this finding is not surprising given that distinct realms with distinct parasite and host pools are being compared at the global scale, implying that species composition is likely to vary significantly, and that these variations would increase with distance. This will result in low predictive power for any factor other than distance, as turnover would be extremely high regardless of environmental differences.

Different parasite groups showed distinct trends in terms of how they responded to climate and spatial distance. Besides helminths being ectothermic animals, most species have complex life-cycles that involve releasing eggs or larvae in the environment [43]. Consequently, during these environmental stages, parasite persistence can be directly affected by local climatic conditions, given that temperature and precipitation can directly influence their survival and infectivity [15,44,45]. This could explain the relevance of climate as broad-scale drivers of helminth beta diversity. We found that trematodes are generally more sensitive to climate than nematodes. Also, the two groups responded to different climatic variables, especially in the neotropics. The higher sensitivity of trematodes to climatic differences may be explained by biological characteristics. For instance, most trematodes have aquatic swimming stages, while many parasitic nematodes (despite their enormous variation) produce larvae and eggs resistant to environmental extremes [43]. This may explain why the former is more vulnerable to climate than the latter, as well as why precipitation affected neotropical trematodes, given that in this region temperature extremes are not as limiting as they are in the Nearctic.

The prominence of the minimum temperature of the coldest month found in the Nearctic models may be explained by either its direct effect on parasites, an indirect effect mediated by hosts, or both. Previous studies have demonstrated that ectotherms such as amphibians have a limited capacity to survive at low temperatures [46]. As a result, physiological tolerance of parasites and hosts to low temperatures could be the primary explanation for these findings. Conversely, in the Neotropical models, spatial distance showed the greatest strength of effect. We also found that the proportional importance of spatial distance in relation to climate increased in the neotropics when compared to the Nearctic. Perhaps this can be explained by host species in the neotropical realm having smaller range sizes in response to low climate variability and high geographic complexity which, in turn, leads to specialization and limits range expansion, see [47].

We only found an effect of host composition on parasite beta diversity for global nematodes (Table 1). This result is hard to interpret and run against the existing theory [10,14] and our predictions. First, host composition may be less important for helminths of amphibians than for other host groups, indicating that perhaps these parasites are more generalists. However, we believe that the most likely explanation is methodological. As shown in Table S2, parasite composition was mostly available for two host species per site. This represents only a subset of the available host pool, which can result in low statistical power to detect a host effect. Moreover, this lack of response may need further investigation. Despite the fact that parasite dissimilarity is unusually high even at the regional scale (see Figure S10 in the Supplementary Material), GDM is quite strong in the face of response data with a large bias towards high dissimilarity values. The non-linear link function used in GDM is intended to address, at least in part, the issues posed by high dissimilarity values, including total dissimilarity, see [37]. Such high dissimilarity also highlight the need of more studies investigating parasite beta diversity both within and between realms, adding valuable sampling sites and host species.

Another interesting finding is that the separate analyses on Nearctic nematodes of Bufonidae, Hylidae and Ranidae revealed contrasting results both among them and when compared to the model with all hosts. Notably, the habits of these anuran families differ. Hylids, for example, are mostly arboreal, whereas bufonids are mostly terrestrial and ranids are semiaquatic [48]. This may warrant further investigation, given that biological differences between hosts can result in diverging pressures for parasite colonization and persistence, resulting in the differences we observed. The take-home message from this discovery could be the importance of specifically incorporating host life history into parasite beta diversity studies at the macroecological level. The general trends may be disproportionately affected by which host group has the majority of data points, especially in studies based on sparse data. Such contingencies should be further discussed, as they can have significant implications for the quest for universal drivers of parasite diversity at broad scales.

One of the main goals of disease macroecology is to predict disease emergence and outbreaks [49]. In this context, a robust understanding of what drives turnover in pathogen diversity at broad spatial scales and, therefore, limits geographical ranges of parasites, is an essential step to reach this end. The central role of spatial distance in most of our models contrasts most current studies on parasite beta diversity. Such differences in the relevance of predictor variables may highlight current disease macroecology's limited ability to have broad expectations about parasite beta diversity. Compared to free-living organisms, parasites are by

far less studied regarding diversity drivers, especially at broad scales. Therefore, it reinforces the need for further investigations, especially on less explored realms, hosts and parasite groups. Amphibians are the most vulnerable group of vertebrate hosts, especially considering the current pace of climate change [46] and disease transmission [50]. Accordingly, combining abiotic and biotic drivers of both parasites and their hosts in a multiscale approach can improve the predictability of macroecology and disease macroecology [21]. Our study contributes to an essential step in this direction and provides an empirical foundation for disease macroecology's goals to be achieved with amphibians.

Author contributions

Paulo Mateus Martins: conceptualization, methodology, formal analysis, investigation, data curation, writing – original draft. Robert Poulin: conceptualization, methodology, writing – review and editing. Thiago Gonçalves-Souza: conceptualization, methodology, writing – review and editing, supervision.

Conflicts of Interests

The authors have no conflicts of interest to disclose.

Data availability

The main R scripts for analysis and figures with respective data are available as supplementary material.

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Table 1. Sum of the I-spline coefficients for each GDM model, followed by the percent of deviance explained by that model and its corresponding root mean square error (RMSE). The strongest variable for each model is highlighted in bold, and the asterisk symbol denotes a marginally significant effect (p=0.06). Near = Nearctic; Buf = Bufonidae family; Hyl = Hylidae family; Ran = Ranidae family.

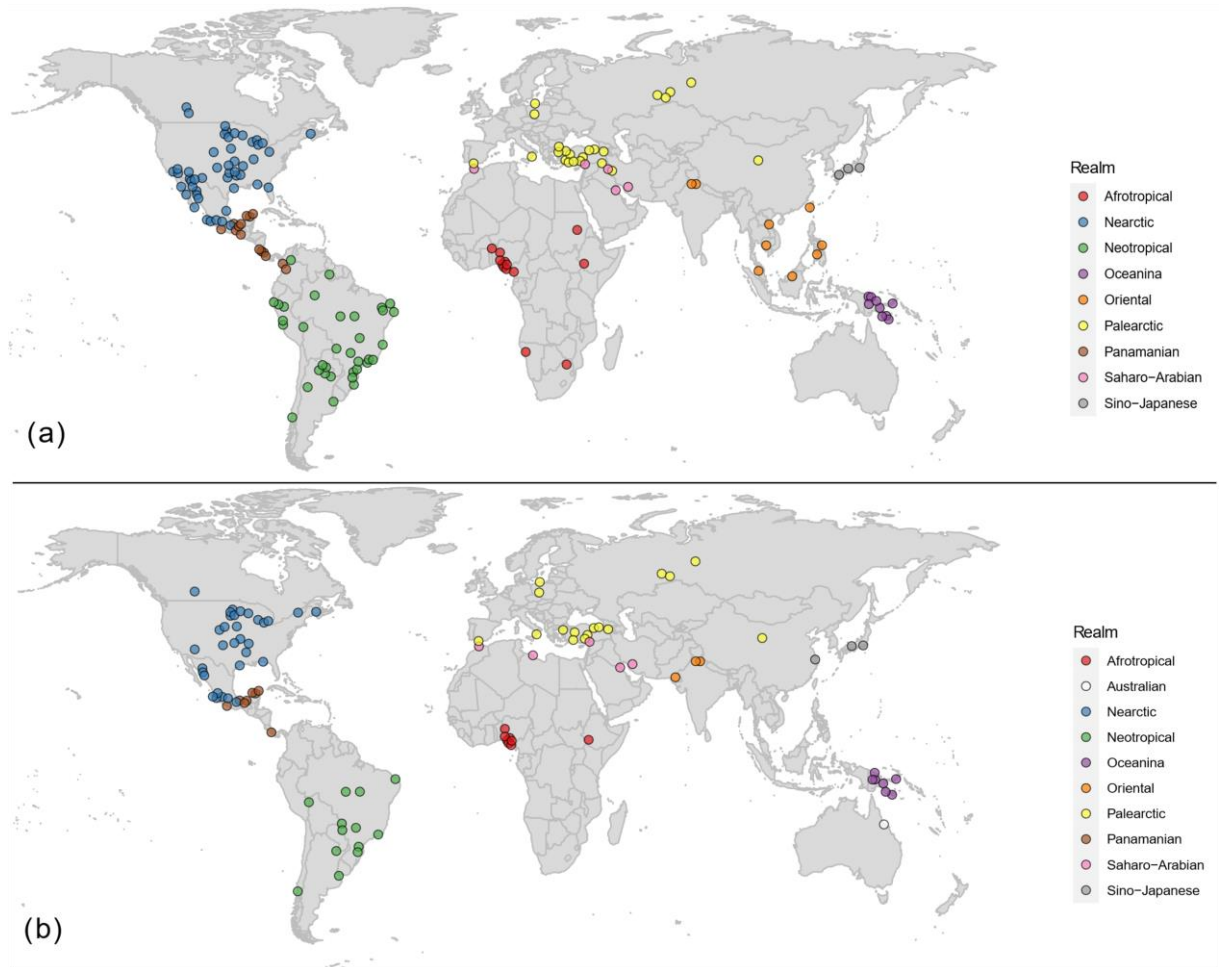|	Nematoda						Trematoda		
	Global	Nearctic	Neotropical	Near Buf	Near Hyl	Near Ran	Global	Nearctic	Neotropical
Spatial Distance	**5.50**	0.60	**2.62**	**1.36**	1.5	< 0.01	**3.82**	< 0.01	**11.95**
Mean Diurnal Temperature Range	NA	1.12	1.44	NA	NA	**2.44**	NA	1.58	NA
Min Temperature of Coldest Month	0.64	**2.23**	NA	NA	NA	NA	2.11	**2.71**	NA
Precipitation of Wettest Month	NA	NA	NA	NA	**4.27**	NA	NA	NA	7.78*
Host Composition	0.63	NA	NA	NA	NA	NA	NA	NA	NA
% Explained	31.51	14.76	11.66	13.17	28.89	15.01	38.13	26.15	22.55
RMSE	0.27	0.32	0.32	0.30	0.27	0.3	0.23	0.30	0.38

Figure 1. Geographical spread of clusters used for the nematode (a) and trematode (b) GDM models. Zoogeographical realms were delimited after [19].
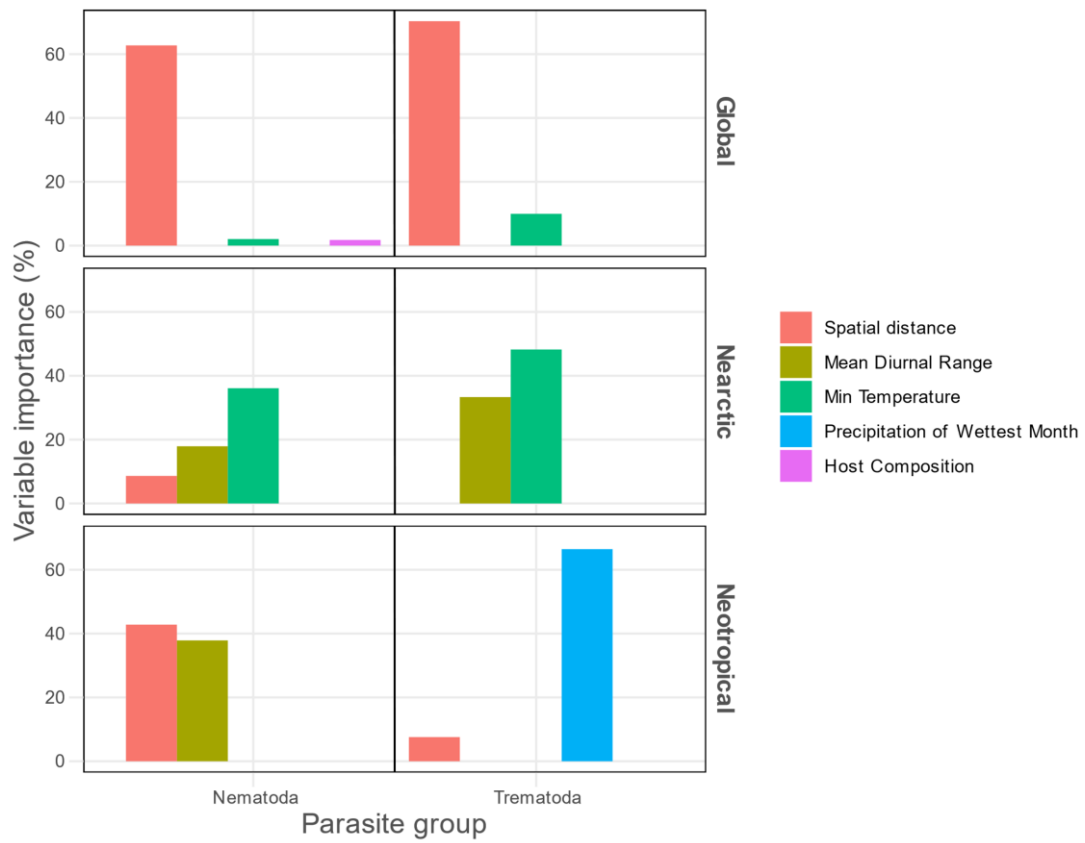
Figure 2. Variable importance for each GDM model according to spatial scale (global, Nearctic and Neotropical) and parasite group (Trematoda and Nematoda).
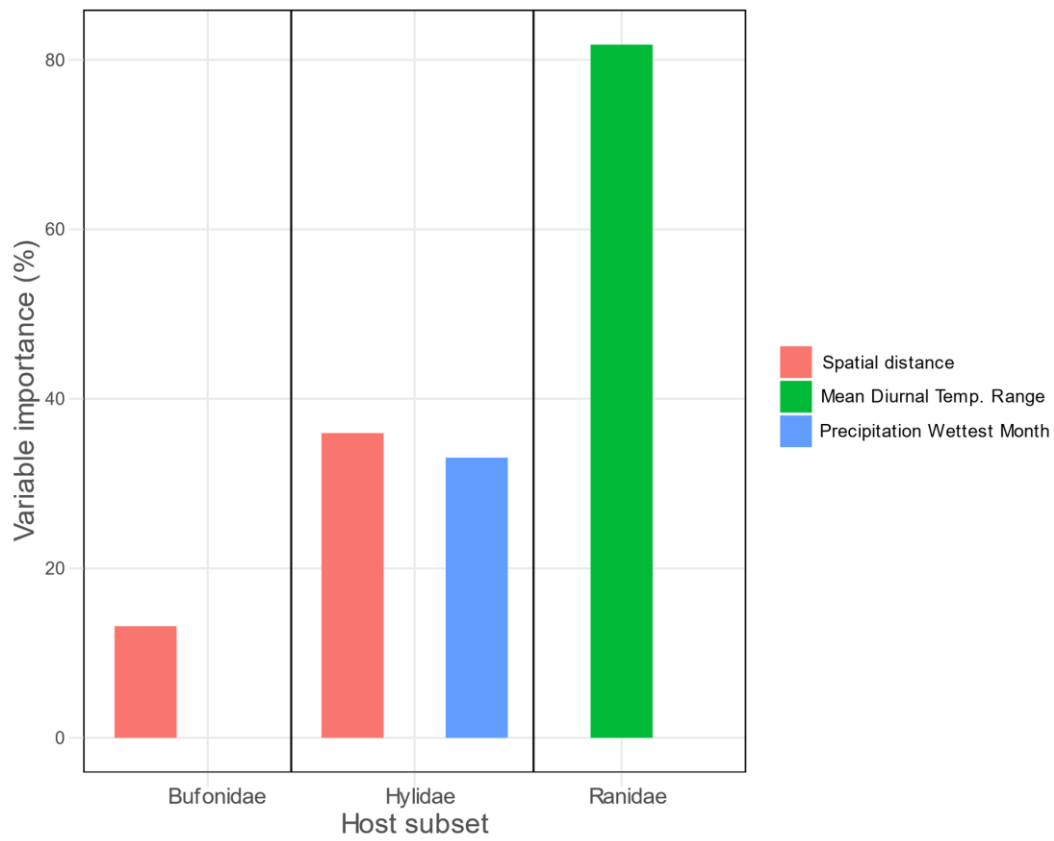
Figure 3. Variable importance for the separate Nematode GDM models according to host family (Bufonide, Hylidae and Ranidae).

Artigo 2: Material Suplementar

Table S1. Number of sites (clusters), parasite species, and host species in the main GDM models (all hosts) when singletons are removed, as well as the I-Spline sum (strength of effect) of each significant variable, percent of deviance explained by the model, and model performance. "NA" stands for absence of effect.

	Global		Nearctic		Neotropical	
	Nematoda	Trematoda	Nematoda	Trematoda	Nematoda	Trematoda
N sites	155	85	49	28	32	8
N parasites	169	35	16	7	16	6
N hosts	170	61	43	19	40	8
Spatial Distance	5.39	2.76	0.59	0.04	1.98	NA
Mean Temp Diurnal Range	NA	NA	1.14	NA	NA	NA
Min Temp Coldest Month	0.72	2.53	2.22	1.87	NA	NA
Host Composition	0.53	NA	NA	NA	NA	NA
% Explained Deviance	32.14	34.30	14.85	14.97	5.69	NA
Mean Square Error (RMSE)	0.27	0.24	0.31	0.25	0.32	NA

Table S2. The total number of sites (clusters), parasite species, surveyed hosts, and the mean(range) number of surveyed hosts and parasite species per cluster for each model and data subset. Near = Nearctic.

Model	Parasite group	Number of sites	Number of parasites	Number of surveyed host species	Mean(range) host/cluster	Mean(range) parasite/cluster
Global	Nematoda	162	134	187	1.72 (1-7)	3.03 (1-13)
Global	Trematoda	99	69	77	1.33 (1-5)	2.01 (1-8)
Nearctic	Nematoda	50	24	44	1.42 (1-3)	2.34 (1-5)
Nearctic	Trematoda	32	16	23	1.25 (1-3)	1.90 (1-5)
Near Bufonidae	Nematoda	15	8	13	1.13 (1-2)	2 (1-4)
Near Hylidae	Nematoda	16	9	11	1.06 (1-2)	1.44 (1-3)
Near Ranidae	Nematoda	22	15	13	1.14 (1-2)	2.09 (1-5)
Neotropical	Nematoda	35	43	45	1.83 (1-7)	3.29 (1-12)
Neotropical	Trematoda	13	19	15	1.54 (1-5)	2.15 (1-8)

Table S3. Mean and range (min, max) values of climatic predictors for each data subset. Near = Nearctic; NA = non-significant variable (p < 0.05).

| Model	Parasite group	Mean Diurnal Temperature Range	Max Temperature of Warmest Month	Min Temperature of Coldest Month	Precipitation of Wettest Month
Global	Nematoda	NA	NA	8.69 (-26.53, 23.16)	NA
Global	Trematoda	NA	30.05 (17.72, 44.20)	4.17 (-26.53, 21.30)	NA
Nearctic	Nematoda	13.47 (8.40, 20.32)	NA	-1.60 (-21.87, 17.25)	NA
Nearctic	Trematoda	NA	NA	-5.31 (-20.31, 17.25)	NA
Near Bufonidae	Nematoda	NA	28.83 (22.43, 36.61)	NA	136 (76, 243)
Near Hylidae	Nematoda	NA	NA	NA	136.6 (22.5, 251.2)
Near Ranidae	Nematoda	12.87 (8.91, 17.81)	NA	NA	NA
Neotropical	Nematoda	10.84 (7.24, 14.43)	NA	NA	NA
Neotropical	Trematoda	NA	NA	NA	207.6 (113, 364)
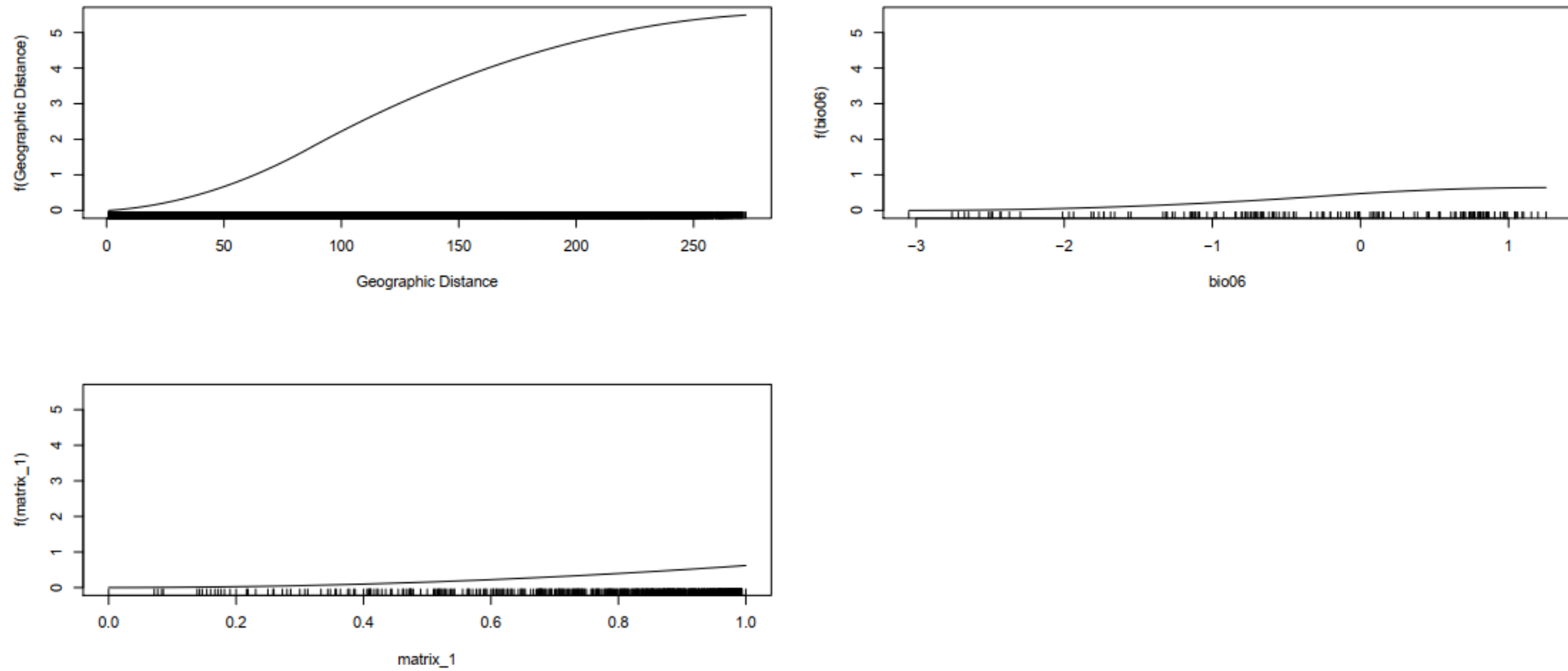
Figure S1. Fitted Generalised Dissimilarity Model I-splines of spatial distance (Geographic Distance), min temperature of coldest month (bio06), and surveyed host composition (matrix_1) as drivers of **global nematode** turnover. The rate of turnover is indicated by the shape of the curve.
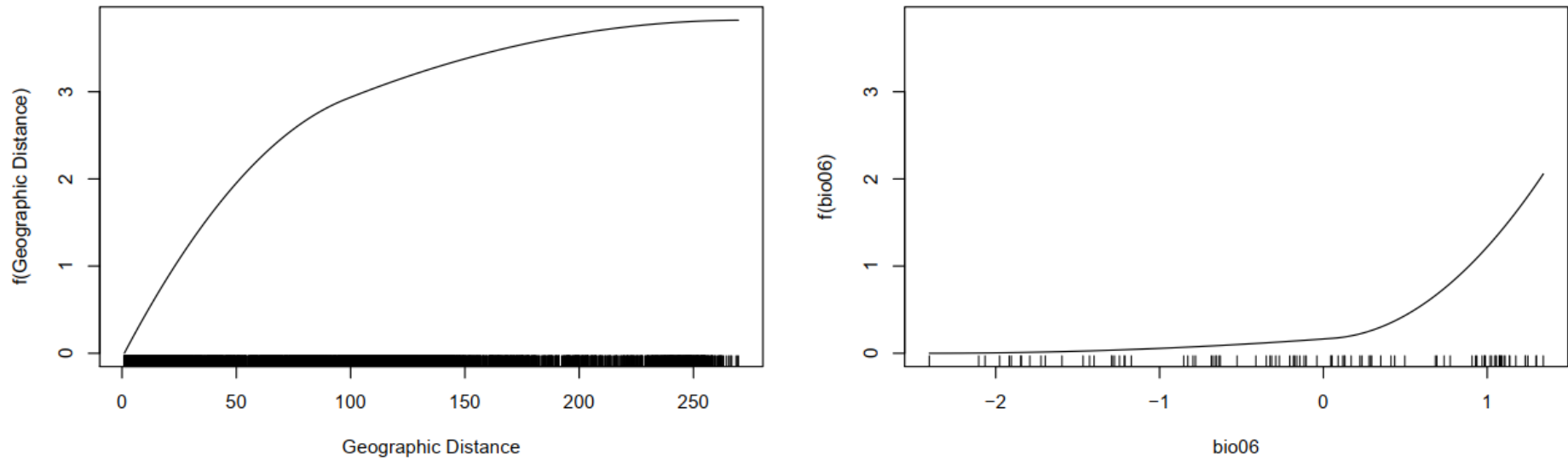
Figure S2. Fitted Generalised Dissimilarity Model I-splines of spatial distance (Geographic Distance) and min temperature of coldest month (bio06) as drivers of **global trematode** turnover. The rate of turnover is indicated by the shape of the curve.
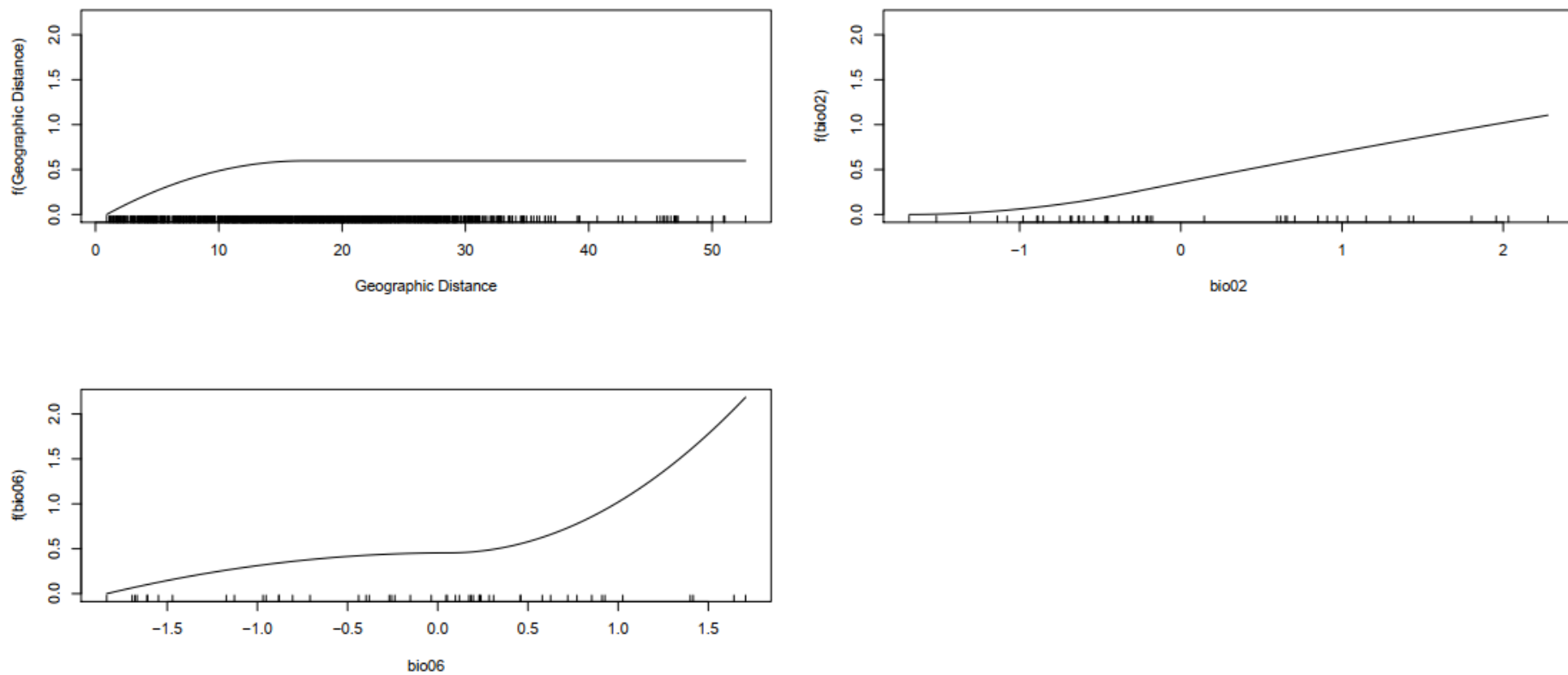
Figure S3. Fitted Generalised Dissimilarity Model I-splines of spatial distance (Geographic Distance), mean diurnal temperature range (bio02), and min temperature of coldest month (bio06) as drivers of **Nearctic nematode** turnover. The rate of turnover is indicated by the shape of the curve.
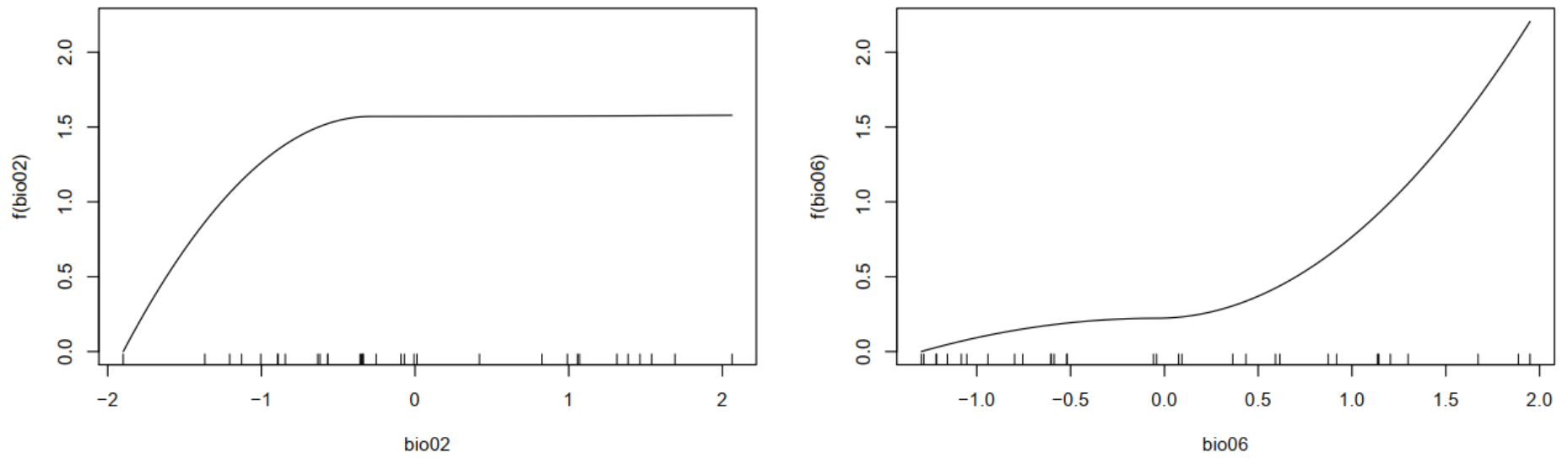
Figure S4. Fitted Generalised Dissimilarity Model I-splines of spatial distance (Geographic Distance) and min temperature of coldest month (bio06) as drivers of **Nearctic trematode** turnover. The rate of turnover is indicated by the shape of the curve.
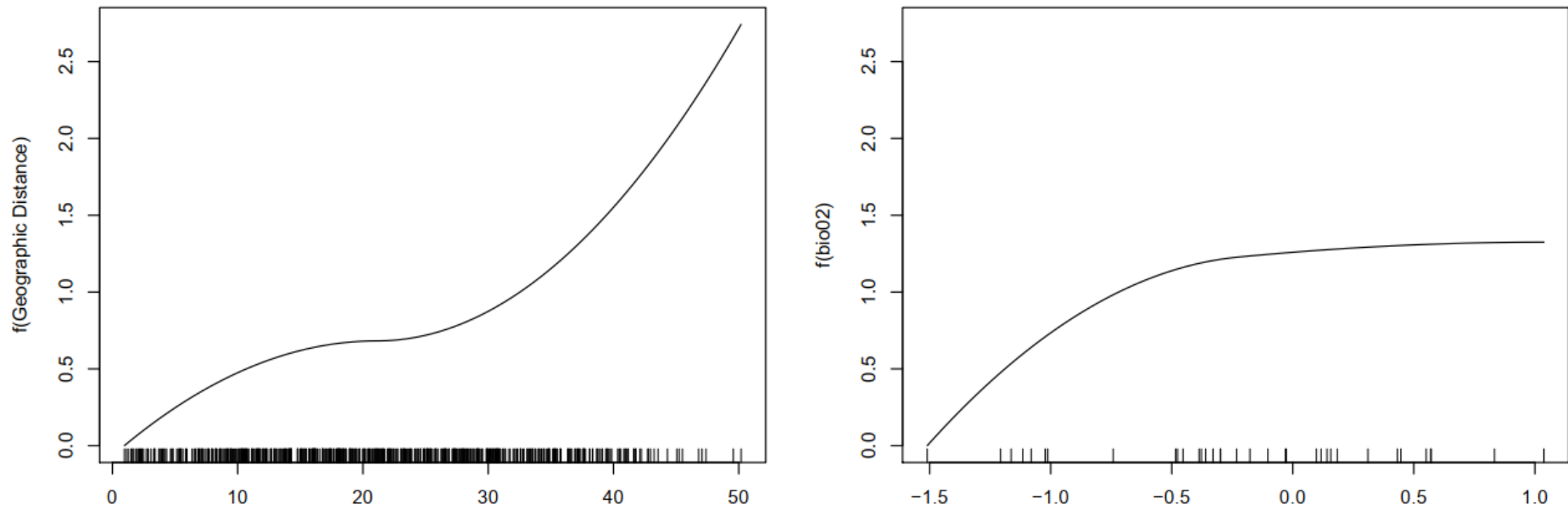
Figure S5. Fitted Generalised Dissimilarity Model I-splines of spatial distance (Geographic Distance) and mean diurnal temperature range (bio02) as drivers of **Neotropical nematode** turnover. The rate of turnover is indicated by the shape of the curve.
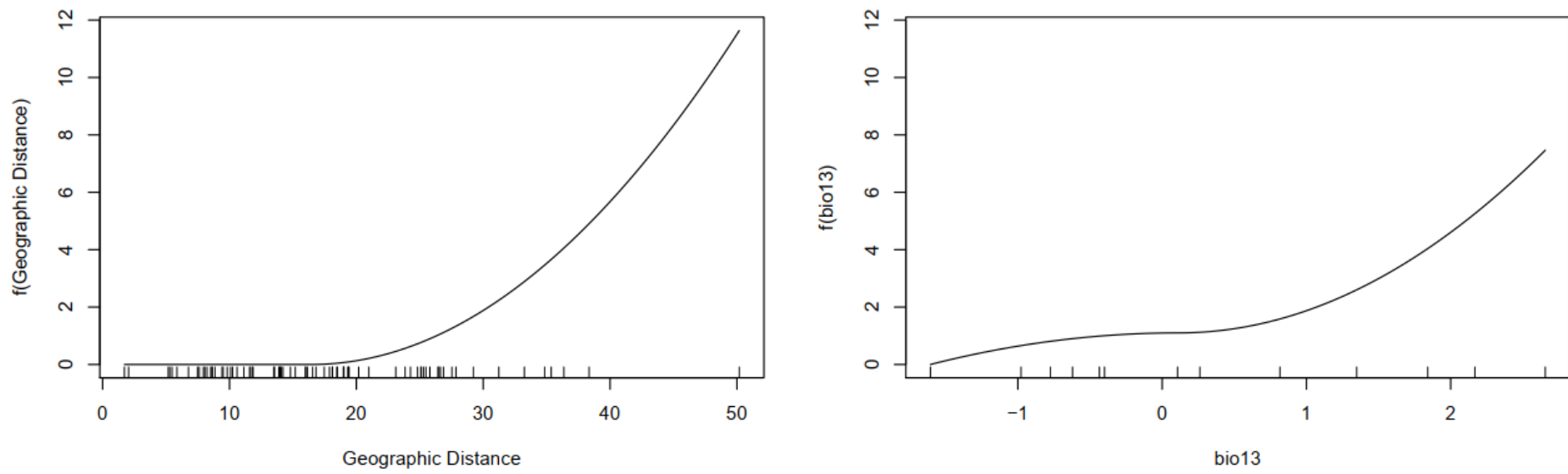
Figure S6. Fitted Generalised Dissimilarity Model I-splines of spatial distance (Geographic Distance) and precipitation of wettest month (bio13) as drivers of **Neotropical trematode** turnover. The rate of turnover is indicated by the shape of the curve.
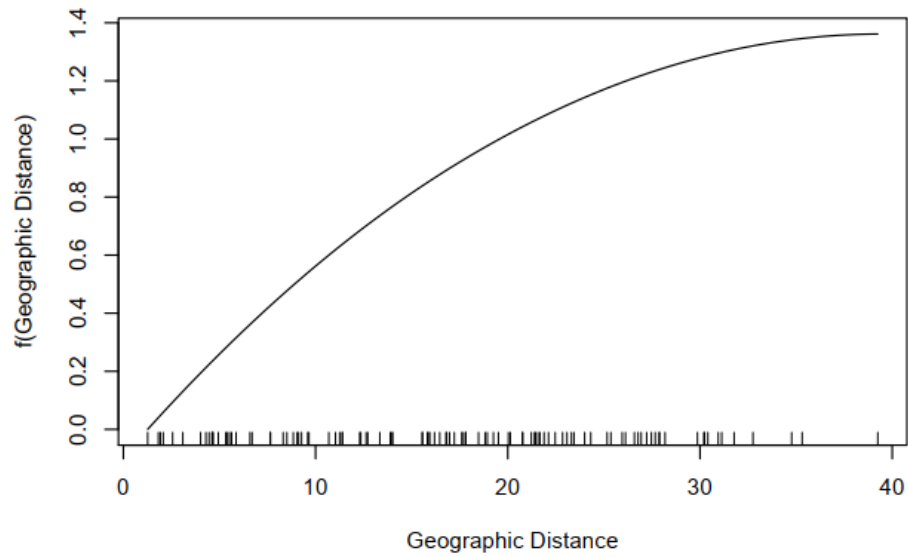
Figure S7. Fitted Generalised Dissimilarity Model I-splines of spatial distance (Geographic Distance) as driver of **bufonid Nearctic nematode** turnover. The rate of turnover is indicated by the shape of the curve.
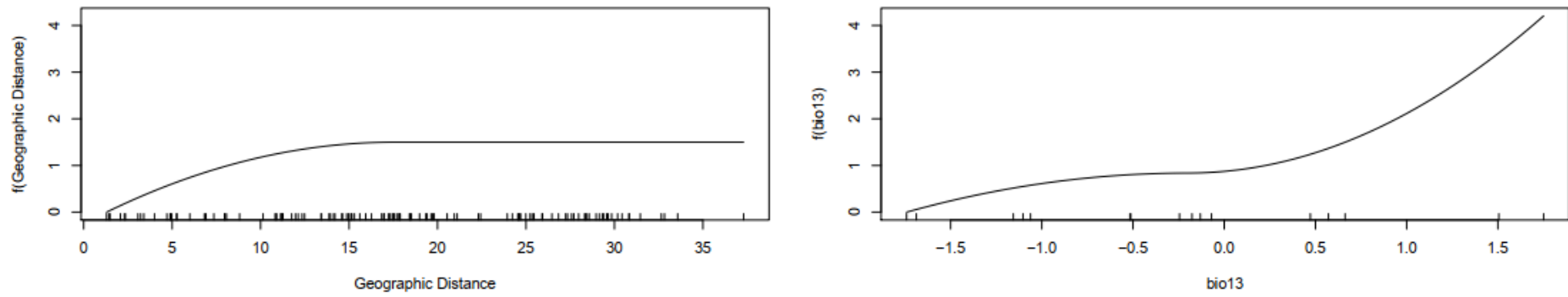
Figure S8. Fitted Generalised Dissimilarity Model I-splines of spatial distance (Geographic Distance) and precipitation of wettest month (bio13) as drivers of **hylid Nearctic nematode** turnover. The rate of turnover is indicated by the shape of the curve.
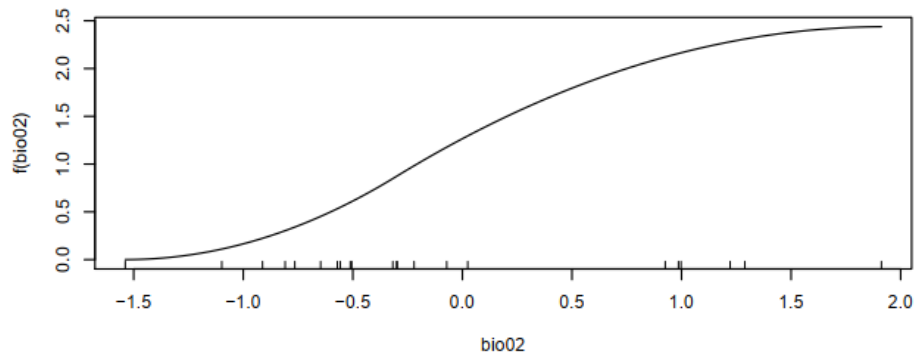
Figure S9. Fitted Generalised Dissimilarity Model I-splines of mean temperature diurnal range (bio02) and composition of surveyed hosts (matrix_1) as drivers of **ranid Nearctic nematode** turnover. The rate of turnover is indicated by the shape of the curve.

Figure S10. Frequency of pairwise parasite Raup-Crick dissimilarity for each main model.
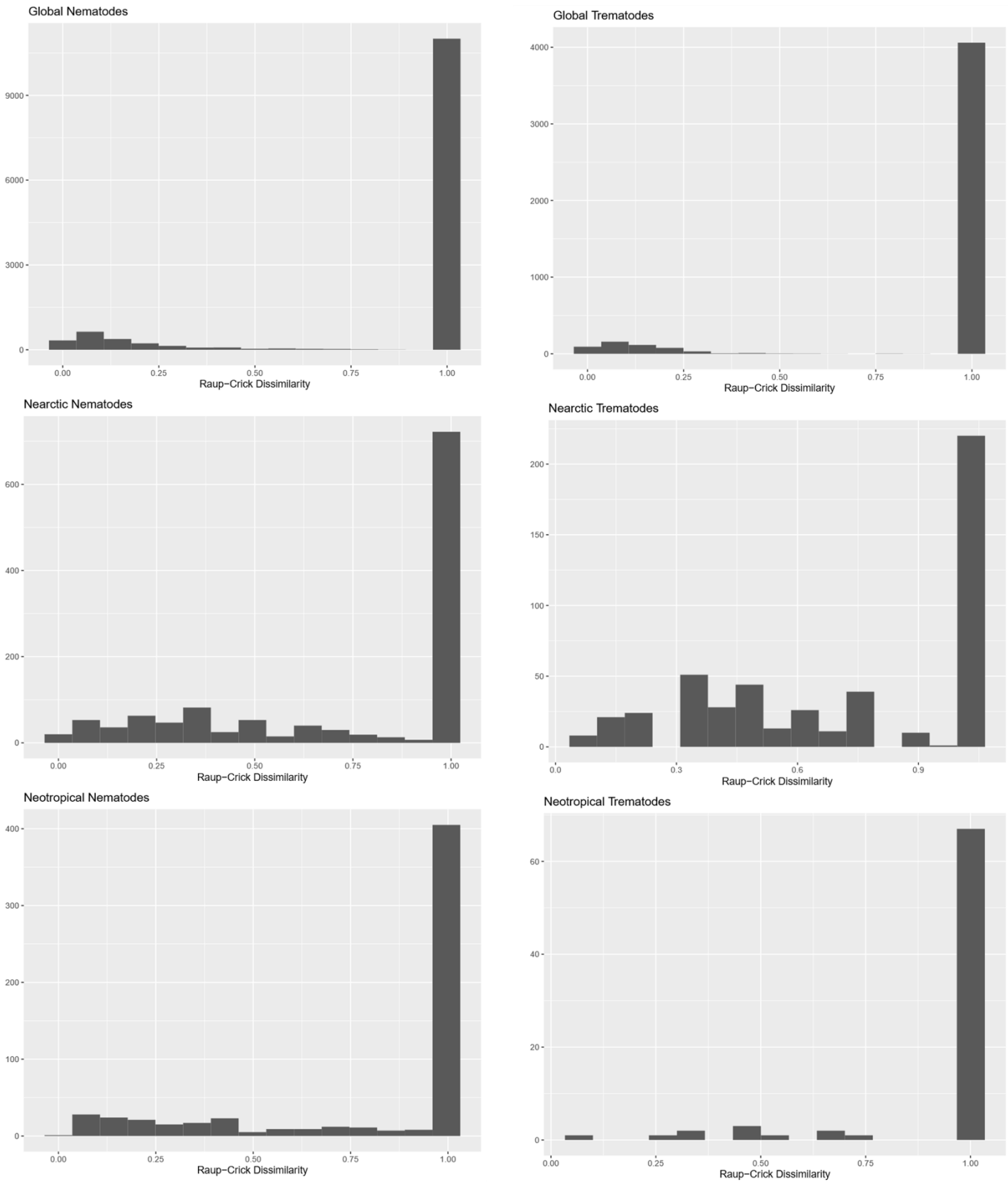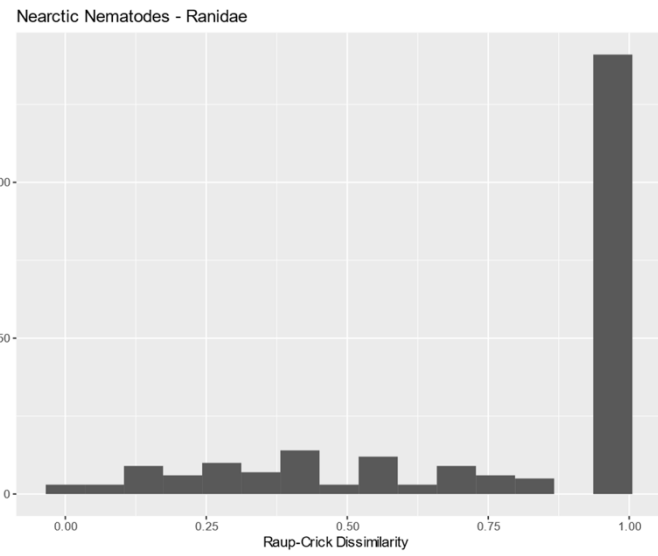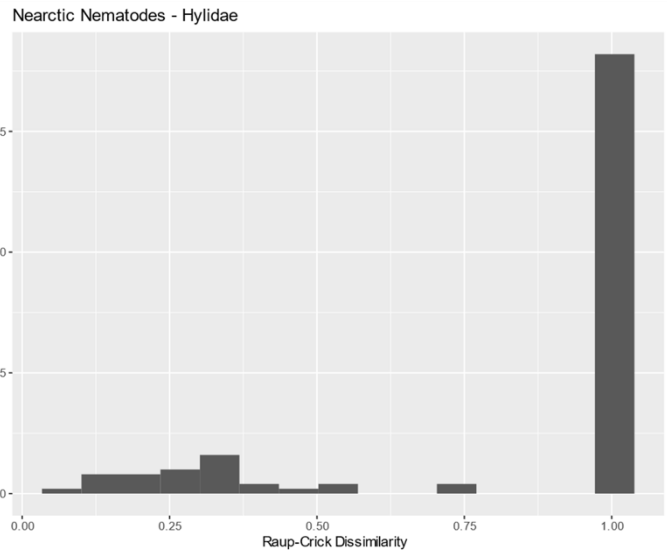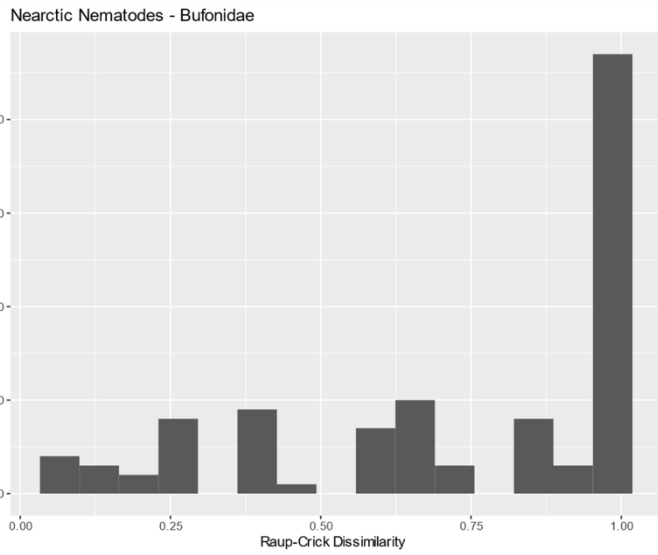
Figure S11. Frequency of pairwise parasite Raup-Crick dissimilarity for each separate analysis on Bufonidae, Hylidae and Ranidae.
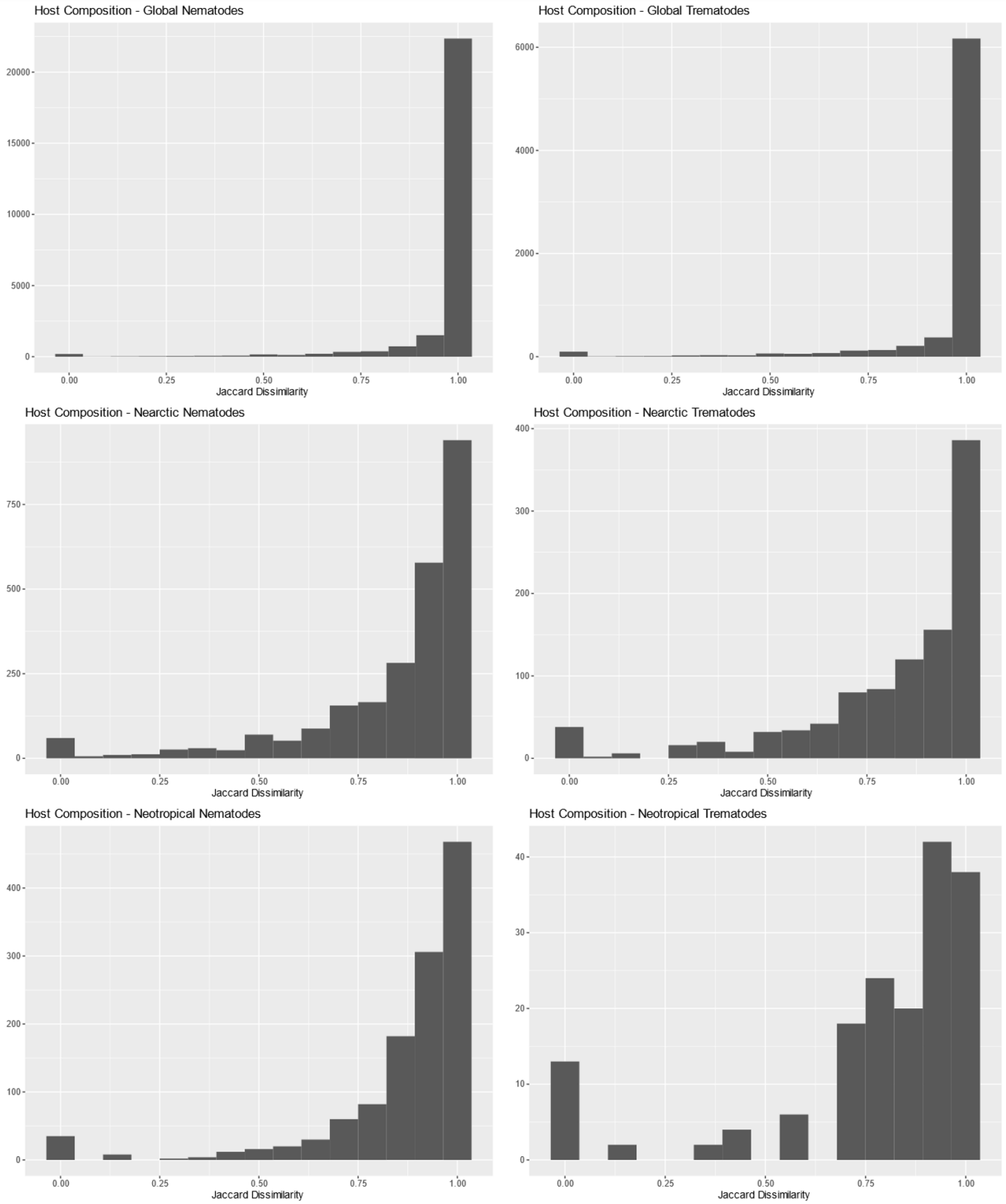
Figure S12. Pairwise dissimilarity of host composition for each data subset.

5. Considerações Finais

5.1. Principais Conclusões

Confirmamos a nossa hipótese de que o clima tem efeitos diretos e indiretos sobre a diversidade global de parasitos de anfíbios. Especificamente, concluímos que a temperatura e a precipitação afetam a diversidade de parasitos tanto diretamente quanto indiretamente pelo seu efeito na riqueza de hospedeiros. No entanto, não houve confirmação para nossa predição de que a precipitação anual teria um efeito direto positivo sobre a riqueza de helmintos, e nem para nossa expectativa de que a sazonalidade da temperatura teria um efeito direto negativo sobre a riqueza de parasitos. A falta de confirmação para essas predições pode estar relacionada ao fato de que os próprios hospedeiros são sensíveis a essas variáveis, o que tem confirmação pela resposta da riqueza de hospedeiros. Como os parasitos são dependentes destes hospedeiros, eles ocorreriam apenas onde é adequado para os seus hospedeiros. Curiosamente, encontramos um efeito positivo direto da sazonalidade sobre a riqueza de parasitos, o que buscamos explicar com base no modo reprodutivo agregado dos anfíbios, especialmente em regiões com maior sazonalidade.

Confirmamos nossa hipótese de que a importância da distância como preditor da substituição de espécies de parasitos diminui com a escala espacial. Os hospedeiros estudados são conhecidos por uma capacidade de dispersão relativamente limitada, especialmente em amplas escalas espaciais, o que pode explicar a proeminência dessa variável. Adicionalmente, confirmamos nossa hipótese de que extremos de temperatura são mais importantes nas regiões temperadas do que nas regiões tropicais. Entender como os preditores variam em função de diferenças biogeográficas é fundamental para o avanço da teoria. Também confirmamos nossa hipótese de que os trematódeos são mais sensíveis às variáveis climáticas do que os nematódeos (ao menos em escala global e no Neártico). Essas diferenças são provavelmente fruto das diferenças na história de vida desses parasitos. Trematódeos possuem estágios larvais mais sensíveis e dependentes de corpos de água, enquanto muitos nematódeos têm ciclos diretos e larvas resistentes a extremos climáticos. Surpreendentemente, não encontramos efeito da composição de hospedeiros sobre a composição de parasitos, o que provavelmente é fruto de uma limitação do estudo.

5.2. Contribuições teóricas e/ou metodológicas da tese

Nosso trabalho contribui para o entendimento do que determina a diversidade alfa e beta de parasitos em escala macroecológica. Primeiro, utilizamos um banco de dados global inédito com um dos grupos de hospedeiros menos estudados em relação à diversidade de parasitos. A exploração de diferentes grupos de hospedeiros é fundamental para o avanço da teoria para além das contingências. Segundo, selecionamos nossas variáveis climáticas através de critérios relacionados à biologia dos grupos ao invés de utilizarmos a latitude como *proxy* ou agruparmos variáveis com métodos de ordenação. Essa decisão representa um avanço no sentido de fazer inferências de causa e efeito de forma direta para elucidar os mecanismos que determinam os padrões de diversidade observados. Terceiro, demonstramos que relações diretas e indiretas devem ser levadas em consideração ao investigar o que determina a riqueza de parasitos. Quarto, até onde temos conhecimento, este foi o primeiro estudo a investigar como a diversidade beta de parasitos em escala macroecológica varia em função da escala espacial e regiões zoogeográficas. Entender como esses dois fatores afetam a diversidade beta é também fundamental para a construção de uma teoria mais geral. Além dessas contribuições teóricas e metodológicas, esta tese compilou o maior banco de dados de parasitas de anfíbios anuros no globo, o que certamente irá permitir o teste de novas hipóteses ou até mesmo de um *datapaper* que pode ser revisado e ampliado.

5.3. Principais limitações do estudo

O nosso banco de dados foi construído a partir da junção de vários estudos primários independentes, o que certamente traz uma série de vieses. Na nossa opinião, algumas das principais incluem: (i) muitos dos estudos primários estão separados por mais de uma década, (ii) um viés geográfico claro onde a maior parte dos estudos primários foram realizados no Neártico, apesar dessa não ser a maior biorregião do planeta, (iii) apenas um subconjunto das espécies de hospedeiros disponíveis foi analisada, e (iv) encontramos muita variação relacionada ao esforço amostral. No entanto, acredito que fizemos o que estava ao nosso alcance no tratamento desses vieses, sendo criteriosos na escolha dos estudos que comporiam o banco de dados, estabelecendo limites mínimos de hospedeiros analisados, considerando as diferenças no esforço amostral no processo de ajuste dos modelos e adotando modelos de validação cruzada. Além destas, esse é um campo

5.4. Propostas de investigações futuras

Poderíamos destacar pelo menos dois resultados interessantes que requerem uma maior atenção em estudos futuros. Em primeiro lugar, precisamos entender os padrões distintos de diversidade de parasitos relacionados às biorregiões, entendendo como os processos históricos e biogeográficos ligados às biorregiões afetam a diversidade de parasitos diretamente e indiretamente via hospedeiros. Em segundo lugar, percebemos que os resultados das análises de diversidade beta variam em função da família de hospedeiros. Isso pode evidenciar a necessidade de um entendimento mais direto acerca de como aspectos da história natural dos hospedeiros afetam os padrões de diversidade beta de parasitos. A desconsideração desse fator pode fazer com que nossos resultados sejam enviesados pelos grupos de hospedeiros mais bem representados, gerando pouco poder de generalização.

5.5. Orçamento

A tese foi desenvolvida com base em uma revisão sistemática da literatura, portanto, este trabalho não contou com fontes externas de financiamento além da bolsa de doutorado concedida a mim por 42 meses (R$ 92,400) pela Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) Além desta, a CAPES também me proveu mais sete bolsas (US$ 11,900) através do programa Ciência Sem Fronteiras para realização do doutorado sanduíche na Universidade de Otago (Nova Zelândia).

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