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REGINALDO AUGUSTO FARIAS DE GUSMÃO

INTEGRANDO CARACTERÍSTICAS DAS ESPÉCIES NA RESPOSTA DA BIODIVERSIDADE ÀS MUDANÇAS AMBIENTAIS EM ESCALA GLOBAL E LOCAL

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Tese apresentada ao Programa de Pós-graduação em Etnobiologia e Conservação da Natureza (UFRPE, UEPB, URCA e UFPE) como parte dos requisitos para obtenção do título de doutor.

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SUMÁRIO

RESUMO

A ecologia vem buscando desde seu surgimento compreender como o ambiente molda a estrutura das comunidades biológicas e estas questões tem ganho cada vez mais poder devido ao forte impacto das ações antrópicas nos filtros ecológicos. A resposta das espécies aos filtros ambientais pode diferir no espaço, a depender da escala observada e entre os táxons avaliados. No entanto, ainda há uma lacuna em compreender os mecanismos envolvidos nestas relações visando explicar as diferentes respostas observadas. Desta forma, ao longo da tese buscamos contribuir com a compreensão dos mecanismos envolvidos na montagem de comunidades em escala global e local. Para isso, realizamos um estudo em macro escala avaliando como o clima atual e a instabilidade climática determinam a riqueza de espécies de tetrápodes. Por meio deste primeiro estudo evidenciamos que as características das espécies é um forte mediador do efeito do clima na riqueza de espécies, porém atuam de forma distinta para cada táxon devido as singularidades metabólicas e fisiológicas destes grupos. Assim, ressaltamos a importância de se integrar diferentes bases teóricas para compreender os mecanismos envolvidos. No segundo capítulo, conduzimos um experimento local para compreender como a invasão biológica e a deposição de nutrientes afetam comunidades de artropodes, destacando o papel do nível trófico para compreender a resposta assimetrica entre herbivoros e predadores ao ambiente. Contrariando expectativas, a adição de nutrientes não teve efeito significativo, enquanto a invasão biológica emergiu como um fator crucial, principalmente na estrutura das comunidades de artrópodes predadores. Demonstramos que as interações tróficas, incluindo controle top-down e bottom-up, são essenciais para compreender as respostas das comunidades à invasão biológica. Portanto, nesta tese evidenciamos os mecanismos pelo qual diferentes fatores ambientais, em escala global e local, determinam a estrutura de comunidade e destacamos o papel das características da espécies para determinar a resposta destas comunidades.

Palavras-chaves: Ecologia; Comunidades Biológicas; Filtros Ecológicos; Invasão Biológica; Clima; Interações Tróficas

ABSTRACT

Ecology has been seeking its adaptation as the environment shapes the structure of biological communities and these questions have gained more and more power due to the strong impact of tropic actions on ecological filters. Thus, recent study has shown that the response of species to environmental filters may differ in space, it depends on the observed scale and among the evaluated taxa. However, there is a gap in understanding the resources still contemplated to contemplate the different solutions observed. In this way, throughout the thesis we seek to contribute to the understanding of the groups involved in the assembly of communities on a global and local scale. For this, we carried out a macro-scale study evaluating how the contemporary climate and historical climate change determine the richness of tetrapod species. Through this study, we show that species characteristics are a strong mediator of the climate effect on species richness, but they are relevant in a different way for each of the metabolic and physiological singularities of these groups. Thus, we emphasize the importance of integrating the theory to understand the different bases developed. In the second chapter, we conducted a local experiment to understand how biological invasion and nutrient deposition affect communities, highlighting the role of trophic level in responding to the environment. Contrary to expectations, nutrient addition had no significant effect, while biological invasion emerged as a crucial factor, especially in the structure of predatory arthropod communities. We demonstrated that trophic interactions, including top-down and bottom-up control, are essential for understanding community responses to biological invasion. Therefore, in this thesis we highlight the mechanisms by which different environmental factors, on a global and local scale, determine community structure and highlight the role of species characteristics in determining the response of these communities.

Keywords: Ecology; Biological Communities; Ecological Filters; Biological Invasion; Climate; Trophic Interactions

INTRODUÇÃO GERAL

OBJETIVOS E QUESTIONAMENTOS

Uma das grandes questões que norteiam as pesquisas em ecologia é como os filtros ambientais atuam na montagem das comunidades (HILLERISLAMBERS et al., 2012). Esta questão tem cada vez mais espaço, pois sabe-se que estes filtros vem sendo alterados pela ação do homem ao modificar a paisagem (ARAÚJO; RAHBEK, 2012; HAWKINS et al., 2007; PIELKE, 2005). Assim, a ecologia tem avançado em considerar o efeito não só dos filtros naturais, como também dos antrópicos. Porém ainda há lacunas na compreensão dos mecanismos envolvidos na montagem das comunidades. Nesta tese buscamos compreender de que forma a estrutura trófica e o tamanho corporal determinam as respostas das comunidades aos filtros naturais e antrópicos.

Assim, esta tese abordará os processos de seleção de espécies por fatores abióticos (e.x., clima e nutrientes do solo) e bióticos (e.x., predação e competição) que atuam como filtros ecológicos determinando quais e quantas espécies ocorrem em uma comunidade (HILLERISLAMBERS et al., 2012). Por exemplo, há evidencias de que maiores temperaturas favorecem riqueza de espécies de aves (HAWKINS et al., 2007; MCARTHUR; MCARTHUR, 1961). No entanto, estes filtros não atuam de forma homogênea em todas as espécies (FICETOLA et al., 2021; SANTOS et al., 2020). A partir disso, observou-se uma lacuna no conhecimento acerca dos mecanismos que produzem as distintas resposta entre diferentes táxons em relação aos filtros ecológicos.

Diferentes espécies responderão de diferentes formas às variações no hábitat. Desta forma, há táxons que apresentarão maior sensibilidade aos fatores abióticos e bióticos (BROWN et al., 2004; FICETOLA et al., 2021; VOIGT et al., 2003). Sabe-se que espécies com maior tamanho corporal e/ou nível trófico tendem a ser mais sensíveis a alterações nos filtros ecológicos (BROWN et al., 2004; VOIGT et al., 2003). Assim, ao considerarmos as mudanças ambientais ocasionadas pela atividade humana, é esperado um rápido declínio de espécies maiores e de níveis tróficos superiores (VOIGT et al., 2003). Desta forma, podemos esperar que a estrutura trófica e do tamanho corporal atuem como mediadores do efeito dos filtros ecológicos na estrutura das comunidades (i.e., riqueza de espécies, abundância e composição).

No entanto, antes de compreender como os filtros alterados pela atividade humana determinam a montagem das comunidades, é fundamental entender como este processo ocorre de forma independente da ação antrópica (HILLERISLAMBERS et al., 2012). Por exemplo, estudos recentes têm demonstrado que o padrão de distribuição atual foi determinado não só pelo clima atual, mas pelas mudanças históricas do clima (SANTOS et al., 2020). Resultado o qual pode ser incorporado para desassociar o impacto natural da variação climática e do aquecimento global ocasionado pela atividade humana. Portanto, sentimos a necessidade de inicialmente responder às seguintes perguntas: Como o clima determina a estrutura das comunidades por meio das características das espécies? Maiores tamanhos corporais reduzem a riqueza de espécies? A predominância de predadores reduz a riqueza de espécies?

Por outro lado, a ação antrópica tem ocasionado forte declínio da diversidade de espécies, principalmente em decorrência da invasão biológica e das mudanças climáticas (JETZ; WILCOVE; DOBSON, 2007; VALIENTE-BANUET et al., 2014). Sabe-se que a invasão biológica e a deposição de nutrientes no solo em decorrência das mudanças climáticas atuam de forma sinergética ocasionando o forte declínio da riqueza de espécies (MACDOUGALL; TURKINGTON, 2005). No entanto, de forma distinta ao clima, a adição de nutrientes e a invasão biológica têm um efeito em cascata bottom-up na comunidade, perdendo seu efeito ao longo da cadeia trófica (ESTES et al., 2011; VOIGT et al., 2003). Desta forma, esperamos compreender como as ações antrópicas determinam a montagem de comunidades e seus mecanismos reguladores, assim como suas consequências para todos os níveis tróficos.

ESTRATÉGIAS DE PESQUISA

Visando responder como as características das espécies atuam como mediadoras da relação entre o clima e a montagem das comunidades, usamos duas distintas abordagens. Realizamos um estudo em macro escala usando dados secundários e um segundo trabalho em escala local por meio de um experimento. Apesar de usarmos sistemas biológicos distintos, as diferenças de escalas dos dois métodos utilizados permitem uma generalização maior dos achados ao compreender como caracteristicas das espécies (i.e., tamanho corporal e nível trofico) moldam a resposta das comunidades aos fatores ambientais. Portanto, apesar das limitações associadas a cada método existente, a robustez dos nossos achados permitem uma maior generalização.

Nossa primeira abordagem teve o intuito de integrar a macroecologia clássica com a teoria metabólica e trófica. Estudos recentes que tem buscado essa integração da macroecologia com outras áreas tem demonstrado que características das espécies (e.x., estratégia de termia) podem explicar a distinta resposta da riqueza de espécies ao clima (FICETOLA et al., 2021;

SANTOS et al., 2020). No entanto, estes estudos não consideram a relação entre o clima e essas características das espécies. Desta forma, ao considerar a relação entre o clima e a estrutura trofica e do tamanho corporal das comunidades, será possível compreender melhor como elas medeiam o efeito do clima nos diferentes padrões de diversidade cada grupo de tetrápode.

A segunda abordagem foi por meio de um experimento que faz parte da rede global NutNet, que visa entender o efeito da adição de nutrientes e invasão biológica. No entanto, as principais redes globais de experimentos estão concentradas principalmente em regiões temperadas (FRASER et al., 2012; GROSSMAN et al., 2018). Como resultado, os achados dessas redes ainda são limitados e pouco generalizáveis. Por exemplo, a partir da teoria de montagem de comunidades, os fatores abióticos e bióticos apresentam importância relativa diferente nas regiões temperadas e tropicais. Desta forma, os resultados destas redes de experimento ainda são restritivas (ROMERO et al., 2018). Assim, nossos resultados contribuem para a generalização do conhecimento das redes globais, e são fundamentais para embasar a compreensão acerca dos efeitos em cascata desencadeados por ações antrópicas nas comunidades.

ESTRUTURA DA TESE

A tese é composta por quatro capítulos. Sendo eles: (I) Fundamentação teórica; (II) Artigo - Body size and trophic structure explain global asymmetric response of tetrapod diversity to climate effects; (III) Artigo - Biological invasion, but not nutrient supply, impacts arthropod communities through bottom-up and top-down effects; e (IV) considerações finais. Apesar de ambos os artigos apresentarem abordagens distintas, buscam identificar como as características das espécies medeiam o efeito do ambiente na montagem de comunidades. Desta forma, esperamos contribuir para uma melhor compreensão dos mecanismos envolvidos na montagem das comunidades biológicas.

A fundamentação teórica, nosso primeiro capítulo, aborda de maneira abrangente a complexa interação entre fatores abióticos e bióticos na montagem de comunidades biológicas, destacando a influência variável desses fatores em diferentes regiões. Ao considerar simultaneamente as ações antrópicas, como mudanças climáticas, invasão biológica e adição de nutrientes, oferecemos uma visão ampla dos impactos humanos na biodiversidade. Além disso, destacamos que uma abordagem multitrófica e que abranja múltiplos fatores ambientais pode revelar *insights* sobre os efeitos sinérgicos e indiretos desses fatores ambientais nas comunidades biológicas. Nós também destacamos lacunas teóricas, especialmente em regiões tropicais, oferecendo uma valiosa contribuição para a compreensão integrada das respostas das comunidades biológicas às pressões antrópicas em escalas local e global.

Em nosso segundo capítulo buscamos entender como a estrutura trófica e o tamanho corporal mediam o efeito do clima atual. São consideradas também as mudanças históricas do clima na riqueza de tetrápodes. Nós integramos o framework da teoria metabólica e de nicho com a macroecologia clássica para explicar como o clima determina distintos padrões de distribuição dos tetrápodes. Assim, identificamos que as características das espécies explicam respostas assimétricas de aves, mamíferos, anfíbios e répteis ao clima. Enquanto o clima contemporâneo diretamente influencia a riqueza de espécies de tetrápodes, a instabilidade climática afeta apenas aves e répteis, por meio de características da comunidade. Neste capítulo destacamos a importância de unificar teorias para compreender padrões de diversidade e aprimorar previsões macroecológicas. Sendo este artigo a ser publicado na revista *Ecology and Evolution*.

Já em nosso terceiro capítulo, que temos como revista pretendida a *Ecology*, nós buscamos identificar como ações antrópicas como a adição de nutrientes e invasão biológica influenciam a comunidade de artrópodes. Estudos prévios que avaliaram perguntas similares, acabam por negligenciar o efeito em cascata na estrutura trófica existente na comunidade. Desta forma, além dos efeitos diretos da adição de nutrientes e invasão biológica em nosso estudo, consideramos os efeitos indiretos por meio do efeito em cascata nos níveis tróficos. Portanto, neste capítulo mostramos que a adição de nutrientes não tem efeitos agudos nas comunidades de artrópodes, mas pode ter efeitos crônicos. Por outro lado, a invasão biológica emerge como fator crucial, influenciando biomassa e riqueza de espécies de artrópodes predadores. Além disso, mostramos que há redução na riqueza de plantas nativas devido à invasão. Este resultado destaca a importância da competição entre espécies invasoras e nativas com efeitos cascata nas interações tróficas e a importância da preservação da vegetação nativa para níveis tróficos superiores.Por fim, no quarto capítulo, nós apresentamos as considerações finais apresentamos um fechamento demonstrando as principais conclusões da tese, destacando lacunas teoricas a serem exploradas por futuros estudos.

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CAPÍTULO I: FUNDAMENTAÇÃO TEÓRICA

O padrão de distribuição das espécies é determinado por fatores abióticos (ex., temperatura e precipitação) e biótico (ex., predação e competição) que atuam como filtros determinando a montagem das comunidades (HILLERISLAMBERS et al., 2012). Porém, a importância relativa dos fatores bióticos e abióticos podem variar entre regiões e entre as facetas da diversidade. Por exemplo, nas regiões tropicais é apontada uma maior força dos fatores bióticos em relação aos abióticos (ROMERO et al., 2018). Estes fatores ambientais irão determinar diversas características das comunidades biológicas, tais como a riqueza de espécies (diversidade alfa) e a composição de espécies (diversidade beta) (HILLERISLAMBERS et al., 2012; VELLEND, 2010). Desta forma, os diferentes fatores abióticos e bióticos vão determinar as distintas estruturas das comunidades biológicas.

Assim, mudanças nos filtros ambientais ocasionadas pelas ações antrópicas (ex. mudanças climáticas, poluição e introdução de espécies invasora) têm modificado os filtros abióticos e bióticos, mudando ao longo do tempo os padrões de distribuição das espécies (JETZ; WILCOVE; DOBSON, 2007; TUANMU; JETZ, 2014). Já foi demonstrado que o aumento da temperatura e redução da precipitação modificam as interações, assim como o aumento da competição devido à invasão biológica, têm consequências negativas para a estrutura das comunidades (WALTHER et al., 2002). Desta forma, as ações antrópicas têm ocasionado um drástico declínio da diversidade (taxonômica, funcional e filogenética), homogeneização biótica e, consequentemente, perda da capacidade de fornecimento de bens e serviços ecossistêmicos (JETZ; WILCOVE; DOBSON, 2007; VALIENTE-BANUET et al., 2014). Portanto, se faz necessário compreender como as ações antrópicas alteram os filtros ambientais e as interações ecológicas, e de que forma afetam a estrutura de comunidades.

O processo de extinção em decorrência de mudanças nos filtros ambientais não ocorre de forma aleatória, uma vez que as espécies com maior risco de extinção geralmente apresentam maior massa, e linhagens mais basais apresentam menor resistência aos efeitos deletérios das ações antrópicas (FRISHKOFF et al., 2014; REZENDE et al., 2007). Por exemplo, estudos apontam que as ações antrópicas afetam principalmente predadores e, consequentemente, ocasiona a redução do controle “top-down” das comunidades, podendo alterar a estrutura das pirâmides tróficas (MCCAULEY et al., 2018). Porém, os efeitos das variações ambientais (ex. mudanças climáticas, adição de nutrientes e invasão biológica) sobre características funcionais e histórias evolutivas de vertebrados e invertebrados ainda são pouco generalizáveis, uma vez que os estudos são limitados a poucos biomas e dados funcionais destes organismos são limitados (FLYNN et al., 2009). Desta forma, para uma melhor compreensão dos efeitos das ações antrópicas e do clima nas comunidades, devemos considerar as características das espécies e a estrutura trófica das comunidades.

Ao alterar os filtros ambientais, as ações antrópicas têm ocasionado o declínio da biodiversidade e alterado a dinâmica de restauração em diversos ecossistemas (ANDERSON-TEIXEIRA et al., 2013; CARLSON et al., 2017; JETZ; WILCOVE; DOBSON, 2007; NEWBOLD et al., 2015; WALTHER et al., 2002). Projeções apontam que as mudanças climáticas apresentam grande consequências para a biodiversidade global, sendo previsto mudanças na distribuição das espécies (ARAÚJO; RAHBEK, 2012) e grandes declínios da diversidade de espécies em diversos grupos taxonômicos (CARLSON et al., 2017; JETZ; WILCOVE; DOBSON, 2007; SALA et al., 2000). Assim, acredita-se que ainda no antropoceno, mais de 75% das espécies conhecidas poderão ser extintas, porém esta estimativa pode estar subestimada por focar em vertebrados (BARNOSKY et al., 2011). Ressaltando assim, a importância do clima como um principal fator a determinar a diversidade, especialmente quando se considera a temperatura e a precipitação, por influenciar a entrada de energia no ecossistema e disponibilidade de água (HAWKINS et al., 2003).

As mudanças climáticas ao serem acentuadas pelas atividades antrópicas, tais como uso do solo e poluição atmosférica, são responsáveis por acentuar as mudanças climáticas, consequentemente, ocasionando alterações na temperatura e na chuva (HAWKINS et al., 2003; RITO et al., 2017). Entre as consequências da alteração do regime de chuva temos o acréscimo da evapotranspiração que pode gerar danos à diversidade, devido à redução na produtividade primária que aumenta o risco de extinção das espécies e reduz resistência dos ecossistemas diante um distúrbio (ANDERSON-TEIXEIRA et al., 2013; ZHAO; RUNNING, 2010). Como resultado, estas regiões apresentam uma maior diversidade vegetal, aumentando a disponibilidade de recursos disponíveis para grupos tróficos superiores, consequentemente, permitindo a manutenção de teias alimentares mais complexas (HAWKINS et al., 2003; MCCAIN, 2007). Desta forma, variações climáticas tem um papel fundamental como fator determinante da riqueza de espécies, principalmente nas regiões neotropicais e florestas secas, além de aumentar a heterogeneidade dos habitats (HAWKINS et al., 2003).

Além disto, a transformação de áreas naturais pelo homem em decorrência expansão agrícola e crescimento populacional é uma das principais causas da homogeneização biótica (FLYNN et al., 2009; HADDAD et al., 2017; PACIFICI et al., 2017). Por exemplo, sabe-se que a homogeneização é favorecida pela colonização de espécies exóticas e invasoras. Uma vez estabelecidas, passam a ampliar rapidamente sua área de distribuição e a prejudicar o desenvolvimento de espécies nativas, apresentando um efeito em cascata em todo ecossistema (YOUNG et al., 2017). Assim, a introdução de espécies invasoras é apontada como responsável pelo declínio da riqueza de diversos grupos taxonômicos, entre eles plantas e artrópodes, respectivamente, 28 e 19% das espécies destes grupos (MOLLOT; PANTEL; ROMANUK, 2017). Desta forma, a invasão biológica é considerada uma das principais causas do declínio da diversidade em todo o mundo.

Apesar das consequências das mudanças climáticas e da invasão biológica serem bem debatidas de forma independente, e considerando os efeitos diretos sobre a diversidade, poucos estudos levam em consideração os efeitos de mais de uma ação antrópica simultaneamente (WALTHER et al., 2009). Por exemplo, as mudanças climáticas favorecem a invasão por espécies exóticas da etapa de colonização até a propagação, respectivamente, por meio do aumento da sobrevivência e dispersão destas espécies (SCHWEIGER et al., 2010; WALTHER et al., 2009). Sendo registrado que temperaturas mais elevadas, principalmente em regiões temperadas, favorecem o estabelecimento de invasoras e aumentam a atividade de voo por dispersores, permitindo que estas espécies alcancem áreas antes inacessíveis (SCHWEIGER et al., 2010; WALTHER et al., 2009). Portanto, essas evidências da influência do clima sobre a invasão de espécies, ressaltando a importância de se considerar os efeitos indiretos e simultâneos destes processos (DUKES; MOONEY, 1999; WALTHER et al., 2009).

Nas regiões do semiárido brasileiro a população é predominantemente rural, e com baixo índice de desenvolvimento humano (IDH). Como estratégia de subsistência, os moradores locais transformam parte da paisagem em agriculturas, pastagens e pequenos fragmentos (ANTONGIOVANNI; VENTICINQUE; FONSECA, 2018; QUESADA et al., 2009). Projeções indicam a contração de mais de 80% da distribuição de espécies nativas e o aumento da distribuição de espécies que são deliberadamente introduzidas no ecossistema (ALMEIDA et al., 2015; CAVALCANTE; DUARTE; OMETTO, 2020). Neste processo de transformação da paisagem, diversas espécies exóticas são introduzidas. As gramíneas, popularmente cultivadas e destinadas para alimentação animal, são consideradas uma forte ameaça às espécies nativas. A possível extinção de espécies nativas, impulsionada pela presença destas gramíneas invasoras, pode contribuir fortemente para a homogeneização biótica, impedindo o processo de sucessão natural na região (ANDRADE; FABRICANTE; OLIVEIRA, 2009; MILTON; DEAN, 2010). Assim, a invasão biológica tem se mostrado um fator predominante em regiões como a Caatinga no Brasil.

Além disso, as consequências da invasão biológica são acentuadas pelas mudanças climáticas. A redução da precipitação, o aumento da temperatura e o excesso de nutrientes no solo são variações já previstas para as regiões do semiárido (HARPOLE; TILMAN, 2007; MAGRIN et al., 2014). Estudos tem demonstrado que as plantas invasoras são “passageiras” de mudanças ambientais, ou seja, a propagação e prevalência da invasão biológica é favorecida por estas alterações, tal como o aumento da disponibilidade de nitrogênio no solo (MACDOUGALL; TURKINGTON, 2005). Portanto, este resultado demonstra que há um efeito sinergético positivo entre a invasão biológica e a deposição de nutrientes no solo. Desta forma, ressalta-se a importância de considerarmos múltiplos estressores ambientais simultaneamente.

A configuração da montagem de comunidades está intimamente relacionada com a disponibilidade e concentração de nutrientes no solo, especialmente o nitrogênio (N), o fosforo (P) e o potássio (K). Estes nutrientes são determinantes para a produtividade, fisiologia vegetal e diversidade biológica (FAY et al., 2015; HARPOLE; TILMAN, 2007). Além disso, são limitantes da produtividade em vários ecossistemas terrestres e aquáticos (ELSER et al., 2007; FAY et al., 2015). Assim, a adição de nutrientes elimina o trade-off entre crescimento e competição, permitindo que a energia alocada para coexistência seja direcionada para o crescimento de produtores (i.e. plantas), consequentemente, aumentando a produtividade local (HARPOLE; TILMAN, 2007; HAUTIER, Y; NIKLAUS, P A; HECTOR, 2009). Desta forma, a adição de nutrientes pode apresentar efeitos positivos para os ecossistemas se tornando uma prática da vez mais comum.

A adição de nutrientes (NPKμ) no solo vem sendo aplicada em ambientes agrícolas visando o aumento da produtividade, e tem sido uma prática viável devido ao baixo custo (ELSER et al., 2007; FAY et al., 2015; SEIBOLD et al., 2015). Além disso, também tem se mostrado uma forma eficiente para a restauração de ambientes degradados. Por exemplo, ao favorecer a produtividade local, há um maior fluxo de energia no ecossistema e, consequentemente, aumenta também a complexidade das cadeias tróficas (aumenta a diversidade vertical) e a riqueza de espécies em cada nível trófico (diversidade horizontal) (EVANS et al., 2005; HARPOLE; TILMAN, 2007; HAUTIER, Y; NIKLAUS, P A; HECTOR, 2009; JOERN; LAWS, 2013). No entanto, elevadas concentrações de nutrientes em ecossistemas terrestres e aquáticos são causadores da eutrofização e do declínio da riqueza de produtores. Isto ocorre devido à redução do número de fatores limitantes no ecossistema, permitindo que uma ou poucas espécies se estabeleçam, tais como as espécies exóticas, levando à homogeneização biótica (HARPOLE; TILMAN, 2007). Portanto, se faz necessário compreender qual o limiar da concentração de nutrientes em ecossistemas naturais em que o efeito da adição de nutrientes ocasiona o declínio da biodiversidade.

As ações antrópicas não atuam de forma independente. Portanto, existem alguns fatores associados que podem contribuir, tanto ampliando quanto reduzindo seus impactos (HARPOLE; TILMAN, 2007; SCHWEIGER et al., 2010; WALTHER et al., 2009). Com isto, evidencia-se a necessidade de compreender a complexidade destes sistemas. Sabe-se, por exemplo, que a dinâmica entre invasão biológica e adição de nutrientes, considerando o efeito do clima e da instabilidade climática longo do tempo nas comunidades biológicas, pode permitir explicar melhor a respostas das espécies (MACDOUGALL; TURKINGTON, 2005; SANTOS et al., 2020). Por isso, ao longo da tese buscamos compreender os efeitos de múltiplos estressores ambientais (i.e., Cap 2- Clima contemporâneo e instabilidade climática e Cap. 3- Adição de nutrientes e invasão biológica). Portanto, demonstraremos a importância de avançar na utilização de múltiplos fatores ambientais para compreender as respostas ecológicas.

Até o momento, os estudos ecológicos vêm se baseando em ações antrópicas de forma isolada (e.g., clima, nutrientes ou espécie invasora), e focando em grupos taxonômicos exclusivos (SEIBOLD et al., 2015, 2018). Ao considerar, por exemplo, os impactos da adição de nutrientes apenas na comunidade de artrópodes herbívoros sem observar os efeitos na riqueza de plantas (i.e., variedade do recurso), é provável que se perpetue uma lacuna no conhecimento acerca das relações entre diferentes níveis tróficos. Assim, a adoção de uma a abordagem multitrófica busca quebrar o paradigma de estudar apenas um grupo taxonômico ou um nível trófico (comunidades horizontais), focando nas interações entre organismos de todos os níveis tróficos e o ambiente (SEIBOLD et al., 2018; WOOTTON, 1998). Esta abordagem não anula a importância de compreender as respostas das comunidades horizontais, mas atua de forma aditiva, em que a combinação de ambas possibilita um melhor entendimento sobre os estressores em vários níveis tróficos (ex. predador, herbívoro e produtor) para a restauração e manutenção da biodiversidade.

Os estudos na ecologia de comunidades em sua maioria ainda são restritos a um táxon, ou a táxons de um mesmo nível trófico, consequentemente ignorando as relações entre os níveis tróficos. No entanto, através da abordagem multitrófica é possível compreender o efeito das mudanças climáticas, da adição de nutrientes e da invasão de espécies na estrutura trófica, bem como da transferência de biomassa no sistema, permitindo compreender mecanismos que estruturam a biodiversidade e seus reflexos para o ecossistema (MCCAULEY et al., 2018; SEIBOLD et al., 2018). Assim, a ecologia de comunidades pode avançar além de um paradigma histórico que foi a separação da ecologia de plantas e animal. Desta forma, ao adotar e incentivar abordagens multitróficas podemos identificar se fatores exógenos e endógenos podem ocasionar alterações significantes nas comunidades biológicas.

A realização de experimentos em meios naturais é uma das principais formas para entender como as ações antrópicas determinam a montagem de comunidades e seus mecanismos reguladores, assim como suas consequências para todos os níveis tróficos (BORER et al., 2014). Por exemplo, por meio de experimentos é possível avaliar sistemas complexos abordando múltiplos níveis tróficos (BORER et al., 2014; SEIBOLD et al., 2018). No entanto, a criação de redes globais permite a ampliação da generalização dos resultados para escalas macroecológicas. Assim, as redes de experimentos globais têm papel chave em responder perguntas ecológicas complexas nas mais distintas escalas.

As principais redes globais de experimentos, como o TreeDivNet, Droughtnet, NutNet, e DRAGNet (FRASER et al., 2012; GROSSMAN et al., 2018), estão concentradas principalmente em regiões temperadas. Assim, os resultados destas redes ainda são limitados e pouco generalizáveis. Por exemplo, quando tratamos da teoria de montagem de comunidades, considera-se que os fatores abióticos e bióticos apresentam importância relativa diferente entre as regiões temperadas e tropicais, limitando assim os resultados destas redes de experimento (ROMERO et al., 2018). Como resultado disso, ressalta-se a importância desta tese ao fazer parte da rede NutNet, sendo uns dos pioneiros no Brasil a buscar responder perguntas ecológicas atuais usando abordagens inovadoras (i.e., multiestressores e multitrófica), que atacam tanto as necessidades práticas para o desenvolvimento da restauração ecológica, quanto questões teóricas relevantes para entender a montagem de comunidades biológicas. Portanto, os resultados de nosso segundo artigo podem auxiliar em práticas de conservação, como no controle de espécies exóticas/invasoras, e na elaboração de técnicas para o incremento de nutrientes na recuperação de áreas degradadas, acelerando a sucessão ecológica e recuperando suas funções ecológicas.

Tudo que vem sendo apresentado e debatido até aqui, é também aplicado a ecologia de comunidades em macro escala. Por exemplo, sabe-se que os fatores antrópicos (i.e., mudanças climáticas e uso do solo) tem alterado o padrão de distribuição das espécies em todo o globo (NEWBOLD et al., 2015). No entanto, é essencial compreender como as ações antrópicas estão alterando as comunidades, e elencar os mecanismos que atuam como filtros na montagem de comunidades. Desta forma, se faz necessário entender os mecanismos envolvidos na relação entre o ambiente e o padrão de distribuição das espécies.

Atualmente, há uma grande quantidade de dados disponíveis para estudos em macro escala, principalmente com vertebrados. Por exemplo, podemos citar a vasta quantidade de dados climáticos e mapas de distribuição das espécies disponíveis que permitem avaliar o padrão de distribuição das espécies atual e fazer predições futuras (KEITH et al., 2012). Diferente dos experimentos em rede, estes dados ainda são mais generalizáveis, apesar do erro associado ao uso de dados secundários. Portanto, o uso de dados secundários para compreender os fatores que determinam a montagem de comunidades em escala global é uma escolha razoável.

A compreensão dos mecanismos que mediam o efeito do ambiente e das interações bióticas na montagem de comunidade é escassa em estudos de escala local (i.e., experimentos) e global (i.e., uso de dados secundários) (BORER et al., 2014; MCGILL, 2019). Por exemplo, as abordagens clássicas macroecológicas buscam compreender os efeitos diretos do clima ou ação antrópica nos padrões de diversidade ou nas características das espécies (NEWBOLD et al., 2014, 2015). Porém, estudos mais recentes vêm buscando integrar várias bases teóricas para entender os mecanismos que envolvidos nestas relações (BUCKLEY; HURLBERT; JETZ, 2012). Desta forma, buscaremos esclarecer o framework teórico da teoria metabólica e trófica para compreender os mecanismos em macro escala que influenciam a estrutura das comunidades biológicas.

Ao compreender de forma multifatorial os mecanismos envolvidos na montagem de comunidades em macro escala, podemos responder questões chaves na macroecologia, tais como: por que há distintos padrões de riqueza entre grupos taxonômicos? Como se dá a seleção de espécies de uma comunidade? Qual o papel das características das espécies na montagem de comunidade? Como demonstrado por Buckley et. al., (2012) e Ficetola et al., (2021) as características das espécies são fatores que podem explicar os diferentes padrões existentes de riqueza de espécies, tais características como a estratégia de termia e a capacidade de dispersão. Assim, ao considerarmos as características das espécies na relação entre ambiente e resposta das comunidades ecológicas, poderemos realizar predições mais precisas. Portanto, por meio de uma abordagem integrativa, buscamos embasar as respostas para estas perguntas.

Além disso, são vastos os estudos macroecológicos que demonstram a relação entre clima e o padrão de espécies para os mais distintos grupos (BUCKLEY; HURLBERT; JETZ, 2012; FICETOLA et al., 2021). No entanto, há evidências de que os padrões macro ecológicos atuais não são determinados somente pelo clima atual, mas também pelas mudanças climáticas históricas (SANTOS et al., 2020). No qual, considerar não só o clima atual, mas as mudanças históricas permitem uma melhor compreensão dos padrões atuais e projeções mais precisas da resposta das espécies as ações antrópicas. Desta forma, abordagens que considerem fatores climáticos atuais e históricos, além das características de cada grupo, estão atualmente na ponta da lança na macroecologia.

Estudos recentes têm buscado explicar os distintos padrões de distribuição das espécies. Por exemplo, tem se demonstrados que mamíferos e aves têm a seu padrão de distribuição de espécies mais bem explicado pelo clima atual do que pela variação do clima (SANTOS et al., 2020). Sendo este resultado oposto a anfíbios e repteis, o que é atribuído à menor capacidade de dispersão destes grupos. Assim, diferenças em características das espécies podem mediar o efeito do clima na montagem das comunidades.

A distinta resposta das espécies pode ser em decorrência a características como tamanho corporal e nível trófico que tem forte influência no metabolismo e fisiologia das espécies

(BUCKLEY; HURLBERT; JETZ, 2012; FICETOLA et al., 2021). Sabe-se que o aumento do tamanho corporal e nível trófico aumentam o requerimento energético e recurso utilizado pelas espécies (BROWN et al., 2004; TOMLINSON et al., 2017). Assim, estas espécies tendem a ser mais sensíveis a variações ambientais resultando em distintos padrões de distribuição (BROWN et al., 2004; VOIGT et al., 2003). Desta forma, compreender como as características das espécies podem explicar a resposta ao clima das espécies permitirá esclarecer os distintos padrões de distribuição de espécies.

Por fim, nesta tese buscamos compreender quais mecanismos atuam na resposta das espécies ao ambiente em escala local e macro escala. Assim, em nosso primeiro capítulo avaliamos como o clima atual e as mudanças históricas determinam o padrão de riqueza de tetrápodes em todo o globo por meio das características das espécies (i.e., tamanho corporal e nível trófico), e em nosso segundo capítulo investigamos como a adição de nutrientes e a invasão biológica determina a montagem da comunidade de artrópodes, levando em consideração o efeito em cascata em cada nível trófico na comunidade. Ambos os capítulos convergem em compreender os mecanismos relacionados ao efeito do ambiente nas comunidades biológicas. Portando, esperamos demonstrar como as características das espécies medeiam o efeito do ambiente na estrutura de comunidades, usando em escala global a distribuição de tetrápodes, e em escala local a riqueza e abundância de artrópodes.

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CAPÍTULO 2: BODY SIZE AND TROPHIC STRUCTURE EXPLAIN GLOBAL ASYMMETRIC RESPONSE OF TETRAPOD DIVERSITY TO CLIMATE EFFECTS

Short running title: Direct and indirect drivers of global tetrapod diversity

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ABSTRACT

Although climate-based hypotheses are widely used to explain large-scale diversity patterns, they fall short of explaining the spatial variation among taxonomic groups. Integrating food web and metabolic theories into macroecology is a promising step forward, as they allow including explicit taxon-specific traits that can potentially mediate the relationship between climate and diversity. Our investigation focuses on the role of body size and trophic structure in mediating the influence of contemporary climate and historical climate change on global tetrapods species richness. We used piecewise structural equation modeling to assess the direct effects of contemporary climate and climate instability of species richness and the indirect effects of climate on tetrapod richness mediated by community-wide species traits. We found that birds and mammals are less sensitive to the direct effect of contemporary climate than amphibians and squamates. Contemporary climate and climate instability favored the species richness of mammals and amphibians. However, for birds and squamates, this link is only associated with contemporary climate. Moreover, we showed that community-wide traits are correlated with species richness gradients. However, we highlight that this relationship is dependent upon the specific traits and taxonomic groups. Specifically, bird communities with smaller bodies and bottom-heavy structures support higher species richness. Squamates also tend to be more diverse in communities with prevalence of smaller bodies, while mammals are correlated with top-heavy structures. Moreover, we showed that higher contemporary climate and climate instability reduce the species richness of birds and mammals through community-wide traits and indirectly increase squamate species richness. We also showed that body size and trophic structure are driving a global asymmetric response of tetrapod diversity to climate effects, which highlights the limitation to use the "typical" climate-based hypotheses. Furthermore, by combining multiple theories, our research contributes to a more realistic and mechanistic understanding of diversity patterns across taxonomic groups.

Keywords: Functional traits; Macroecology; food web theory; metabolic theory; species pattern; climate instability; contemporary climate

INTRODUCTION

The most difficult challenge for ecological theory has been explaining the non-homogeneous distribution of species, which has encouraged the development of various hypotheses with varying degrees of support (Pianka, 1996; Willig *et al.*, 2003). Climate-based hypotheses have been shown to be the most effective in explaining patterns of global diversity (Gillman & Wright, 2014). However, empirical studies criticized these hypotheses because species from different trophic levels and metabolic rates respond asymmetrically to climate (Voigt *et al.*, 2003; Brown *et al.*, 2004). Thus, a tangle of diffuse explanations requires synthesis to understand the mechanisms underlying the climate-based hypotheses (McGill, 2019).

Contemporary temperature and precipitation (hereafter, contemporary climate) have been widely established in the literature as the main drivers of species richness (Evans *et al.*, 2005; Whittaker *et al.*, 2007; Table 1a). Moreover, climate change from the Last Glacial Maximum (LGM, a measure of climate instability) also explains broad scale diversity patterns, adding fuel to a debate concerning whether contemporary climate or climate instability are better predictors of global species richness (Araújo & Rahbek, 2006; Santos et al., 2020; Table 1b). Despite this central relevance of climate-based hypotheses to macroecology, this theory has yet not fully untangled the strength and direction of the asymmetric effect of contemporary climate and climate instability on species richness, which can vary depending on species traits and taxonomic groups (Barreto *et al.*, 2021; Ficetola *et al.*, 2021; Fig. 1- (I)). For instance, bird and mammal diversity are less sensitive to the contemporary climate because they have a broader thermal tolerance range than amphibians and squamates (Buckley *et al.*, 2012; Ficetola *et al.*, 2021). However, compared to birds and mammals, amphibians and squamates are more vulnerable to climate instability due to their smaller bodies reducing their ability to disperse (Ficetola *et al.*, 2021). Additionally, the responses to climate could also vary within the same taxon when comparing across trophic levels (Voigt *et al.*, 2003; Sandel *et al.*, 2011). For example, species of higher trophic levels are more sensitive to climate than lower trophic levels mainly because higher trophic levels require more energy and resources (Voigt et al., 2003). These trait or taxon dependent responses to climate suggest that two major questions remain unanswered: How do the mechanisms involved in the relationship between climate and species richness differ between taxonomic groups? How do community-wide species traits (e.g., size and trophic structure at the community scale) explain the disparities in global diversity patterns among tetrapods?

The number of species supported by a community can be determined by the link between climate and size structure (i.e., body size and variance of body size) of a community (Hillebrand & Azovsky, 2001). Communities dominated by larger species tend to have lower species richness because larger species may have lower generational rate and population size resulting in a reduced speciation rate and increased extinction rate (Brown *et al.*, 2004; Evans *et al.*, 2005; Peralta-Maraver & Rezende, 2021). Metabolic theory allows for more refined predictions regarding the relationship between climate and species richness within each tetrapod group. For instance, the theory predicts regions characterized by lower temperatures, drier and higher climatic instability are likely to host larger-bodied bird and mammal species (Phillips & Heath, 1995; Brown *et al.*, 2004). This increase in body size is attributed to the organisms' reduced surface-to-volume ratio, which reduces heat and water losses improving survival and reproductive success, in accordance with Bergmann's rule (Phillips & Heath, 1995; Rapacciuolo *et al.*, 2017). Bergmann’s rule expresses that species tend to be larger in higher latitudes (closer to the poles) and smaller in lower latitudes (closer to the equator), mainly to mammals and birds (Rapacciuolo *et al.*, 2017). In contrast, there is a reverse latitudinal pattern of body size distribution to amphibians and squamates because larger-bodied species in higher temperatures have greater potential for heat gain (Ashton & Feldman, 2003; Olalla-Tarraga et al., 2006; Rapacciuolo *et al.*, 2017; see Table 1c). As a result, the conclusions of Bergmann's rule tend to be either ambiguous or limited, particularly in the case of some taxonomic groups such as ectotherms. This ambiguity arises due to the existence of either positive, negative, or nonlinear patterns in body size-latitude correlation, or sometimes no discernible pattern at all (Ashton & Feldman, 2003; Johnson et al., 2023; Meiri & Dayan, 2003; Rapacciuolo et al., 2017). This lack of generality may be caused by the fact that the body size is determined by multiple simultaneous pressures, which are linked with other traits such as body size variation and trophic level. Therefore, these distinct relationships between climate and body size within tetrapod groups might determine the indirect effect of climate on species richness through body size and the relationship between multiple traits (see Fig.1- (II)).

Additionally, the climate also might determine the species richness of a community through the body size variance in a community. For instance, studies suggest that colder and drier regions favor an evolutionary convergence to larger-bodied species due to climatic pressure acting as a stronger filter (Bothwell *et al.*, 2015; Rapacciuolo *et al.*, 2017; Read *et al.*, 2018; Table 1c). As a result, this convergence leads to increased niche overlap and competition, particularly among larger species that have higher energetic demands for food resources (Pawar, 2015; Hopwood *et al.*, 2016; Read *et al.*, 2018). Hence, the intensified competition driven by climate limits the coexistence of species, ultimately resulting in a reduction in species richness (Pawar, 2015; Hopwood et al., 2016; see Fig. 1 – (IV)).

In addition to altering the size structure, climate also has a significant impact on the trophic structure, which in turn can affect the number of species in a region. Based on food-web theory, precipitation also favors plant biomass, which might cascade up throughout the trophic chain, allowing the community to support a greater number of species at each trophic level (Hopwood *et al.*, 2016). As a result, precipitation can result in more bottom-heavy food-web pyramids (i.e., communities with higher biomass or species richness on lower trophic levels) with greater bottom-up control (Hatton *et al.*, 2015). Higher temperatures, on the other hand, increase activity time, food consumption rates, and reproductive rates, reducing abundance at lower trophic levels and favoring top-heavy chains (i.e., communities with higher biomass or species richness on higher trophic levels) and top-down control (Romero et al., 2018; Welti et al., 2020a; Danet et al., 2021; see Fig.1 - (III) and Table 1c). Additionally, predators are more sensitive to climate changes than primary consumers because they have a higher habitat requirement, in fact, previous evidence demonstrated that predator with larger bodies were extinct in greater proportion in regions with higher climatic instability since the Last Maximum Glacial (Voigt *et al.*, 2003; Sandel *et al.*, 2011). Consequently, regions with lower climatic instability are a refuge to predators, resulting in an imbalance in the predator-prey relationships, increasing the dominance of some predator species with larger body size and favoring top-heavy chains compared to regions with higher climatic instability. However, the bottom-up control generally has higher importance to determine species richness patterns at the macroscale than top-down control (Sandom *et al.*, 2013). Thus, communities with bottom-heavy chains tend to be more diverse than top-heavy chains at global scales (Sandom et al., 2013; Danet et al., 2021; Fig. 1 – (V)).

In this study, we seek to integrate macroecological theory with metabolic ecology and food web theories to explain the direct (climate -> species richness) and indirect (climate -> trait -> species richness) effects of the contemporary climate and climate instability on the global richness of tetrapods (Fig. S1). Specifically, we test the following predictions (detailed in Table 1):

(1) Warmer and rainier regions with lower climatic instability has greater species richness for all tetrapod groups than colder and drier regions with higher climatic instability; this relationship will be stronger in amphibians and squamates than in birds and mammals (Fig. 1 – (I)).

(2) Warmer and rainier regions with lower climatic instability has smaller birds and mammals, and larger amphibian and squamate species than colder and drier regions with higher climatic instability (Fig. 1 – (II)).

(3) Greater size variation and top-heavy pyramids of tetrapods are correlated with warmer and rainier regions with lower climatic instability (Fig. 1 – (III)).

(4) Warmer and rainier regions with lower climatic instability have an indirect, positive effect on species richness by favoring body size reduction and increasing size variation. In contrast, these climates favor top-heavy pyramids and indirectly reduce species richness (Fig. 1 – (VII) Unifying theories).

METHODS

Species distribution matrices

The distribution polygons for amphibians, birds, mammals, and squamates from the International Union for Conservation of Nature (IUCN, 2023) were utilized to calculate species richness per grid cell. We compiled the IUCN occurrence polygons for 15.788 tetrapod species containing 220 amphibians, 2.512 squamates, 7.949 birds, and 5.107 mammals. We standardized taxon-specific distribution polygons to the same spatial resolution and projection (i.e., Mollweide projection) to create 2° grids (i.e., ~220 km) covering all terrestrial ecosystems in the globe. Then, we extracted the number of species on each grid and used these grids as the sampling unit in statistical analysis. Hereafter, we will refer to the species found on each grid as a “community” because this scale encompasses all species that potentially live and interact (Fauth *et al.*, 1996).

Defining trophic structure and body size to calculate grid-scale trait information

To gain a more realistic understanding of how climate influences species richness, we focus on two key community-wide species traits: size structure and trophic structure. Community-wide species traits represent the average trait shared by multiple species within a community (Ibarra-Isassi *et al.*, 2023). These traits reflect physiological characteristics, ecological interactions, and resource utilization. The median body size provides insights into the physiological limits and energy requirements of species in relation to climate (Brown *et al.*, 2004). Additionally, body size variance captures the diverse range of body sizes within a community, facilitating niche differentiation and reducing competition for resources (Hopwood *et al.*, 2016). On the other hand, trophic structure considers the feeding relationships and positions of organisms within the food chain, influencing energy flow and species interactions (Voigt *et al.*, 2003; Brown *et al.*, 2004). By studying these traits, we can uncover the mechanisms through which climate impacts species richness, while considering the physiological and ecological dynamics associated with resource use and requirements.

We obtained the body size and diet of species using specialized databases for amphibians (Oliveira *et al.*, 2017), squamates (Feldman *et al.*, 2016; Meiri, 2018), birds (Wilman *et al.*, 2014), and mammals (Faurby *et al.*, 2018). We used the body mass in grams as a size measure that is comparable across all taxa because to each group the body size is measured in a different way. Thus, these databases considered: For amphibians, body size is the maximum adult body mass; for squamates is the conversion of snout–vent length (SVL) or total length (TL) to body mass by clade-specific allometric equations; for mammals, the body size is the mass in species level and, whilst in the absence of data, body mass was estimated based on morphological correlates or phylogenetic imputation; and for birds, body size is geometric mean of average values of body mass provided for both sexes or mass-length relationships parameterized at family level.

We used the “Taxize” package and expertise of each group to standardize the taxonomic names between the IUCN and traits databases (Foster *et al.*, 2018). After this, we removed species with missing information about body size and trophic level in traits databases. Our final occurrence database had 12.034 tetrapod species with trait information, corresponding to 76.2% of the IUCN database. Specifically, we used 178 amphibian species, 1.501 squamates, 6.607 birds, and 3.748 mammals in the analyses.

Body size was defined as the median value of body mass (in grams) of all species in a grid cell, whereas body size variation was calculated on each cell. The disparity in body sizes in a grid increases as body size variation increases. Additionally, we use the logarithm of median body size in the statistical models because body size has a skewed right distribution with higher predominance of lower body size species (Kozłowski & Gawelczyk, 2002).

We categorized species diets into three trophic levels to define the trophic structure at the community level: (i) primary consumers, which are represented by organisms that have more than 90% of their diet predominantly composed of leaves, flowers, seeds, and fruits; (ii) secondary consumers, representing organisms with a diet composed predominantly (>90%) of invertebrates and vertebrates; (iii) omnivores, organisms with a mixed diet without predominance of plant or animal components (<90%). After defining the trophic level of each species, we calculated trophic structure of communities across tetrapods group by estimating the predominance of higher trophic levels by grid and assigning a weight to each category: primary consumers received a weight of 2, omnivores 2.5, and secondary consumers 3 (Welti et al., 2020a,b). We defined this weight for each trophic level based on previous studies with N isotopes, which determine an intermediate position to omnivores relative to primary and secondary consumers (see Welti et al., 2020a,b). Furthermore, the trophic structure was estimated by the average trophic level weights of species of each tetrapod group that occur in each grid. Values close to 2 indicate a given grid has a bottom-heavy pyramid with greater dominance of herbivores, whereas values close to 3 reflect a top-heavy pyramid with greater dominance of predators and omnivores (McCauley *et al.*, 2018; Welti *et al.*, 2020a).

Species richness

We used the final occurrence data containing only species with traits information to calculate species richness per grid. The species richness was calculated by summing all species whose polygons intersect the center of each grid. We excluded grids with less than three species from statistical analyses to reduce the sampling bias. The final species matrix included 2,722 cells covering each tetrapod group distributed across all continents (from 54°S to 69°N and 161°W to 178°E, covering an area of ~13,353 km of latitude and ~37,629 km of longitude) (Fig. 2).

Environmental data

Climatic variables were extracted from WorldClim v.2.0 at a spatial resolution of 10 Arcmin (Fick & Hijmans, 2017). Initially, we created 2° grids to extract the contemporary annual mean temperature (Bio 1) and mean precipitation (Bio 12), using coordinates of grid centroids. Furthermore, we obtained each grid temperature and precipitation in the Last Glacial Maximum (~21,000 years BP) by using the MIROC-ESM model. Temperature and precipitation anomalies are characterized by the difference between actual mean temperature (Bio 1) and mean precipitation (Bio 12) and from historical annual mean temperature or precipitation of last glacial maximum (e.g., García-Andrade et al., 2021). When the difference between the current and historical values is close to zero, imply a lower temperature and precipitation anomaly, which indicates that the projected climatic change might be less pronounced or negligible in that region (Hortal *et al.*, 2011). We emphasize that despite the uncertainties linked to models of climate reconstruction, it has been demonstrated that the inclusion of paleoclimatic information is fundamental to understanding current macroecological patterns (Hortal et al., 2011; García-Andrade et al., 2021).

Composite variables

Composite variables are used to represent multivariate and complex theoretical concepts and their effect on response variables (Grace & Keeley, 2006; Santos *et al.*, 2020). As a result, combining multiple operational variables into a single conceptual variable in the model reduces the number of interactions which, in turn, prevents an inflated model and allows a better interpretation of the relationships between the composite variables and the response variable (Grace & Keeley, 2006; Santos *et al.*, 2020). We estimated the composite variables using a multiple regression between operational variables and response variables (see Appendix S1). Then, we multiplied the values of operational variables by their coefficient regression and summed them to estimate the values of composite variables to use in the structural models (Grace & Keeley, 2006).

We used three composite variables: (1) contemporary climate, which is represented by combining the contemporary temperature and precipitation, with higher values indicating warmer and wetter regions (Fig. S2); (2) climatic instability, which is composed of temperature and precipitation anomalies, with lower values representing regions with lower climatic variation since last maximum glacial; and (3) community-wide species traits, composed of body size, size variation, and trophic structure that have a unique relationship to each group (Fig. 3 and Fig. S3). As a result, the combined effect of the component operational variables on the response variable is represented by this new path through the composite variable: operational variables -> composite variable -> response variable). For example, the effect of contemporary temperature and precipitation on species richness is represented by the effect of a unique composite variable (i.e., contemporary climate) on the number of species.

Statistical analyses

We used the piecewise Structural Equation Model (pSEM) to test how community-wide species traits mediate the effects of contemporary climate averages and climate instability on species richness of each tetrapod group. Thus, we performed a pSEM containing the composite variables based on the theoretical model (Fig. S1). We used separate pSEM in the following subgroups: birds, mammals, amphibians, and squamates. Before running the final pSEM model, we excluded the variables that were highly correlated ($r > 0.7$) based on the models with the lower Akaike Information Criterion (AIC) (see Fig. S2 and Appendix S1).

The pSEM models enable for the simultaneous testing of multiple hypotheses in which the variables act as response and explanatory variables, allowing for the partitioning of the total effects of the variables into direct (i.e., the relationship is not explained by another variable) and indirect effects (i.e., the relationship is explained by another variable) (Lefcheck, 2016). We defined contemporary climate (temperature and precipitation averages) and climate instability (temperature and precipitation anomaly) as exogenous variables, while community-wide species traits act as endogenous variables to explain tetrapod richness; species richness can be directly affected by exogenous variables or indirectly by factoring out the link between exogenous and endogenous variables (Fig. S1). This model also allows the inclusion of the correlation between endogenous variables.

Furthermore, each pSEM was composed of four ordinary least squares (OLS) that assess: (1) effects of contemporary climate, climate instability, and community-wide species traits per grid on tetrapod species richness; (2) effects of contemporary climate and climate instability on the (a) trophic structure, (b) on species body size, and (c) on species size variation. In addition, we also considered the correlation between body size, size variation, and trophic structure on composite variable community-wide species traits (see Appendix 1). We also performed a “Distance-based Moran's eigenvector analysis” to obtain the eigenvectors (MEMs) representing the shortest distance connecting the locations with the highest autocorrelation (Dray *et al.*, 2012). By including the MEMs in the models, we were able to explicitly estimate the effects of the spatial autocorrelation on the results. We first performed the OLS analysis for each response variable. Then, we extracted the residuals to select the MEMs to be added in each model, thus we minimized the autocorrelation in the residuals (MIR method- Bauman et al. 2018). Later, we used OLS adding the spatial vectors (MEMs) to evaluate the spatial autocorrelation of each model with Moran’s I that presented values lower than 0.8 (Table S1). Thus, we deal with the trade-off between minimizing spatial autocorrelation and inflating the model by including a greater number of eigenvectors (Lefcheck, 2016; Santos *et al.*, 2020). Although there is still autocorrelation in the models, we have minimized the effect of spatial autocorrelation on variables that are highly spatially structured. Finally, we used the four OLS models adding selected MEMs as structural models of our pSEM to each tetrapod group. The pSEM was performed using the R "piecewiseSEM" package (Lefcheck, 2016). All analyzes were performed using the R 3.5 software (R Core Team, 2019).

The strength and direction of direct and indirect effects were interpreted based on the standardized effect size of each link between two variables. The indirect effects of the exogenous variables were obtained from the multiplication of the direct effects (Lefcheck, 2016; García-Andrade *et al.*, 2021). To understand the role of contemporary climate, climate instability, and community-wide species traits on species richness, we summed the direct and indirect effects of each variable to individually obtain each total effect (see Appendix 1). However, we point that the random variation attributed to species traits variables may be a result of phylogenetic relatedness, but because our analyses are conducted at the assemblage-level, this effect is reduced, although species traits do exhibit some phylogenetic signal.

RESULTS

We found a latitudinal pattern in the distribution of species and traits of tetrapods, with regions closer to the equator (e.i., regions with higher contemporary climate and lower climate instability, see Fig. S4) having more species, more variation in body size, and species with smaller body sizes than those farther away from the equator (Fig. 2 a-c). For example, moving from 10° of latitude to the equator increases the average species richness and body size variation, respectively, by 9.7% and 0.3%, and decreases body size by 2.2% for all tetrapods. However, there is no clear latitudinal pattern in trophic structure, suggesting a similar proportion of primary consumers, secondary consumers, and omnivores in tropical and temperate regions (Fig. 2d).

Although the latitudinal pattern of species richness is similar for all groups, there are distinct patterns to traits across tetrapod groups (Fig. S5). Specifically, birds and mammals tend to be smaller, while squamates are larger. In these groups, there is also higher size variation next to the equator and has no clear latitudinal pattern to trophic structure. On the other hand, the amphibians have no clear pattern to body size and size variation but tend to have more top-heavy structures on temperate regions. We also could observe that there is predominance of omnivores to birds and mammals, but the secondary consumers are predominant to amphibians and squamates (Fig. S6). Thus, bird and mammal communities tend to be more bottom-heavy than amphibians and squamates communities.

Contemporary climate, climate instability, and community-wide species traits explained, on average, 69% of the variation in species richness to each tetrapod group (details of each model on Table S1). The contemporary climate (temperature and precipitation average) and climate instability (temperature and precipitation anomaly) showed a positive relationship with species richness to mammals and amphibians, but only to contemporary climate is related to bird and squamate species richness. Still, this effect was stronger in amphibians and squamates (Fig. 3a-d). We also found a positive correlation between community-wide species traits with species richness for all groups, except for amphibians. In addition, communities with higher species richness are mostly associated with smaller bodies and more bottom-heavy structures in birds and smaller bodies in mammals and squamates. Thus, we showed distinct routes in which contemporary climate and climate instability affect species richness through the community-wide species traits.

Direct effects of climate on species richness

We observed that regions with higher temperature, precipitation, and higher climatic instability have more tetrapod species (Table S2). However, the contemporary climate and climate instability have different relative importance to each group (Figs. 3, 4). Bird and mammal richness response to contemporary climate and climate instability is comparatively lower than that of amphibians and squamates. Nonetheless, bird and squamate species richness is only affected by contemporary climate, while amphibians and mammals are determined by both contemporary climate and climate instability. More specifically, contemporary climate and climate instability have similar importance to mammals, but amphibians species richness is mostly influenced by climate instability (Table S2).

Correlation between climate and community-wide species traits

Likewise, contemporary climate and climate instability affected species richness and community-wide species traits, but their relative importance varied among tetrapod groups (Figs. 3, 4). Warmer and rainy regions have bird species with larger body sizes (standardized β= 0.14) and less size variation (standardized β= -0.58) than in colder and drier regions. Additionally, higher climatic instability has species with higher body sizes (standardized β= 0.29) and less body variation (standardized β= -0.44) (Figs. 3a and 5). Thus, the contemporary climate and climate instability acting in a synergistic way to favor larger-bodied birds and lower size variation in warmer, wetter, and higher climatic instability. Nevertheless, contemporary climate is the main drive to body size, while climate instability determines the body size variation (Table S2). Moreover, climate instability is the only determinant of the trophic structure, favoring bottom-heavy pyramids in birds in higher climatic instability (β climate instability = -0.12, $p < 0.001$, Figs. 3a and 5, Table S2).

For mammals, we demonstrated that the contemporary climate and climate instability have a combined effect on body size and trophic structure (Figs. 3b and 5). Warmer and rainier regions with higher climatic instability have mammal species with smaller bodies, lower body size variance, and top-heavy pyramids (Table S2). The contemporary climate (i.e., temperature and precipitation average) and climate instability has a similar negative effect on body size. Conversely, the influence of climate instability on body size variation and the trophic structure is around 2.8 times stronger than the contemporary climate (Table S2). Thus, climate instability outperforms the contemporary climate as a global driver of trophic structure and body size variation of mammals, while contemporary climate and climate instability has similar importance to determine the body size of mammals.

In warm and wetter regions with higher climatic instability, the squamate communities have top-heavy pyramids, larger species, and higher size variation. Furthermore, contemporary climate and climate instability act synergistically favoring this size and trophic structure on squamates (Fig. 3c). However, the contemporary climate is the primary driver of body size and size variation, although it has similar importance to climate instability in determining trophic structure (Table S2). Finally, we find that community-wide species traits of amphibians are less influenced by climate than other tetrapods, with their body size variance being the only dependent variable influenced by climate (Figs. 3 and 5, Table S2). The increase in temperature, humidity, and climate instability favors more body size variance in amphibians (Fig. 3d).

Climate plays a role in the correlation between species richness and community-wide species trait

We found that community-wide species traits were correlated with higher species richness, but the strength and way of this relationship varied among tetrapod groups. For example, the species richness of birds is favored by community-wide species traits around four times more than that of other tetrapod groups. Therefore, smaller-bodied species and bottom-heavy structures are likely to be associated with higher species richness (Fig. S3). In similar ways, squamate communities with smaller species tend to have greater richness, but mammal species richness is favored mainly by top-heavy structures. However, the direct route between species traits (body size and trophic structure) at the community level did not influence the number of amphibian species. Therefore, despite the community-wide species traits favoring species richness on birds, mammals, and squamates, these groups have distinct size and trophic structure.

We demonstrated that the contemporary climate and climate instability indirectly reduce the bird and mammal richness through community-wide species traits. Notably, these indirect pathways differ between birds and mammals communities (Fig. 4). We found that warmer, wetter climates and higher climatic instability indirectly reduce the bird species richness because they favor similar size between the species and bottom-heavy communities. However, these climates have a weak positive effect on bird species richness through increasing the body size. About mammals, we showed that indirect reduction in species richness occurs due to the stronger effect of reduction on body size and size variation by contemporary climate and climate instability, despite a top-heavy structure indirectly favoring species richness.

On the one hand, we found that the contemporary climate and climate instability indirectly increases the species richness through community-wide species traits in squamates and it has no effect on amphibians (Fig. 4). On squamates communities, higher contemporary climate and climate instability favor larger-bodied species, higher size variation, and top-heavy structures, consequently, indirectly increasing the species richness. Furthermore, body size, size variation, and trophic structure are mediators of the contemporary climate and climate instability effects on birds, mammals, and squamates, but they have no indirect effect on amphibian species richness.

DISCUSSION

Our study is the first one demonstrating that community-wide species traits mediate the effects of contemporary climate and climate instability on global species richness, which emphasizes the importance of integrating climate-based hypotheses into a more mechanistic framework in macroecology (Baiser *et al.*, 2019; McGill, 2019). We first predicted that warmer and rainier regions with lower climatic instability have greater species richness for all tetrapod groups, but the climate effect could be stronger in amphibians and squamates than in birds and mammals. As expected, warmer and wetter regions have greater species richness for all tetrapod groups. However, we revealed that regions with higher climatic instability generally have higher species richness of mammals and amphibians. We also found that amphibians and squamates species richness are more affected by contemporary climate and climate instability than birds and mammals, supporting our prediction 1. Moreover, we observed that different traits at the community scale determine the response of tetrapod groups to contemporary climate and climate instability. More specifically, smaller mammals, larger squamates, and birds were associated with warmer and wetter climates with lower climatic instability. However, the body size of amphibians did not correlate with climate. This outcome contradicts our prediction 2 for birds but supports it for mammals and squamates. Additionally, in these regions, birds and mammals exhibit similarity in body size. However, there is lower similarity in body size for squamates and amphibians. This result is partially in line with our third prediction. Top-heavy pyramids for mammals and squamates are more favored in warmer and wetter climates with lower climatic instability, whereas bottom-heavy pyramids for birds are more prevalent. Finally, we showed that contemporary climate and climate instability on species richness through community-wide species traits have distinct direction, strength, and route to all tetrapod groups, except amphibians that there is no indirect effect. The observed pattern may be explained by limited data availability, which highlights the importance of further research. Therefore, it is urgent that a new investigation is performed to better understand the relationship between climate, traits, and amphibian biodiversity (see, e.g., Guirguis et al. 2023).

Direct effects of climate on tetrapod richness

Species richness of all tetrapod groups respond to contemporary climate, but only mammals and amphibian species richness directly respond to climate instability. Overall, regions with higher temperatures present greater thermal and kinetic energy resulting in higher speciation rates, whereas higher rainfall is associated with greater resource availability, allowing larger populations and lower extinction rates (Brown *et al.*, 2004; Gillman & Wright, 2014). These results support the metabolic theory, which predicts warmer and wetter regions have greater species richness due to higher resource and energy availability, and consequently, greater survival under these conditions (Brown *et al.*, 2004; Currie *et al.*, 2004; O'Brien, 2006).

On the other hand, contrary to expected, we found that regions with higher climatic instability tend to be more diverse than regions with lower climatic instability to mammals and amphibians, while birds and squamates are unaffected by climate instability. These regions with higher climatic instability tend to promote new habitats or expand existing ones, becoming certain areas suitable for new species, and promote evolutionary adaptation and speciation to better adapt to the new environment increasing the species richness (Carnaval *et al.*, 2009; Rangel *et al.*, 2018). This result aligns with the hypothesis of ecological opportunity demonstrating how climatic instability can create opportunities for rapid speciation allowing a better understanding of the evolution of the latitudinal gradient (see Schluter, 2016). Thus, climate instability can favor higher species richness through the creation of new habitats, the promotion of evolutionary adaptation, and speciation that could cause significant changes on latitudinal patterns over time. These results contradict the prevailing hypothesis of climate stability, which suggests that regions with lower climate instability harbor more diversity due to reduced extinction rates and increased speciation (Fine, 2015). This difference between our findings and previous studies may be explained by two reasons: first, most studies did not directly assess climate instability or do not assess it simultaneously with the contemporary climate.

The bird and mammal species richness showed a response weaker to the contemporary climate and climate instability compared to squamates and amphibians, thereby lending support there are asymmetric relationship of climate and global species richness between ectotherms and endotherms (Marin *et al.*, 2018; Barreto *et al.*, 2021). The greatest response of squamates and amphibians richness to climate may be related to a narrow thermotolerance range and lower dispersal ability compared to mammals and birds, which results in a higher geographical turnover (Buckley *et al.*, 2012; Ficetola *et al.*, 2021). Moreover, we found that climate instability is a better predictor than contemporary climate to amphibians and both climates has similar strength to mammals, while the contemporary climate is the unique predictor to birds and squamates. Importantly, as current macroecological theory frequently uses patterns observed in endotherms to generalize to ectotherms (see Pincheira-Donoso et al., 2021), our findings demonstrate that endotherms and ectotherms have distinct macroecological patterns and provide an enhanced mechanism for explain the macroecology of ectotherms. In addition, our results reinforce the importance of climate instability to predict the species richness mainly of bad-disperser and narrow-ranging groups (Araújo *et al.*, 2008). For example, birds' higher dispersal capacity allows them to move between regions and track appropriate climates to avoid climate changes (Jetz *et al.*, 2007; Buckley *et al.*, 2012; Ficetola *et al.*, 2021). In contrast, mammals and amphibians are more constrained by geographical barriers, making them the most sensitive tetrapod to climate instability (Ficetola *et al.*, 2021). Additionally, squamates have a narrow term tolerance and low dispersal capacity than birds might also become constrained by geographic barriers due to the similarity of their response to that of amphibians (Buckley et al., 2012; Araujo et al., 2013). Taken together, these results emphasize the importance of ecological traits (e.g., body size and dispersal ability) and metabolic factors (e.g., heat tolerance) to understand the correlation between climate instability and species richness patterns at the global scale.

Correlations between climate and community-wide species traits improve predictions of species richness at large scales

We found that the contemporary climate and climate instability have different correlation patterns with size structure (i.e., median and variance) of tetrapods. Thus, warmer and wetter climates with higher climatic instability have smaller mammals, but larger squamates and birds, than colder and drier regions. However, they do not affect amphibian's body size. Our findings support the Bergmann's rule for mammals (Meiri & Dayan, 2003), the reverse pattern for squamates (Ashton & Feldman, 2003), no support for amphibians (Adams & Church, 2008; Johnson et al., 2023), although it is opposite the expected pattern for birds (Meiri & Dayan, 2003; Salewski & Watt, 2017). These nuances of Bergmann's rule are highly debated and other explanations for Bergmann-type clines, like precipitation, primary plant productivity, trophic level and competition have a key role acting simultaneously with temperature to determine the latitudinal body size pattern (Alhajeri & Steppan, 2016; Hantak et al., 2021). Furthermore, the contrasting result observed in birds may stem from the possibility that previous studies did not account multiple climatic variables and traits, including body size variation and trophic structure. This could lead to a bias in assessing the effect of climate on body size. Moreover, we showed that higher contemporary climate (i.e, higher temperature and precipitation) on lower latitudes are correlated with larger birds, but similar body size, and predominance of lower trophic levels. We also highlight that the use of only the mean or median of body size is limited, because the mean is biased due to the influence of extreme values that are more present at lower latitudes because of higher body size variation (Fig. 2c). Moreover, the use of only the median of body size reduces the influence of extreme values but does not represent the variation in body size of the species. Furthermore, we reinforce the importance of simultaneous use of the median and variation of body size (i.e., size structure) to allow an unbiased and mechanistic understanding of the response of the community to climate (see Appendix S2).

The decrease of body size of mammals in regions with lower climatic instability could be due to smaller species being able to withstand climate change for longer periods than larger species, as expected by the metabolic theory (Gardner *et al.*, 2011; Peralta-Maraver & Rezende, 2021). Previous studies have shown that larger species are more affected by the warming climate than smaller species, mainly via changes in the length of their reproductive or feeding season (Gardner *et al.*, 2011). However, we also found that birds and squamates tend to be larger bodied in regions with lower climatic instability that due these groups have different dispersal abilities and physiological tolerance. For instance, birds that are better at dispersing than other tetrapod groups could have their body size more determined by higher resource availability on regions with lower climatic instability than climatic tolerance (Ficetola *et al.*, 2021). Nonetheless, the larger-bodied squamates in regions with lower climatic instability could be due higher climatic tolerance of ectotherms than allow higher survival to climatic changes (Buckley *et al.*, 2012; Ficetola *et al.*, 2021). Moreover, we also found that these relationships between climate and body size indirectly favor higher species richness in communities with smaller mammals, and larger birds and squamates, supporting the “species packing” hypothesis (Ritchie & Olff, 1999). This hypothesis predicts that smaller species require lower resources and space, and may have lower specialized ecological requirements, consequently, allowing higher coexistence in a given area (Ritchie & Olff, 1999). Furthermore, the negative relationship between body size and richness suggests that climatic-mediated reductions in species body size favor resource partitioning, which drives macroecological diversity patterns.

Contrary to our expectations, birds and mammals have lower size variations in warmer and wetter climates with higher climatic instability, consequently decreasing the species richness. Higher temperatures and precipitation may reduce the interspecific competition of birds and mammals due to greater food availability allowing similar-sized species to coexist (Buckley *et al.*, 2012; Hopwood *et al.*, 2016). Additionally, bodies tend to converge to a similar size in higher climatic instability climates, increasing the survival rate (Phillips & Heath, 1995; Araújo *et al.*, 2013). However, the relevant climate variables driving size variation are distinct between birds and mammals. The contemporary climate is the main determinant of bird size variation, while climate instability is more important to mammals. This distinct importance of contemporary climate and climate instability can result from the lower dispersal ability of mammals than birds to avoid climate instability (Ficetola *et al.*, 2021). Moreover, we found that this reduction of size variation by contemporary climate and climate instability has indirectly reduced the species richness of birds and mammals. This reduction of species richness occurs due higher similarity of body size increasing the niche overlap and competition, consequently, reducing the number of coexisting species (Hopwood *et al.*, 2016).

We found that warmer and wetter regions have a remarkable squamate and amphibian size variation and these regions have higher coexistence of species. In warmer regions, squamate and amphibian species experience higher competition due to elevated temperatures favoring more time activity and larger species, but the simultaneous presence of higher precipitation increases availability of resources (Buckley *et al.*, 2012; Hopwood *et al.*, 2016). To squamates, the higher size variation could be linked to occupying distinct niches, accessing underutilized resources, and reducing competition intensity. Additionally, we also found that warmer and wetter climates with lower climatic instability are indirectly associated with increased squamate species richness through higher size variation. Thus, these results show that greater size variation to avoid competition is a primary drive to favor the species richness, despite that it is expected a higher interspecific competition reducing coexistence on squamate (Buckley *et al.*, 2012; Peralta-Maraver & Rezende, 2021). On the other hand, despite the climate favoring the size variation on amphibians, there is no effect on species richness. This absence of effect could be due to narrow variance of body size and predominance of predators on amphibian communities.

Lastly, the contemporary climate and climate instability are correlated with top-heavy pyramids to mammals and squamates but bottom-heavy to birds. Warmer and wetter regions feature pyramids of mammals and squamates that tend to be top-heavy, as predicted by the food-web theory (Welti *et al.*, 2020a). Despite corroborating this to mammals and squamates, we found no correlation between climate and trophic structure of amphibians that suggests this trend described in literature may be a bias of change on other variables, such as the variance in body size that favor top-heavy pyramids when have lower size variation. Moreover, the association between higher climatic instability climates and top-heavy pyramids of mammals and squamates may be due to decreasing plant abundance since the last glacial maximum, which reduces resource availability mainly to herbivores than omnivores and predators (McCauley *et al.*, 2018). We found that top-heavy pyramids tend to have lower bird species richness but, contrary to expectations, have greater mammal and squamates species richness. To birds, these results support the hypothesis that the top-heavy trophic structure has lower species richness due to greater predation force that reduces the species abundance and consequently, species richness in lower trophic levels (Brown *et al.*, 2004; Romero *et al.*, 2018; Welti *et al.*, 2020a). However, the increase of mammal and squamate species richness in top-heavy pyramids can be due to these groups having the main predators or higher abundance of predatory species, consequently, have higher top-down control reducing the dominance of some herbivore species (Estes *et al.*, 2011). Furthermore, we showed that warmer and wetter climates with higher climatic instability reduce bird species richness but favors mammal and squamate species richness through top-heavy pyramids.

CONCLUSION

In this study, we provided a macroecological synthesis that integrates multiple hypotheses linking direct and indirect pathways by which contemporary climate and climate instability determine in complex and different ways the global distribution of birds, mammals, amphibians, and squamates. We provide a more detailed and mechanistic explanation supporting that endotherms and ectotherms have distinct macroecological patterns and response to climate, each influenced by different traits, allowing a better understanding of the current pattern of species distribution and the refinement of the risk of extinction due to climate change. Although the contemporary climate directly determines the species richness of all tetrapod groups, climate instability only influences bird and squamate species richness through community-wide species traits. Additionally, we showed that contemporary climate and instability indirectly affect all tetrapod species richness, except amphibians, by altering body size and trophic structure. Thus, we demonstrated that species traits can explain the asymmetric responses of tetrapod species to climate. Likewise, macroecological studies using traits at the community scale may be benefitted by using different trait facets such as size structure and multiple traits averages. Our findings demonstrate that unifying multiple theories improves our knowledge of large-scale diversity patterns across taxonomic groups by allowing us to make realistic and mechanistic predictions, which can improve macroecological theory.

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Data availability statement: All data and script are provided in submission as a supporting information and deposited on https://doi.org/10.5061/dryad.bzkh189f0. All data also can acess by this github.

FIGURES CAPTIONS

Figure 1. Conceptual framework containing predictions to each separate theory and predictions integrating the theories to the asymmetric response by tetrapods to climate.

Figure 2. Latitudinal pattern of tetrapod (A) species richness, (B) body size, (C) body size variance, and (D) predominance of higher trophic levels.

Figure 3. Structural model of piecewise Structural Equation Model (pSEM) showing the relationship between the predictor and response variables emphasizing the direction and effect size on species richness to each tetrapod group. We represented only those significant relationships ($p < 0.05$). The blue and red colors represent, respectively, positive and negative relationships between the variables.

Figure 4. Effect size of composite variables (i.e., contemporary climate, climate instability, and species traits) on species richness of each tetrapod group. Fill color represents positive (blue) and negative (red) relationships between variables and circle size represents the strength of these relationships (standardize estimates).

Figure 5. Effect size of composite variables (i.e., contemporary climate and climate instability) on species traits that compose the composite variable species traits of each taxon (i.e., body size, body size variance and trophic structure). Fill color represents positive (blue) and negative (red) relationships between variables and circle size represents the strength of these relationships.

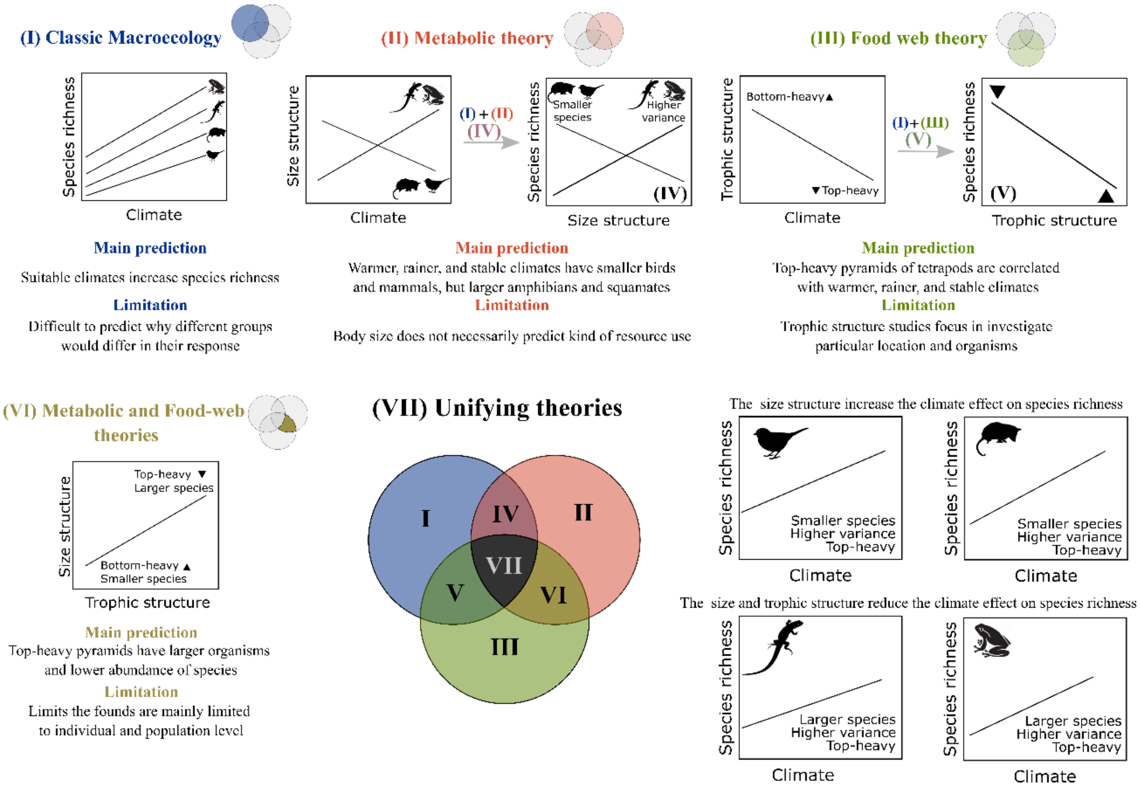

(I) Classic Macroecology
Species richness
Climate
Main prediction
Suitable climates increase species richness
Limitation
Difficult to predict why different groups would differ in their response
(II) Metabolic theory
Size structure
Climate
(I) + (II)
(IV)
Species richness
Smaller species
Higher variance
(IV)
Size structure
Main prediction
Warmer, rainer, and stable climates have smaller birds and mammals, but larger amphibians and squamates
Limitation
Body size does not necessarily predict kind of resource use
(III) Food web theory
Trophic structure
Bottom-heavy ▲
▼Top-heavy
Climate
(I)+(III)
(V)
Species richness
▼
(V)
▲
Trophic structure
Main prediction
Top-heavy pyramids of tetrapods are correlated with warmer, rainer, and stable climates
Limitation
Trophic structure studies focus in investigate particular location and organisms
(VI) Metabolic and Food-web theories
Size structure
Top-heavy ▼
Larger species
Bottom-heavy ▲
Smaller species
Trophic structure
Main prediction
Top-heavy pyramids have larger organisms and lower abundance of species
Limitation
Limits the founds are mainly limited to individual and population level
(VII) Unifying theories
I
IV
II
VII
V
VI
III
The size structure increase the climate effect on species richness
Species richness
Smaller species
Higher variance
Top-heavy
Climate
Species richness
Smaller species
Higher variance
Top-heavy
Climate
The size and trophic structure reduce the climate effect on species richness
Species richness
Larger species
Higher variance
Top-heavy
Climate
Species richness
Larger species
Higher variance
Top-heavy
Climate

Figure 1

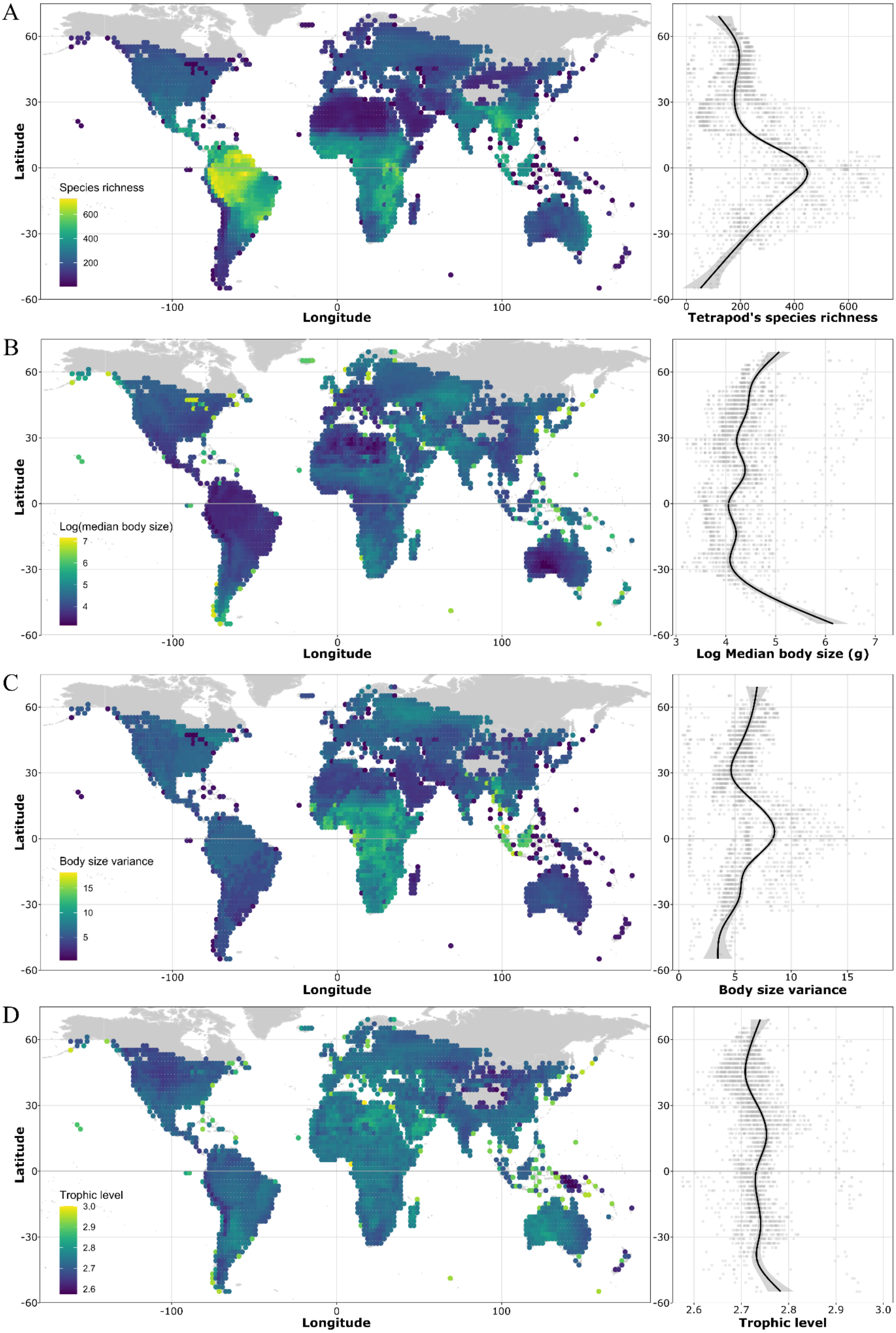

A
Species richness
600
400
200
Tetrapod's species richness
B
Log(median body size)
7
6
5
4
Log Median body size (g)
C
Body size variance
15
10
5
Body size variance
D
Trophic level
3.0
2.9
2.8
2.7
2.6
Trophic level
Latitude
60
30
0
-30
-60
Longitude
-100
0
100

Figure 2

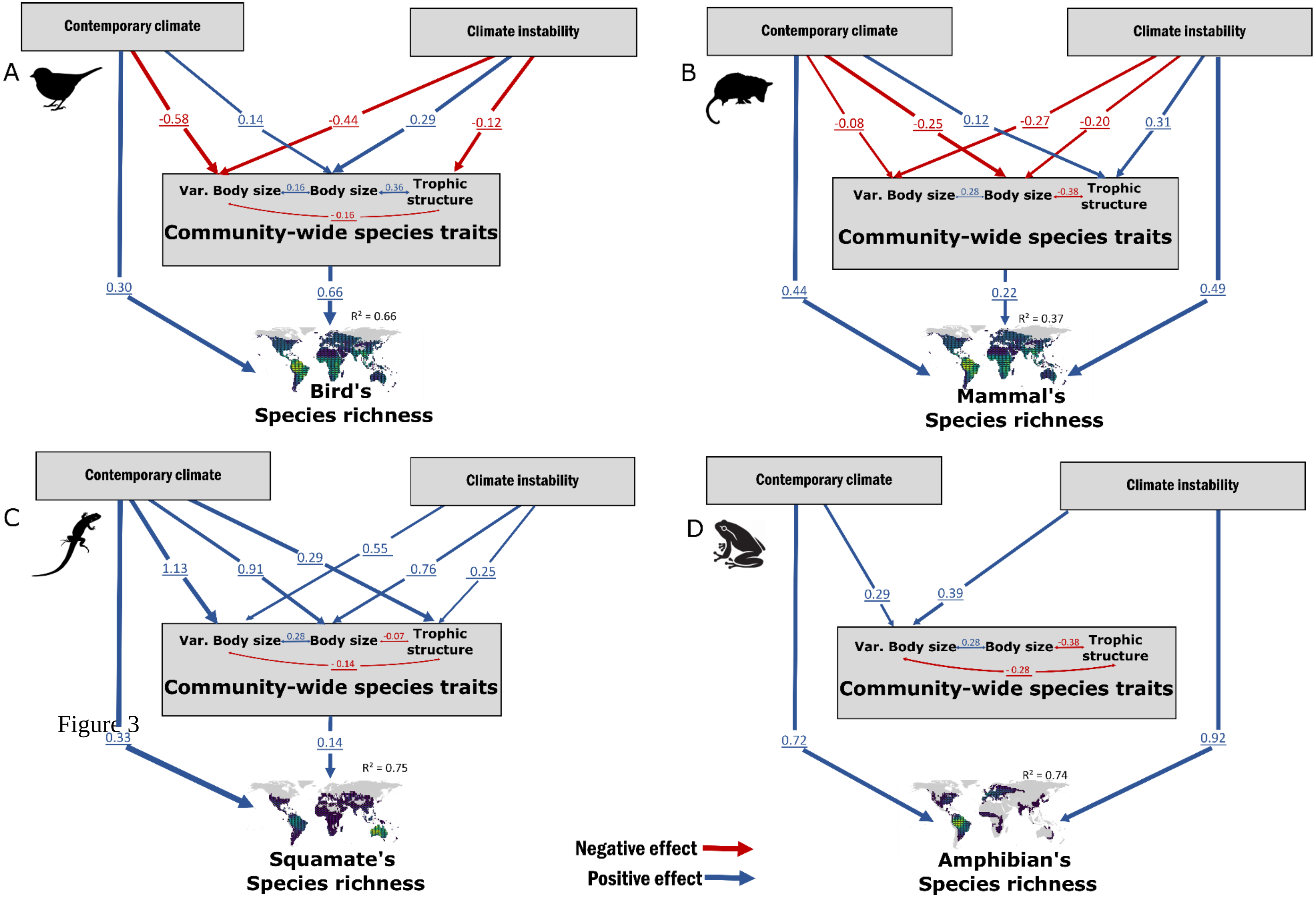

A
Contemporary climate
Climate instability
-0.58
0.14
-0.44
0.29
-0.12
Var. Body size
0.16
Body size
0.36
Trophic structure
-0.16
Community-wide species traits
0.30
0.66
R² = 0.66
Bird's Species richness
B
Contemporary climate
Climate instability
-0.08
-0.25
0.12
-0.27
-0.20
0.31
Var. Body size
0.28
Body size
-0.38
Trophic structure
Community-wide species traits
0.44
0.22
0.49
R² = 0.37
Mammal's Species richness
C
Contemporary climate
Climate instability
1.13
0.91
0.29
0.55
0.76
0.25
Var. Body size
0.28
Body size
-0.07
Trophic structure
-0.14
Community-wide species traits
0.33
0.14
R² = 0.75
Squamate's Species richness
D
Contemporary climate
Climate instability
0.29
0.39
Var. Body size
0.28
Body size
-0.38
Trophic structure
-0.28
Community-wide species traits
0.72
0.92
R² = 0.74
Amphibian's Species richness
Negative effect
Positive effect

Figure 3

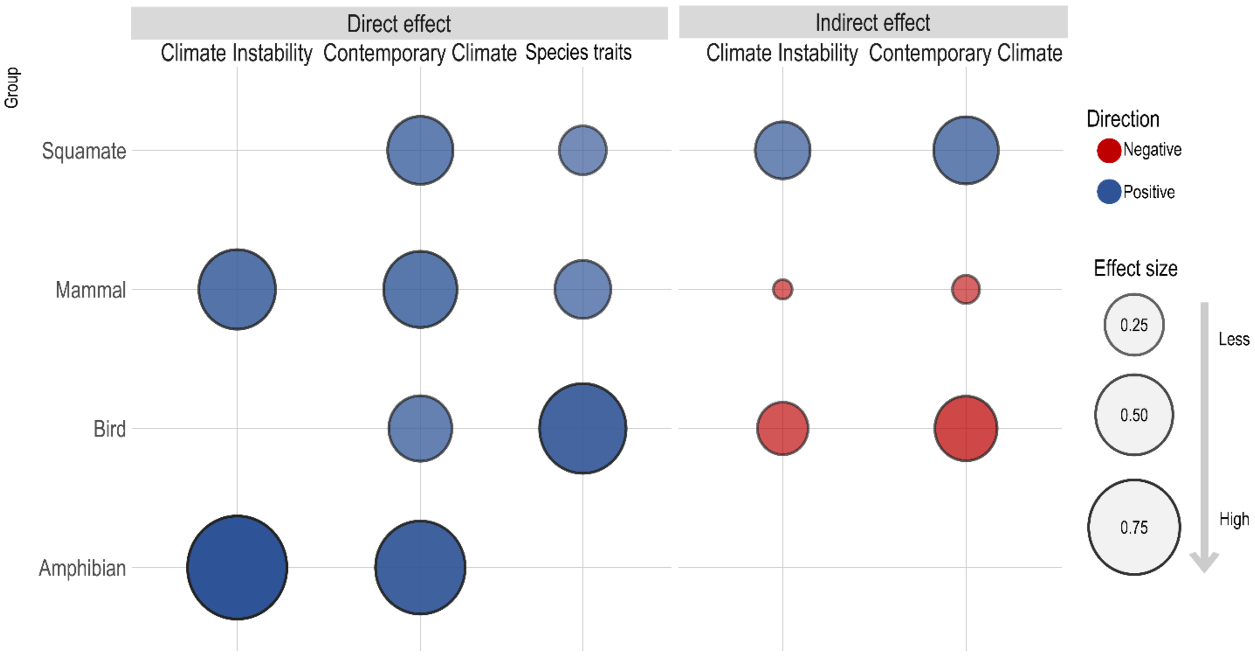

Direct effect
Indirect effect
Climate Instability
Contemporary Climate
Species traits
Climate Instability
Contemporary Climate
Group
Squamate
Mammal
Bird
Amphibian
Direction
Negative
Positive
Effect size
0.25
0.50
0.75
Less
High

Figure 4

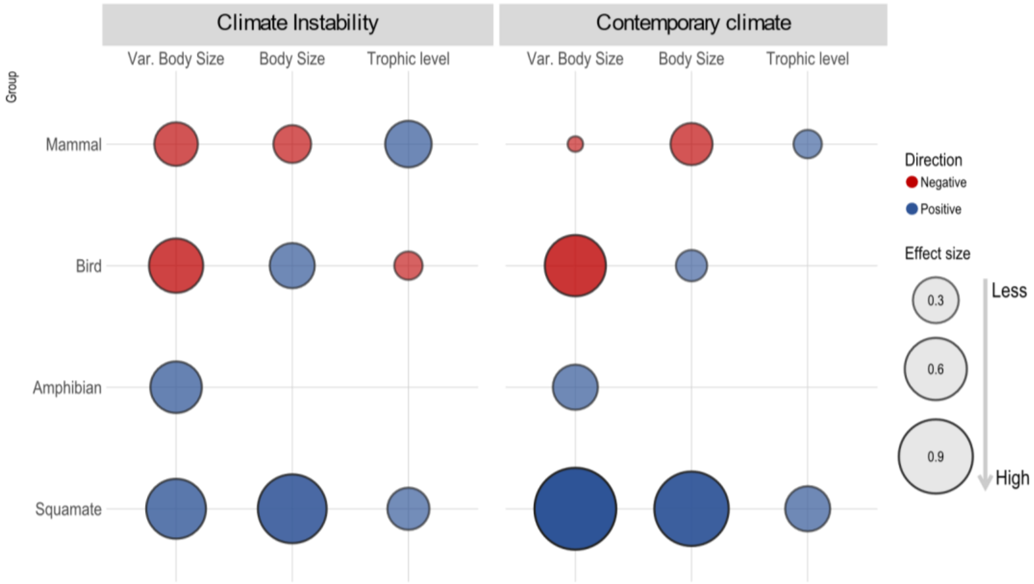

Climate Instability
Contemporary climate
Var. Body Size
Body Size
Trophic level
Var. Body Size
Body Size
Trophic level
Group
Mammal
Bird
Amphibian
Squamate
Direction
Negative
Positive
Effect size
0.3
0.6
0.9
Less
High

Figure 5

TABLE CAPTIONS

Table 1. The assumptions and predictions of effect of theoretical variables and its respective predictor variables on tetrapod species richness.

Theoretical variable	Predictor Variable	Premises	Predictions
a) Contemporary climate	Temperature	Temperature is positively linked to increased energy availability, favoring diversification and the number of coexisting species (Clarke & Gaston, 2006; Gillman & Wright, 2014; Fig.1 – (I) Classic macroecology). Furthermore, increasing temperature decreases the average size of species because smaller bodies have a reduced heat loss (Phillips & Heath, 1995). The temperature tends to reduce the variance of body size favoring an evolutionary convergence among coexisting species to increase the survival rate (Araújo et al., 2013; Rapacciuolo et al., 2017; Fig.1 – (II) Metabolic theory). Lastly, warmer climates have higher energy availability allowing more species of higher trophic levels favoring top-heavy pyramids (Danet et al., 2021; Fig.1 – (III) Food web theory).	Higher temperature favors tetrapod species richness and positive indirect effects on species richness by reducing body size and size variation. Moreover, temperatures reduce species richness indirectly by decreasing size variation and increasing the presence of higher trophic levels (see community-wide species traits).
	Precipitation	Precipitation is linked to increased numbers of individuals, which increase diversification rate, and ultimately favoring species diversity (Tieleman et al., 2003; Gillman et al., 2015; Fig.1 – (I) Classic macroecology). Wetter climates have more resource availability favoring larger species, and higher body size variance which, in turn, increases the number of species at each trophic level (bottom-heavy pyramids) due to greater niche availability (Hopwood	Precipitation may have a direct and positive effect on tetrapod species richness and may also have a negative indirect effect through body size and a positive indirect effect by size variation and trophic structure (see community-wide species traits).

		et al., 2016; Fig.1 – (II) Metabolic theory and (III) Food web theory).	
b) Climate instability	Temperature anomaly	Higher temperature anomaly may be associated with a less diverse community due to a lower speciation rate and higher extinction rate (Hortal et al., 2011; Fig.1 – (I) Classic macroecology). These communities have larger species that are highly resistant to climatic anomaly, which favors convergence of body size (Buckley et al., 2012; Hopwood et al., 2016; Fig.1 – (II) Metabolic theory). On the other hand, food-web theory shows that predators are more sensitive to climatic anomalies, so higher temperature anomalies can decline the number of species of higher trophic level (Voigt et al., 2003; Fig.1 – (III) Food web theory).	Temperature anomalies decrease tetrapod species richness. Higher temperature anomalies reduce species richness indirectly through body size and variation in body size. Conversely, temperature anomalies indirectly increase species richness by decreasing the presence of species from higher trophic levels.
	Precipitation anomaly	Reduced precipitation anomaly is linked to lower productivity and higher water stress, which leads to a reduction in the number of individuals and species (Araújo et al., 2008; Fig.1 – (I) Classic macroecology). There is an evolutionary trend toward larger species that support conditions with water stress and there is reduction of body size variance (Tieleman et al., 2003; Peralta-Maraver & Rezende, 2021; Fig.1 – (II) Metabolic theory). Another effect of lower precipitation anomaly is that the reduction in resources reduces predator species through a bottom-up effect (Voigt et al., 2003; Clarke & Gaston, 2006; Fig.1 – (III) Food web theory).	Higher precipitation anomalies reduce tetrapod species richness. Precipitation anomalies reduce species richness indirectly by favoring larger species and reducing body size variance. Precipitation anomalies, on the other hand, increase species richness by reducing higher trophic level species.

c) Community-wide species traits	Body size	Regions dominated with larger species have a smaller number of individuals per species which, in turn, decreases species richness (Evans *et al.*, 2005). Furthermore, due to higher species requiring more energy, the energy available to support a greater number of trophic levels is reduced (Brown *et al.*, 2004; Evans *et al.*, 2005).	Larger body size directly reduces tetrapod species richness. Moreover, regions dominated with larger species have fewer species richness of predators and omnivores.
	Body size variance	Body size variance reduces interspecific competition due possibly best division of the niche, resulting in greater species coexistence (Evans et al., 2005; Fig.1 – (I) + (III)). This lower competition allows higher species richness and trophic levels.	Body size variance may directly increase tetrapod species richness. Moreover, higher body size variance favors bottom-heavy pyramids.
	Trophic structure	The energy demand is proportional to the trophic level, therefore communities with more species at higher trophic levels require more energy and have greater top-down control (Evans *et al.*, 2005). However, bottom-heavy chains tend to have more species richness than top-heavy chains due stronger effect of bottom-up control on species richness (Sandom et al., 2013; Danet et al., 2021; Fig.1 – (I) + (III)).	Regions with top-heavy pyramids have lower tetrapod species richness.

Table 1

BODY SIZE AND TROPHIC STRUCTURE EXPLAIN GLOBAL ASYMMETRIC RESPONSE OF TETRAPOD DIVERSITY TO CLIMATE EFFECTS

Short running title: Direct and indirect ecological drivers of global tetrapod diversity

SUPPORTING INFORMATION

Appendix

Appendix S1. Detail of piecewise Structural Equation Model (pSEM).

1. Composite variables

The composite variables could be determined as the sum of the effect's values of individual variables, with each operational variable having a distinct weight (statistical composite) on the composite variable. The weight of each variable is based on the coefficient of an ordinary least square (OLS). Thus, we used an ordinary least square (OLS) to evaluate operational variables' effect on species richness. After this, the values of each operational variable were multiplied by their coefficients (weight) and summed to generate the factor scores (composite variables).

We conducted an OLS on each tetrapod group assessing the effect of temperature (Bio 1), precipitation (Bio 12), anomaly temperature, anomaly precipitation, mean trophic level, median body size, and variance of body size on species richness. We then developed each composite variable as follows:

1- Contemporary climate: We multiplied the coefficient of contemporary temperature (Bio1) and precipitation (Bio12) by their coefficients and summed them to obtain the factor score to use on the structural model.

2- Climate instability: We multiplied the coefficient of temperature and precipitation anomalies by their coefficients and summed them to obtain the factor score.

3- Species traits: We multiplied the coefficient of mean trophic level, median and variance body size by their coefficients and summed them to obtain the factor score that it used on the structural model.

2. Selecting variables

We evaluated the correlation between our operational and composite variables in each tetrapod group (Fig. S2). Thus, we used Spearman's correlation to avoid correlation problems between the variables and avoid inflating the models. We removed variables with strong correlations ($r > 0.7$) and evaluated the models with and without these variables. We observed that all tetrapod groups have a substantial correlation ($r < 0.7$) between temperature and temperature anomaly (Fig. S2). As a result, we removed the temperature anomaly variables that have lower p values, and ran the OLS models again selecting the models that had lower Akaike Information Criterion (AIC) values for each tetrapod group. The models with temperature and anomalous temperature show lower AIC than models with simply temperature for all tetrapod groups, except for birds (see Tab. S3)

3. Structural equation to Piecewise Structural Equation Model (pSEM)

After selecting the variables, we defined our theoretical model (Fig. S1) of the effects of composite variables on species richness. Based on the theoretical model, we created four structural equations for pSEM. We used the Ordinary Least Square (OLS) to perform structural equations that evaluate the (1) effect of composite variables (i.e., contemporary climate, climate instability and community-wide species traits) on species richness; (2) the effect of contemporary climate and climate instability on the (a) trophic structure, (b) on species body size, and (c) on species size variation. We follow this structure to each tetrapod group (i.e., bird, mammals, amphibian, and squamate). Furthermore, each group has four OLS models, totaling 16 structural models (Table S2).

4. Distance-based Moran's eigenvector analysis

We used the "Distance-based Moran's eigenvector analysis" to reduce spatial autocorrelation. We performed each model and used the residuals (Shown above - Topic 3) to obtain the eigenvectors (MEMs) that represent the highest autocorrelation with the response variable ($p<0.05$) (MIR method- Dray *et al.*, 2012). Then, we added the select MEMs to the OLS models with the function 'listw.select' of the package adespatial and ran the models once again (see selected MEMs – Table S2). Next, we assessed the spatial autocorrelation of each model using Moran's I, which was calculated with the residuals from our models. To perform this analysis, we employed the 'lm.morantest' function from the 'spdep' package. This calculation involved utilizing a spatial weights matrix (W) that defines the spatial relationships among our grid and the residuals of each model. Our observation revealed that models with R^2 values below 0.8 (as indicated in Table S1 - Moran's I) exhibited yet a spatial autocorrelation.Thus, we reduce the spatial autocorrelation on response variables and avoid inflating our models by including more eigenvectors although there is still autocorrelation in the models, although some variable responses remain spatially structured (Lefcheck 2016; see Appendix 3).

5. Piecewise Structural Equation Model (pSEM)

We used the piecewise Structural Equation model (pSEM) to evaluate composite variables' direct and indirect effects on the species richness of each tetrapod group (Fig. S2 e Table S1). We performed one pSEM to each tetrapod group using the five structural equations with the selected MEMs (Shown above – Topic 3 and 4, Table S1). We used the function ‘psem’ of the package “piecewiseSEM”. Moreover, we added to our pSEM the correlation relationships between the body size, size variance, and trophic level to avoid inflating the model using the ‘%~~%’. After performing the pSEM, we used the directed separation test to evaluate the independence claims in our pSEM (‘dSep’ function), as shown in our theoretical model (Fig. S1). We present Ficher’s C and R^2 values of each pSEM on Table S1.

Direct and indirect effects were interpreted based on the standardized effect sizes that link the variables (Table S2). The strength and direction of direct effect is the standardized effect size of these relationships, and we represented only significant effects ($p > 0.05$) in Figure 3. The indirect effects were obtained from the multiplication of the direct effects on a specific route of pSEM (Lefcheck, 2016; García-Andrade *et al.*, 2021). For example, the indirect effect of contemporary climate on species richness through species traits (pSEM route = contemporary climate -> species traits -> species richness) was calculated by multiplication of standardized estimate of contemporary climate effect on species richness, species traits on species richness, and contemporary climate effect on specie traits. Besides that, to understand the role of contemporary climate, climate instability, and species traits on species richness, we summed the direct and indirect effects of each variable to obtain each total effect (Figure 4 and 5).

Reference

Dray, S., Pélissier, R., Couteron, P., Fortin, M.J., Legendre, P., Peres-Neto, P.R., Bellier, E., Bivand, R., Blanchet, F.G., de Cáceres, M., Dufour, A.B., Heegaard, E., Jombart, T., Munoz, F., Oksanen, J., Thioulouse, J. & Wagner, H.H. (2012) Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs*, **82**, 257–275.

García-Andrade, A.B., Carvajal-Quintero, J.D., Tedesco, P.A. & Villalobos, F. (2021) Evolutionary and environmental drivers of species richness in poeciliid fishes across the Americas. *Global Ecology and Biogeography*, **30**, 1245–1257.

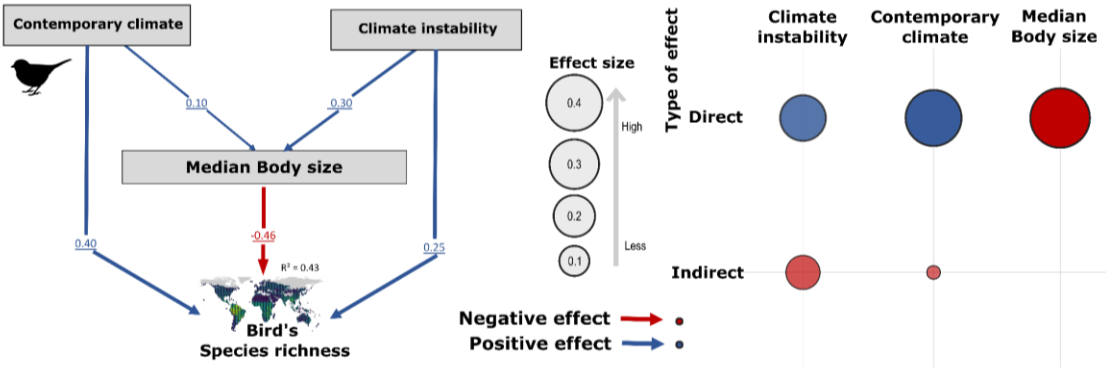
Lefcheck, J.S. (2016) piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, **7**, 573–579.

Appendix S2. Complementary analysis to understand the importance of community-wide species traits on body size and climate relationship.

We conducted a supplementary analysis using piecewise Structural Equation Models (pSEM), focusing solely on the median body size as a mediator of climate effects. By doing this, we repeated all analyses on the bird dataset replacing composite-wide species traits with the median body size (see Methods, main text). Previous studies indicate that communities with larger birds tended to exhibit lower species richness (Evans *et al.*, 2005). We corroborated these results when analysis using only the body size (Fig. 1). Thus, we showed that higher contemporary climate and climate stability favor higher species richness through reducing body size. However, upon examining community-wide species traits, we observed that the variance in body size plays a pivotal role in counteracting the increase in median body size and higher trophic level (see results Fig. 3a). We also reinforce that our model with all traits (R = 0.66) has higher power than the body size model (R= 0.43) to explain the species richness pattern to birds. Furthermore, the use of community-wide species traits provides us with a more comprehensive understanding of how species traits mediate the impact of climate on species richness. Therefore, our results highlight the importance of not relying solely on a single trait, as doing so could lead to biased interpretations regarding how climate influences species richness. For a more detailed discussion, please refer to the section titled "Correlations between climate and community-wide species traits improve predictions of species richness at large scales" in our discussion.

Figure 1. Structural model of piecewise Structural Equation Model (pSEM) We showed the relationship between the predictor and response variables emphasizing the direction and effect size on bird species richness using only body size with mediator. We

represented only those significant relationships ($p < 0.05$). The blue and red colors represent, respectively, positive and negative relationships between the variables. We also showed the effect size of composite variables (i.e., contemporary climate, climate instability, and median body size) on bird species richness. Fill color represents positive (blue) and negative (red) relationships between variables and circle size represents the strength of these relationships (standardize estimates).



Reference

Evans, K.L., Warren, P.H. & Gaston, K.J. (2005) Species-energy relationships at the macroecological scale: A review of the mechanisms. Biological Reviews of the Cambridge Philosophical Society, 80, 1–25.

Appendix S3. Complementary analysis to understand the influence of spatial autocorrelation on results.

Although we use Ordinary least squares models (OLS) with "Distance-based

Moran's eigenvector analysis” to minimize the influence of space on the results (see methods and Appendix S1), we observed that residuals were still spatially-structured (Tab. S1). Thus, we re-evaluated our models with the generalized least squares (GLS) analysis because it explicitly adjusts the models with correlated residuals using latitude and longitude (Pinheiro and Bates, 2000). Therefore, comparing our models with OLS + MEMs with GLS allows us to assess the robustness of the results despite the potential effects of the autocorrelated structure of the residuals. We found that similarly to OLS + MEMs, GLS was unable to fully control the spatial structure of the data across tetrapod groups (Fig. S3-1 to S3-4). This result indicates that there is a strong spatial structure that can slightly affect our models. It is important to emphasize, however, that OLS + MEMs models have higher R^2 and lower residuals than GLS models. We observed that OLS + MEMs and GLS models minimize in similar ways the autocorrelation to amphibians, squamates, and mammals data (Fig. S3-1 to S3-3), but OLS + MEMs models were better than GLS models to birds (Fig. 4). To make it consistent, we used OLS + MEMs analysis in the main manuscript because it is the most common method used in similar studies: Diniz-Filho *et. al.*, 2009 and Santos *et. al.*, 2020).

Figure 1. Variogram to Ordinary least squares (OLS) with the Moran’s eigenvector maps (MEM) and to generalize least squares (GLS) models to amphibian data.

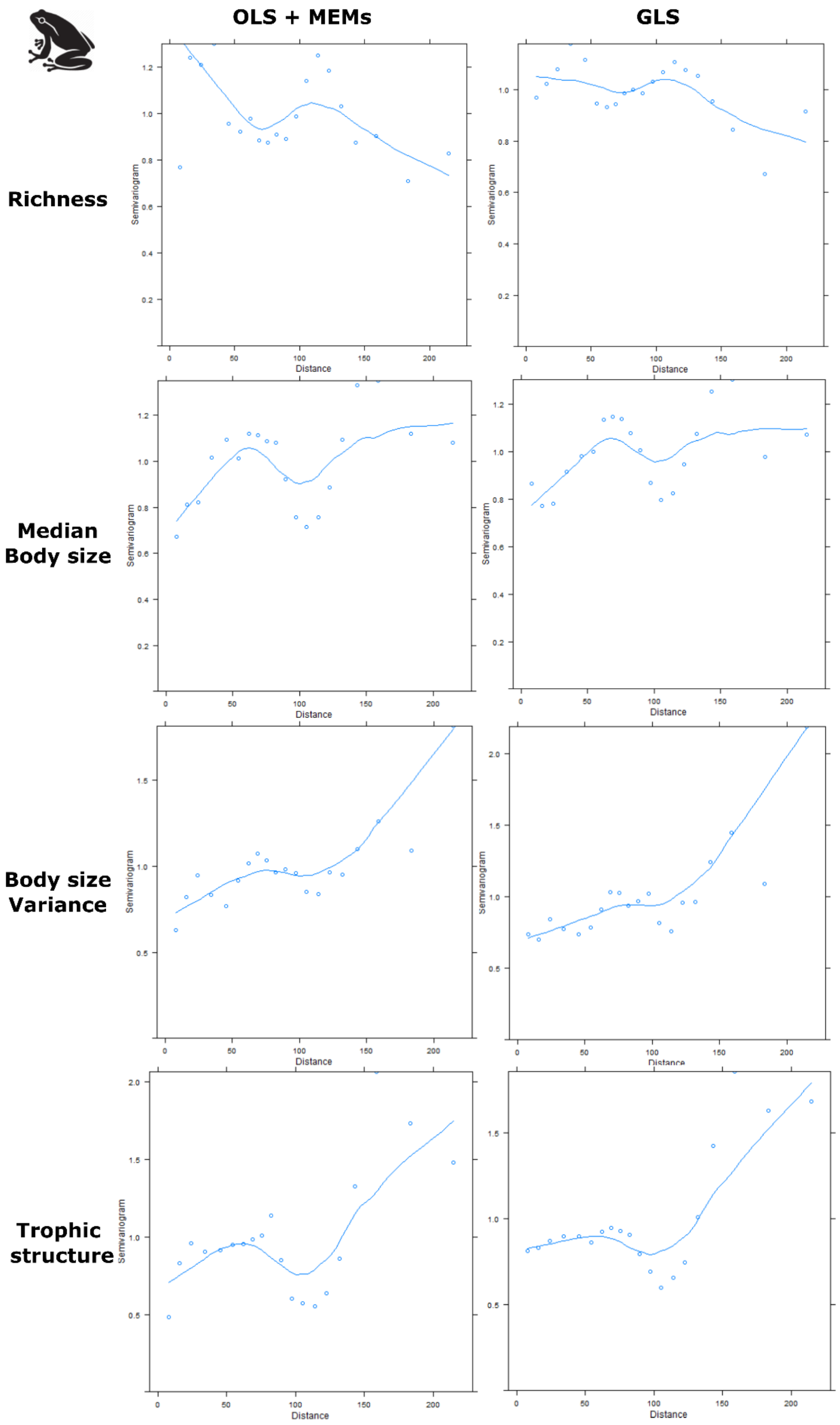


Figure 2. Variogram to Ordinary least squares (OLS) with the Moran's eigenvector maps (MEM) and to generalize least squares (GLS) models to squamates data.

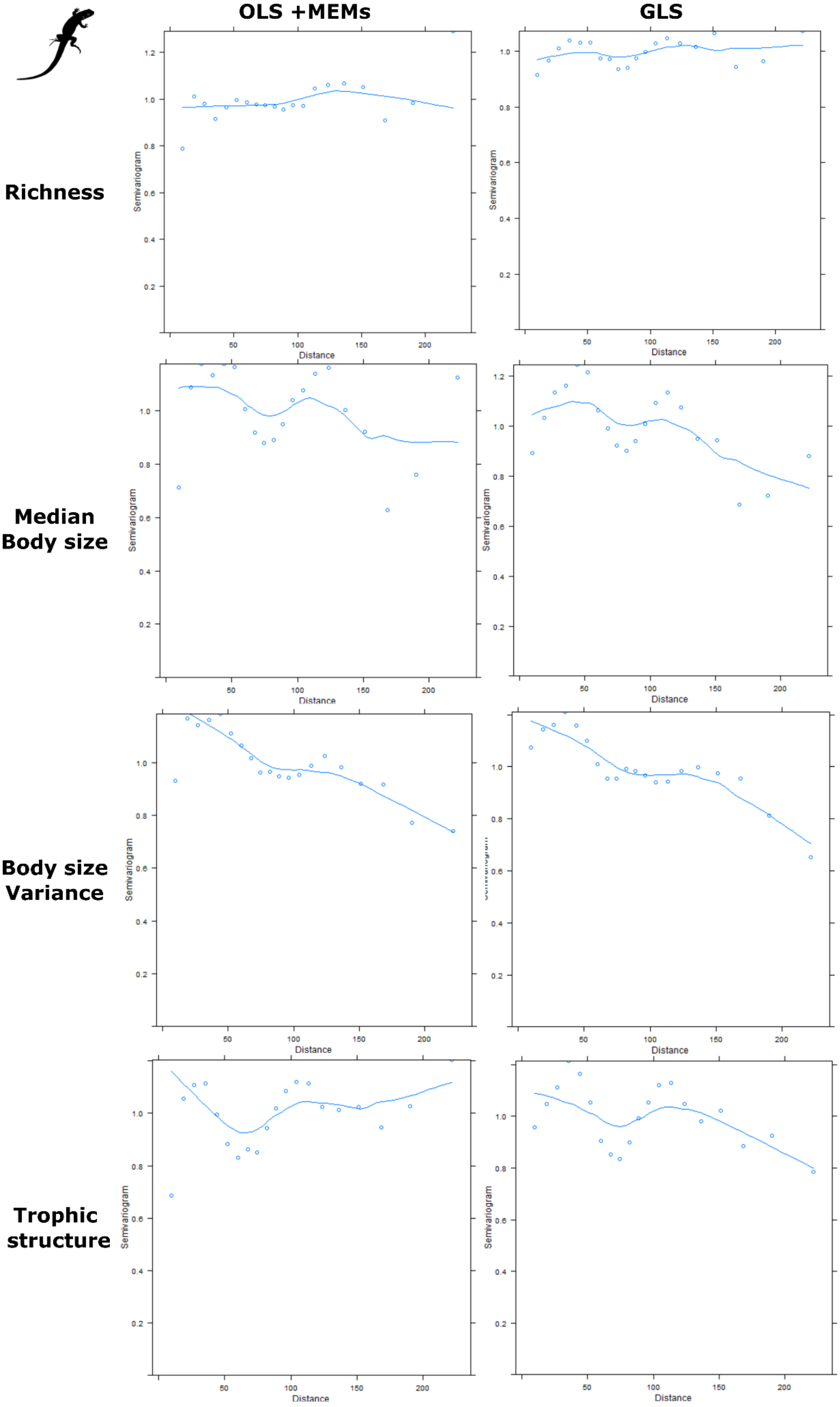


Figure 3. Variogram to Ordinary least squares (OLS) with the Moran's eigenvector maps (MEM) and to Generalize least squares (GLS) models to mammals data.

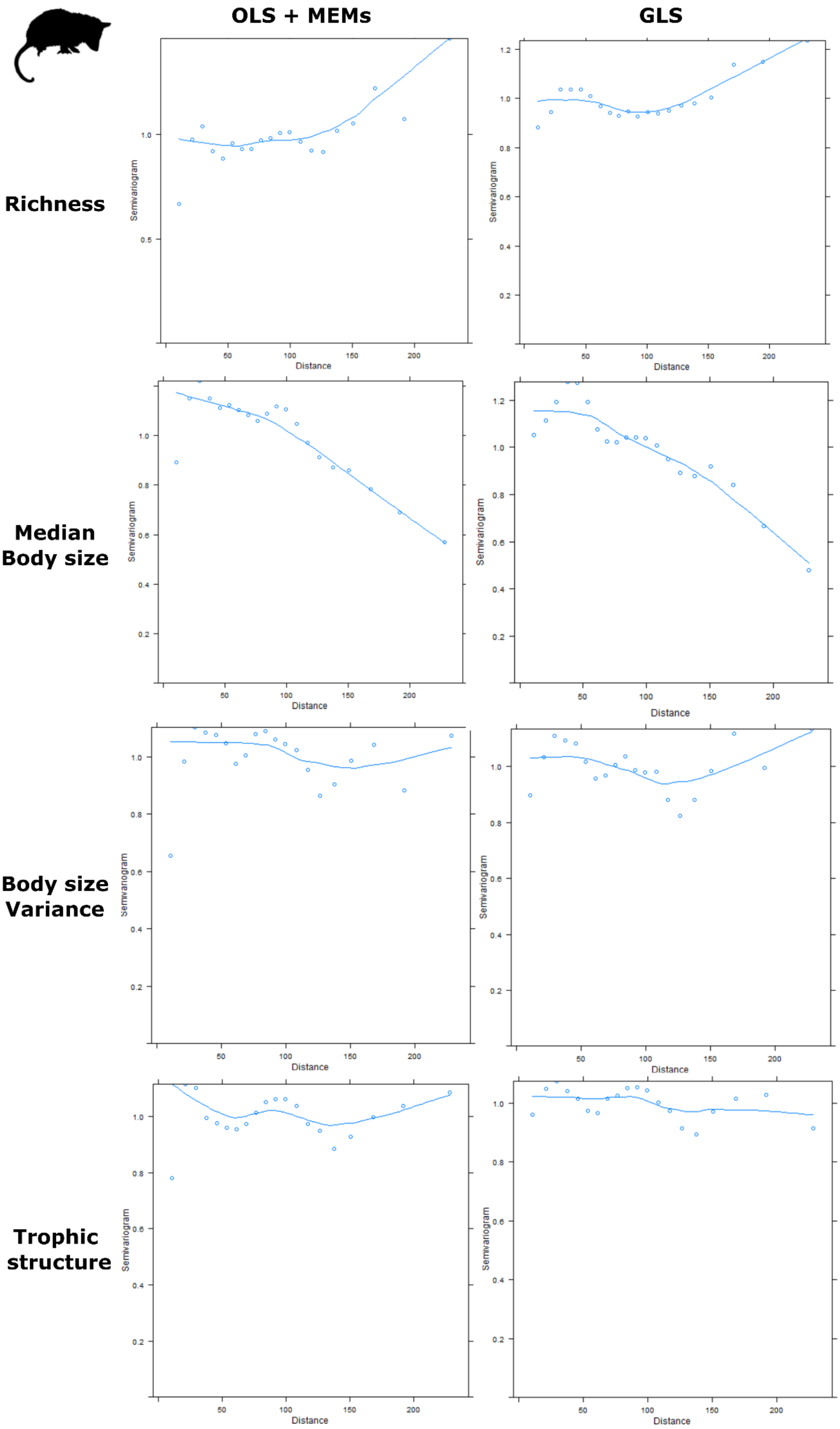
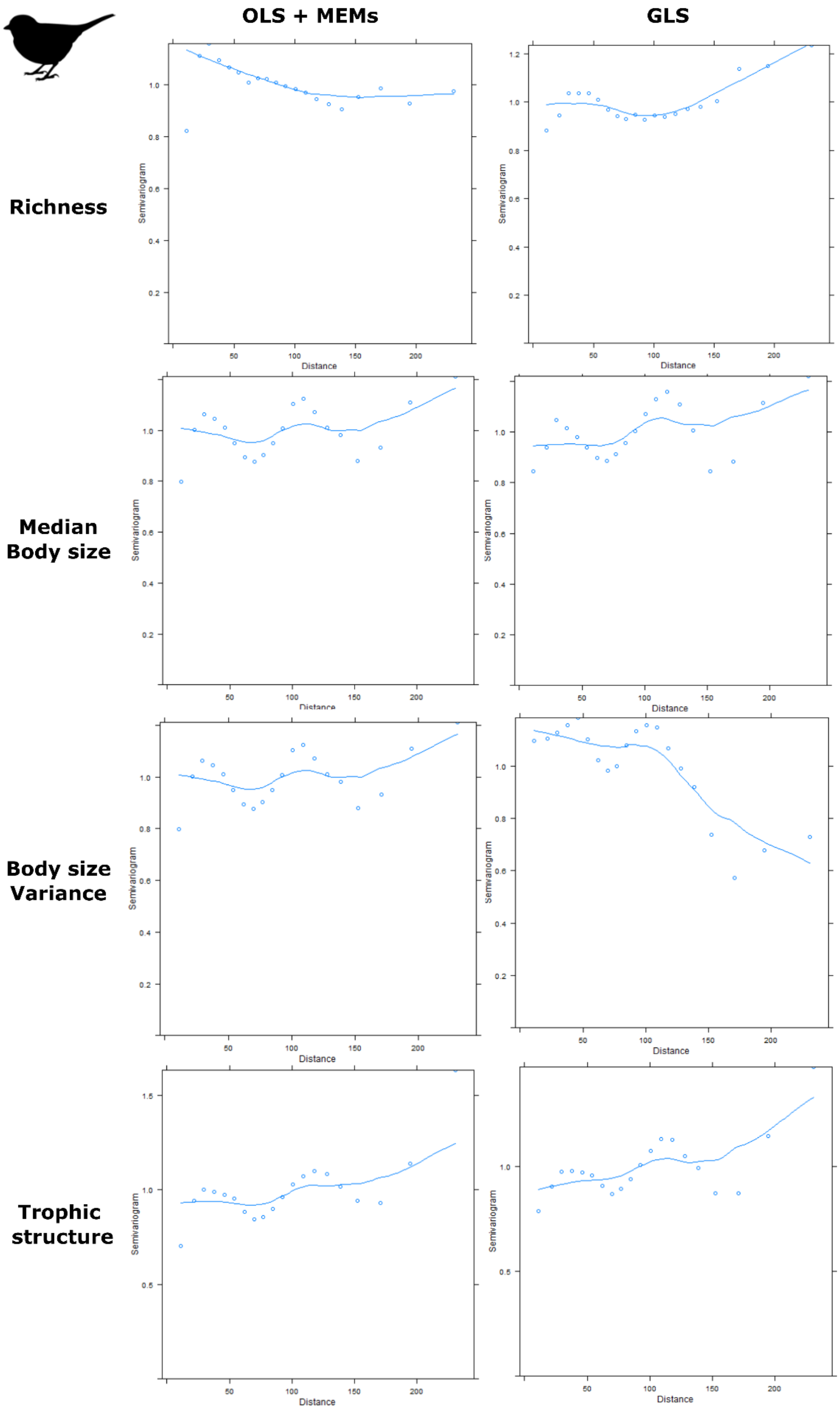


Figure 4. Variogram to Ordinary least squares (OLS) with the Moran’s eigenvector maps (MEM) and to Generalize least squares (GLS) models to birds data.



Reference

Diniz-Filho, J. A. F., Rodríguez, M. Á., Bini, L. M., Olalla-Tarraga, M. Á., Cardillo, M., Nabout, J. C., et al. (2009). Climate history, human impacts and global body size of Carnivora (Mammalia: Eutheria) at multiple evolutionary scales. Journal of Biogeography 36, 2222–2236. doi: 10.1111/j.1365-2699.2009.02163.x.

Santos, A. M. C., Cianciaruso, M. V., Barbosa, A. M., Bini, L. M., Diniz-Filho, J. A. F., Faleiro, F. V., et al. (2020). Current climate, but also long-term climate changes and human impacts, determine the geographic distribution of European mammal diversity. Global Ecol. Biogeogr. 29, 1758–1769. doi: 10.1111/geb.13148.

Figures

Figure S1. Theoretical structural model used in *piecewise Structural Equation Model* (pSEM). The expected relationships between exogenous (i.e., contemporary climate and climate instability) and endogenous variables (i.e., species traits) were used to understand their effect on species richness. The colors represent positive (blue) and negative (red) relationships between the variables.

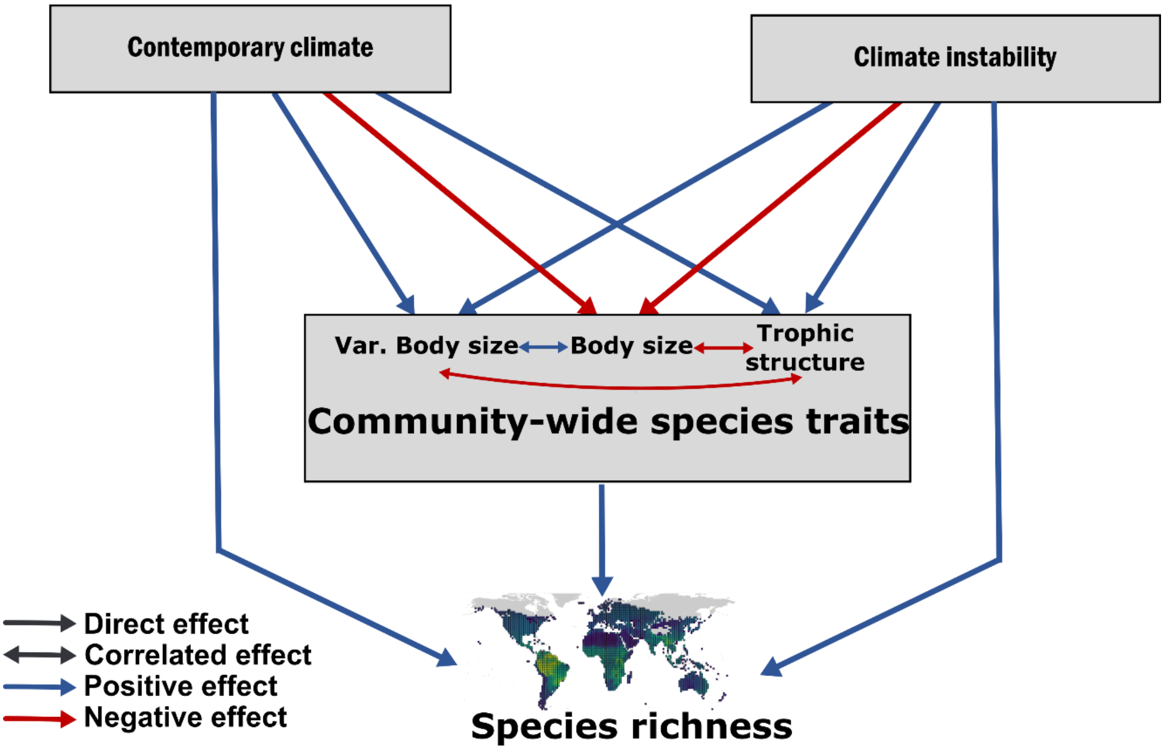


Figure S2. Correlation between the predictor variables used to structure the models. We avoided using a correlation higher than 0.7 between component variables (Green) and composite variables (Black) to each taxon: (A) bird, (B) mammal, (C) squamate, and (D) amphibian.

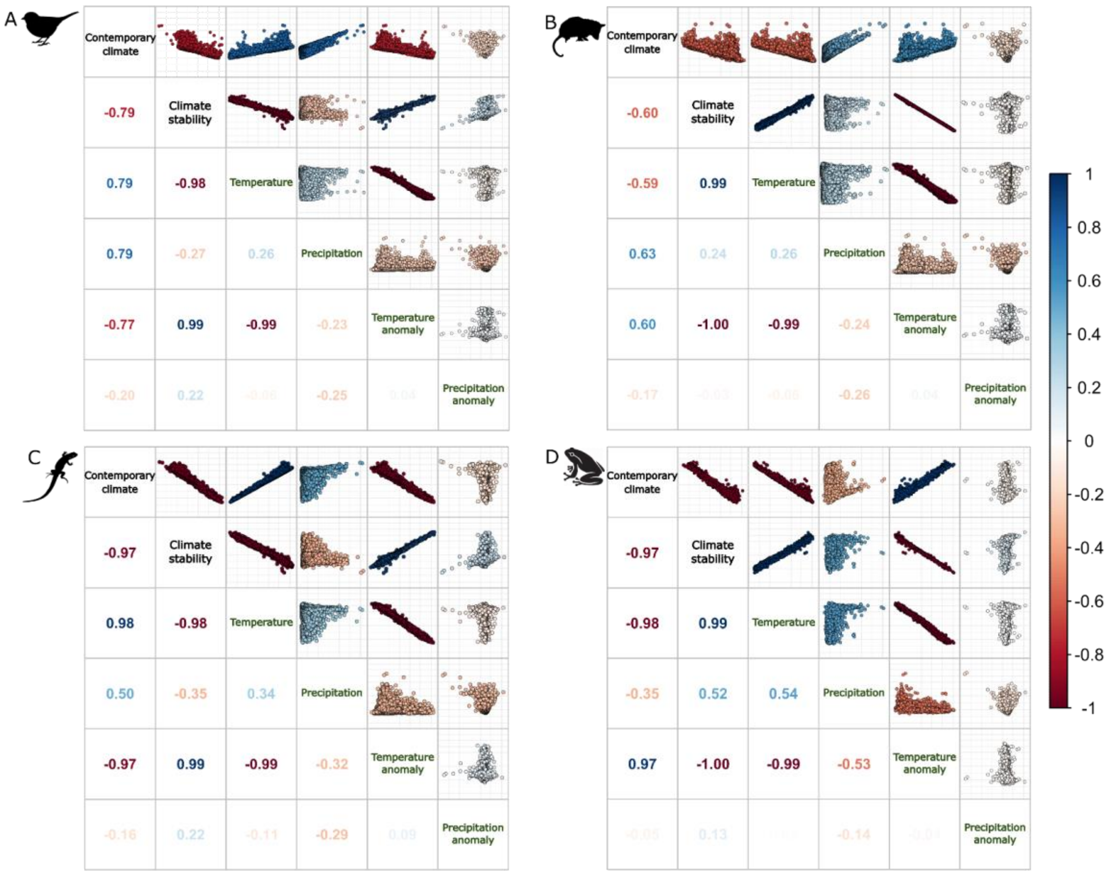


Figure S3. Correlation between the species traits variables to explain the relationship between component variables (Green) and composite variable (Black) to each taxon:

(A) bird, (B) mammal, (C) squamate, and (D) amphibian.

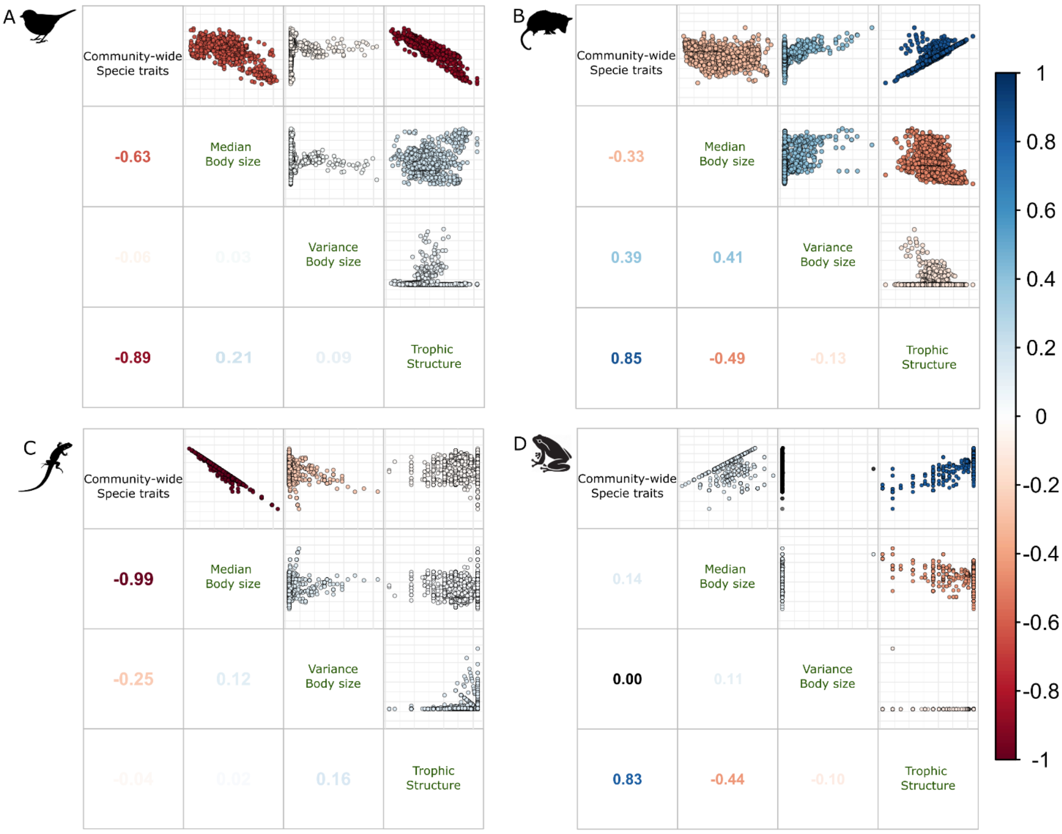


Figure S4. Latitudinal pattern of tetrapod (A) Current climate and (B) Climate instability.

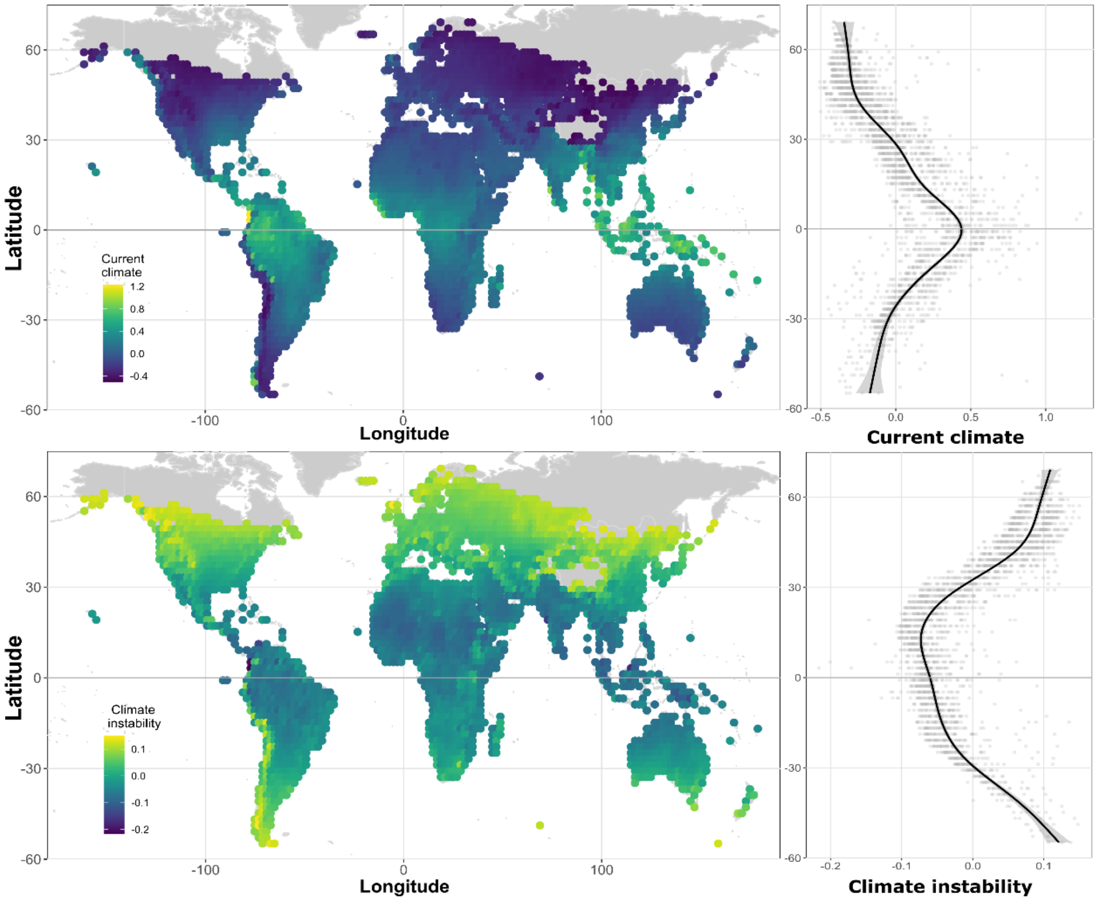


Figure S5. Latitudinal pattern of tetrapod species richness, body size,body size variance, and (D) trophic structure to (A) birds, (B) mammals, (C) squamates , and

(D)amphibians.

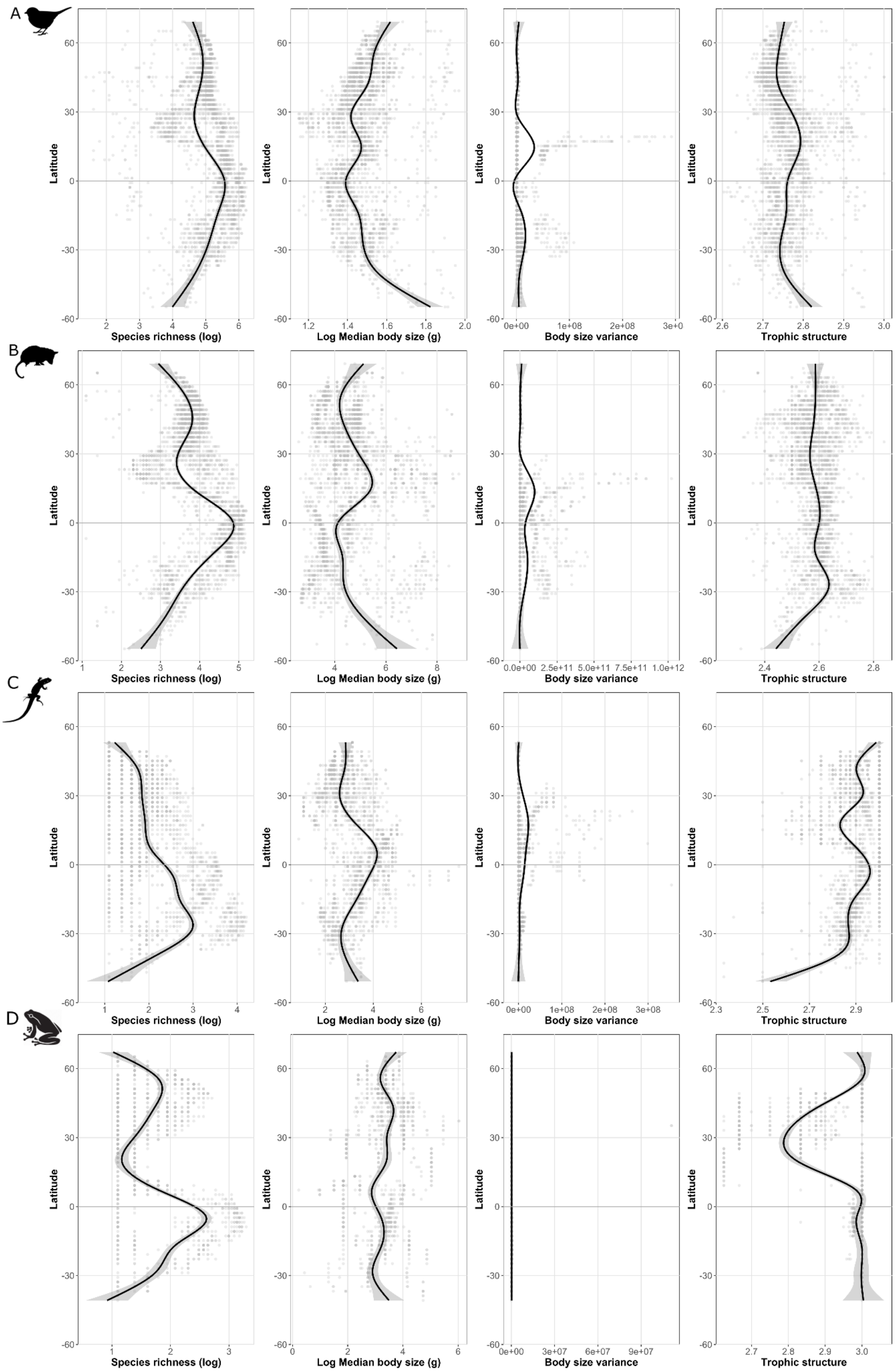
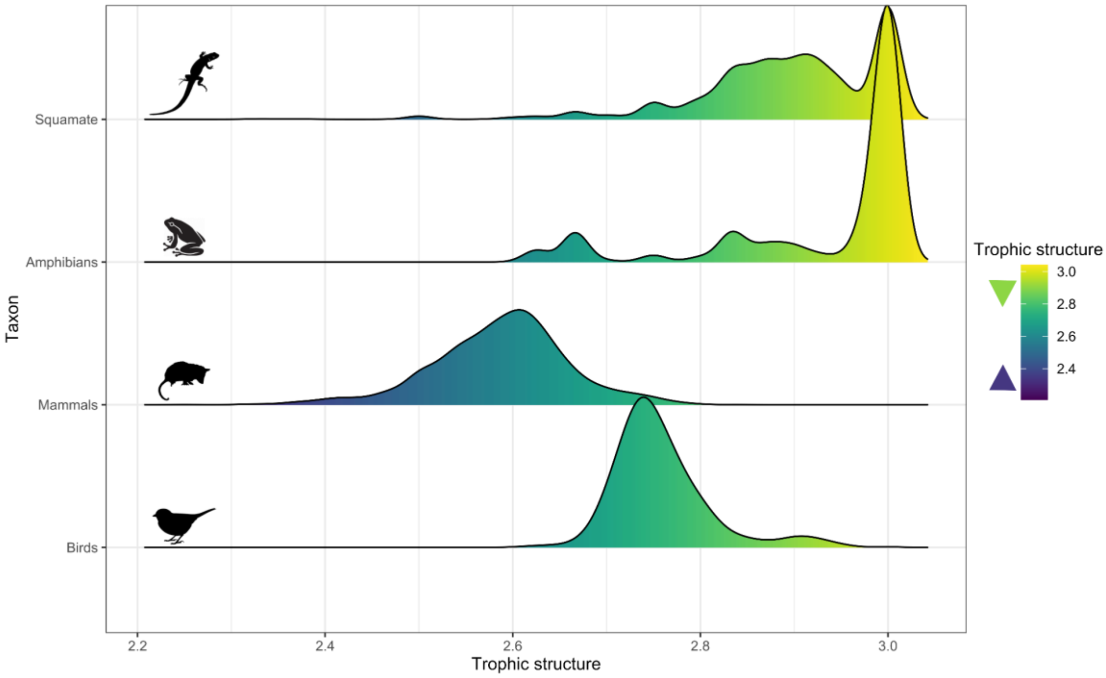


Figure S6. Density of trophic structure by group (i.e.,Birds, Mammals, Amphibians, and Squamates). Values of trophic structure next to 3 higher top-heavy structures and values next to 2 represent bottom-heavy structures.



Tables

Table S1. Details of the structural equation of pSEM containing the composite variables and the MEMs selected (see Table S2).

Taxon	Model	Response Variable	Predictor Variable	Moran's I	Fisher's C	p value	DF	R^2
Bird	M_{B1}	Species Richness	Contemporary climate + Climate instability + Community-wide species traits + Selected MEMs	0.61	1130	0.001	68	0.66
	M_{B2}	Trophic Structure	Contemporary climate + Climate instability + Selected MEMs	0.39				0.30
	M_{B3}	Median Body size	Contemporary climate + Climate instability + Selected MEMs	0.52				0.32
	M_{B4}	Variance Body size	Contemporary climate + Climate instability + Selected MEMs	0.81				0.12
Mammal	M_{M1}	Species Richness	Contemporary climate + Climate instability + Community-wide species traits + Selected MEMs	0.71	1713	0.001	78	0.61
	M_{M2}	Trophic Structure	Contemporary climate +	0.72				0.30

			Climate instability + Selected MEMs					
	M_{M3}	Median Body size	Contemporary climate + Climate instability + Selected MEMs	0.69				0.45
	M_{M4}	Variance Body size	Contemporary climate + Climate instability + Selected MEMs	0.69				0.57
Amphibian	M_{A1}	Species Richness	Contemporary climate + Climate instability + Community-wide species traits + Selected MEMs	0.73	1101	0.001	52	0.74
	M_{A2}	Trophic Structure	Contemporary climate + Climate instability + Selected MEMs	0.77				0.74
	M_{A3}	Median Body size	Composite contemporary + Climate instability + Selected MEMs	0.63				0.34
	M_{A4}	Variance Body size	Contemporary climate + Climate instability + Selected MEMs	0.67				0.44
Squamate	M_{S1}	Species Richness	Contemporary climate +	0.64	859	0.001	62	0.75

		Climate instability + Community-wide species traits + Selected MEMs			
M_{S2}	Trophic structure	Contemporary climate + Climate instability + Selected MEMs	0.72		0.18
M_{S3}	Median Body size	Contemporary climate + Climate instability + Selected MEMs	0.50		0.40
M_{S4}	Variance Body size	Contemporary climate + Climate instability + Selected MEMs	0.33		0.33

Table S2. Details of relationship between variable responses and predictors obtained in the SEM models containing the composite climatic variables and the MEMs selected.

Taxon	Response	Predictor	p value	Std. Estimate
Mammals	**Species richness**	**Contemporary climate**	**<0.001**	**0.44**
	Species richness	**Climate instability**	**<0.001**	**0.49**
	Species richness	**Community-wide species trait**	**<0.001**	**0.22**
	Species richness	MEM4	<0.001	0.16
	Species richness	MEM8	<0.001	-0.26
	Species richness	MEM5	<0.001	0.16
	Species richness	MEM1	<0.001	0.22
	Species richness	MEM7	<0.001	-0.23
	Species richness	MEM2	<0.001	0.13
	Species richness	MEM6	<0.001	-0.06
	Species richness	MEM11	<0.001	0.11
	Species richness	MEM18	<0.001	0.08
	Species richness	MEM22	<0.001	-0.09
	Body size	**Contemporary climate**	**<0.001**	**-0.25**
	Body size	**Climate instability**	**<0.001**	**-0.20**
	Body size	MEM4	<0.001	0.33
	Body size	MEM6	<0.001	-0.23
	Body size	MEM1	<0.001	-0.24
	Body size	MEM7	<0.001	-0.14
	Body size	MEM10	<0.001	-0.16
	Body size	MEM3	<0.001	-0.19
	Body size	MEM8	<0.001	-0.09
	Body size	MEM13	<0.001	0.14
	Body size	MEM11	<0.001	-0.13
	Body size	MEM18	<0.001	-0.11
	Body size	MEM2	0.537	-0.01
	Var. body size	**Contemporary**	**<0.001**	**-0.08**

		climate		
	Var. body size	**Climate instability**	**<0.001**	**-0.27**
	Var. body size	MEM8	<0.001	-0.26
	Var. body size	MEM1	<0.001	-0.58
	Var. body size	MEM4	<0.001	0.31
	Var. body size	MEM7	<0.001	-0.14
	Var. body size	MEM5	<0.001	0.15
	Var. body size	MEM13	<0.001	0.22
	Var. body size	MEM11	<0.001	0.07
	Var. body size	MEM18	<0.001	-0.06
	Trophic structure	**Contemporary climate**	**<0.001**	**0.12**
	Trophic structure	**Climate instability**	**<0.001**	**0.31**
	Trophic structure	MEM3	<0.001	0.09
	Trophic structure	MEM6	<0.001	0.35
	Trophic structure	MEM4	<0.001	-0.20
	Trophic structure	MEM7	<0.001	0.11
	Trophic structure	MEM21	<0.001	0.27
	Trophic structure	MEM15	<0.001	-0.13
	~~ Body size	**~~ Var. body size**	**<0.001**	**0.28**
	~~ Body size	**~~ Trophic structure**	**<0.001**	**-0.38**
	~~ Var. body size	**~~ Trophic structure**	**0.219**	**-0.01**
Bird	**Species richness**	**Contemporary climate**	**<0.001**	**0.30**
	Species richness	**Climate instability**	**0.1655**	**-0.02**
	Species richness	**Community-wide species trait**	**<0.001**	**0.66**
	Species richness	MEM5	<0.001	-0.22
	Species richness	MEM4	<0.001	-0.13
	Species richness	MEM7	<0.001	0.18
	Species richness	MEM8	<0.001	-0.16

	Species richness	MEM6	<0.001	0.04
	Species richness	MEM26	<0.001	-0.09
	Body size	**Contemporary climate**	**<0.001**	**0.14**
	Body size	**Climate instability**	**<0.001**	**0.29**
	Body size	MEM2	<0.001	0.26
	Body size	MEM6	<0.001	-0.32
	Body size	MEM1	<0.001	-0.14
	Body size	MEM8	<0.001	-0.08
	Body size	MEM13	<0.001	0.18
	Body size	MEM3	<0.001	0.11
	Body size	MEM12	<0.001	0.08
	Body size	MEM9	<0.001	0.11
	Var. body size	**Contemporary climate**	**<0.001**	**-0.58**
	Var. body size	**Climate instability**	**<0.001**	**-0.44**
	Var. body size	MEM2	<0.001	-0.08
	Var. body size	MEM1	0.76	-0.006
	Trophic structure	**Contemporary climate**	**0.70**	**0.01**
	Trophic structure	**Climate instability**	**<0.001**	**-0.12**
	Trophic structure	MEM1	<0.001	-0.39
	Trophic structure	MEM6	<0.001	0.08
	Trophic structure	MEM4	<0.001	-0.11
	Trophic structure	MEM7	<0.001	0.05
	Trophic structure	MEM8	<0.001	0.15
	Trophic structure	MEM12	<0.001	0.16
	~~ Body size	**~~ Var. body size**	**<0.001**	**0.16**
	~~ Body size	**~~ Trophic structure**	**<0.001**	**0.36**
	~~ Var. body size	**~~ Trophic structure**	**<0.001**	**-0.16**
Amphibi	**Species richness**	**Contemporary**	**<0.001**	**0.77**

an		**climate**		
	Species richness	**Climate instability**	**<0.001**	**0.92**
	Species richness	**Community-wide species trait**	**0.300**	**-0.02**
	Species richness	MEM3	<0.001	-0.45
	Species richness	MEM1	<0.001	-0.38
	Species richness	MEM2	<0.001	-0.33
	Species richness	MEM4	<0.001	-0.20
	Species richness	MEM5	0.132	0.02
	Species richness	MEM8	0.051	-0.02
	Species richness	MEM6	<0.001	0.06
	Species richness	MEM11	<0.001	-0.10
	Body size	**Contemporary climate**	**0.358**	**0.09**
	Body size	**Anomaly precipitation**	**0.382**	**-0.09**
	Body size	MEM5	<0.001	-0.30
	Body size	MEM8	<0.001	0.24
	Body size	MEM1	<0.001	-0.16
	Body size	MEM7	<0.001	-0.12
	Body size	MEM2	<0.001	0.09
	Body size	MEM3	<0.001	-0.15
	Body size	MEM12	<0.001	0.19
	Body size	MEM15	<0.001	0.20
	Var. body size	**Contemporary climate**	**<0.001**	**0.29**
	Var. body size	**Climate instability**	**<0.001**	**0.39**
	Var. body size	MEM2	<0.001	0.23
	Var. body size	MEM8	<0.001	0.46
	Var. body size	MEM3	<0.001	-0.08
	Var. body size	MEM1	<0.001	0.15
	Var. body size	MEM5	<0.001	-0.10
	Var. body size	MEM14	<0.001	-0.09
	Var. body size	MEM15	<0.001	-0.20

	Var. body size	MEM10	<0.001	0.21
	Trophic structure	**Contemporary climate**	**0.244**	**-0.08**
	Trophic structure	**Climate instability**	**0.187**	**-0.10**
	Trophic structure	MEM3	<0.001	-0.18
	Trophic structure	MEM2	<0.001	-0.49
	Trophic structure	MEM5	<0.001	0.58
	Trophic structure	MEM4	<0.001	-0.17
	Trophic structure	MEM7	<0.001	0.13
	Trophic structure	MEM10	<0.001	0.09
	Trophic structure	MEM14	<0.001	0.22
	Trophic structure	MEM6	0.571	0.01
	Trophic structure	MEM1	<0.001	-0.14
	~~ Body size	**~~ Var. body size**	**<0.001**	**0.28**
	~~ Body size	**~~ Trophic structure**	**<0.001**	**-0.38**
	~~ Var. body size	**~~ Trophic structure**	**<0.001**	**-0.028**
Squamate	**Species richness**	**Contemporary climate**	**<0.001**	**0.33**
	Species richness	**Climate instability**	**0.337**	**0.05**
	Species richness	**Community-wide species trait**	**<0.001**	**0.14**
	Species richness	MEM3	<0.001	-0.23
	Species richness	MEM1	<0.001	-0.51
	Species richness	MEM12	<0.001	0.14
	Species richness	MEM7	<0.001	0.06
	Species richness	MEM5	<0.001	-0.40
	Species richness	MEM8	<0.001	0.14
	Species richness	MEM6	<0.001	0.18
	Species richness	MEM11	0.667	-0.006
	Species richness	MEM18	<0.001	0.12
	Body size	**Contemporary**	**<0.001**	**0.91**

	climate		
Body size	**Climate instability**	**<0.001**	**0.76**
Body size	MEM4	<0.001	0.30
Body size	MEM6	<0.001	-0.17
Body size	MEM1	<0.001	0.24
Body size	MEM5	<0.001	0.08
Body size	MEM2	<0.001	-0.26
Body size	MEM3	<0.001	0.09
Body size	MEM9	<0.001	-0.14
Var. body size	**Contemporary climate**	**<0.001**	**1.13**
Var. body size	**Climate instability**	**<0.001**	**0.55**
Var. body size	MEM2	<0.001	0.24
Var. body size	MEM6	<0.001	0.16
Var. body size	MEM13	<0.001	0.13
Var. body size	MEM9	<0.001	-0.09
Var. body size	MEM1	<0.001	-0.22
Var. body size	MEM5	<0.001	-0.16
Var. body size	MEM4	<0.001	-0.05
Var. body size	MEM11	<0.001	-0.12
Var. body size	MEM10	<0.001	0.08
Trophic structure	**Contemporary climate**	**<0.001**	**0.37**
Trophic structure	**Climate instability**	**<0.001**	**0.29**
Trophic structure	MEM3	<0.001	-0.14
Trophic structure	MEM2	<0.001	0.16
Trophic structure	MEM9	<0.001	0.14
Trophic structure	MEM4	<0.001	0.21
Trophic structure	MEM7	<0.001	0.12
Trophic structure	MEM10	<0.001	-0.09
Trophic structure	MEM13	<0.001	0.13
Trophic structure	MEM1	0.031	0.05
~~ Body size	**~~ Var. body size**	**<0.001**	**0.27**

	~~ Body size	**~~ Trophic structure**	**0.003**	**-0.07**
	~~ Var. body size	**~~ Trophic structure**	**<0.001**	**-0.14**

Table S3. Details of evaluated ordinary least squares (OLS) models with strong correlated variables. Values of correlated variables could be observed on Figure S2. Selected models with lower Akaike Information Criterion (AIC) are in bold.

Group	**Correlated variables on Models**	**AIC**	**p value**
Bird	Temperature and Anomaly of temperature	**690.04**	0.365
	Only with temperature	690.25	
Mammals	Temperature and Anomaly of temperature	**772.09**	<0.001
	Only with temperature	779.77	
Amphibians	Temperature and Anomaly of temperature	**261.65**	<0.001
	Only with temperature	288.25	
Squamates	Temperature and Anomaly of temperature	**905.25**	<0.001
	Only with temperature	956.10	

CAPÍTULO 3: BIOLOGICAL INVASION, BUT NOT NUTRIENT SUPPLY, IMPACTS ARTHROPOD COMMUNITIES THROUGH BOTTOM-UP AND TOP-DOWN EFFECTS

Short running title: Nutrient Supply and Invasion Impact on Arthropod Communities

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Statement of authorship: R.G. e T.G-S conceived the idea and study design; R.G. assembled the data and performed the statistical analyses with inputs from T.G-S; R.G. wrote the first draft of the manuscript, and T.G-S contributed substantially to reviewing and editing the manuscript.

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Supporting Information: The online version contains supplementary material available at RMarkdown.

BIOLOGICAL INVASION, BUT NOT NUTRIENT SUPPLY, IMPACTS ARTHROPOD COMMUNITIES THROUGH BOTTOM-UP AND TOP-DOWN EFFECTS

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ABSTRACT

Anthropogenic activities, including eutrophication and biological invasion, contribute significantly to the global decline of biodiversity, potentially leading to biotic homogenization and a reduction in taxonomic and functional diversity. However, it has been demonstrated that the response of each trophic level is not homogeneous, in which, predator species tend to be more sensitive to environmental changes than herbivorous species. Thus, understanding how each trophic level responds to human activities can allow more efficient mitigation and recovery actions on affected ecosystems. Here, recognizing the need to unravel these mechanisms by which biological invasion and nutrient supply determine change the community structure of herbivorous and predatory. Moreover, we evaluate the importance of top-down and bottom-up effect on trophic chain to determine the response of arthropods communities. For that, we conducted an experiment with treatments of biological invasion and nutrient addition on dry forest for one year and collect species richness and biomass primary consumers and secondary consumers arthropods. We used Piecewise structural equation modeling to assess the effects of biological invasion and nutrient addition on the richness and biomass of herbivorous and predatory arthropods thought plant species richness and trophic chain effects. We found that nutrient addition exhibited no effects on the arthropod communities. Conversely, biological invasion caused a reduction of 21% in the number of native plant species and indirectly impacted predator biomass through the decline in native plants. The incorporation of top-down and bottom-up effects improved our comprehension of herbivore and predator species richness. Notably, the bottom-up effect revealed a new pathway where biological invasion improves predator species richness. This asymmetrical response between primary and secondary consumers underscores the interplay between invasive species and community dynamics. In conclusion, our study emphasizes the need to comprehend the multifaceted mechanisms through which nutrient addition and biological invasion shape communities, especially in trophic interactions. The observed asymmetry in response of each trophic level highlights the complexity of biological invasion effects and key role of bottom-up effect to determine the response of arthropod communities, providing valuable insights for biodiversity conservation and ecosystem management.

INTRODUCTION

Anthropogenic activities have led to a reduction in biodiversity, generating biotic homogenization, a decline in taxonomic and functional diversity, and a loss of capacity to provide ecosystem goods and services to the human species (Jetz et al. 2007, Valiente-Banuet et al. 2015). These activities increase habitat loss and eutrophication, which alters nutrient and species dynamics in the remaining habitats and the surrounding matrix. This is because changes in land use include activities such as intense agriculture, which contribute to the increased deposition of nitrogen and phosphorus in the soil (Compton and Boone 2000). Moreover, agricultural practices are generally associated with the spread of exotic species. As a result, by altering nutrient availability and introducing new species, these practices can drastically affect native communities (Römermann at. al. 2008, Boscutti et. al. 2018). One of the best-known effects of adding nutrients is to increase the establishment of invasive species, which can result in the biotic homogenization of natural ecosystems (Muthukrishnan & Larkin, 2020; Daru et. al., 2021). However, the effects of nutrient addition and biological invasion on terrestrial communities are often conducted independently and the distinct response between trophic levels is overlooked (Joern & Laws, 2013). Furthermore, our understanding of the underlying mechanisms through which nutrient addition and biological invasion shape community structure, along with their impact on trophic interactions, remains limited and lacks generalizability (HilleRisLambers et al. 2012, Filgueiras et al. 2021).

The impacts of biological invasions on biodiversity are multifaceted, encompassing the entire community structure in an ecosystem (see. Ehrenfeld, 2010). Invasive plants compete for resources with native plants (i.e. within the same trophic level), such as nutrients, water, and space (Forti *et. al.*, 2017). The invasive grass *Megathysus maximus*, known as Guinea grass, has been impacting biodiversity around the world, reducing soil nutriments and microhabitats availability (Rhodes *et. al.*, 2022). Additionally, biological invasion can have a cascading effect on the arthropod community reducing overall biomass and species richness (Van Hengstum *et. al.*, 2014). However, each trophic level could response distinctly, for example, invaded areas tend to have a lower biomass of herbivorous arthropods and a higher richness of predatory species due to a decrease in the availability of food and an increase in the availability of microhabitats, respectively (Gallé *et. al.*, 2023, Gusmão *et. al. in press*). In this way, biological invasion tends to have direct and indirect effects on the arthropod community, but herbivores and predators tend to respond differently.

Another anthropogenic impact is the addition of nutrients that has been used to increase crop productivity (Fay et al., 2015). The use of nutrients to improve productivity is because nitrogen (N), phosphorus (P) and potassium (K) are the main nutrients limiting productivity in many ecosystems (Elser et al., 2007; Fay et al., 2015). The increased concentration of these nutrients eliminates the trade-off between competition and development, which contributes to an increase in the biomass of producers, and thus cause a cascade effect throughout the trophic web (Harpole & Tilman, 2007; Hautier *et. al.*, 2009). For example, higher nutrient supply tends to increase the productivity, consequently, might favors the diversity of herbivorous arthropods and predators through a bottom-up effect (Evans et al., 2005; Joern & Laws, 2013). However, despite an increase in richness at higher trophic levels, the richness of producers tends to be reduced or maintained when subjected to conditions of excess nutrients in the soil (Harpole & Tilman, 2007; Joern & Laws, 2013). For example, nutrient deposition is responsible for a 6% decline in overall plant richness and for accentuating the presence of acquisitive plants (e.g. invasive species) that due higher nutrient absorption tends to limit the nutrients available to other species at the same trophic level (Boch et al. 2021; Gallego-Zamorano et al. 2022). In addition, this negative effect can also propagate throughout the trophic chain by reducing the food resource for the higher trophic levels (*i.e.*, bottom-up control) (Ehrenfeld, 2010; Gallé *et. al.*, 2023). Therefore, it is necessary to understand the mechanisms by which nutrient addition alters the structure of communities in a direct and cascading way between each trophic level and how the nutrient addition could increase the impact of other anthropogenic impacts, like the biological invasion (Walther et al. 2009, Borer and Stevens 2022).

Moreover, the addition of nutrients and biological invasion can have a synergistic effect on the decline in diversity by favoring the establishment of invasive species from the colonization stage to propagation (Araújo and Rahbek 2006, Walther et al. 2009, Milton and Dean 2010). Invasive species are favored by environmental changes (e.g. increased nutrient availability and temperature), increasing their dominance through the combined effect of facilitation and suppression of competing species (Battisti et al. 2006, Walther et al. 2009, Schweiger et al. 2010). As a result, it is expected across the globe an increase of up to 35% in biological invasion by 2050 (Essl *et al.,* 2020; Seebens *et al.,* 2021). Thus, it should be emphasized that the addition of nutrients and biological invasion are anthropogenic processes that need to be evaluated simultaneously and that the nutrient addition has an indirect effect on the communities through the biological invasion.

Here, we investigate how soil fertilization and biological invasion impact arthropod richness and biomass across trophic levels. In this study, we used an experimental module to simultaneously and individually evaluate the effect of nutrient enrichment (i.e., NPK) and invasion by a grass (*i.e. Megathyrsus maximus*) on biomass and species richness of herbivorous and predatory arthropod communities in a dry forest. We expect that: (i) increasing nutrient supply and invasive grass cover affect the biomass and species richness in a asymmetric way to each trophic levels; specifically, we expected that the nutrient supply reduce the biomass and species richness of herbivorous and predator arthropods, while the biological invasion favored the biomass and species richness of predator but reduce to herbivores arthropods; (ii) the effect of biological invasion is stronger than the effect of nutrient addition on species richness and biomass to all trophic levels but (iii) lower trophic levels (i.e., producers and primary consumers) will be more sensitive to these drives than higher trophic levels (i.e., secondary consumers) due bottom-up effects (Fig.1). Hence, the trophic pyramid's structure can shift from being bottom-heavy to being more top-heavy as a result of higher nutrition supply and biological invasion. Therefore, understanding how each trophic level responds to environmental changes improves our capacity to predict and mitigate anthropogenic impacts on ecosystems.

METHODS

STUDY AREA

The experiment described here was carried out in the Catimbau National Park (PNC), located in the semi-arid region of the state of Pernambuco (8° 34’ 02” S, 37° 14’ 24” W), more specifically in the Caatinga biome. The Caatinga biome is highly populated and marked by extreme poverty and water scarcity (Silva et al. 2017). Thus, a mosaic is established in the Brazilian Caatinga biome with distinct land use and anthropogenic pressure on the local biota that exhibits a high degree of endemism (Silva et al. 2017). In order to gain food and a source of additional revenue, the local people are known to have introduced exotic plants to the area, which are now dispersed and poorly managed in every location, and nutrient addition to increase productivity (Cavalcante and Major 2006, Silva et al. 2017). The experimental site is a good representative of this scenario, in which it is an area of pasture abandoned since 2012 immersed in a forest matrix (Fig. S1). In this area was introduced the Guine grass (*Megathyrsus* *maximus*) to use for cattle and goat pasture. Moreover, in the experimental area, the addition of nutrients was never carried out prior to the study. The experimental site has a sandy soil, which tends to be nutrient limited, mainly by nitrogen (Fay et. al., 2015). Additionality, the average annual temperature is 23 ºC and the average annual precipitation is 700 mm. However, Precipitation is concentrated mainly two times of the year, around 65% occurs from March to July and the remainder occurs between September and January.

We implemented an experimental module using the setup defined in the Nutrient Network (https://nutnet.org/). For the construction of this experiment, we used as reference international experiments that were already well established and that were successful in their development as the global experiment network, such as TreeDivNet, Drought-Net, NutNet and DRAGNet (Fraser et al. 2013, Borer *et. al.*, 2014, Grossman et al. 2018). The module where the experiment was carried out consists of 200 plots (36m²) arranged in parallel and 1 meter apart (Fig. S1 and S2). Each plot is subdivided into 4 subplots of 9m², and for the experimental design we randomly selected one subplot to collect information (see below).

EXPERIMENT DESIGN

Our experiment was installed in April 2021 and incorporates biological invasion treatments along with nutrient-enriched treatments to comprehend the response of arthropod communities We first used a drone to take aerial photographs of the module, plots and subplots from a height of 40 meters. By doing so, we were able to quantify plant cover for each sampling unit. The software ImageJ (Schneider *et. al.* 2012) was used to calculate the percentage of cover of the invasive species (*Megathyrsus maximus*) on each plot/subplot. Then, we used the information about the cover of the invasive species in all plots to select the treatments based on plots sharing a similar cover percentage on all subplots and categorized in two groups: with low and high coverage percentage. All plots with similar cover percentual have a positively skewed distribution, in which there is a predominance of plots (mode) with lower cover percentage than average (Fig. S3). Thus, we used the quartiles to define the categories of invasion: lower invasion, with 0 to 6% coverage of the invasive species (i.e., 1º and 2º quantile); and higher biological invasion, with 7 to 60% coverage of the invasive species (i.e., 3º and 4º quantile). We randomly selected 24 plots from each invasion category. Therefore, we have two treatments of species invasion (i.e., lower invasion and higher invasion) each with 24 plots that received nutrient treatments.

Each of the selected 48 plots received a type of treatment in relation to the amount of nutrients, namely: no addition of nutrients (N_0); lower dose with addition of 0.5 g m-2(N_1); intermediate dose with the addition of 2.5 g m-2r (N_2); and a higher dose of addition 5 g m-2(N_3). The addition of nutrients occurred twice a year at the beginning and after 6 months of the first addition, always containing nitrogen, phosphorus, and potassium in the same proportions (10:10:10), following the protocols established by NutNet. Furthermore, the experiment has 6 replicates of each of the 4 nutrient addition treatments (i.e., no addition, 0.5 g m-2, 2.5 g m-2, and 5.0 g m-2) in lower invasion plots and 6 duplicates in higher invasion plots (Fig. S2).

This arrangement of treatments, in which there is an increasing addition of nutrients, allows assessing whether there is a threshold that the addition of nutrients change the response of the arthropod community. Moreover, we adapted the NutNet methods to test theoretical and practical ecological issues and their implications for the restoration of the Caatinga. We separated the nutrient addition two times a year to take advantage of the rainy season, avoiding the need to irrigate the area, increasing nutrient absorption. In which, the addition of nutrients during the rainy season has been a practice carried out by Caatinga residents to reduce costs.

DATA COLLECT AND SPECIES TRAITS

Field campaigns commenced in May 2021, one month after the first nutrient addition, and recurred every two months for a year, totalizing 6 campaigns. Each campaign had an average duration of 6 days in which they obtained data on plant richness, as well as the richness and abundance of arthropods per subplot. Arthropods were collected utilizing entomological umbrellas and nets. The collected arthropods were photographed with a scale of 10 mm to identify, thus ensuring greater accuracy in identification, with the help of specialists until identification was obtained at the lowest possible taxonomic level. Most arthropods were classified at the family level. The photos with scales were also used to estimate individual body size using ImageJ. When direct measurement of body size was not possible, the value was estimated using the average of other individuals of the same species that were included in the same sample. Thus, we used the body size and biomass formula of each family to obtain biomass for each individual (Hodár, 1996). Additionally, the level trophic of arthropods was obtained based on mouthparts and specialized literature to each group separating in two main groups: primary and secondary consumers representing. Primary consumers represent herbivore species, while secondary consumers are represented by predators and omnivorous.

Finally, we used the biomass and trophic level to calculate the average of biomass of primary and secondary consumers on each plot.

STATISTICAL ANALYSIS

In order to comprehend the direct and indirect effects of biological invasion and nutrient addition on the arthropod communities, we used a piecewise structural equation model (pSEM) (Lefcheck 2016). We separated the arthropod community according to trophic levels (i.e., herbivores and predators) for the construction of structural models, allowing us to understand the cascade effect of treatments in the entire arthropod community and take into account the different responses to environmental stressors between each trophic level. Therefore, we performed three routes using pSEM: (i) environment effect, (ii) top-down effect, and (iii) bottom-up effect (see. Sandom *et. al.*, 2013). The structure to evaluate the environment effect considers that there is a correlation between biomass and species richness of primary and secondary consumers; to evaluate the top-down effect, ours model considers a causal relationship between biomass and species richness of secondary consumers on biomass and species richness of primary consumers (*i.e*, secondary consumers communities -> primary consumers communities); and the structure to bottom-up effect considers that biomass and species richness of primary consumers determine biomass and species richness of secondary consumers (i.e, primary consumers communities -> secondary consumers communities).

Therefore, each pSEM was made up of five structural models according to our theoretical model (Fig. 1). The three pSEM have like structural models the effect of biological invasion and nutrient addition on plant richness (i). However, each pSEM has specific models to evaluate each effect (i.e, environmental, top-down and bottom-up effect). To environment effect, the additional models are: effect of treatments and plant richness on biomass (ii) and on richness (iii) of primary consumers arthropods; the effect of treatments, plant richness on biomass (iv) and species richness (v) of secondary consumers. Moreover, we added the correlation between biomass of primary and secondary consumers. To top-down effect pSEM, the structural models are effect of treatments, plant richness, and biomass of secondary arthropods on biomass of primary consumers (ii); plant richness, and species richness of secondary arthropods on species richness of primary consumers (iii); the effect of treatments, plant richness on biomass (iv) and species richness (v) of secondary consumers. All three pSEM also considered the correlation between species richness and biomass on each trophic level.

For the structural models, we used Generalized Mixed Models (GLMM), with plots and samples as random factors. In addition, species richness and biomass data were standardized and used the Gaussian distribution on models. Moreover, we considered the interaction between nutrient addition and biological invasion, but we simplified the models based on Akaike (AIC) and selected the model with lower value (Zuur, 2009). Thus, we found there is no interaction between nutrient addition and biological invasion and that the simplified models, without the interaction, have lower AIC. Furthermore, we used to interpretation the modes without the interaction between nutrient addiction and biological invasion. We determine the direction and magnitude of indirect effects by multiplying standardized estimates of the variables into each pathway between exogenous and endogenous factors. Moreover, all analyses were conducted out using the R 3.5 software and the "lme4" package for GLMM and the "piecewiseSEM" package for pSEM.

RESULTS

We registered 44 plant species and 298 morphospecies (6,509 individuals) of arthropods, from 133 of herbivores and 166 of secondary consumers (omnivores and predators). The average species richness of native plants on each plot was 6 species (sd = 2), to primary consumers was 4 species (sd = 2), and to secondary consumers was 6 species (sd = 3). About the biomass of primary and secondary consumers was observed respectively at an average of 92.5 mg and 518mg on each plot.

We showed that there is no interaction between nutrient addition and biological invasion. However, individuality, the nutrient addition has no effect on plant, primary and secondary arthropods communities, while higher biological invasion reduces the plant species richness and indirectly reduces the secondary consumers biomass. Additionally, the biological invasion could have a direct effect on secondary consumers species richness considering the bottom-up interactions. We highlight that the addition of top-down and bottom-up interaction between primary and secondary consumers increases the explanation of species richness compared to environmental interaction (primary $r^2 = 0.13$, secondary $r^2 = 0.04$), but there is no influence to explain the biomass of primary and secondary consumers (Tab. S1). Specifically, the inclusion of top-down effect increases around 2.5 times the explanation of species richness primary consumers ($r^2 = 0.33$), while the bottom-up effect increases 6.5 times the explanation of species richness secondary consumers ($r^2 = 0.26$). Thus, the bottom-up effect has a stronger contribution to global explanation of the models than top-down effect or environment effect.

We showed that nutrient addition did not affect plant species richness, biomass and species richness of primary and secondary consumers (Fig. 2a). Moreover, we found that the biological invasion reduces the species richness of native plants on all three models (β = 0.35, $p < 0.001$, Tab. 2). We showed that invaded plots have around 21% lower native species than non-invaded plots. However, the biological invasion has no effect on primary and secondary consumers (*i.e.*, biomass and species richness) (Fig. 2a). However, the addition of bottom-up effect revealed a new path, in which, the higher biological invasion improves the secondary consumer species richness (β = 0.11, $p < 0.05$, Tab. S2). Thus, there are around 10% more species of secondary consumers in higher invaded areas than lower invaded areas considering the bottom-up effect.

Moreover, we demonstrated a positive relationship between increased species richness of native plants and the secondary consumer biomass (β = 0.17, $p < 0.05$, Tab. S2). Thus, for every more native species, there is a significant 0.2 mg rise in the biomass of secondary consumers. In turn, the biomass of primary consumers and species richness of both primary and secondary consumers were not shown to be affected by native plant species richness (Fig. 2a). Additionally, our result showed that the biological invasion indirectly affects the secondary consumer biomass through native plant species richness. Thus, although biological invasion does not directly affect the community of secondary consumers, it tends to reduce the biomass of these communities due to the reduction in native species richness.

We also showed that there is a correlation between biomass and species richness to primary consumers arthropods, but there is no correlation of biomass and species richness to secondary consumers (Fig. 2a). Thus, communities of primary consumers with higher biomass tend to have higher species richness than communities with lower biomass. This link has a similar importance independent of environmental, top-down, and bottom-up effects (Fig. 2b and c). On the other hand, we found that the relationship between primary and secondary consumers is only through species richness independently of environmental, top-down, and bottom-up effects and with similar strengths of effect, but there is any relationship through biomass between these trophic levels (Fig. 2).

DISCUSSION

We found evidence that the biological invasion, but not nutrient supply, determined the arthropods communities, but herbivores and predatory arthropods responded distinctly to higher biological invasion. Our results showed that the nutrient addition has no discernible impact on the diversity of plant species, herbivores, and predatory arthropods, as well as on the total biomass of arthropod communities. On the other hand, the biological invasion tends to reduce the native plant species richness and, consequently, the biomass of predator arthropods. Additionally, we observed that the relationship between the communities of herbivore and predator arthropods occurs through only species richness with similar importance to environment, top-down and bottom-up effect. Nevertheless, the bottom-up effect has a higher importance to explain the studied system. Considering the bottom-up effect, the biological invasion also tends to improve the species richness of predator arthropods. However, this effect of the biological invasion does not act in cascade on trophic structure because it is associated with the bottom-up effect of species richness of herbivores arthropods.

The biological invasion was unique to determine the plant and arthropod communities, while the addition of nutrients has no effect on productor and arthropod communities. Contrary to our prediction that increasing nutrient supply reduces native plant species richness and biomass and species richness of arthropod communities. Some studies have shown that the effect of enrichment of nutrients is chronic and detected in producer communities after around 3 years of continued addition (Harpole *et. al.,* 2016*;* Seabloom *et. al.,* 2021). Additionally, the nutrient effect increases more slowly at sites with lower litter and sandy soils, such as Caatinga (Santana *et. al.*, 2022). For example, the Caatinga have a limited stock of nutrients mainly defined by lower incorporation into the soil and higher mineralization, respectively, due to water deficit and high radiation (Santana *et. al.,* 2022). Furthermore, we highlight that the addition of nutrients has no acute effect, mainly in sites with sandy soils, might this effect be chronic.

Moreover, we showed that biological invasion affects distinctly each trophic level. The biological invasion reduces the native plants species richness and biomass and species richness of predator arthropods, but there is no effect on herbivore arthropods. The reduction of species richness of native plants due the biological invasion is supported on distinct ecosystems due the competition with native species (Bradley *et. al.,* 2019). Thus, the *Megathyrsus maximus* has an extensive rhizome system and is fast-growing, therefore, it might have better water absorption, a limiting factor in dry forests, and occupies spaces in exposed soil more quickly than native species (Soti & Thomas, 2022). However, we also showed that native plant species richness increases the biomass of predatory arthropods. This relationship can be explained by the greater diversity of plants that promote refuge to predators and higher capture rate allowing to maintain a greater biomass of predator species (Blaise *et. al.,* 2022). Furthermore, the biological invasion reduces the biomass of predatory arthropods through plant native diversity due the loss of refuges to predators and, consequently, capture rate of prey.

However, contrary to our prediction, we showed that predator arthropods tend to be more sensitive to biological invasion than herbivore arthropods due to bottom-up control. Despite the indirect effect of biological invasion on biomass of predator arthropods, we observed that, considering the bottom-up effect, the biological invasion tends to increase the species richness of predators. The invasion biologically tends to improve the species richness of predatory species through changes on vegetation structure and microhabitat quality (Gallé *et. al.,* 2023). Moreover, this effect is accentuated by the diversity of generalist species and sand soils present on dry forest and dunes (Carvalho *et. al.,* 2011; Gallé *et. al.,* 2023). However, we only observed this effect when we consider the bottom-up effect, in which, it's necessary higher diversity to herbivores to improve the species richness of predator arthropods. In this way, It may be that the increase in predator richness in invaded areas is dependent on greater prey diversity.

CONCLUSION

Here, we demonstrated that the nutrient addition has no effects on the structure of arthropod communities, while biological invasion emerged as a pivotal factor influencing the biomass and species richness of predator arthropods. The reduction of native plant species richness due to biological invasion, highlighting the competition between invasive and native species. Intriguingly, this invasion did not directly impact primary and secondary consumer biomass or species richness. However, the inclusion of top-down and bottom-up effects significantly enhanced our understanding of species richness compared to environmental factors. Thus, we also revealed the cascade effects of biological invasion on trophic levels and the importance of biologic interaction to understand the ecosystem response to biological invasion. The biological invasion tends to reduce the biomass of predator arthropods through the reduction of native plant species richness shed light on the importance of preserving native vegetation for maintaining higher trophic levels. Furthermore, when considering the bottom-up effect, the invasion was associated with an increase in predator species richness.

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FIGURES CAPTIONS

Figure 1. Conceptual framework containing predictions to each model effect (i.e. environmental, top-down, and bottom-up) to the asymmetric response by arthropods to nutrient addition and biological invasion.

Figure 2. Structural model of piecewise Structural Equation Model (pSEM) showing the relationship between the predictor and response variables emphasizing the direction and effect size on biomass and species richness to primary and secondary consumers. We represented only those significant relationships ($p < 0.05$). The blue and red colors represent, respectively, positive and negative relationships between the variables.

FIGURES

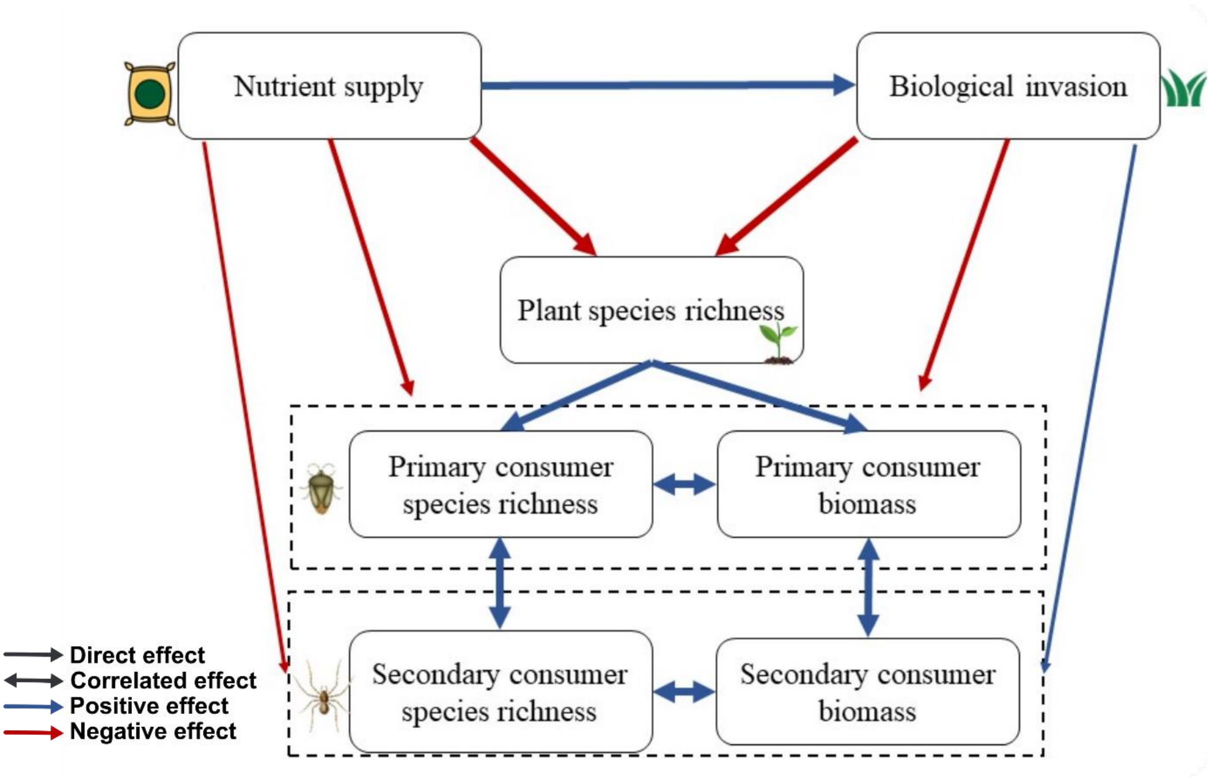


Figure 1

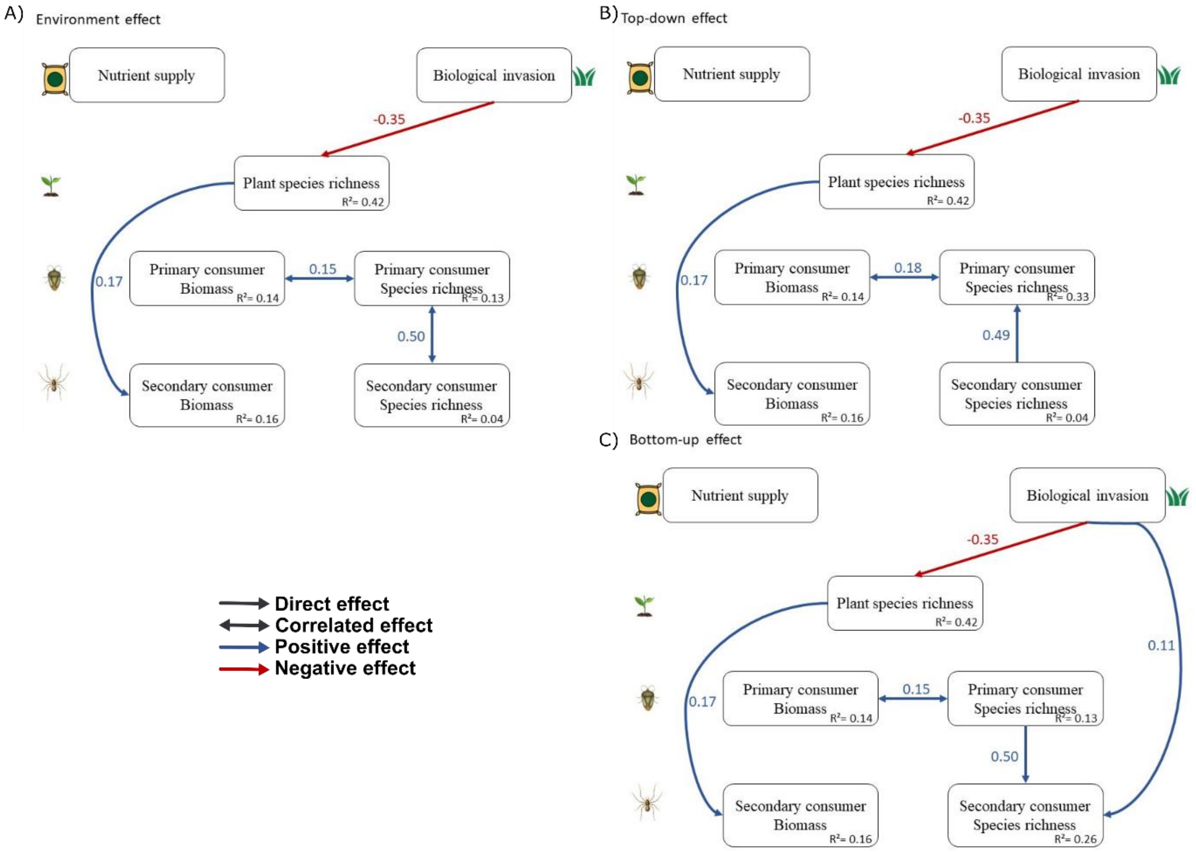

A) Environment effect
Nutrient supply
Biological invasion
-0.35
Plant species richness
R²= 0.42
0.17
Primary consumer Biomass
R²= 0.14
0.15
Primary consumer Species richness
R²= 0.13
0.50
Secondary consumer Biomass
R²= 0.16
Secondary consumer Species richness
R²= 0.04
B) Top-down effect
Nutrient supply
Biological invasion
-0.35
Plant species richness
R²= 0.42
0.17
Primary consumer Biomass
R²= 0.14
0.18
Primary consumer Species richness
R²= 0.33
0.49
Secondary consumer Biomass
R²= 0.16
Secondary consumer Species richness
R²= 0.04
C) Bottom-up effect
Nutrient supply
Biological invasion
-0.35
0.11
Plant species richness
R²= 0.42
0.17
Primary consumer Biomass
R²= 0.14
0.15
Primary consumer Species richness
R²= 0.13
0.50
Secondary consumer Biomass
R²= 0.16
Secondary consumer Species richness
R²= 0.26
Direct effect
Correlated effect
Positive effect
Negative effect

Figure 2

BIOLOGICAL INVASION, BUT NOT NUTRIENT SUPPLY, IMPACTS ARTHROPOD COMMUNITIES THROUGH BOTTOM-UP AND TOP-DOWN EFFECTS

Short running title: Nutrient Supply and Invasion Impact on Arthropod Communities

Reginaldo A. F. Gusmão[1] & Thiago Gonçalves-Souza[1,2*]

SUPPORTING INFORMATION

Figures

Figure S1. Photograph of the experimental module highlighting the forest matrix in which it is located.

Figure S2. Location (A-B) and experimental design (C-D). The experimental module is located in the semi-arid region of the state of Pernambuco/Brazil (A), more specifically in the Caatinga biome (B – Caatinga biome in brown and experimental site in green). The experimental site has 200 plots, in which, 48 plots were randomly selected (C). The 48 plots correspond to 6 replicates of each of the 8 treatments. The 8 treatments are: 4 nutrient addition treatments (*i.e.*, no addition, 0.5 g m-2, 2.5 g m-2, and 5.0 g m-2) in lower invasion plots and duplicates in higher invasion plots (D).

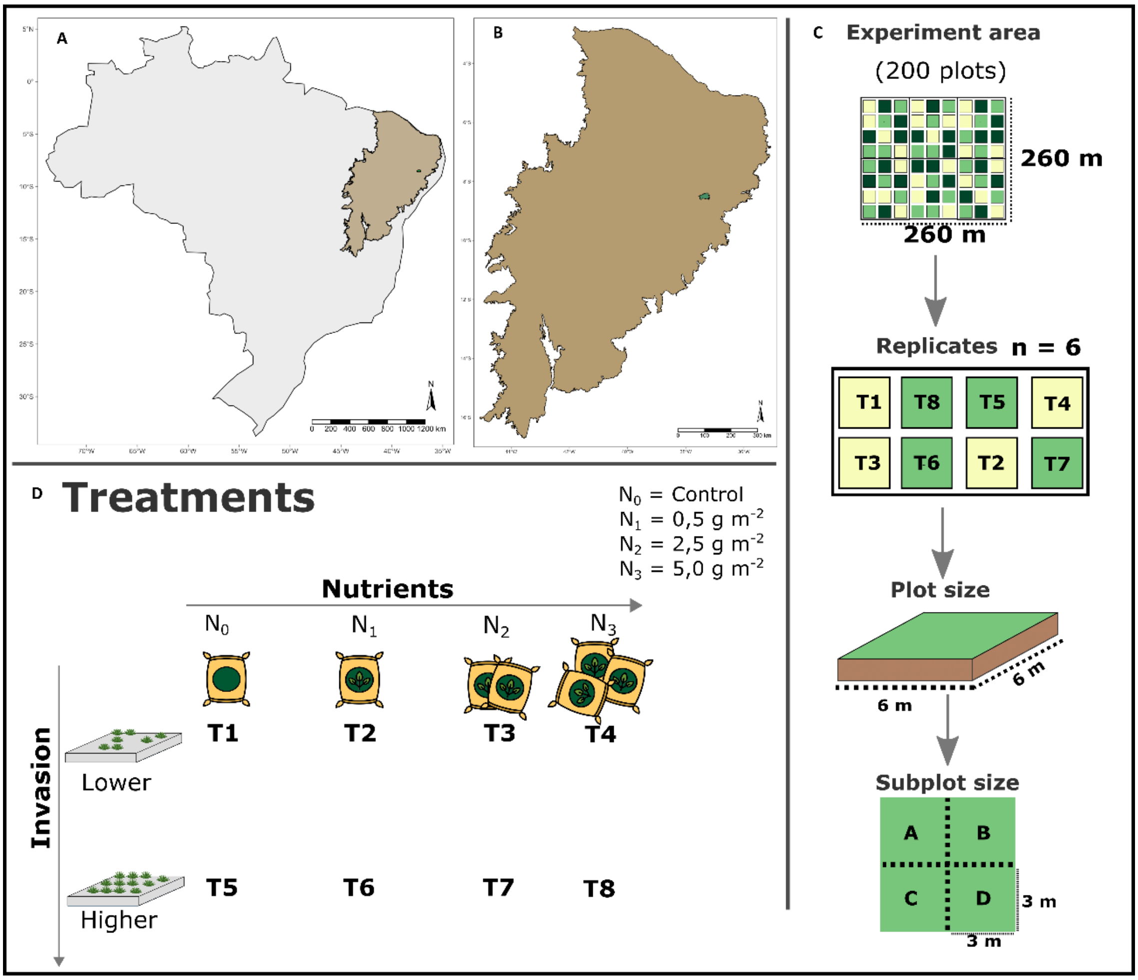
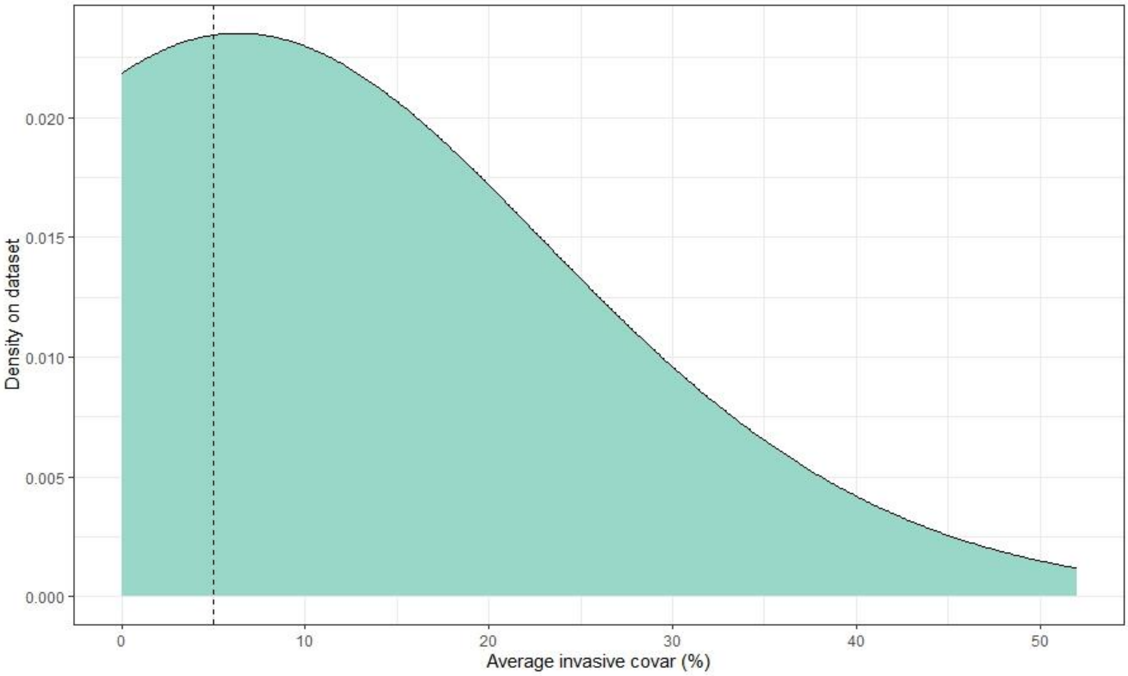


Figure S3. Density on dataset of invasive plant coverage in each.



Tables

Table S1. Details of the structural equation of pSEM to environmental, top-down, and bottom-up effect (see Table S2).

Effect	Response Variable	Predictor Variable	Fisher's C	p value	DF	R²
Enviroment	Plant Species Richness	Biological invasion + Addition of nutrient	2.75	0.599	4	0.42
	Primary consumer Species Richness	Biological invasion + Addition of nutriente + Plant species richness				0.13
	Primary consumer Biomass	Biological invasion + Addition of nutriente + Plant species richness				0.16
	Secondary consumer Species Richness	Biological invasion + Addition of nutriente + Plant species richness				0.04
	Secondary consumer Biomass	Biological invasion + Addition of nutriente + Plant species richness				0.16
Top-down	Plant Species Richness	Biological invasion + Addition of nutrient	3.54	0.472	4	0.42
	Primary consumer Species Richness	Biological invasion + Addition of nutriente + Plant + Secondary consumer species richness				0.33
	Primary consumer Biomass	Biological invasion + Addition of nutriente + Plant + Secondary consumer biomass				0.14
	Secondary consumer	Biological invasion + Addition of				0.04

	Species Richness	nutriente + Plant species richness				
	Secondary consumer Biomass	Biological invasion + Addition of nutriente + Plant species richness				0.16
Bottom-up	Plant Species Richness	Biological invasion + Addition of nutrient	8.16	0.086	4	0.42
	Primary consumer Species Richness	Biological invasion + Addition of nutriente + Plant species richness				0.13
	Primary consumer Biomass	Biological invasion + Addition of nutriente + Plant species richness				0.14
	Secondary consumer Species Richness	Biological invasion + Addition of nutriente + Plant + Primary consumer species richness				0.26
	Secondary consumer Biomass	Biological invasion + Addition of nutriente + Plant + Primary consumer biomass				0.16

Table S2. Details of relationship between variable responses and predictors obtained in the SEM models to environmental, top-down, and bottom-up effect.

Effect	**Response**	**Predictor**	**p value**	**Std. Estimate**
Environmental	**Plant Species richness**	**Biological invasion**	**<0.001**	**-0.35**
	Plant Species richness	Nutrient addition	0.349	-0.08
	Primary consumers biomass	Biological invasion	0.762	0.02
	Primary consumers biomass	Nutrient addition	0.603	0.03
	Primary consumers biomass	Plant species richness	0.526	-0.04
	Primary consumers species richness	Biological invasion	0.586	-0.03
	Primary consumers species richness	Nutrient addition	0.415	0.05
	Primary consumers species richness	Plant species richness	0.427	0.05
	Secondary consumers biomass	Biological invasion	0.743	0.02
	Secondary consumers biomass	Nutrient addition	0.581	0.03
	Secondary consumers biomass	**Plant species richness**	**0.005**	**0.17**
	Secondary consumers species richness	Biological invasion	0.108	0.10
	Secondary consumers specie richness	Nutrient addition	0.835	-0.01
	Secondary	Plant species richness	0.611	0.03

	consumers specie richness			
	~~ Secondary consumers specie richness	~~ Secondary consumers biomass	0.488	0.001
	~~ Primary consumers specie richness	**~~ Primary consumers biomass**	**0.004**	**0.15**
	~~ Primary consumers specie richness	**~~ Secondary consumers species richness**	**<0.001**	**0.50**
	~~ Primary consumers biomass	~~ Secondary consumers biomass	0.459	-0.006
Top-down	**Plant Species richness**	**Biological invasion**	**0.0001**	**-0.35**
	Plant Species richness	Nutrient addition	0.349	-0.08
	Primary consumers biomass	Biological invasion	0.762	0.02
	Primary consumers biomass	Nutrient addition	0.602	0.03
	Primary consumers biomass	Plant species richness	0.540	-0.04
	Primary consumers biomass	Secondary consumers biomass	0.942	-0.004
	Primary consumers species richness	Biological invasion	0.095	-0.09
	Primary consumers species richness	Nutrient addition	0.224	0.06
	Primary consumers species richness	Plant species richness	0.671	0.02
	Primary consumers species richness	**Secondary consumers species**	**<0.001**	**0.49**

		richness		
	Secondary consumers biomass	Biological invasion	0.743	0.02
	Secondary consumers biomass	Nutrient addition	0.581	0.03
	Secondary consumers biomass	**Plant species richness**	**0.005**	**0.17**
	Secondary consumers species richness	Biological invasion	0.108	0.10
	Secondary consumers specie richness	Nutrient addition	0.835	-0.01
	Secondary consumers specie richness	Plant species richness	0.611	0.03
	~~ Primary consumers specie richness	**~~ Primary consumers biomass**	**0.0007**	**0.18**
	~~ Primary consumers specie richness	~~ Primary consumers biomass	0.488	0.001
Bottom-up	**Plant Species richness**	**Biological invasion**	**<0.001**	**-0.35**
	Plant Species richness	Nutrient addition	0.349	-0.08
	Primary consumers biomass	Biological invasion	0.762	0.02
	Primary consumers biomass	Nutrient addition	0.603	0.03
	Primary consumers biomass	Plant species richness	0.526	-0.04
	Primary consumers	Biological invasion	0.586	-0.03

species richness			
Primary consumers species richness	Nutrient addition	0.415	0.05
Primary consumers species richness	Plant species richness	0.427	0.05
Secondary consumers biomass	Biological invasion	0.743	0.02
Secondary consumers biomass	Nutrient addition	0.580	0.03
Secondary consumers biomass	Plant species richness	0.005	0.17
Secondary consumers species richness	**Biological invasion**	**0.032**	**0.11**
Secondary consumers specie richness	Nutrient addition	0.489	-0.03
Secondary consumers specie richness	Plant specie richness	0.873	0.008
Secondary consumers specie richness	**Primary consumer species richness**	**<0.001**	**0.50**
~~ Primary consumers specie richness	**~~ Primary consumers biomass**	0.004	0.15
~~ Primary consumers specie richness	~~ Primary consumers biomass	0.239	0.04

CAPÍTULO 4: CONSIDERAÇÕES FINAIS

Principais conclusões e Avanços Teóricos:

Nesta tese, nós trazemos contribuições significativas para a compreensão das dinâmicas ecológicas em diferentes escalas e destacamos a importância da inclusão das caracteristicas das espécies para compreender suas respostas a mudanças ambientais. Além disso, observamos que as características das espécies a nivel de comunidade é independente destes dos fatores ambientais e da escala avaliada. Assim, demonstramos que a compreensão de forma mais mecanistica sobre influência dos fatores ambientais nas estruturas de comunidades pode direcionar predições sobre mudanças ambientais futuras.

Especificamente, no primeiro estudo, a síntese macroecológica revela padrões distintos nas respostas de tretapodes às variações climáticas, enfatizando a importância de considerar as características específicas das espécies. A distinção entre os efeitos diretos e indiretos do clima e sua relação com atributos como tamanho corporal e estrutura trófica aprimora as previsões realistas e mecanísticas, aperfeiçoando as teorias macroecológicas. Além disso, a consideração de múltiplos fatores ecológicos e de comunidade oferece uma visão mais completa e integrada dos padrões de diversidade em grupos taxonômicos distintos. No segundo estudo, destaca-se a identificação da adição de nutrientes como não tendo efeitos nas comunidades de artrópodes, enquanto a invasão biológica emerge como fator crucial na biomassa e riqueza de espécies de artrópodes predadores. A complexa interação entre invasores e espécies nativas, destacada pela competição por recursos, ressalta a importância da preservação da vegetação nativa para manter os níveis tróficos superiores. A análise de efeitos cascata da invasão biológica nos diferentes níveis tróficos, incorporando efeitos de cima para baixo e de baixo para cima, enriquece a compreensão das respostas do ecossistema a esse fenômeno.

Em suma, a tese apresenta avanços teóricos no campo da ecologia, sendo eles: a importância das características das espécies, proporcionando uma compreensão mais aprofundada das respostas da comunidade biologicas; distinção entre os efeitos diretos e indiretos dos fatores ambientais (i.e., clima contemporaneo, instabilidade climatica, invasão biologica e adição de nutrientes); explorar o papel dos atributos das espécies, como tamanho corporal e estrutura trófica, possibilitando previsões mais realistas e mecanísticas.

Limitações:

Ambos os estudos, no entanto, apresentam limitações importantes. No primeiro estudo, apesar da abordagem abrangente, as conclusões são baseadas em sínteses macroecológicas, e a validação desses padrões em escalas locais pode ser necessária para maior robustez. Ademais, a falta de consideração específica de certos atributos ecológicos pode limitar a generalização dos resultados. No segundo estudo, a análise das comunidades de artrópodes pode não capturar completamente a complexidade das interações em ecossistemas mais amplos, e a influência de outros fatores ambientais merece mais investigação. Em ambos os casos, essas limitações ressaltam a necessidade contínua de pesquisa para aprimorar e refinar as conclusões apresentadas.

Propostas de estudos futuros:

Com base nos avanços teóricos desenvolvidos nesta tese, apresentamos alguns direcionamentos para estudos futuros que poderiam aprofundar ainda mais nossa compreensão da ecologia e contribuir para a conservação dos ecossistemas naturais. Sendo essas sugestões:

1. Integração de Múltiplos Estudos Macroecológicos: Realizar uma síntese abrangente que integre dados de múltiplos, abordando diferentes grupos taxonômicos e ecossistemas. Além disso, pode ser adotada uma abordagem macroecologica para experimentos globais, tais como NutNet e DragNet.

2. Impacto de Invasões Biológicas em Diferentes Contextos Ecológicos: Investigar o impacto das invasões biológicas em diferentes contextos ecológicos, considerando variações nas características das espécies invasoras e as caracteristicas do ambiente. Isso poderia fornecer insights sobre estratégias de manejo adaptativas para minimizar os efeitos negativos das invasões.

3. Estudos Experimentais sobre Adição de Nutrientes: Realizar estudos experimentais mais detalhados para investigar os efeitos da adição de nutrientes em diferentes tipos de ecossistemas, levando em consideração os diferentes tipos de de solo, a presença de espécies específicas e as condições climáticas. Isso poderia esclarecer a importancia do tipo de solo como mediador do efeito da adição de nutrientes nas comunidades biologicas.

4. Dinâmica de Efeitos Cascata: Desenvolver modelos dinâmicos que simulem os efeitos cascata da invasão biológica nos diferentes níveis tróficos ao longo do tempo. Isso poderia ajudar na previsão de mudanças a longo prazo nos ecossistemas e na identificação de pontos críticos para intervenção.

5. Avaliação da Resiliência dos Ecossistemas:Avaliar a resiliência dos ecossistemas frente às variações climáticas, considerando não apenas as características das espécies, mas também a interação entre fatores climáticos, mudanças na vegetação nativa e possíveis perturbações antropogênicas.

Destcamos que essas sugestões representam apenas algumas das possíveis direções para estudos futuros, e a combinação de abordagens empíricas, experimentais e macroecologicas podem enriquecer ainda mais nosso entendimento das complexas interações ecológicas.