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Padrões e processos macroevolutivos na origem e diversificação de vertebrados terrestres da Floresta Atlântica

Matheus de Toledo Moroti

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Padrões e processos macroevolutivos envolvidos na origem e diversificação de vertebrados terrestres da Mata Atlântica

Matheus de Toledo Moroti

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Orientador: Dr. Diogo Borges Provete
Coorientador: Dr. Fernando Rodrigues da Silva

Banca avaliadora

Dra. Thaís Guedes,
Universidade Estadual de Campinas – UNICAMP

Dr. Gabriel Nakamura,
Texas A&M University

Dr. Renan Maestri,
Universidade Federal do Rio Grande do Sul - UFRGS

Dr. Gustavo Graciolli,
Universidade Federal do Mato Grosso do Sul - UFMS

Dr. Fabrício Villalobos
Instituto de Ecologia - INECOL

Dra. Carina Levi,
Universidade Federal de Jataí - UFJ

Dr. Rafael Guariento,
Universidade Federal do Mato Grosso do Sul - UFMS

“A guerra que nos reaproximou de nós
É a mesma que me pôs a repensar meus sonhos
O quanto neles era só publicidade?
Fazendo acreditar que eram meus próprios planos
Medo de fazer meus próprios planos serem
Nossos planos mesmo que eu tombe antes de vê-los
Agora vendo florescerem
Inevitavelmente eu sei que estarei lá
No dia que eles finalmente cheguem
Um dia desse eu tava meio cabreiro
Sem saber o que pode me acontecer
E não ver o fruto que eu plantei em algum janeiro
Mas tive um relampejo de que já estão aí
E a gente pode ser feliz agora mesmo
Apesar da batalha, o pente cheio
As tecnologias ancestrais nós temos
Pra induzir o sonho dentro de um pesadelo
Entre um traçante e outro
Dilatar o tempo e imaginar um mundo novo

***A única luta que se perde é a que se abandona** e nós nunca abandonamos a luta.*
*Hay que **endurecer sem nunca perder a ternura**”*

Don L, trecho de “Primavera”.

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Índice

Resumo geral

A Floresta Atlântica é um dos hotspots globais de biodiversidade devido ao grande número de espécies endêmicas sob alto grau de ameaça. Várias hipóteses têm sido propostas para explicar as causas da alta biodiversidade neste bioma, como a hipótese dos refúgios. Por outro lado, barreiras de dispersão e especiação alopátrica parecem ser importantes para determinar a diversidade genética em algumas espécies. No entanto, ainda não existe consenso sobre a importância relativa destes processos ou como eles variam ao longo do espaço e entre organismos com diferentes habilidades de dispersão e tolerância térmica. Logo, iniciativas que integram abordagens de áreas como ecologia, macroevolução e evolução fenotípica podem contribuir para melhorar o entendimento sobre os processos chave envolvidos na formação da biota da Floresta Atlântica. O objetivo dessa tese foi identificar os processos macroevolutivos envolvidos na origem e diversidade de vertebrados terrestres da Floresta Atlântica. A tese está dividida em dois capítulos: o primeiro intitulado "*Productivity interacts with diversification rate in determining species richness and trait diversity of tetrapods in a global hotspot*" e o segundo "*The effects of climatic niche on the rate of body size evolution in terrestrial vertebrates*". No primeiro capítulo estávamos interessados em investigar quais variáveis das dinâmicas de equilíbrio (topografia, clima e produtividade primária) e de não-equilíbrio (taxa de diversificação e idade da assembleia) explicam a riqueza de espécies e a diversidade funcional dos quatro clados de vertebrados terrestres (anfíbios anuros, répteis squamata, aves e mamíferos não-voadores) na Floresta Atlântica. Também investigamos se ospadrões espaciais são congruentes entre os grupos. Encontramos que a riqueza de espécies e a diversidade funcional têm os mesmos preditores nas linhagens de vertebrados, mas operam de maneira diferente no espaço. A diversidade de clados não foi afetada pelo tempo de especiação, enquanto a taxa de diversificação teve uma grande influência positiva na diversidade funcional e na riqueza de espécies. Nossos resultados reforçam a necessidade de avaliar múltiplos táxons ao testar explicações alternativas para padrões de diversidade. No segundo capítulo, estávamos interessados em testar se a taxa de evolução do tamanho do corpo de vertebrados terrestres é impactada pelo nicho climático. Encontramos que os vertebrados terrestres apresentam padrões idiossincráticos de evolução fenotípica ao longo do tempo, com algumas linhagens acelerando e outras desacelerando suas taxas evolutivas. Além disso, não encontramos uma relação significativa entre as taxas de evolução fenotípica e o nicho climático. No entanto, a

amplitude influencia mais a variação das taxas do que a sua posição do nicho. Esses resultados ressaltam a importância das pressões seletivas e das características específicas de cada grupo na evolução fenotípica. Ainda, é possível que diferentes eixos do nicho ecológico das espécies impactem as taxas evolutivas do tamanho do corpo nos vertebrados terrestres. Juntos, esses capítulos fornecem uma visão mais completa dos processos que moldaram a biota da Floresta Atlântica, abrangendo tanto aspectos macroecológicos quanto macroevolutivos das comunidades de vertebrados terrestres. Nossas descobertas têm implicações para nossa compreensão dos impulsionadores de biodiversidade e das mudanças evolutivas nas taxas fenotípicas de vertebrados, assim como dos fatores que moldam os padrões de biodiversidade em escalas regionais.

General abstract

The Atlantic Forest is one of the global hotspots of biodiversity due to the high number of endemic species under a high degree of threat. Several hypotheses have been proposed to explain the causes of high biodiversity in this biome, such as the refuge hypothesis. On the other hand, barriers to dispersal and allopatric speciation seem to be important in determining genetic diversity in some species. However, there is still no consensus on the relative importance of these processes or how they vary across space and among organisms with different dispersal abilities and thermal tolerance. Therefore, initiatives that integrate approaches from areas such as ecology, macroevolution, and phenotypic evolution can contribute to a better understanding of the key processes involved in the formation of the Atlantic Forest biota. The objective of this thesis was to identify the macroevolutionary processes involved in the origin and diversity of terrestrial vertebrates in the Atlantic Forest. The thesis is divided into two chapters: the first entitled "*Productivity interacts with diversification rate in determining species richness and trait diversity of tetrapods in a global hotspot*" and the second "*The effects of climatic niche on the rate of body size evolution in terrestrial vertebrates*". In the first chapter, we were interested in investigating which variables from equilibrium dynamics (topography, climate, and primary productivity) and non-equilibrium dynamics (diversification rate and assemblage age) explain species richness and functional diversity of the four clades of terrestrial vertebrates (anuran amphibians, squamata reptiles, birds and non-volant mammals) in the Atlantic Forest. We also investigated whether their spatial patterns are congruent among the groups. We found that species richness and functional diversity have the same predictors in vertebrate lineages but operate differently in space. The clade diversity was not affected by speciation time, while diversification rate had a strong positive influence on functional diversity and species richness. Our results emphasize the need to evaluate multiple taxa when testing alternative explanations for diversity patterns. In the second chapter, we were interested in testing whether the rate of body size evolution in terrestrial vertebrates is impacted by the climatic niche. We found that terrestrial vertebrates exhibit idiosyncratic patterns of phenotypic evolution over time, with some lineages accelerating and others decelerating their evolutionary rates. Additionally, we did not find a significant relationship between phenotypic evolution rates and the climatic niche. However, amplitude influences the variation in rates more than niche position. These results highlight the importance of selective pressures and specific characteristics

of each group in phenotypic evolution. Furthermore, it is possible that different axes of the species' ecological niche impact the evolutionary rates of body size in terrestrial vertebrates. Together, these chapters provide a more complete view of the processes that shaped the Atlantic Forest biota, encompassing both macroecological and macroevolutionary aspects of terrestrial vertebrate communities. Our findings have implications for our understanding of the drivers of biodiversity and evolutionary changes in vertebrate phenotypic rates, as well as the factors that shape biodiversity patterns at regional scales.

Introdução geral

A Floresta Atlântica é a segunda maior floresta tropical da América do Sul, abrangendo uma área de 1.6 milhões de hectares (Muylaert et al., 2018). Essa floresta tropical também é conhecida por ser uma das regiões mais biodiversas do planeta, sendo considerada um dos 35 *hotposts* globais de interesse em conservação com uma alta riqueza de espécies endêmicas (Mittermier et al., 2011; Marques et al., 2021). Originalmente, a Floresta Atlântica se estendia da costa nordeste do Brasil até o norte do Paraguai e Argentina (Ribeiro et al., 2009) cobrindo uma extensa área latitudinal (3ºS-30ºS), longitudinal (35º-60ºW) e com variações acentuadas na altitude (0-2900m do nível do mar). Essa heterogeneidade reflete em um elevado gradiente climático, com áreas de menor (1000 mm) e maior precipitação (4200 mm), contribuindo para a formação de uma grande variedade de fisionomias florestais, como florestas ombrófilas, semidecíduas, decíduas, manguezais, pântanos, restingas, campos rupestres em grandes altitudes entre outras formações (revisado em Marques et al., 2021).

Diversas evidências palinológicas e filogeográficas apontam conexões entre a Floresta Amazônica e a Mata Atlântica no passado, como as que ocorreram no Último Máximo Glacial no período do Quaternário, a aproximadamente 25 a 33 mil anos atrás (Sobral-Souza et al., 2015). As conexões passadas dessas florestas ocorreram como resultado de flutuações climáticas, fazendo com que a formação dessa floresta possua uma complexa história evolutiva (Carnaval & Moritz, 2008; Sobral-Souza et al., 2015). Essas conexões facilitaram a dispersão de muitas linhagens e o isolamento de outras, contribuindo diretamente para a formação de comunidades em florestas ripárias na Diagonal Seca (Cabanne et al., 2011; Sobral-Souza et al., 2015) e a colonização e extinção de espécies ao longo do gradiente climático e espacial da Floresta Atlântica. Portanto, a formação desse domínio parece ser o resultado da dinâmica geológica das florestas tropicais da América do Sul, com acentuada contribuição do conjunto de espécies que colonizaram a Floresta Atlântica nos últimos 20 mil anos (Marques et al., 2021).

Diferentes estudos têm apontado mecanismos envolvidos na formação e origem da alta diversidade de espécies da Floresta Atlântica (revisados em Dantas et al., 2011, Batalha-Filho & Miyaki, 2011, da Silva et al., 2011). Atualmente, existem ao menos três hipóteses não excludentes para explicar a diversificação de espécies no domínio: (1) Refúgios do Plio-Pleistoceno, que consistiram em fragmentos florestais que ficaram isolados durante as flutuações climáticas que ocorreram ao longo do tempo, levando à acumulação de novas linhagens nessas áreas (Ab'Saber, 1979) e formação de centros de endemismo (Carnaval & Moritz, 2008); (2) Soerguimento de montanhas e rios que podem atuar como barreiras geográficas, ou até como agentes de modificações na paisagem. Essa hipótese está alinhada com a ideia de que o surgimento de montanhas como a Serra do Mar no sudeste do Brasil, além de atuarem como barreiras também modificariam o clima e potencialmente criaram condições para diversificação das linhagens (Simpson, 1953). Além disso, rios de grande porte como o rio São Francisco, rio Doce, rio Parapanema poderiam isolar reprodutivamente as populações promovendo especiação alopátrica (e.g. Menezes et al., 2016). Por fim (3) a hipótese de gradientes ecológicos que diz que a transição gradual entre florestas úmidas e secas criam regimes de seleção (e.g., Cabanne et al., 2011), podendo promover divergência e consequentemente especiação parapátrica. Embora essas hipóteses sejam comumente utilizadas para explicar a biodiversidade da Floresta Atlântica em largas escalas espaciais, processos de diversificação podem variar entre linhagens (Buckley et al., 2012; Rolland et al., 2018), e ainda não há um estudo que vise integrar linhas de evidências distintas e de diferentes grupos para determinar as causas dessa alta biodiversidade.

A macroecologia e a macroevolução se concentram em identificar padrões e processos que ocorrem em escalas geográficas e temporais amplas, usando ferramentas estatísticas para compreender a distribuição e a evolução da biodiversidade a partir de uma perspectiva integrativa (Keith et al., 2012). A macroecologia, como linha de pesquisa, surgiu há mais de duas décadas em resposta as explicações baseadas em processos locais e em pequenas escalas que visavam entender as causas da distribuição das espécies (Gaston and Blackburn, 2000). Processos locais podem ser dominados por respostas das espécies a pressões seletivas específicas a essa área, o que pode não refletir a dinâmica mais ampla da biodiversidade em diferentes regiões. Portanto, uma abordagem macroecológica pode ser útil para identificar como diferentes mecanismos evolutivos moldaram a biodiversidade na Mata Atlântica ao longo do tempo, identificando radiações adaptativas, processos de especiação e extinção que moldaram a diversidade de espécies na região (Gaston and Blackburn, 2000). Além disso, em uma mesma área geográfica, onde as variações históricas e contemporâneas relacionadas à geologia e às condições climáticas atuam como modelo geográfico para todos os grupos biológicos, é possível detectar como as diferenças de história de vida dos grupos podem responder aos diferentes processos espaciais e temporais. Por exemplo, a distribuição da riqueza em anfíbios, mamíferos terrestres e aves atinge o pico na porção central e costeira da Mata Atlântica, especialmente na região da Serra do Mar (Figueiredo et al., 2021). A maior riqueza de répteis também está na porção central, porém mais interna do continente (Figueiredo et al., 2021). Esses padrões espaciais podem também diferir em outras facetas da biodiversidade (e.g., funcional e filogenética), influenciadas por diferentes mecanismos evolutivos (e.g., Oliveira et al., 2016). Por essa complexidade, a Floresta Atlântica pode ser considerada um bom modelo para responder questões macroecológicas e macroevolutivas sobre os processos responsáveis por gerar a biodiversidade, e como diferentes grupos com capacidades fisiológicas distintas (endotérmicos e ectotérmicos).

As espécies diferem em suas capacidades fisiológicas, que por sua vez influenciam atributos de história de vida (Mammola et al., 2021). Por exemplo, o comportamento de ectotérmicos é diferente dos endotérmicos em temperaturas extremas devido às diferenças na capacidade de termorregulação (Rolland et al., 2018; Gouveia et al., 2019). Logo, isso poderia limitar a dispersão de linhagens de vertebrados de maneira diferente (Buckley et al., 2012). Avaliar apenas a riqueza nesse contexto pode mascarar padrões e processos na montagem das comunidades que estão mais relacionados ao nicho ecológico (Hutchinson, 1957) do que com a identidade taxonômica. Medidas da biodiversidade que forneçam uma medida mais acurada do espaço do nicho, tais como diversidade funcional (Weiher, 2011, Violle et al., 2007) podem ajudar a desvendar padrões de biodiversidade em larga escala. Por exemplo, em escala global, a riqueza de mamíferos está mais relacionada com variáveis climáticas, enquanto a diversidade funcional é mais afetada pelo tempo evolutivo (Oliveira et al., 2016). No entanto, estas questões na Floresta Atlântica têm sido geralmente investigadas utilizando riqueza de espécies, enquanto facetas alternativas da biodiversidade, tais como as diversidades funcional e filogenética, têm sido pouco exploradas (Violle et al., 2014). Logo, a Floresta Atlântica e sua complexa formação constituem um modelo de estudo importante para integrar diferentes facetas da biodiversidade (funcional e taxonômica), comparando como cada grupo biológico responde aos mecanismos ecológicos e evolutivos envolvidos na estruturação das comunidades.

Assim como os padrões de distribuição da biodiversidade, diversos fatores bióticos e abióticos podem determinar a taxa de variação fenotípica em escalas macroevolutivas (Harmon, 2017). O tamanho corporal, por exemplo, é um dos atributos mais importantes na sobrevivência de um organismo, com requisitos fisiológicos e ecológicos podendo ser determinados por ele (Peters, 1986). Por essa razão, é esperado que endotérmicos e ectotérmicos possam apresentar diferenças na evolução desse atributo, uma vez que apresentam tolerâncias térmicas distintas (Buckley et al., 2012; Rolland et al., 2018), além de poder apresentar diferenças marcantes na distribuição desse atributo pela Floresta Atlântica devido a severidade climática presente na região (e.g. Millien et al., 2006). Enquanto essas questões têm sido avaliadas em escala global ou utilizando linhagens específicas, pouco se sabe como condições ambientais (e.g., sazonalidade de temperatura e precipitação) podem ter moldado o nicho climático de linhagens que ocorrem em biomas climaticamente complexos e influenciado taxas de evolução de atributos ecologicamente relevantes como o tamanho de corpo. Dessa forma, investigar como o tamanho do corpo evoluiu em espécies que ocorrem em uma mesma região como a Floresta Atlântica pode lançar luz sobre os processos envolvidos na diversificação de fenótipos e consequentemente na formação do seu pool de espécies. Semelhantemente, entender como a relação entre fenótipo e ambiente varia em escala macroevolutiva pode lançar luz sobre mecanismos que regulam a adaptação de linhagens aos seus hábitats (Harmon, 2017).

Portanto, o objetivo geral da tese é investigar os mecanismos macroevolutivos envolvidos na origem e diversidade dos vertebrados terrestres na Floresta Atlântica. Foram analisados dados de ecologia funcional, identidade taxonômica e relações filogenéticas para identificar fatores históricos e climáticos que influenciaram a diversificação e a evolução fenotípica dos vertebrados terrestres. Essa abordagem integrada nos permitirá compreender os processos ecológicos e evolutivos que moldaram a riqueza de espécies e as características dos vertebrados terrestres na Floresta Atlântica, contribuindo para o conhecimento e a conservação desse bioma diverso que abriga a maior parcela da população brasileira. Especificamente, esta tese está dividida em dois capítulos: 1) "*Productivity interacts with diversification rate in determining species richness and trait diversity of tetrapods in a global hotspot*" submetido para o periódico *Global Ecology and Biogeography*; e 2) "*Effects of climatic niche on the rate of body size evolution in terrestrial vertebrates*" em preparação para submissão ao periódico *Evolution*.

Referências

Ab'Saber, A.N. (1979). Geomorfologia e espeleologia. Espeleo-Tema, nº12. ANAIS do 12º Congresso Brasileiro de Espeleologia

Batalha-Filho, H., & Miyaki, C.Y. (2011). Filogeografia da Mata Atlântica. *Revista da Biologia*, **7**, 31–34.

Buckley, L.B., Hurlbert, A.H., & Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, **21**, 873–885.

Cabanne, G.S., D'Horta, F.M., Meyer, D., Silva, J.M., & Miyaki, C.Y. (2011). Evolution of *Dendrocolaptes platyrostris* (Aves: Furnariidae) between the South American open vegetation corridor and the Atlantic forest. *Biological Journal of the Linnean Society,* **103**(4), 801–820.

Carnaval, A.C., & Moritz, C. (2008). Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography*, **35**(7), 1187–1201.

Da Silva, M.B., Pinto-da-Rocha, R., & De Souza, A.M. (2011). História biogeográfica da Mata Atlântica: opiliões (Arachnida) como modelo para sua inferência. In *Biogeografia da América do Sul - Padrões e Processos*. Roca, São Paulo, 221–238.

Dantas, G.P.M., Cabanne, G.S., & Santos, F.R. (2011). How past vicariant events can explain the Atlantic Forest biodiversity. *Ecosystems Biodiversity*, 429–442.

Figueiredo, M.D.S.L., Weber, M.M., Brasileiro, C.A., Cerqueira, R., Grelle, C.E., Jenkins, C.N., ... & Lorini, M.L. (2021). Tetrapod diversity in the Atlantic Forest: maps and gaps. In *The Atlantic Forest: History, Biodiversity, Threats and Opportunities of the Mega-diverse Forest,* Springer, São Paulo, 185–204.

Gouveia, S.F., Bovo, R.P., Rubalcaba, J.G., Da Silva, F.R., Maciel, N.M., Andrade, D.V., & Martinez, P.A. (2019). Biophysical modeling of water economy can explain geographic gradient of body size in anurans. *The American Naturalist*, **193**(1), 51–58.

Hutchinson, F. (1957). The distance that a radical formed by ionizing radiation can diffuse in a yeast cell. *Radiation Research*, **7**(5), 473–483.

Mammola, S., Carmona, C.P., Guillerme, T., & Cardoso, P. (2021). Concepts and applications in functional diversity. *Functional Ecology*, **35**(9), 1869–1885.

Marques, M.C., Trindade, W., Bohn, A., & Grelle, C.E. (2021). The Atlantic Forest: an introduction to the megadiverse forest of South America. In *The Atlantic Forest: History, Biodiversity, Threats and Opportunities of the Mega-diverse Forest*, Springer, São Paulo, 3–23.

Menezes, L., Canedo, C., Batalha-Filho, H., Garda, A. A., Gehara, M., & Napoli, M. F. (2016). Multilocus phylogeography of the treefrog *Scinax eurydice* (Anura, Hylidae) reveals a plio-pleistocene diversification in the Atlantic Forest. *PLoS One*, **11**(6), e0154626.

Millien, V., Lyons, S.K., Olson, L., Smith, F.A., Wilson, A.B., & Yom-Tov, Y. (2006). Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters*, **9**(7), 853–869.

Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M. & Gascon, C. (2011). Global biodiversity conservation: the critical role of hotspots. *Biodiversity hotspots*, Springer, 3–22

Muylaert, R.L., Vancine, M.H., Bernardo, R., Oshima, J.E.F., Sobral-Souza, T., Tonetti, V.R., Niebuhr, B.B. & Ribeiro, M.C. (2018). Uma nota sobre os limites territoriais da Mata Atlântica. *Oecologia Australis*, **22**(3), 302–311.

Oliveira, B.F., Machac, A., Costa, G.C., Brooks, T.M., Davidson, A.D., Rondinini, C., & Graham, C.H. (2016). Species and functional diversity accumulate differently in mammals. *Global Ecology and Biogeography*, **25**(9), 1119–1130.

Peters, R.H. (1986). *The ecological implications of body size*. Cambridge: Cambridge university press.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., & Hirota, M.M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological conservation*, **142**(6), 1141–1153.

Rolland, J., Silvestro, D., Schluter, D., Guisan, A., Broennimann, O., & Salamin, N. (2018). The impact of endothermy on the climatic niche evolution and the distribution of vertebrate diversity. *Nature Ecology and Evolution*, **2**, 459–464.

Sobral-Souza, T., Lima-Ribeiro, M.S., & Solferini, V.N. (2015). Biogeography of Neotropical Rainforests: past connections between Amazon and Atlantic Forest detected by ecological niche modeling. *Evolutionary Ecology*, **29**, 643–655.

Simpson, G.G. (1953). *The Major Features of Evolution*. Columbia University Press.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. *Oikos* **116**, 882–892.

Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J., & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences*, **111**(38), 13690–13696.

Weiher, E. 2011. A primer of trait and functional diversity. In *Biological diversity: frontiers in measurement and assessment*. Oxford University Press, Oxford, 175–193

Productivity interacts with diversification rate in determining species richness and trait diversity of tetrapods in a global hotspot

Matheus de Toledo Moroti[1,2], Alexander Skeels[3,4], Fernando R. Da Silva[5], Diogo B. Provete[2,6*]

[1] Pós-Graduação em Ecologia e Conservação, Instituto de Biociências, Universidade Federal do Mato Grosso do Sul, Campo Grande, Mato Grosso do Sul, Brazil.

[2] Instituto de Biociências, Universidade Federal do Mato Grosso do Sul, Campo Grande, Mato Grosso do Sul, 79002-970, Brazil.

[3] Landscape Ecology, Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zürich, Zürich, CH-8092, Switzerland.

[4] Swiss Federal Research Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, CH-8903, Switzerland.

[5] Laboratório de Ecologia Teórica: Integrando Tempo, Biologia e Espaço (LET.IT.BE), Departamento de Ciências Ambientais, Universidade Federal de São Carlos, Sorocaba, São Paulo, Brazil.

[6] Gothenburg Global Biodiversity Centre, Box 100, S-405 30, Göteborg, Sweden.

*Corresponding author: diogo.provete@ufms.br

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Author’s contribution statement

DBP and FRS conceived the study. MTM obtained all data, conducted data analysis, and wrote the first version of the manuscript. AS contributed to the final version of the text and gave input on figure presentation and data analysis.

Conflict of Interest Statement

Authors declare they have no conflict of interest.

Data Availability Statement

All data and associated R scripts are available at https://github.com/mmoroti/biogeo_vertebrates and https://doi.org/10.6084/m9.figshare.19735552.v1

Productivity interacts with diversification rate in determining species richness and trait diversity of tetrapods in a global hotspot

Short title: Terrestrial vertebrates drivers in the Atlantic Forest

Abstract

Aim

The effects of equilibrium and non-equilibrium dynamics on generating biodiversity patterns are generally investigated using species richness of a single biological group. However, little is known about how these two classes of processes affect trait diversity and richness of multiple taxa within the same geographical region. Here, we evaluated which variables representing equilibrium (topography, climate, and primary productivity) and non-equilibrium (diversification rate and assemblage age) dynamics best explain species richness and trait diversity of four vertebrate clades in a global hotspot. We also investigated whether their spatial patterns are congruent between groups.

Location

Atlantic Rainforest

Time period

Contemporary.

Major taxa studied

Terrestrial vertebrates.

Methods

We tested whether trait diversity, species richness, diversification rate, and assemblage age between groups are spatially correlated. In addition, we estimated functional dispersion as a measure of trait diversity. After that, we used spatially explicit structural equation model based on Generalised Least Square models to test how species richness and trait diversity are influenced by variables representing equilibrium and non-equilibrium mechanisms.

Results

Diversification rate positively influenced both species richness and trait diversity, while productivity was both a direct and an indirect negative driver of species richness and trait diversity. Furthermore, we observed a consistent pattern of distribution of species richness between the two endotherm groups, as well as between endotherms and ectotherms, but we did not find this same pattern between the two ectotherm groups. In contrast, the spatial distribution of trait diversity, assemblage age, and diversification rate was distinct for each group.

Main conclusions

Species richness and trait diversity have the same predictors across tetrapod lineages but show diferente patterns in space. In contrast to a recent synthesis, diversity of younger clades was not affected by time-for-speciation, whereas diversification rate had a major positive influence on both trait diversity and species richness across tetrapods. Our results reinforce the need to evaluate multiple taxa when testing alternative explanations for diversity patterns.

Keywords: Brazilian Atlantic Forest, community assembly, equilibrium dynamics, macroecology, Functional traits, non-equilibrium dynamics, time-for-speciation.

Introduction

Geographical gradients of species richness and trait diversity are fundamentally determined by speciation, extinction, dispersal and trait evolution (Ricklefs, 2004, 2006; Wiens & Donoghue, 2004). These four fundamental processes are in turn influenced by environmental, ecological, and evolutionary factors, such as the time for speciation, frequency of colonization of regions, or the biotic or abiotic selection dynamics of the environment (reviewed in Li & Wiens, 2019). These factors are not mutually exclusive and may interact with each other to explain species distribution at broad scales. The relative roles of macroevolutionary processes, such as time-for-speciation effect (Wiens & Donoghue, 2004) and environmental constraints in dictating diversity gradients are often interpreted under the lens of equilibrium and non-equilibrium dynamics (Rhode, 2006; Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015; Pontarp & Wiens, 2017).

Currently, there are two classes of mechanisms pointed out as opposing explanations to explain patterns of biodiversity, known as equilibrium (review in Rabosky & Hurlbert, 2015) and non-equilibrium dynamics (review in Harmon & Harrison, 2015). Under equilibrium dynamics, features of the present-day environment, and specifically the amount of resource availability (such as net primary productivity) or resource diversity (such as environmental heterogeneity), are expected to be the strongest predictors of species and trait diversity (Rhode, 2006; Rabosky & Hurlbert, 2015). This is because more resources, or kinds of resources, can facilitate differentiation of resource-use between species, driving speciation, ecological divergence, and allowing more species to colonize the area and coexist (Rhode, 2006). Also, climatically stable areas can allow the long-term persistence of species, reducing extinction rates and increasing species richness (Rolland et al., 2018). Therefore, environmental conditions set ecological limits and opportunities for niche partitioning, dictating the maximum number of species a region can support (Rhode, 2006; Rabosky & Hurlbert, 2015). As a result, speciation and extinction dynamics would be controlled by factors like environmental carrying capacity and interspecific competition that could decouple species richness from assemblage age or diversification rate (Rabosky, 2013). Yet regions do not only differ in present-day measures of resource diversity and availability, they also differ in their geological and environmental histories, which may determine the presence or absence of factors driving speciation, extinction, and colonization dynamics through deep-time (Ricklefs, 2004; 2006). Under non-equilibrium dynamics, species and trait diversity within regions should be more closely related to the historical dynamics that shape the accumulation of species and divergence of traits relative to other regions (Ricklefs, 2004; 2006; Harmon & Harrison 2015), such as a greater time-for-speciation (Wiens, 2011) or a faster rate of lineage diversification or trait evolution, than to the present-day environment. Consequently, species richness on a continental scale would be subjected to stochastic dynamics that constantly change the limits of species and environmental carrying capacity (Harmon & Harrison, 2015). While these two views are not necessarily exclusive (Pontarp & Wiens 2017), studies investigating their relative support in explaining present-day biodiversity gradients have shown mixed results (e.g., Oliveira et al., 2016). Furthermore, most studies investigating the relative importance of these dynamics focus on single clades and species richness (Li & Wiens, 2019). Consequently, the strength of equilibrium and non-equilibrium dynamics in explaining different facets of biodiversity, such as variation in trait diversity and richness patterns, is unclear. Disentangling the relative importance of these two dynamics is one of the key questions at the interface between macroecology and macroevolution (McGill et al., 2019), providing a multifaceted understanding of species diversity.

The relative importance of equilibrium vs. non-equilibrium dynamics may vary depending on ecological traits that determine resource use and physiological tolerances to environmental variation, including metabolic rates, thermoregulatory modes, and dispersal ability (Buckley et al., 2012). Hence, traits can better represent niche axes of species and how they respond to environmental variation (Violle et al., 2014). For example, body size is directly related to metabolic capacity in ectotherms and endotherms (Peters, 1986). Likewise, diel activity affects foraging patterns in birds and mammals, and is related to risk of desiccation in ectotherms, especially in amphibians (Kronfeld-Schor et al., 2001). Ectotherms also typically have narrower environmental tolerances and more selective habitat preferences, which leads to slower rates of climatic niche evolution, smaller geographic ranges, and narrower latitudinal and elevational ranges (Rolland et al., 2018). In addition, ectotherms generally have lower dispersal capacity (Buckley et al., 2012; Rolland et al., 2018), which in combination with narrow environmental preferences, could mean that these species are less able to colonise new regions or novel habitats through time. This could make ectotherms more susceptible to environmental stochasticity, climate changes and more dependent on climatic refuges (Carnaval et al., 2009), which would increase rates of extinction though range collapse, or increase rates of speciation through range fragmentation (Li & Wiens, 2022), leading to different patterns of species distributions (e.g., Schweizer et al., 2014; MacDougall et al., 2019). In ectotherms, activity time is limited by available environmental energy, while endotherms can remain highly active if resource consumption meets their metabolic demands (Buckley et al., 2012). As a result, endotherms require more resources than ectotherms to thermoregulate, particularly in colder environments (Clarke & Gaston, 2006). Therefore, it is expected that highly productive regions could harbour a greater number of endotherm species due to the greater supply of resources, as well as a great diversity of ecological niches to be explored (Oliveira et al., 2016). Therefore, fundamental metabolic and dispersal constraints between ectotherms and endotherms may drive differences in resource use and niche partitioning under an equilibrium model and rates of diversification and/or occupation times under a non-equilibrium model. Trait diversity provides a better estimation of the variety of ecological strategies found in a region than species richness (Violle et al., 2014), while also allowing the comparison of different groups based on a common element. As such, trait diversity could more efficiently capture the underlying processes related to the species' ecological niche. Therefore, it is a useful approach to identify the causes of the dynamics that regulate the variation of species biodiversity in space.

In a geographic area, where historical and contemporary variations related to geology and climate conditions create a single region for all biological groups, it is possible to detect how species and trait diversities of ectotherms and endotherms are determined by equilibrium and non-equilibrium dynamics. The Brazilian Atlantic Forest harbours an outstanding diversity and endemism of terrestrial vertebrate species (Figueiredo et al., 2021). Due to its wide latitudinal (from 5 to 33° S) and longitudinal (from 35 to 55° W) ranges, the Atlantic Forest is a heterogeneous environment that varies in climatic gradients, such as annual rainfall (from 800 to 4,000 mm), mean annual temperature (from 15 to 25 °C), and topography (from sea level to 2,200 m a.s.l.). Species richness in amphibians, terrestrial mammals, and birds peak in the highly productive central and coastal portion of the Atlantic Forest, especially in the Serra do Mar mountain range (Vasconcelos et al., 2019; Figueiredo et al., 2021). It is possible that this disjunct distribution is related to differences related to the regional microclimate that this region has. While the Serra do Mar is a more humid region, the region in contact with the Cerrado is drier and hotter throughout the year (Figueiredo et al., 2021). This suggests that environmental productivity could be a major determinant of species diversity. However, while reptiles also present greater richness in this region, they are closer to the region of contact with dry savannas in the inner part of the continent (Figueiredo et al., 2021). In addition to present-day climatic differences, historical climate change was important in shaping species distributions in a geographical region. For example, phylogeographic studies have found high genetic diversity in frogs (Carnaval et al., 2009), birds and lizards in the central region of the Atlantic Forest (reviewed in Peres et al., 2020), which was more climatically stable during the Pleistocene. Further, there is evidence of recent colonization and population expansion in areas that were less stable in the past, such as the southern portion (reviewed in Peres et al., 2020), indicating that past climate conditions might be associated with species geographic range expansion and extinction, thereby regulating the size and composition of regional species pools (Benício et al., 2021). Thus, its exceptional biodiversity, marked climatic gradients and dynamic climatic history, make the Atlantic Forest biome an excellent model for understanding the spatial distribution patterns of multiple diversity components for different taxa within the same geographical region. With this, add new evidence to the dynamics classified as equilibrium vs. non-equilibrium.

Here, we evaluated the relative importance and spatial congruence of variables representing equilibrium and non-equilibrium dynamics explaining variation in species richness and trait diversity of terrestrial vertebrates in the Atlantic Forest. Specifically, we tested (1) how species richness and trait diversity are related to assemblage age, diversification rate, productivity, climate, and topographical heterogeneity (Figure 1). Under an equilibrium model, we predict that species or trait diversity will be positively, and directly, related to climate, productivity, or topographical heterogeneity, as these factors set ecological limits on biodiversity (green lines in Figure 1a; Rabosky & Hurlbert, 2015). Areas with more stable climates have higher carrying capacity that supports more species (Rabosky & Hurlbert, 2015). Climatic variables determine range limits in vertebrates (e.g., Wiens et al., 2006; Botero et al., 2014), and potentially influence large-scale species distributions (Hua & Wiens, 2013). High productivity and resource availability can sustain more individuals, more viable populations, and more species (i.e., the “more individuals” hypothesis; Brown, 1981). Similarly, areas with greater elevational heterogeneity have greater habitat complexity, at the same time which imposes barriers to dispersal, creating more opportunities for local adaptation and speciation (Rhode, 2006; McGill et al., 2019). Under a non-equilibrium model, we predict that species and trait diversity will be directly and positively related to diversification rates or assemblage age (blue lines in Figure 1b; Harmon & Harrison, 2015). Alternatively, topography, productivity or climate could indirectly drive species and trait diversity via their effect on diversification rates or assemblage age (dashed green and blue lines in Figure 1c). This could be because topography and climate can shape rates of speciation through allopatric divergence or increase extinction rates through climate change. Furthermore, as different biomes have different ages (Ricklefs, 2006; Jetz & Fine, 2012; Pontarp & Wiens, 2017), and different regions have acted as climatic refugia through time (Carnaval et al., 2009), these variables might also reflect the age and stability of assemblages. This means that areas with lower extinction rates and/or higher rates of speciation would be more species rich and have greater trait diversity, or that older communities would allow species to accumulate more trait differences over time (Wiens & Donoghue, 2004; Wiens, 2011) and diversify in the same area. In addition, we tested (2) whether the distribution of vertebrate communities is spatially congruent in terms of diversification rate, assemblage age, trait diversity, and species richness. Considering that amphibians and reptiles have narrower physiological requirements and lower dispersal ability than endotherms, which are usually better trackers of ecological limits than ectotherms (e.g., Araújo & Pearson, 2005; Rolland et al., 2018), we expect more spatial similarity between ectotherms than between endotherms and ectotherms.

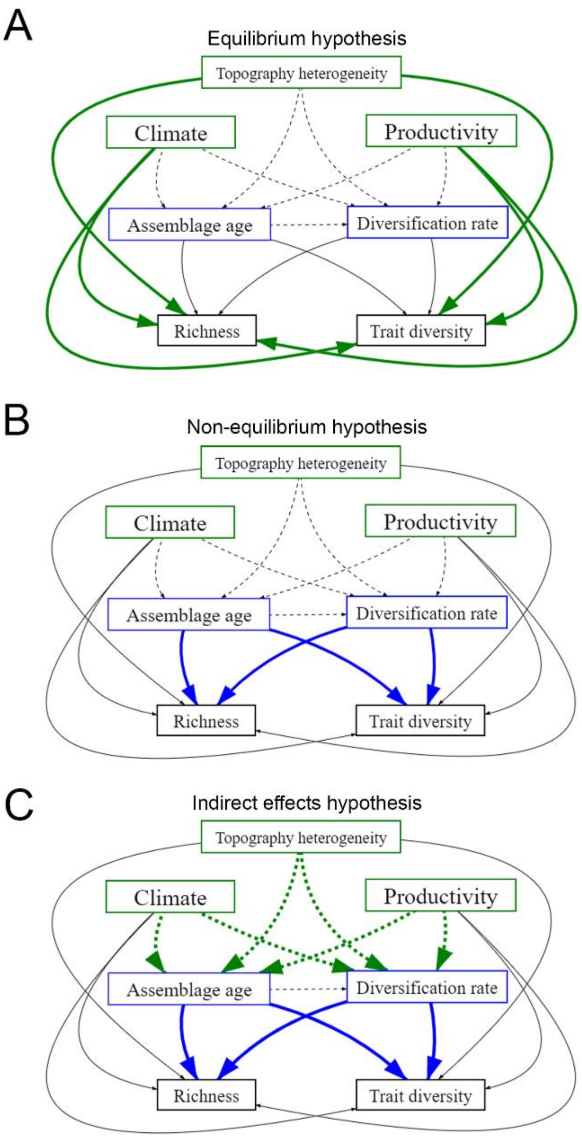


Figure 1. Alternative hypotheses tested in this paper referring to each class of dynamics. The pathway connecting productivity to species richness represents the more-individuals hypothesis, while the pathways connecting topographic heterogeneity/climate/productivity to trait diversity reflect ecological niche partitioning. Blue colour indicates non-equilibrium mechanisms, while green represents equilibrium mechanisms. Climate is a statistical composite variable.

Material and Methods

Species geographical data

We built a 10 x 10 km grid with 0.5º cells overlaid on the Atlantic Forest consensus extent (Muylaert et al., 2018) in QGIS software (QGIS Development Team, 2019). We excluded cells with less than 50% continental coverage, resulting in 424 cells. We obtained extent-of-occurrence polygons of vertebrates. We opted for this treshhold to avoid underestimating cells that have little continental shelf surface, leading to underestimated coastal communities. In addittion, although these polygons are scale dependent (Hurlbert & White, 2005) and include commission errors, recent studies (e.g., da Silva et al., 2016) have found congruence between point occurrence data and range maps for 10 x 10 Km scales for amphibians in the Atlantic Forest, whose distribution is less known than other taxa. For amphibians, we used data from IUCN (2021), complemented by shapefiles from (Vasconcelos et al., 2019). For squamates, we used data from Roll et al (2017). For birds, we used data from BirdLife International (2015). For terrestrial mammals, we used data from IUCN (2021). We obtained presence-absence matrices separately for each group by overlapping polygons on the grid using the *letsR* R package (Vilela & Villalobos, 2015), considering that at least 50% of the polygon covered the cell. We defined our Atlantic Forest species pool as the result of overlapping polygons in the grids, keeping only native (excluding exotic) and non-migratory (not temporary visitors) species.Finally, our presence-absence matrices contained 518 species of frogs, 402 squamates, 815 birds, and 236 mammals. We applied the same species nomenclature of the phylogeny to the trait data and polygons for each group.

Trait data

We used three response traits to describe the trait space of assemblages at large spatial scales: body mass for endotherms or body size for ectotherms, diel activity, and habitat (Table S1). We chose these traits because they reflect different niche dimensions, in addition to being directly related to climatic gradients (e.g., Oliveira et al., 2016; Vasconcelos et al., 2019).

We obtained trait data from the following sources: i) amphiBIO (Oliveira et al., 2017) and Vasconcelos *et al.* (2019) for frogs; ii) Marques et al (2019) for squamates; iii)

Elton Traits (Wilman et al., 2014) for birds and mammals, and complement with PanTHERIA (Jones et al., 2009) and Phylacine (Faurby et al., 2018) for mammals. We also complemented them with the literature for 9% of frogs, 22% of squamates, and 10% of mammals (see Moroti et al., 2022). However, 84 frog (~17%), 135 squamate (~34%), 107 bird (~13%), and 41 mammal species (~17%) had missing trait values. Thus, they were excluded from the analyses, resulting in a trait database with 434, 267, 708, and 195 species, respectively.

Phylogeny

We used the maximum clade credibility tree (MCCT) for amphibians containing 7,239 species of Jetz & Pyron (2018). For squamates, we used the fully-sampled consensus tree with 9,754 species of Tonini et al (2016). For birds, we used the tree proposed by Jetz et al (2012), with 9,993 bird species. For mammals, we used the fully-sampled tree of Upham et al (2019). Birds are the only group to which a consensus tree is not provided. Thus, following Rubolini et al (2015), we generated 10,000 posterior trees to our species pool based on the 'Hackett' backbone (Jetz et al., 2012). Then, we built a MCCT with the *DendroPy* and *SumTrees* packages in Python.

We pruned the species to which we had occurrence and trait data from the respective phylogenies using the R package *picante* (Kembel et al., 2010). Yet, 24 frog (~3%), 70 birds (~10%), and 28 mammals (~14%) species had not been sampled in the phylogenies and were removed from analysis. Thus, our final dataset contained 421 frog, 261 squamates, 638 birds, and 167 non-flying mammal species. Our final dataset corresponds to ~60% of frog richness (707 species), ~53% of reptiles (492 species), 62.2% of birds (1,025 species), and ~64% of mammals (262 species) known to occur in the Atlantic Forest (Figueiredo et al., 2021).

Trait Diversity

To describe the community trait space, we calculated Functional Dispersion (FDis; Laliberté & Legendre, 2010), which here we call trait diversity, using the trait distance and presence-absence matrices in the FD package (Laliberté et al., 2014). Simulation studies (Kuebbing et al., 2017; McPherson et al., 2018) have shown that FDis has a good performance to detect community assembly mechanisms and is also less prone to outliers. To calculate the trait dissimilarity matrix, we used the Gower index that allows for mixed data (Pavoine et al., 2009) in the R package *ade4* (Dray & Dufour, 2007). In addittion, we chose this metric because it can identify hotspots regions of trait divergence. Specifically, FDis is the average Euclidean distance of species to the centroid of the trait volume each grid (Laliberté & Legendre, 2010). Therefore, the metric measures how dispersed the community trait space is (Mammola et al., 2021), independently from species richness (Fig. S6).

Variables related to equilibrium dynamics

We used three environmental variables that reflect the amount and variety of resources available to represent equilibrium dynamics: i) Topographical heterogeneity; We obtained the coefficient of variation of elevation at 1 km from Amatulli et al (2018); ii) Productivity; For each grid cell, we calculated the mean of potential net primary productivity (NPP) obtained from the CHELSA dataset (Brun et al., 2022). NPP represents the amount of carbon dioxide that is removed from the atmosphere, so it is a proxy to indicate the amount of biomass that is produced, a key function of the ecosystem (Schimel, 1995); and iii) Climate; We firstly choose nine bioclimatic variables from CHELSA dataset (Brun et al., 2022): Mean annual air temperature (BIO1), Mean Diurnal Temperature Range (BIO2), Isothermality (BIO3), Temperature Seasonality (BIO4), Temperature Annual Range (BIO7), Mean Temperature of Coldest Quarter (BIO11), Annual precipitation amount (BIO12), Precipitation Seasonality (BIO15), and Precipitation of Driest Quarter (BIO17). After testing for multicollinearity, we excluded BIO1 and BIO11 that had Variation Inflation Factor >10 from further analysis. The climatic and NPP variables obtained from CHELSA correspond to the average of their collection period: 1981–2010.

To reduce model complexity, BIO3, BIO4, BIO7, BIO12, and BIO15 were further combined into a statistical composite variable (Grace & Bollen, 2008; Grace et al., 2010) called ‘climate’ created separately for each group. In all groups, the variable with the highest loading was BIO3 (Isothermality). Thus, positive coefficients for ‘climate’ represent a less stable climate, that is, with more pronounced daily temperature oscillations in relation to the annual temperature range. This analysis was performed in the R software (R Core Team, 2020).

Variables related to non-equilibrium dynamics

We calculated two predictor variables to represent non-equilibrium dynamics separately for each group: i) Assemblage age as a measure of the evolutionary time of each community (Van Dijk et al., 2021) – This metric (see supplementary methods) is based on an ancestral area estimation using the BioGeoBEARS R package (Matzke, 2013). This method includes the diversification and dispersal of species on a regional scale, thus, we performed biogeographical regionalization in the set of species that make up the Atlantic Forest. Specifically, we calculate the age of each assemblage as the average age at which the ancestors of each current species arrived and settled in the region of a given cell. As such, assemblage age could be used to represent non-equilibrium mechanisms if higher species and trait diversity accumulate in older areas (time-for-speciation effect, Wiens & Donoghue, 2004), which would indicate a longer evolutionary time to overcome niche conservatism (e.g., Oliveira et al., 2016; Hua & Wiens, 2013; Pontarp & Wiens, 2017); ii) diversification rates. We calculated a revised version of the Jetz et al (2012) tip-level diversification rate (DR) in the R package *Herodotools* (Nakamura et al., 2023). Subsequently, we took the harmonic mean of the DR for each grid cell. Rapidly diversifying lineages have high DR values (Jetz et al., 2012).

There is no consensus on how accurate speciation rate estimated using different tip metrics or diversification models is (Velasco & Pinto-Ledezma, 2022). These may potentially bias net diversification rate towards high rates of speciation, while down-weighting extinction (Title & Rabosky 2019). However, DR is a suitable metric to test our hypotheses, as it is a species level metric, incorporates the number of split events, and distances between nodes from the root to tips of a phylogeny, while giving greater weight to branches closer to the present (Jetz et al., 2012; Nakamura et al., 2023). However, the metric proposed by Jetz et al. (2012) does not consider the dynamics of local colonization and assumes that diversification occurs only at the species' place of origin. This may not fully capture diversification processes, especially in highly dispersive groups, such as birds, which are part of our focus. In these groups, historical migration can play a significant role in regional diversity. Therefore, we are using a revised metric that takes this dynamic into account (Nakamura et al., 2023).

Data Analysis

Missing trait data is expected in global databases and can lead to bias in functional metrics (Johnson et al., 2021). To check how missing data could alter our conclusions, we first calculated Pearson's correlation between harmonized (reduced set of species with all polygons, traits, and phylogeny) and the full dataset (species with polygons and phylogeny, but with missing traits). We also calculated phylogenetic signal of missing traits using Fritz' *D* (Fritz & Purvis, 2010) in the R package SensiPhy (Paterno et al., 2018). Species richness estimated using both datasets were highly correlated (>0.8) for all groups (Figure S7; Table S2). However, assemblage age differed considerably between datasets (Figure S8), which indicates that the conclusions may change if we do not use the complete dataset. As diversification rate also depends on ancestral range reconstruction, we used the complete dataset for calculating DR and assemblage age. Missingness pattern in most traits was random or slightly clumped in all groups (Table S3, Figures S9-12), indicating that it likely has little impact on FDis estimation. In sum, species richness and FDis were calculated using the harmonized dataset (421 frog, 261 squamates, 638 birds, and 167 non-flying mammal species), while DR and assemblage age were calculated using the full dataset (487 frog, 382 squamates, 695 birds, and 196 non-flying mammal species). To test whether there is spatial congruence in species richness, FDis, assemblage age, and DR between the four groups, we used Dutilleul's modified *t*-test (Dutilleul, 1993) in the *SpatialPack* R package (Vallejos et al., 2020).

To explore the direct and indirect relationships between predictor variables and species richness and FDis, we built spatially-explicit structural equation models (SEM). We normalized predictor variables using the R package *vegan* (Oksanen et al., 2022) before entering in the analysis. We first fit four Generalized Least Squares (GLS) models to test how each predictor variable (climatic, productivity, topographical heterogeneity, diversification rate, and assemblage age) was related to FDis and species richness separately for each group (Figure 1), namely:

(1) FDis ~ climate + elevation + productivity + DR + Assemblage age

(2) Richness ~ climate + elevation + productivity + DR + Assemblage age

(3) Assemblage age ~ climate + elevation + productivity

(4) DR ~ Assemblage age + climate + elevation + productivity.

We tested five correlation structures (exponential, Gaussian, linear, ratio, and spherical) in GLS models. This procedure resulted in 20 models for each group (Table S5). Then, we selected the best-fit model based on the Akaike information criterion (AIC), on the spatial correlogram, and visual diagnosis of residuals (Figures S13-17). This analysis was performed in the *nlme* R package (Pinheiro et al., 2017). Subsequently, we included the four best-fitting GLS for each group (in the formulas above) in a SEM using the *piecewiseSEM* R package (Lefcheck, 2016). Results of the SEM models represent standardized beta coefficients.

Results

Spatial distribution

We found a highly positive spatial congruence between the richness of the two groups of endotherms in the central portion of the Atlantic Forest, specifically in the Serra do Mar mountain range (Figure 2). Likewise, there was a positive and significant congruence between frog richness and the two groups of endotherms (Table 1), notably in the central portion (Figure 2). We also observed a positive congruence of the richness of squamates and mammals (Table 1), but slightly weaker and not significant with birds. However, spatial congruence, although positive, was not significant between the two groups of ectotherms, with the highest richness of squamates more concentrated in the interior region of the continent and that of frogs in the coastal region of the Atlantic Forest (Figure 2), specifically from the southeast to the northeast (Table 1).

We found a significant negative congruence for trait diversity between squamates and birds (Table 1). While squamates had greater trait diversity in the northern portion, trait diversity of birds was greater in the southern portion of the Atlantic Forest. The greatest trait diversity of frogs is found in the coastal region, coincident with its species richness (Figure S6). However, the greatest trait diversity for mammals is concentrated in the transition with the Brazilian Cerrado, in the innermost portion of the continent, and in the central region.

We found idiosyncratic spatial patterns for diversification rate and assemblage age for all groups (Figure 2), with no significant congruence (Table 1). The lowest diversification rates for frogs were in the north, and the highest rates in the south and in the central portion in the transition with the Cerrado. A similar pattern is observed for squamates, with higher diversification rates concentrated in the southern portion and lower rates in the north. The highest diversification rates for birds were in the transition with the Cerrado and Serra do Mar, while that for mammals were in the southern portion. The oldest communities of frogs and squamates were concentrated in the central region of the Atlantic Forest, while those for birds were also in the central region and in the transition with the Cerrado. Interestingly, the oldest communities of mammals are scattered throughout the Atlantic Forest.

Table 1. Pairwise spatial correlation of Richness, Trait diversity, Diversification Rate, and Assemblage age between tetrapod clades in the Atlantic Forest. Values correspond to Dutilleul's modified *t*-test; bold face represents *P* values < 0.06.

Richness	**Frogs**	**Squamates**	**Birds**
Squamates	0.387	-	-
Birds	**0.655**	0.549	-
Mammals	**0.700**	**0.703**	**0.776**
Trait diversity			
Squamates	0.196	-	-
Birds	-0.414	**-0.701**	-
Mammals	-0.162	0.241	-0.441
Diversification rate			
Squamates	0.657	-	-
Birds	0.050	-0.296	-
Mammals	0.105	0.431	-0.424
Assemblage age			
Squamates	0.169	-	-
Birds	0.072	0.251	-
Mammals	0.131	0.097	-0.163

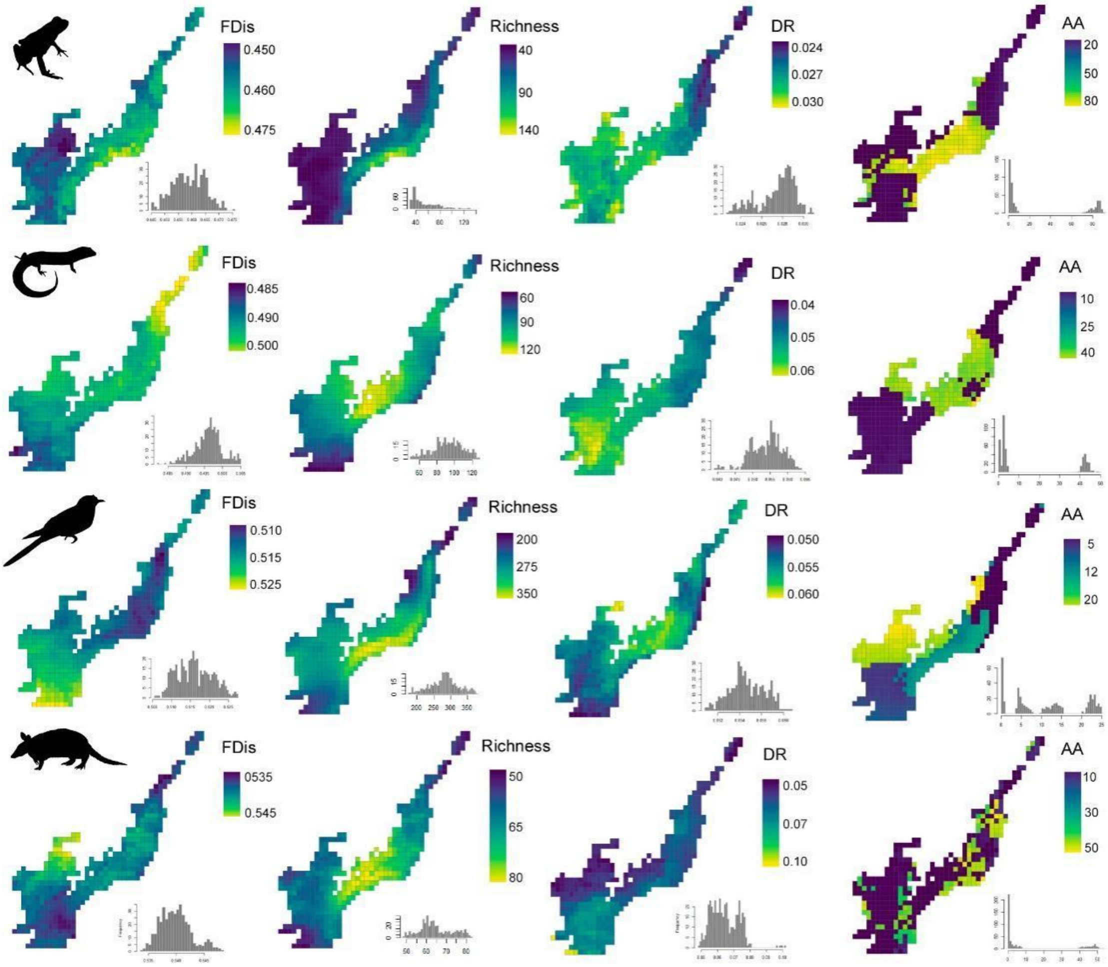


Figure 2. Geographical patterns of trait diversity (FDis), species richness, diversification rate (DR), and mean assemblage age, in Millions of Years (AA) of frogs, squamates, birds, and non-flying mammals of the Atlantic Forest. Silhouettes are CC-BY from PhyloPic.

Structural equation models

SEMs for birds (Fisher's C= 0.527, $P = 0.768$) and frogs (Fisher's C= 2.194, $P = 0.334$) had a good fit to the data, but not for squamates (Fisher's C= 53.076, $P < 0.001$) and mammals (Fisher's C= 106.178, $P < 0.001$). This is probably due to missing paths not relevant to our hypothesis or the linear relationship between FDis and species richness in these two groups (Figure S6), instead of erroneous model specification (see also Hertzog 2019). We found that equilibrium (climate, productivity, and topographic heterogeneity) and non-equilibrium (diversification rate) predictors interacted to explain trait diversity and richness in Atlantic Forest tetrapods. Productivity had a negative effect on the richness of all groups, as well as on trait diversity of frogs, squamates, and mammals. In contrast, diversification rate was strongly, positively associated with richness and trait diversity across all groups. Climate had a direct and positive influence on species richness only for birds. But interestingly, it had an indirect negative effect on species richness of mammals and frogs via diversification rate. Our model better explained the variation in trait diversity, than species richness (Figure 3). Variation in diversification rate was better explained by equilibrium predictors, than assemblage age (Figure 3).

Diversification rate had a strong and positive influence on trait diversity of frogs, squamates, and birds (Figure 3). Conversely, productivity was negatively related with trait diversity ($\beta = -0.567$, $P < 0.001$) and richness ($\beta = -0.682$, $P < 0.001$) of mammals. Species richness of frogs, squamates, and mammals had a more negative influence of productivity than a positive influence of diversification rates (Figure 3). In birds, both species richness and trait diversity were better explained by diversification rate, than equilibrium predictors (Figure 3).

Assemblage age was positively influenced by climate in ectotherms (frogs $\beta= 0.591$, squamates $\beta= 0.388$, $P < 0.001$), but not in endotherms. Climate also had a negative influence on trait diversity of frogs and mammals, and a lesser one in birds. In addition, climate negatively impacted frog and mammal diversification rates, while topographic heterogeneity positively affected diversification rate of all groups (Figure 3). Surprisingly, assemblage age had a negative, direct though small influence on species richness and trait diversity, yet significant for trait diversity of mammals and frogs.

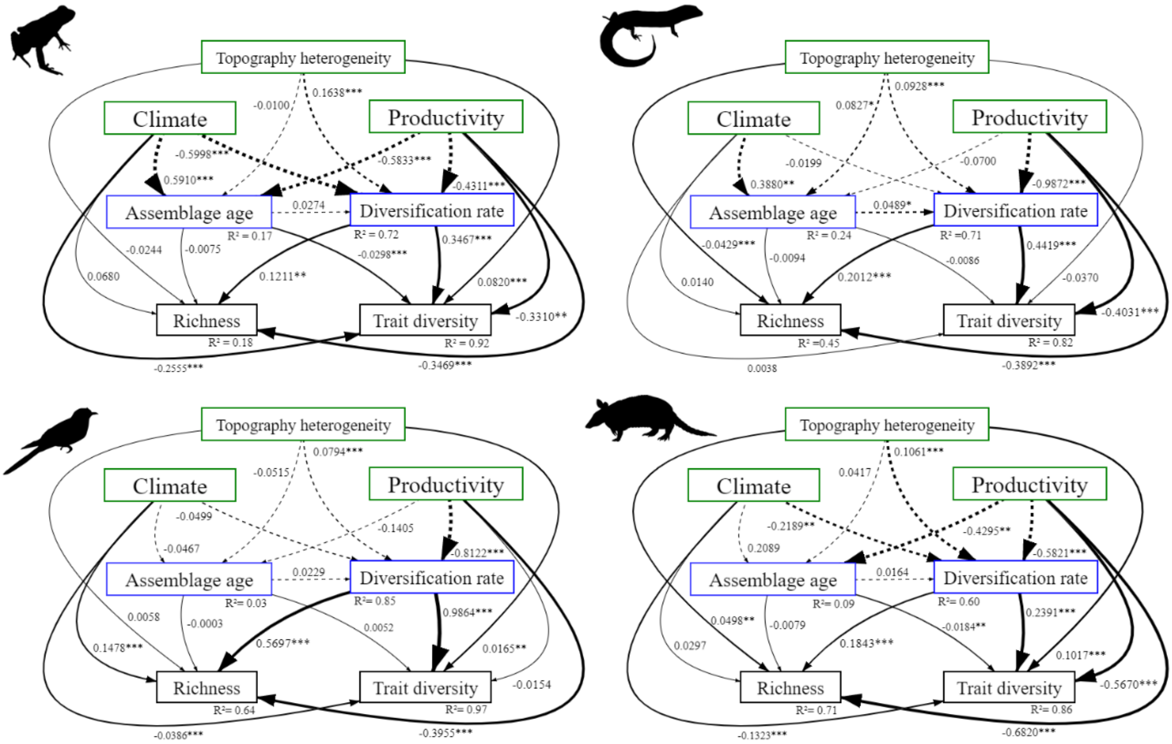


Figure 3. Path diagrams showing the standardized coefficients (β) of models testing the influence of variables representing equilibrium (Climate, productivity, topographic heterogeneity) and non-equilibrium (Assemblage age and Diversification Rate) dynamics on species richness and trait diversity of ectotherms: Frogs and squamates; and endotherms: birds and terrestrial mammals of the Atlantic Forest. Dashed arrows indicate indirect effects of equilibrium predictors on non-equilibrium predictors. Arrow thickness indicates effect size according to standardized coefficients (β). The number of asterisks indicate level of significance (* = *P* < 0.05; ** = *P* < 0.005; and *** *P* < 0.001). Silhouettes are CC-BY from PhyloPic.

Discussion

Here, we use a multifaceted approach including species richness and trait diversity of terrestrial vertebrates to add new lines of evidence about the ecological and evolutionary mechanisms involved in biodiversity patterns in the Atlantic Forest hotspot. One common pattern is that the central region of the biome had the highest species richness for all clades. In contrast, trait diversity had idiosyncratic spatial patterns among taxa, as well as the assemblage age and diversification rate (DR). Overall, we found that equilibrium predictors (Productivity for all groups, and climate for frogs and mammals) influenced species and trait diversity only indirectly via non-equilibrium predictors (DR). Specifically, Diversification rate was a strong positive driver of species richness and trait diversity, while productivity was both an indirect and direct negative driver of richness and trait diversity. Highly productive areas had lower species richness of amphibians, squamates, and mammals. Importantly, our results challenge the current view (Pontarp & Wiens, 2017; Li & Wiens, 2019) that diversification rate dominates over longer time scales, while colonization time (assemblage age) dominates over shorter time scales.

While the spatial pattern of species richness was congruent among most groups, hotspots of trait diversity had an idiosyncratic distribution. This pattern means that these two variables are decoupled in space among groups in the Atlantic Forest. However, against our prior expectation, we did not find higher spatial similarity between ectotherms, but a highly positive congruence between frogs and endotherms. Yet, both species and trait diversity had the same predictors across tetrapod lineages. Although richness of all groups was concentrated in the central portion of the Atlantic Forest, areas with greatest FDis in birds and mammals were in ecotones. Ecotones might support high trait diversity because they typically have high habitat heterogeneity, which permits a high degree of niche partitioning and co-occurrence of functionally distinct species (Smith et al., 2001). Higher trait disparity in ecotones might also be due to higher rates of trait evolution (Luza et al., 2021), which would allow species to occupy distinct regions of the trait space. Ecotones also harbour high degrees of endemism and uniquely adapted species (Kark et al., 2007). One reason why ecotone harbour high biodiversity is that they drive faster rates of ecological speciation, either along environmental gradients or among habitat patches due to higher heterogeneity (Schilthuizen, 2000).

Diversification rate was a common driver of both trait diversity and species richness across tetrapods in the Atlantic Forest, with little direct impact of assemblage

age. This result reinforces the role of non-equilibrium dynamics in determining biodiversity patterns at continental scales (Harmon & Harrison, 2015. It also challenges the systematic review (Pontarp & Wiens, 2017; Li & Wiens, 2019) that diversification rate dominates over longer time scales, while colonization time (assemblage age) dominates over shorter time scales. A mechanistic simulation (Pontarp & Wiens, 2017) and vote-counting review (Li & Wiens, 2019) argue that the richness of younger clades are more likely to be dominated by colonization time, whereas that of older clades should be dominated by diversification rate. Here, we found that species and trait diversity of younger (mammals and birds) and older (frogs and squamates) clades were equally influenced by diversification rate. This result also means that both species and trait diversity are coupled among groups at the regional scale. Our measure of diversification rate as well as assemblage age (colonization time) took into account the age of arrival of ancestors in the region in which communities are (Van Dijk et al., 2021; Nakamura et al., 2023).

Productivity had a both direct and indirect negative effect on species and trait diversity across tetrapods. This result supports that equilibrium dynamics are playing a major, yet indirect role. More specifically, the relationship between productivity and species richness is usually hump-shaped or positive (Mittlebach et al., 2001), with no consensus if it is scale dependent. However, a negative relationship between species and trait diversity and productivity might occur under high anthropogenic disturbance (Laliberté et al., 2013). Our NPP data describes biomass variation in a relatively recent time frame (1981-2010). This temporal scale is enough to capture the effects of forest fragmentation and biotic homogenization that is promoting the collapse of species and trait diversity in the Atlantic Forest. Under these circumstances, highly productive regions might favour widespread species (winners) with certain traits that confer competitive dominance (Keddy & Laughlin, 2021), resulting in lower functional disparity and species richness (Newbold et al., 2018).

Climate stability had only a weak positive effect on species richness, but a strong and negative direct effect on trait diversity. This means that communities with higher daily temperature variation in relation to annual variation have less dispersed trait spaces, but potentially more species. This pattern is consistent with the fact that harsh climates can be a strong ‘environmental filter’, constraining the trait space (Keddy & Laughlin, 2021) and promoting functional redundancy. Topographic heterogeneity played a direct and positive role in the diversification of all groups, with varying strengths. The same pattern has also been found for amphibians at global and realm scales (García-Rodríguez et al., 2021), indicating that mountains might be acting as speciation pumps in those groups (Graham et al., 2014; Antonelli et al., 2018). The central Atlantic Forest encompasses the Serra do Mar range that experienced climatic stability during the Last Glacial Maximum (Carnaval et al., 2009). The high diversification rates in mountainous areas are likely driven by allopatric and ecological speciation, decreasing extinction rates, and constraining species dispersal (Rahbek et al., 2019; Benício et al., 2021).

Furthermore, we observed a strong and positive relationship between climate and assemblage age in ectotherms, meaning that communities that were colonized earlier have more stable climates. Amphibians and squamates have narrow physiological requirements related to thermal metabolism that impact locomotor performance (Araújo & Pearson, 2005; Buckley et al., 2012). As a result, the climate of the central region of the Atlantic Forest might have played a key role in the concentration of older communities of ectotherms. Additionally, it adds a more nuanced view about the duality between equilibrium and non-equilibrium dynamics, suggesting that both might be relevant to explain continental-scale biodiversity patterns via direct and indirect effects.

We found a significant and positive relationship between trait diversity and DR for all groups. The strong positive association between trait diversity and DR suggests that functionally diverse ecotone regions were formed from higher diversification rates that allowed the accumulation of functionally distinct lineages instead of more time (assemblage age) for the disparification of traits to evolve *in situ* and *ex situ*. Several studies have suggested a positive relationship between phenotypic evolution and lineage diversification in amphibians (Rabosky & Adams, 2012) and ray-finned fish (Rabosky et al., 2013), but not in birds (Crouch & Tobias, 2022; but see Barreto et al., 2023). Our results contribute to this discussion by adding a regional and comparative perspective, given that we found a high influence of DR on trait divergence for all groups occurring in the same geographical region.

Climate negatively influenced the diversification rate of frogs and mammals. Meaning that climatically more stable communities have higher DR. The evolutionary speed hypothesis predicts that higher temperatures support faster speciation rates (Rohde, 2006). Consequently, speciation rates of ectotherms, which regulate their metabolism based on environmental temperatures, should depend more heavily on climate than endotherms (Gillooly & Allen, 2007). Here, diversification rates of an old and a young clade have been influenced by climatic stability, pointing again to the indirect role of equilibrium predictors on non-equilibrium dynamics. Higher diversification rates have been found to be associated with stable climates in some groups (Hua & Wiens, 2013), potentially caused by high rates of climatic niche evolution (Kozak & Wiens, 2010). Climatic niche conservatism might mediate the relationship between diversification and stable climates (Pyron et al., 2015).

Overall, we found that equilibrium and non-equilibrium dynamics together played a role to explain species and trait diversity of ectotherms and endotherms in the Atlantic Forest. This is in line with the idea that continental communities are temporary sets of species in ever-changing environments, in which their assembly over time more likely takes place without defined ecological limits at continental scales (Harmon & Harrison, 2015; Oliveira et al., 2016), with equilibrium forces playing an indirect and secondary role. Our results suggest that high diversification rates are important to generate trait diversity in Atlantic Forest tetrapods. Areas such as ecotones and climatically stable areas with high elevation heterogeneity, such as mountainous regions of the central Atlantic Forest, may be promoting faster rates of ecological speciation along environmental gradients or between patches of habitat due to the greater heterogeneity in these environments. Likewise, in all groups the species richness is concentrated in the central portion of the Atlantic Forest. However, we found idiosyncratic and distinct patterns for each group regarding diversification rate, community age, and trait diversity. Furthermore, our study innovated by mapping the age of communities and diversification rates of terrestrial vertebrates in the Atlantic Forest. This approach allowed us to identify biodiversity hotspots that go beyond species richness, incorporating other facets of functional and phylogenetic diversity. These findings have the potential to more effectively guide conservation efforts and prioritize critical areas for the preservation of this ecosystem.

References

Amatulli, G., Domisch, S., Tuanmu, M.N., Parmentier, B., Ranipeta, A., Malczyk, J. & Jetz, W. (2018). Data Descriptor: A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data*, **5**,1–5.

Antonelli, A., Kissling, W. D., Flantua, S. G. A., Bermúdez, M. A., Mulch, A., Muellner-Riehl, A. N., . . . Hoorn, C. (2018). Geological and climatic influences on mountain biodiversity. *Nature Geoscience, 11*(10), 718-725. doi:10.1038/s41561-018-0236-z

Araújo, M.B. & Pearson, R.G. (2005). Equilibrium of species' distributions with climate. *Ecography*, **28**(5), 693–695

Barreto, E., Lim, M.C., Rojas, D., Dávalos, L.M., Wüest, R.O., Machac, A., & Graham, C.H. (2023). Morphology and niche evolution influence hummingbird speciation rates. *Proceedings of the Royal Society B*, **290**(1997), 20221793.

Benício, R.A., Provete, D.B., Lyra, M.L., Heino, J., Haddad, C.F.B., Rossa-Feres, D. de C. & da Silva, F.R. (2021). Differential speciation rates, colonization time and niche conservatism affect community assembly across adjacent biogeographical regions. *Journal of Biogeography*, **48**(9), 2211–2225.

BirdLife International (2015) BirdLife Data Zone. Downloaded from http://datazone.birdlife.org/ on 17/02/2021.

Botero, C.A., Dor, R., McCain, C.M. & Safran, R.J. (2014). Environmental harshness is positively correlated with intraspecific divergence in mammals and birds. *Molecular Ecology*, **23**, 259–268.

Brown, J. H. (1981). Two Decades of Homage to Santa Rosalia: Toward a General Theory of Diversity. *American Zoologist*, **21**(4), 877–888. doi:10.1093/icb/21.4.877

Brun P., Zimmermann N.E., Hari C., Pellissier L., Karger D.N. (2022). Global climate-related predictors at kilometer resolution for the past and future. *Earth System Science Data*. **14**(12):5573–603. https://doi.org/10.16904/envidat.332

Buckley, L.B., Hurlbert, A.H. & Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and*

Biogeography, **21**, 873–885.

Carnaval, A.C., Hickerson, M.J., Haddad, C.F.B., Rodrigues, M.T. & Moritz, C. (2009). Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science*, **323**, 785–789.

Clarke, A. & Gaston, K.J. (2006). Climate, energy and diversity. *Proceedings of the Royal Society B: Biological Sciences*, **273**(1599), 2257–2266.

Crouch, N.M. & Tobias, J.A. (2022). The causes and ecological context of rapid morphological evolution in birds. *Ecology Letters*, **25**(3), 611–623.

Da Silva, F.R., Almeida-Neto, M., Do Prado, V.H.M., Haddad, C.F.B. & De Cerqueira Rossa-Feres, D. (2012) Humidity levels drive reproductive modes and phylogenetic diversity of amphibians in the Brazilian Atlantic Forest. *Journal of Biogeography*, **39**, 1720–1732.

Da Silva, F.R., Provete, D.B. & Hawkins, B.A. (2016). Range maps and checklists provide similar estimates of taxonomic and phylogenetic alpha diversity, but less so for beta diversity, of Brazilian Atlantic Forest anurans. *Natureza e Conservação*, **14**, 99–105.

Dray S., Dufour A.B. (2007). The ade4 package: implementing the duality diagram for ecologists. *Journal of statistical software*, **22**, 1–20.

Dutilleul, P. (1993) Modifying the t Test for Assessing the Correlation Between Two Spatial Processes. *Biometrics*, **49**, 305.

Faurby, S., Davis, M., Pedersen, R.Ø., Schowanek, S.D., Antonelli, A. & Svenning, J.C. (2018). PHYLACINE 1.2: the phylogenetic atlas of mammal macroecology. *Ecology*, **99**(11), 2626.

Figueiredo, M. de S.L., Weber, M.M., Brasileiro, C.A., Cerqueira, R., Grelle, C.E. V., Jenkins, C.N., Solidade, C. V., Thomé, M.T.C., Vale, M.M. & Lorini, M.L. (2021). Tetrapod Diversity in the Atlantic Forest: Maps and Gaps. In *The Atlantic Forest*, (pp 185–204). Springer, Cham.

Fritz, S.A. & Purvis, A. (2010) Selectivity in Mammalian Extinction Risk and Threat Types: a New Measure of Phylogenetic Signal Strength in Binary Traits: Selectivity in Extinction Risk. *Conservation Biology*, **24**, 1042–1051.

Garcia-Rodriguez, A., Martinez, P. A., Oliveira, B. F., Velasco, J. A., Pyron, R. A., & Costa, G. C. (2021). Amphibian Speciation Rates Support a General Role of Mountains as Biodiversity Pumps. *American Naturalist,* **198**(3), E68-E79. doi:10.1086/715500

Gillooly, J. F., & Allen, A. P. (2007). Linking global patterns in biodiversity to evolutionary dynamics using metabolic theory. *Ecology,* **88**(8), 1890–1894. doi:10.1890/06-1935.1

Grace, J. B., & Bollen, K. A. (2008). Representing general theoretical concepts in structural equation models: the role of composite variables. *Environmental and Ecological Statistics*, **15**, 191-213

Grace, J. B., Anderson, T. M., Olff, H., & Scheiner, S. M. (2010). On the specification of structural equation models for ecological systems. *Ecological Monographs*, **80**, 67-87.

Graham, C. H., Carnaval, A. C., Cadena, C. D., Zamudio, K. R., Roberts, T. E., Parra, J. L., . . . Sanders, N. J. (2014). The origin and maintenance of montane diversity: integrating evolutionary and ecological processes. *Ecography*, **37**(8), 711-719. doi:10.1111/ecog.00578

Harmon, L.J. & Harrison, S. (2015). Species diversity is dynamic and unbounded at local and continental scales. *American Naturalist*, **185**, 584–593.

Hertzog, L.R. (2019) How robust are Structural Equation Models to model miss-specification? A simulation study. *arXiv* DOI 10.48550/arXiv.1803.06186.

Hua, X. & Wiens, J.J. (2013) How Does Climate Influence Speciation? *American Naturalist*, **182**, 1–12.

Hurlbert, A. H., & White, E. P. (2005). Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications. Ecology Letters, **8**(3), 319-327. doi:10.1111/j.1461-0248.2005.00726.x

IUCN (2021). The *IUCN Red List of Threatened Species. Version 2021-1*. https://www.iucnredlist.org. Downloaded on 15 April 2021.

Jetz, W. & Pyron, R.A. (2018). The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature*

Ecology and Evolution, **2**(5), 850–858.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012). The global diversity of birds in space and time. *Nature*, **491**, 444–448.

Jetz, W., Fine, P.V.A. (2012). Global Gradients in Vertebrate Diversity Predicted by Historical Area-Productivity Dynamics and Contemporary Environment. *PLOS Biology* **10**(3): e1001292. https://doi.org/10.1371/journal.pbio.1001292

Johnson, T.F., Isaac, N.J., Paviolo, A. & González-Suárez, M. (2021). Handling missing values in trait data. *Global Ecology and Biogeography*, **30**(1), pp.51-62.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., Connolly, C., Cutts, M.J., Foster, J.K., Grenyer, R., Habib, M., Plaster, C.A., Price, S.A., Rigby, E.A., Rist, J., Teacher, A., Bininda-Emonds, O.R.P., Gittleman, J.L., Mace, G.M. & Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, **90**, 2648–2648.

Kark, S., Allnutt, T. F., Levin, N., Manne, L. L., & Williams, P. H. (2007). The role of transitional areas as avian biodiversity centres. *Global Ecology and Biogeography,* **16**(2), 187–196. doi:10.1111/j.1466-8238.2006.00274.x

Keddy, P.A. & Laughlin, D.C. (2021) *A Framework for Community Ecology: Species Pools, Filters and Traits*. Cambridge Cambridge University Press.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**(11), 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kronfeld-Schor, N., Dayan, T., Elvert, R., Haim, A., Zisapel, N. and Heldmaier, G. (2001). On the use of the time axis for ecological separation: diel rhythms as an evolutionary constraint. *American Naturalist*, **158**(4), 451–457.

Kozak, K.H. & Wiens, J.J. (2010) Accelerated rates of climatic-niche evolution underlie rapid species diversification: Niche evolution and rapid diversification. *Ecology Letters*, **13**, 1378–1389.

Kuebbing, S.E., Maynard, D.S. & Bradford, M.A. (2018). Linking functional diversity and ecosystem processes: A framework for using functional diversity metrics to predict the ecosystem impact of functionally unique species. *Journal of Ecology*. **106**(2), 687–698.

Laliberte, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**(1), 299–305.

Laliberté, E., Legendre, P., Shipley, B. and Laliberté, M.E. (2014). Measuring functional diversity from multiple traits, and other tools for functional ecology. *R package version*, **1**, 1–12.

Lefcheck, J.S. (2016). PiecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, **7**(5), 573–579.

Li, H. & Wiens, J.J. (2019). Time explains regional richness patterns within clades more often than diversification rates or area. *American Naturalist*, **193**(4), 514–529.

Li, P. & Wiens, J.J. (2022) What drives diversification? Range expansion tops climate, life history, habitat and size in lizards and snakes. *Journal of Biogeography*, **49**, 237–247.

Luza, A.L., Maestri, R., Debastiani, V.J., Patterson, B.D., Hartz, S.M. & Duarte, L.D.S. (2021) Is evolution faster at ecotones? A test using rates and tempo of diet transitions in Neotropical Sigmodontinae (Rodentia, Cricetidae). *Ecology and Evolution*, **11**, 18676–18690.

MacDougall, M.J., Brocklehurst, N. & Fröbisch, J. (2019). Species richness and disparity of parareptiles across the end-Permian mass extinction. *Proceedings of the Royal Society B*, **286**(1899), 20182572

Mammola, S., Carmona, C.P., Guillerme, T. & Cardoso, P. (2021). Concepts and applications in functional diversity. *Functional Ecology*, **35**, 1869–1885.

Marques, O., Eterovic, A. & Sazima, I. (2019). *Serpentes da Mata Atlântica: guia ilustrado para as florestas costeiras do Brasil*. Cotia: Ponto A.

Matzke, N.J. (2013) Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Frontiers of Biogeography*, **5**, 242–248.

McGill, B.J., Chase, J.M., Hortal, J., Overcast, I., Rominger, A.J., Rosindell, J., Borges, P.A.V., Emerson, B.C., Etienne, R.S., Hickerson, M.J., Mahler, D.L., Massol, F., McGaughran, A., Neves, P., Parent, C., Patiño, J., Ruffley, M., Wagner, C.E. & Gillespie, R. (2019) Unifying macroecology and macroevolution to answer fundamental questions about biodiversity. *Global Ecology and Biogeography*, **28**, 1925–1936.

Moroti, M., Skeels, A., da Silva, F. R., Provete, D. B. (2022). Non-equilibrium processes prevail in shaping species richness and functional diversity of terrestrial vertebrates in a global hotspot. figshare. Dataset. https://doi.org/10.6084/m9.figshare.19735552.v1

Muylaert, R.L., Vancine, M.H., Bernardo, R., Oshima, J.E.F., Sobral-Souza, T., Tonetti, V.R., Niebuhr, B.B. & Ribeiro, M.C. (2018). Uma nota sobre os limites territoriais da Mata Atlântica. *Oecologia Australis*, **22**(3), 302–311.

Newbold, T., Hudson, L.N., Contu, S., Hill, S.L.L., Beck, J., Liu, Y., Meyer, C., Phillips, H.R.P., Scharlemann, J.P.W. & Purvis, A. (2018) Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. *PLOS Biology*, **16**, e2006841.

Oliveira, B.F., Machac, A., Costa, G.C., Brooks, T.M., Davidson, A.D., Rondinini, C. & Graham, C.H. (2016). Species and functional diversity accumulate differently in mammals. *Global Ecology and Biogeography*, **25**, 1119–1130.

Oliveira, B.F., São-Pedro, V.A., Santos-Barrera, G., Penone, C. & Costa, G.C. (2017). AmphiBIO, a global database for amphibian ecological traits. *Scientific Data*, **4**, 1–7.

Paterno, G. B., Penone, C., & Werner, G. D. A. (2018). sensiPhy: An r-package for sensitivity analysis in phylogenetic comparative methods. *Methods in Ecology and Evolution*, **9**(6), 1461-1467. doi:10.1111/2041-210x.12990

Pavoine, S., Vallet, J., Dufour, A.B., Gachet, S. & Daniel, H. (2009). On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. *Oikos*, **118**(3), 391–402.

Peres, E.A., Pinto-da-Rocha, R., Lohmann, L.G., Michelangeli, F.A., Miyaki, C.Y., Carnaval, A.C. (2020). Patterns of Species and Lineage Diversity in the Atlantic

Rainforest of Brazil. In Rull, V., A. Carnaval (Eds.), *Neotropical Diversification: Patterns and Processes*. Cham: Springer. https://doi.org/10.1007/978-3-030-31167-4_16

Peters, R.H. (1986). *The ecological implications of body size*. Cambridge: Cambridge university press.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B. & Maintainer, R. (2017). Package 'nlme'. Linear and nonlinear mixed effects models, version 3.

Pontarp, M. & Wiens, J.J. (2017) The origin of species richness patterns along environmental gradients: uniting explanations based on time, diversification rate and carrying capacity. *Journal of Biogeography*, **44**, 722–735.

Pyron, R.A., Costa, G.C., Patten, M.A. & Burbrink, F.T. (2015) Phylogenetic niche conservatism and the evolutionary basis of ecological speciation: Niche conservatism and speciation. *Biological Reviews*, **90**, 1248–1262.

Rabosky, D. L. (2013). Diversity-Dependence, Ecological Speciation, and the Role of Competition in Macroevolution. *Annual Review of Ecology, Evolution, and Systematics*, **44**(1), 481-502. doi:10.1146/annurev-ecolsys-110512-135800

Rabosky, D. L. & Hurlbert, A. H. (2015). Species richness at continental scales is dominated by ecological limits. *American Naturalist*, **185**, 572–583.

Rahbek, C., Borregaard, M. K., Colwell, R. K., Dalsgaard, B. O., Holt, B. G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R. J. & Fjeldså, J. (2019). Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science*, **365**(6458), 1108–1113. doi:10.1126/science.aax0149

Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, **7**, 1–15.

Ricklefs, R.E. (2006) Evolutionary diversification and the origin of the diversity–environment relationship. *Ecology*, **87**, S3–S13.

Rohde, K. (2006) *Nonequilibrium Ecology*. Cambridge: Cambridge University Press.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G.R., Dabool, L., Das, I., Doan, T.M., Grismer, L.L., Hoogmoed, M., Itescu, Y., Kraus, F., Lebreton, M., Lewin, A., Martins, M., Maza, E., Meirte, D., Nagy, Z.T., Nogueira, C.D.C., Pauwels, O.S.G., Pincheira-Donoso, D., Powney, G.D., Sindaco, R., Tallowin, O.J.S., Torres-Carvajal, O., Trape, J.F., Vidan, E., Uetz, P., Wagner, P., Wang, Y., Orme, C.D.L., Grenyer, R. & Meiri, S. (2017). The global distribution of Tetrapods reveals a need for targeted reptile conservation. *Nature Ecology and Evolution*, **1**(11), 1677–1682.

Rolland, J., Silvestro, D., Schluter, D., Guisan, A., Broennimann, O. & Salamin, N. (2018). The impact of endothermy on the climatic niche evolution and the distribution of vertebrate diversity. *Nature Ecology and Evolution*, **2**, 459–464.

Rubolini, D., Liker, A., Garamszegi, L.Z., Møller, A.P. & Saino, N. (2015). Using the birdtree.org website to obtain robust phylogenies for avian comparative studies: A primer. *Current Zoology*, **61**(6), 959–965.

Schimel, D.S. (1995). Terrestrial ecosystems and the carbon cycle. *Global change biology*, **1**(1), 77–91.

Schilthuizen, M. (2000). Ecotone: speciation-prone. *Trends in Ecology & Evolution,* **15**(4), 130–131. doi:10.1016/s0169-5347(00)01839-5

Schweizer, M., Hertwig, S.T., & Seehausen, O. (2014). Diversity versus disparity and the role of ecological opportunity in a continental bird radiation. *Journal of Biogeography*, **41**(7), 1301–1312.

Smith, T. B., Kark, S., Schneider, C. J., Wayne, R. K., & Moritz, C. (2001). Biodiversity hotspots and beyond: the need for preserving environmental transitions. *Trends in Ecology & Evolution,* **16**(8). doi:10.1016/s0169-5347(01)02201-7

Title, P. O. & Rabosky, D. L. (2019). Tip rates, phylogenies and diversification: What are we estimating, and how good are the estimates? *Methods in Ecology and Evolution,* **10**(6), 821–834. doi:10.1111/2041-210x.13153

Tonini, J.F.R., Beard, K.H., Ferreira, R.B., Jetz, W. & Pyron, R.A. (2016). Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*, **204**, 23–31.

Upham, N.S., Esselstyn, J.A. & Jetz, W. (2019). Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biology,* **17**(12), e3000494.

Vallejos, R., Osorio, F., Bevilacqua, M. (2020). *Spatial Relationships Between Two Georeferenced Variables: with Applications in R*. Cham: Springer. DOI: 10.1007/978-3-030-56681-4

Van Dijk, A., Nakamura, G., Rodrigues, A. V., Maestri, R., & Duarte, L. (2021). Imprints of tropical niche conservatism and historical dispersal in the radiation of Tyrannidae (Aves: Passeriformes). *Biological Journal of the Linnean Society,* **134**(1), 57–67. https://doi.org/10.1093/biolinnean/blab079

Vasconcelos, T.S., da Silva, F.R., dos Santos, T.G., Prado, V.H.M. & Provete, D.B. (2019). *Biogeographic Patterns of South American Anurans*. Switzerland: Springer International Publishing.

Velasco, J.A. & Pinto-Ledezma, J.N. (2022) Mapping species diversification metrics in macroecology: Prospects and challenges. *Frontiers in Ecology and Evolution,* **10**, DOI 10.3389/fevo.2022.951271.

Vilela, B., & Villalobos, F. (2015). letsR: a new R package for data handling and analysis in macroecology. *Methods in Ecology and Evolution*, **6**(10), 1229-1234. doi:10.1111/2041-210x.12401

Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences of the United States of America*, **111**(38), 13690-13696. doi:10.1073/pnas.1415442111

Wiens, J.J. (2011). The causes of species richness patterns across space, time, and clades and the role of"ecological limits". *Quarterly Review of Biology,* **86**(2), 75–96.

Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, **19**, 639–644.

Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. & Reeder, T.W. (2006). Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: Treefrog trees unearth the roots of high tropical diversity. *American Naturalist*, **168**, 579–596.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, **95**(7), 2027.

Supplementary material

Productivity interacts with diversification rate in determining species richness and trait diversity of tetrapods in a global hotspot

Supplementary Methods

To obtain the metrics of diversification rate (Jetz et al., 2012) and assemblage age (Van Dijk et al., 2021), we used the *Herodotools* R package (Nakamura et al., 2022). Community-level metrics available in *Herodotools* incorporate ancestral range reconstruction and regionalization proposals, allowing one to consider historical biogeography and species dispersal/colonization time. First, we performed a biogeographical regionalization analysis of the Atlantic Forest species pool based on a phylogenetic fuzzy matrix coupled to a Discriminant Principal Component Analysis based on non-hierarchical k-means clustering in the R package evoregions. Evoregions calculates areas corresponding to centers of lineage-independent diversification, reflecting the historical radiation of unique clades (Maestri & Duarte, 2020). The evoregion function will run an automatic procedure based on the "elbow" method to define the maximum number of clusters. This procedure returned four distinct regions for amphibians and squamates, five for birds, and six for mammals in the Brazilian Atlantic Forest. However, community attribution to each evoregion is not equal across cells. Therefore, an affiliation value is assigned to each assemblage, where low affiliation values correspond to areas with high turnover, that is, areas with multiple colonization events by different lineages (Figure 1; Maestri & Duarte, 2020).

After classifying areas in each of the evoregions in a Phyllip file, we fitted the DEC and DEC+J models to the data using the R package BioGeoBEARS. The DEC and DEC+J models implicitly assume that the observed tree is complete, and that lineage-level speciation and extinction are independent of the process of distributional evolution. The only difference is that DEC+J incorporates founder event speciation (+J). After that, we compare model fit using ⊗AICc. The DEC+J model performed better in all vertebrate groups (Table S3). Given we have data on species occurrence, a biogeographical regionalization proposal, and the ancestral range reconstruction, we can use this information to calculate metrics. The 'calc_age_arrival' function calculates the mean age of each assemblage. After that, we calculated the harmonic mean of DR (DR; Jetz et al.,

2012) for each grid cell, using the inverse of the Equal Splits measure (Redding & Mooers, 2006).

References

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012). The global diversity of birds in space and time. *Nature*, **491**, 444–448. https://doi.org/10.1038/nature11631

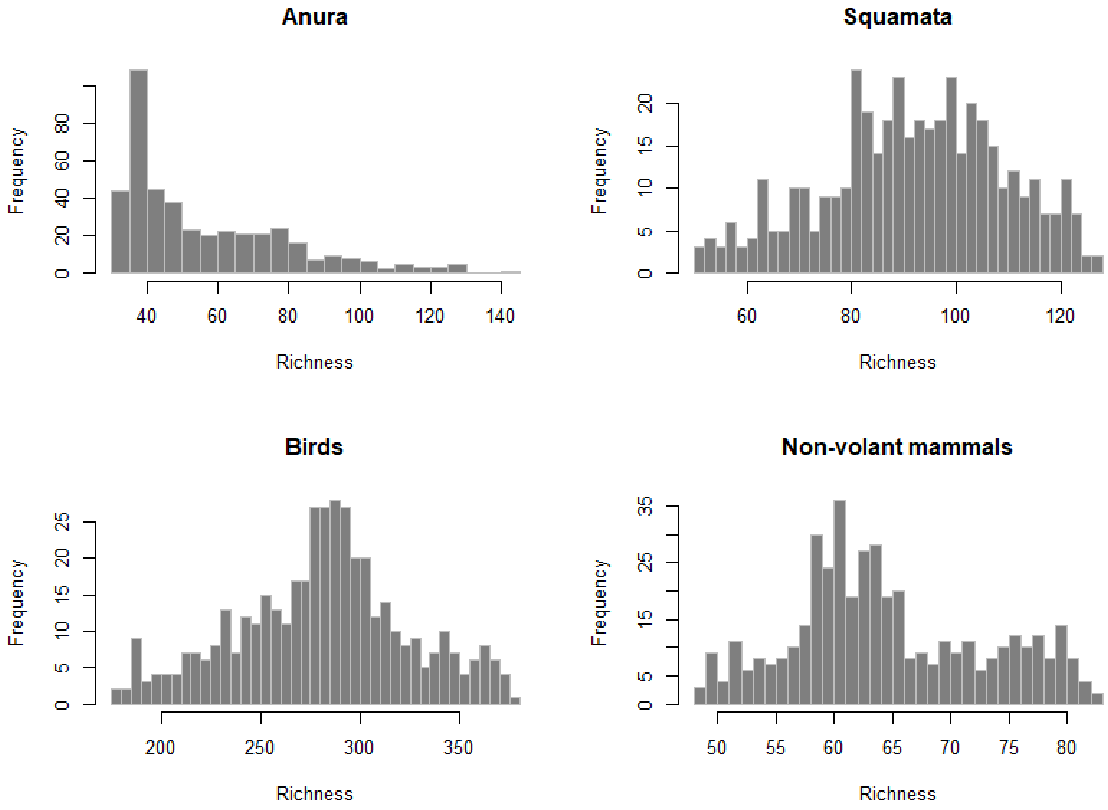
Maestri, R., & Duarte, L.D.S. (2020). Evoregions: Mapping shifts in phylogenetic turnover across biogeographic regions. *Methods in Ecology and Evolution*, **11**(12), 1652–1662. https://doi.org/10.1111/2041-210X.13492

Nakamura, G., Rodrigues, A.V., Luza, A.L., Maestri, R., Debastiani, V. & Duarte, L. (2022). Herodotools: An R package to integrate macroevolution, community ecology, and biogeography. *Journal of Biogeography in press* https://doi.org/10.32942/osf.io/2f6uk

Redding, D.W., & Mooers, A.O. (2006). Incorporating evolutionary measures into conservation prioritization. *Conservation Biology*, **20**(6), 1670–1678. https://doi.org/10.1111/j.1523-6221739.2006.00555.x

Van Dijk, A., Nakamura, G., Rodrigues, A. V., Maestri, R., & Duarte, L. (2021). Imprints of tropical niche conservatism and historical dispersal in the radiation of Tyrannidae (Aves: Passeriformes). *Biological Journal of the Linnean Society*, **134**(1), 57–67. https://doi.org/10.1093/biolinnean/blab079

Figures


Anura
Frequency
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40
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Richness
Squamata
Frequency
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60
80
100
120
Richness
Birds
Frequency
0
5
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15
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25
200
250
300
350
Richness
Non-volant mammals
Frequency
0
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Richness

Fig S1. Frequency distribution of species richness count in the grids for the four clades of terrestrial vertebrates.

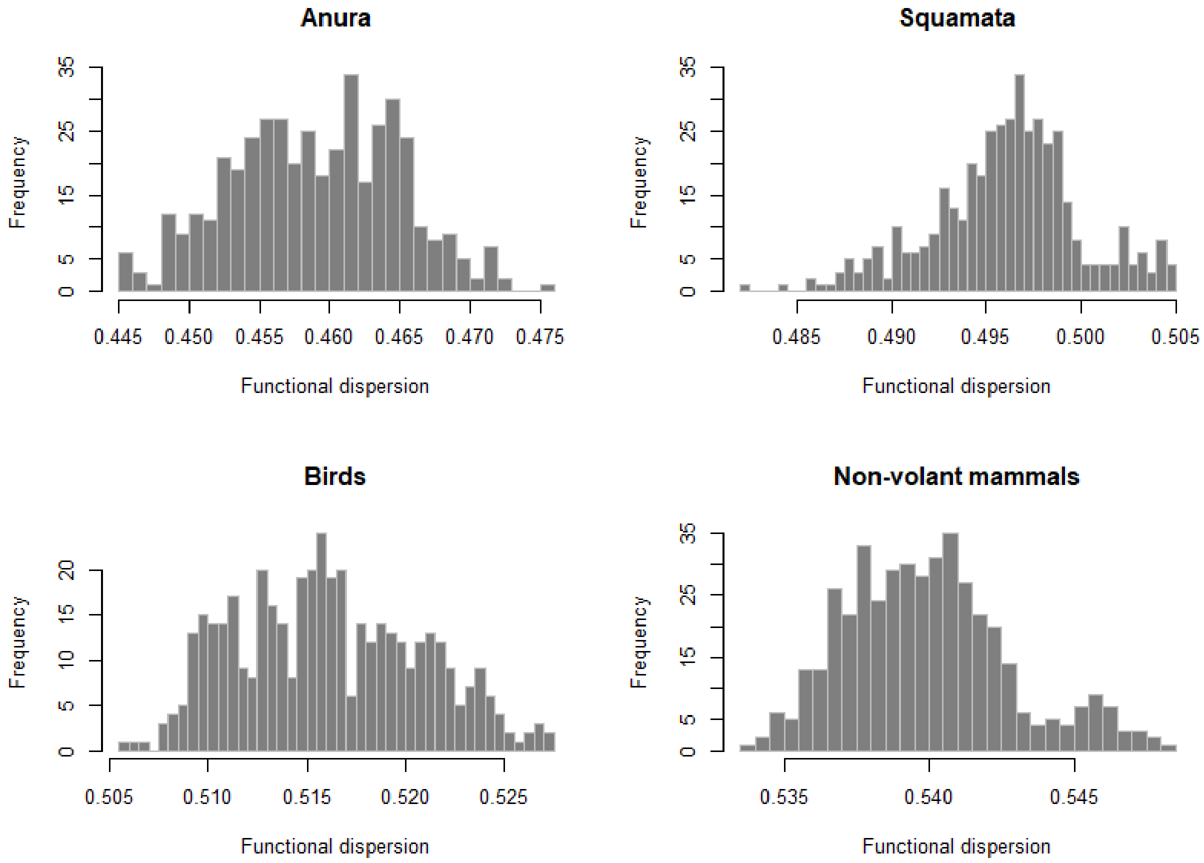

Fig S2. Histograms showing the frequency distribution for the functional dispersion values (FDis) of the four clades of terrestrial vertebrates.

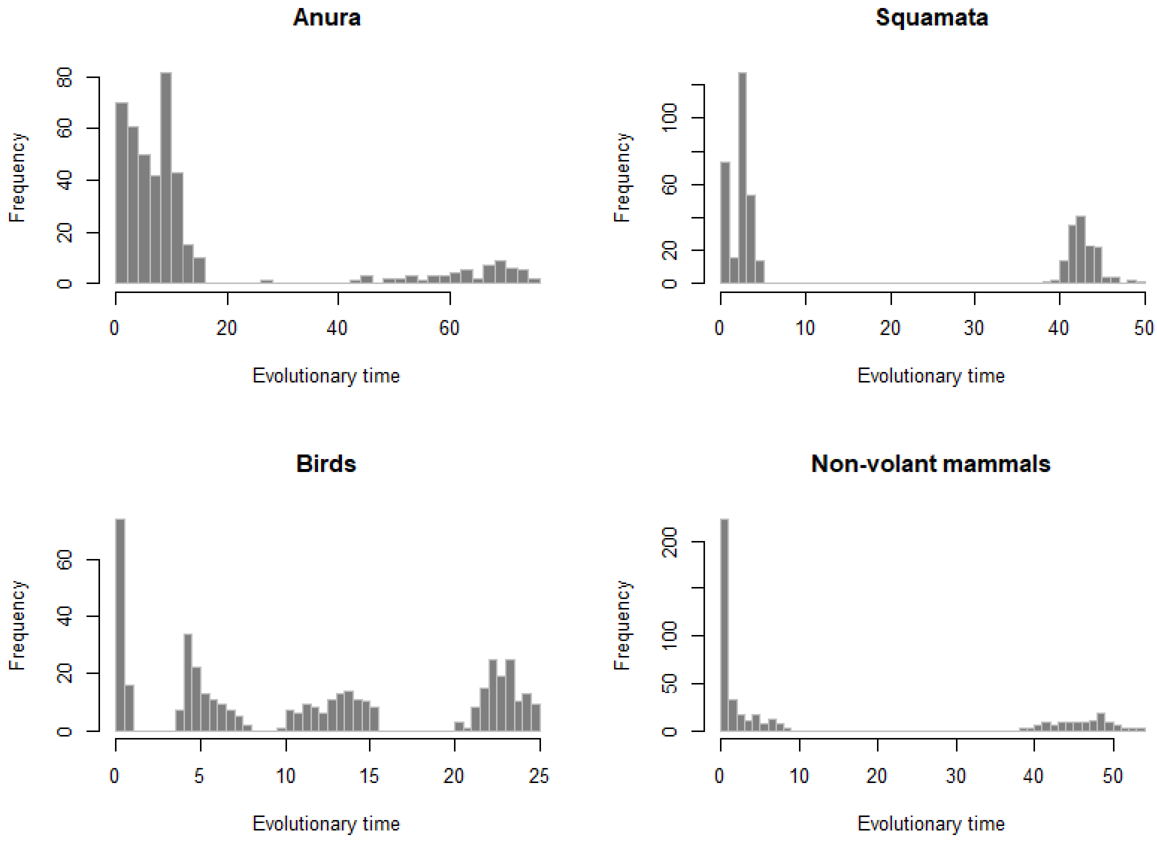

Fig S3. Histogram showing the frequency distribution of assemblage age (evolutionary time) of the four clades of terrestrial vertebrates.

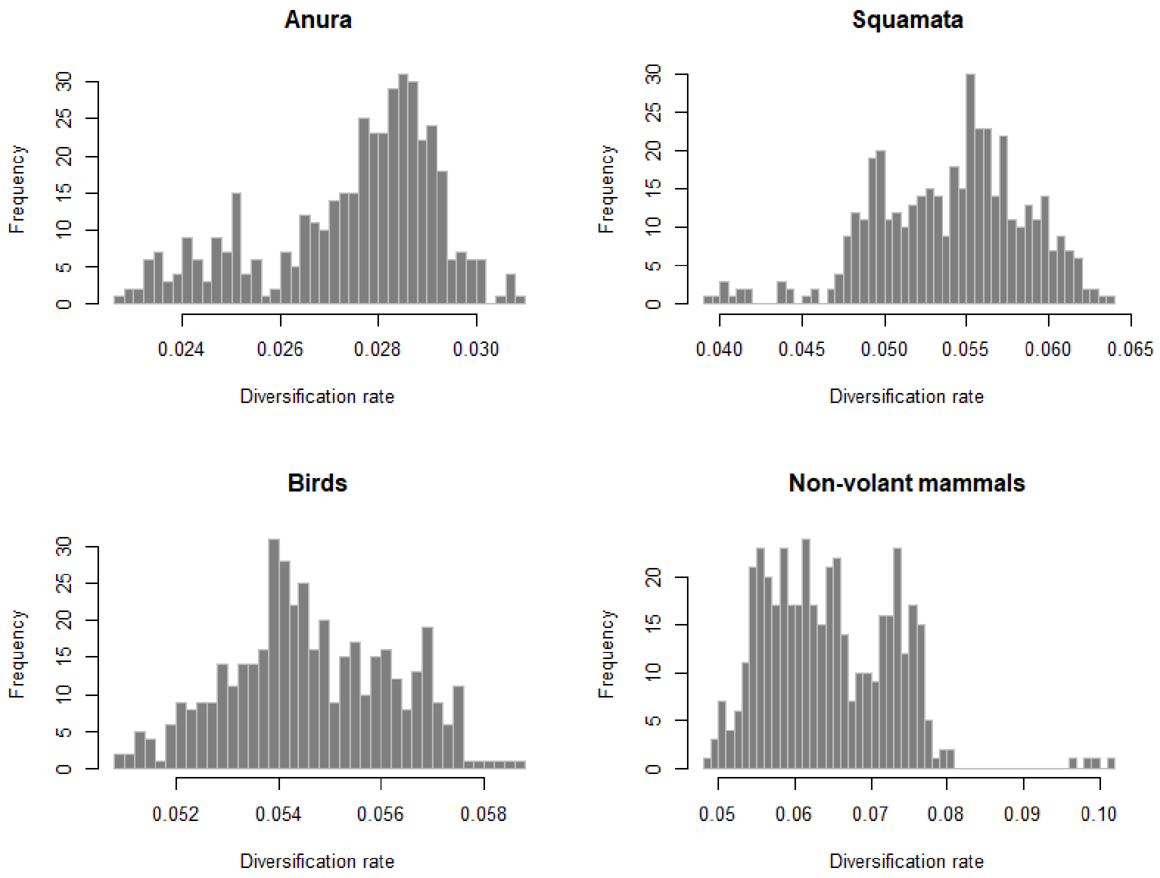

Fig. S4. Histograms showing the frequency distribution of diversification rate of the four clades of terrestrial vertebrates

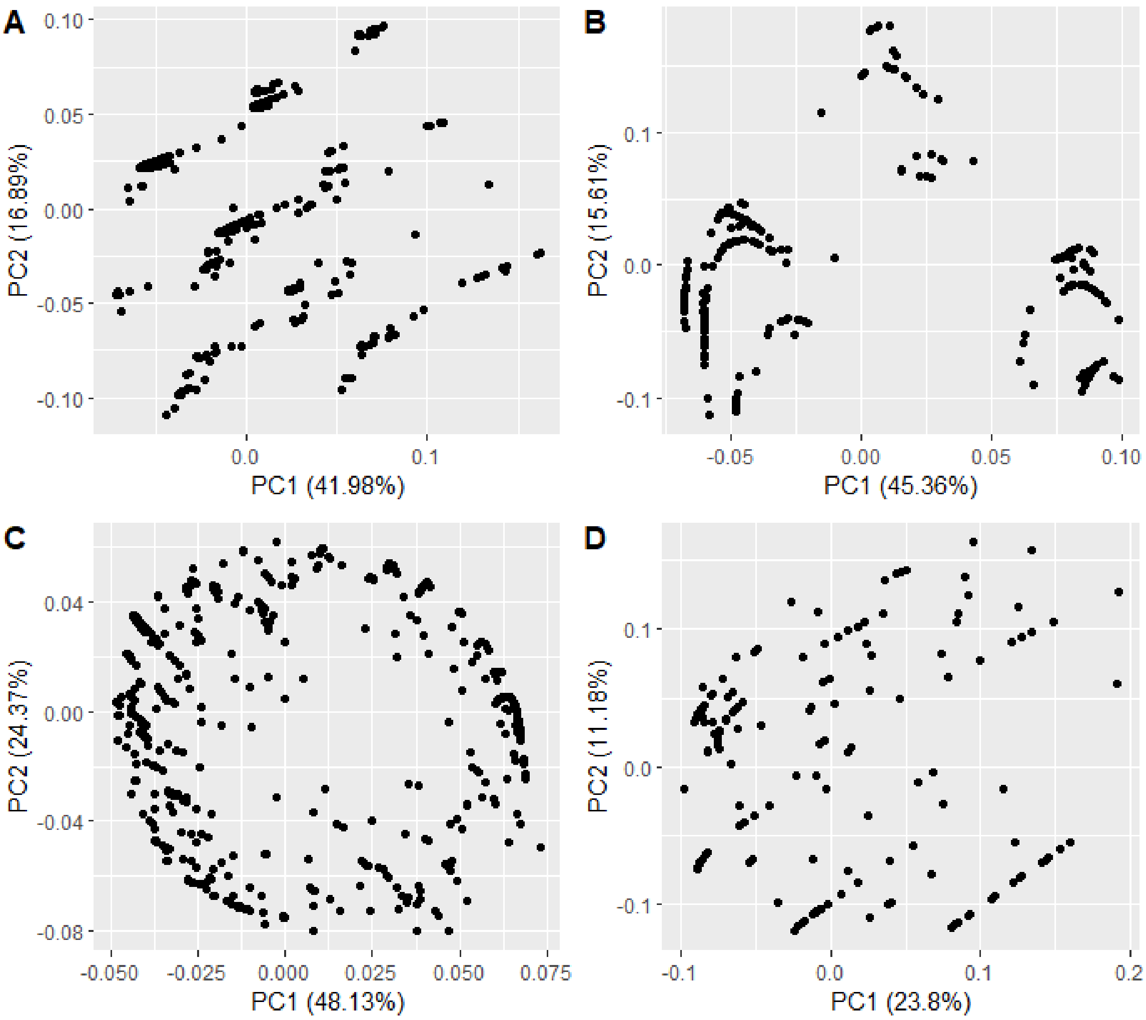

Fig S5. Ordination diagrams showing the first two axes of Principal Coordinates Analyses (PCoA) conducted on the trait distance matrices describing the trait space of the four clades of terrestrial vertebrates (A: Anura; B: Squamates; C: Birds; D: Mammals).

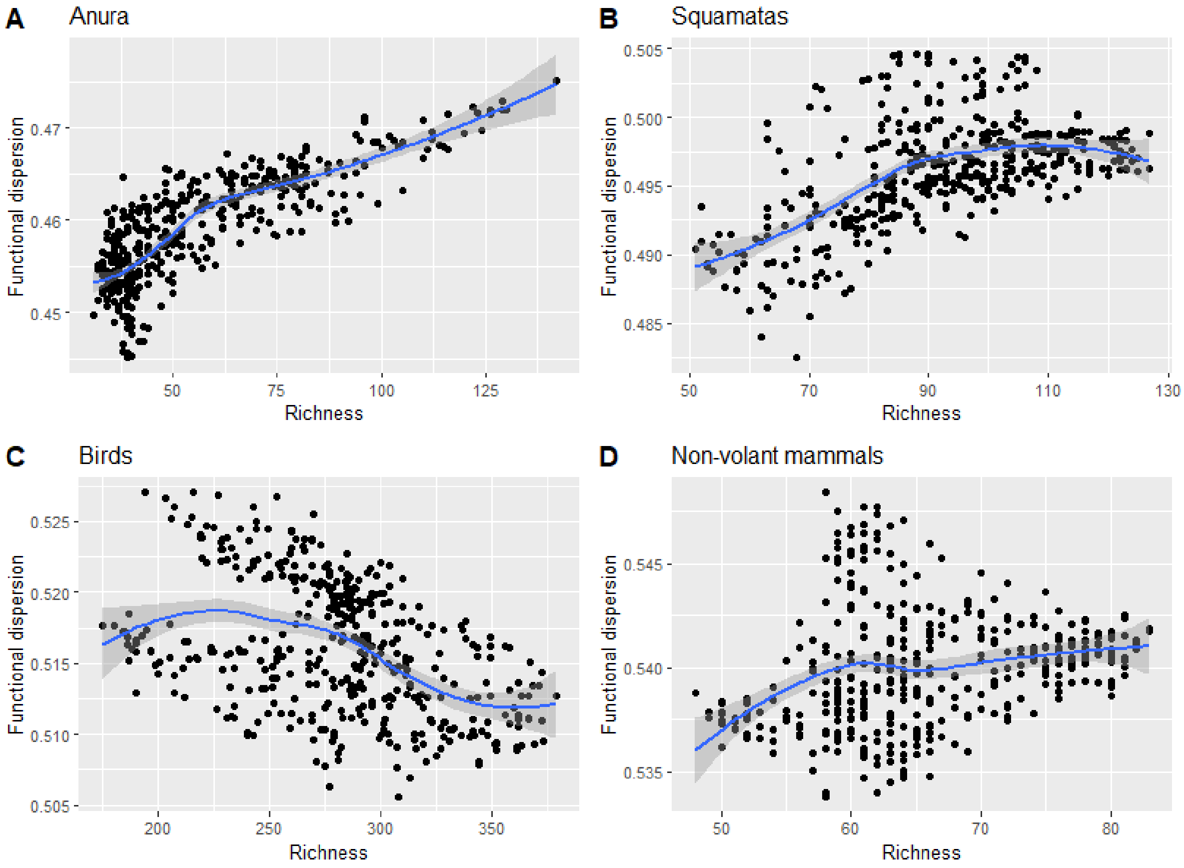

Fig S6. Scatter plots showing the relationship (loess curve) between richness and functional dispersion (FDis) of terrestrial vertebrates.

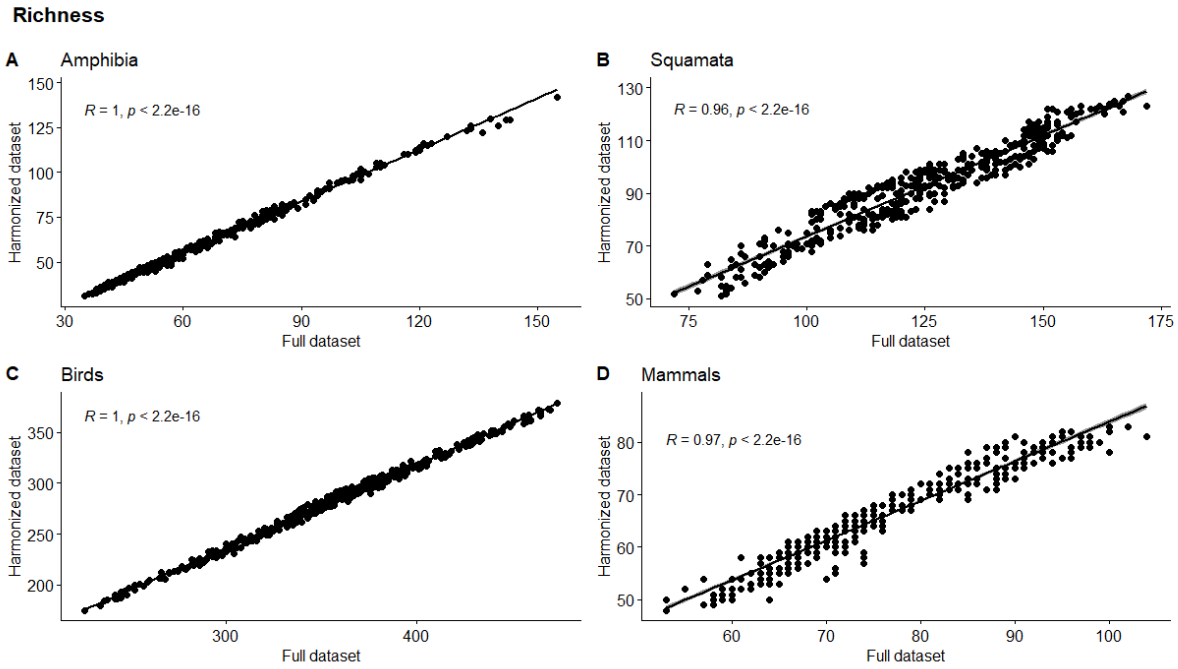

Fig S7. Pearson's correlation between species richness estimated with the harmonized (only species with traits) and the complete dataset.

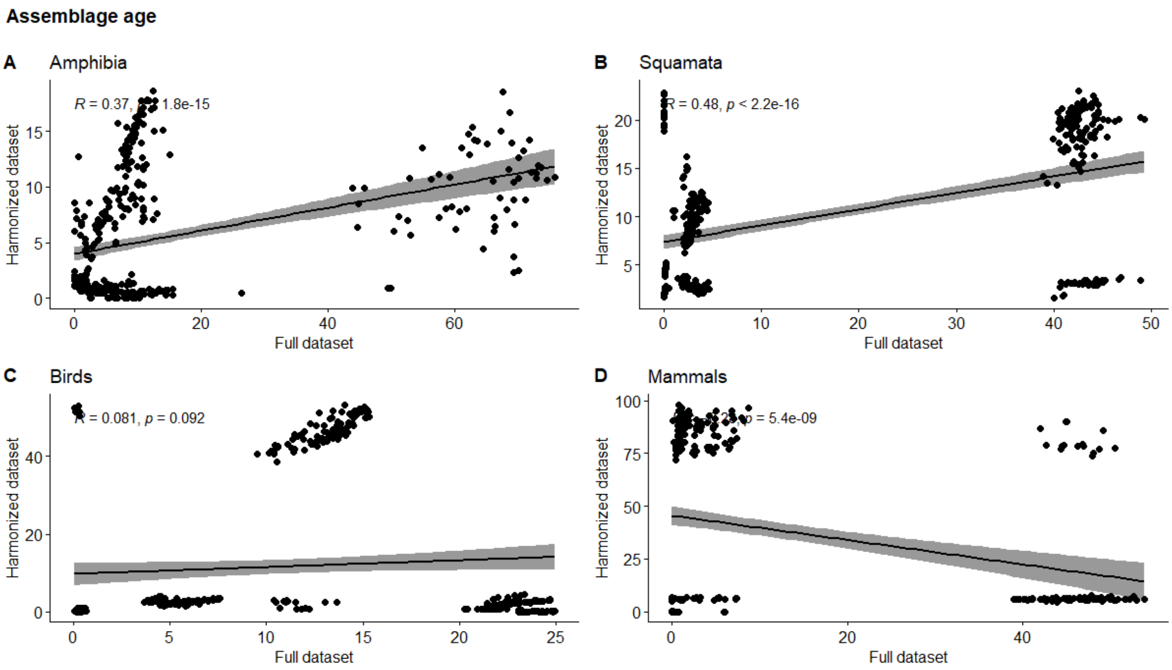

Fig S8. Pearson's correlation between assemblage age estimated with the harmonized (only species with traits) and the complete dataset.

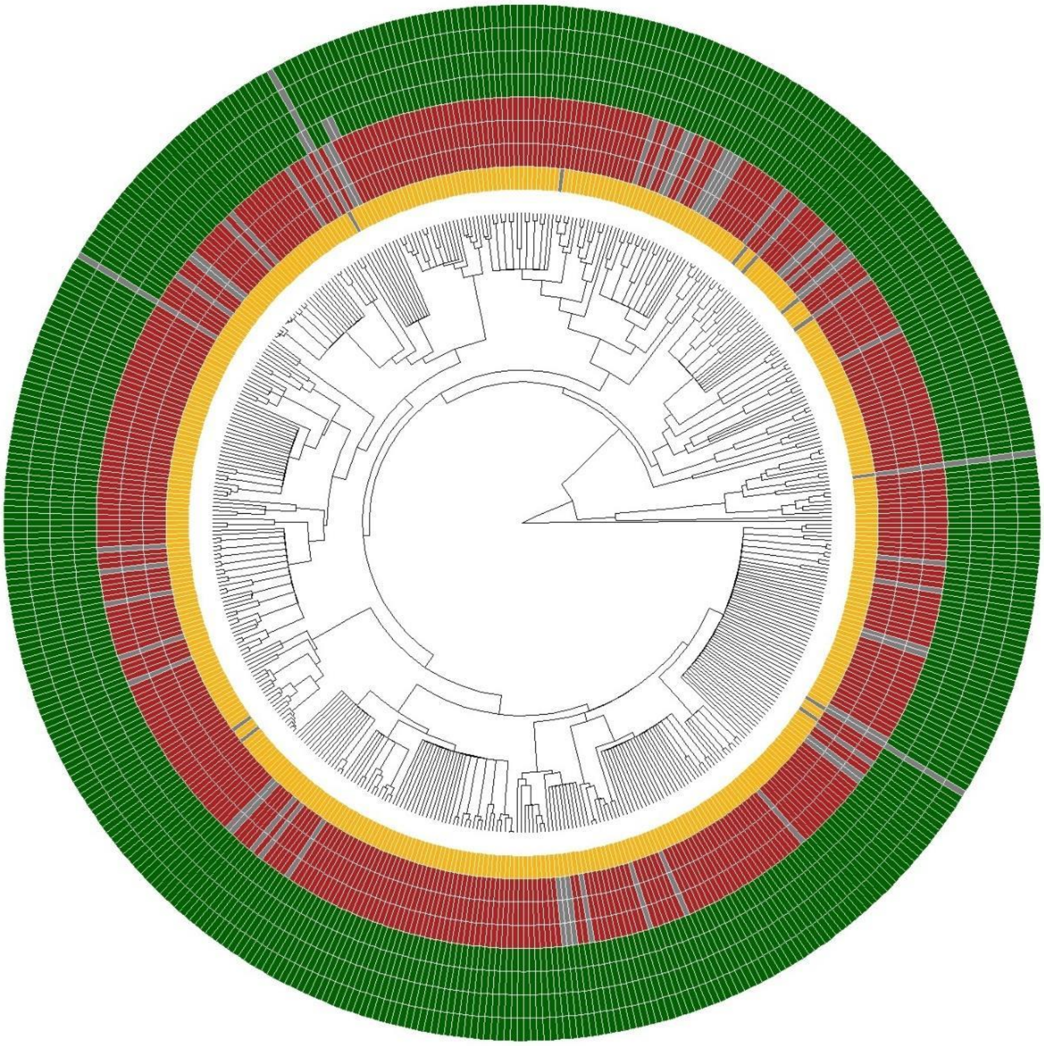

Fig S9. Distribution of missing traits (gray) in the amphibian phylogeny. Body size (yellow), circadian activity (red), and habitat (green). See Table S3 for phylogenetic signal metric. Missingness in habitat is slightly clumped, while body size and circadian activity data are missing mostly at random, with very few species missing all three traits.

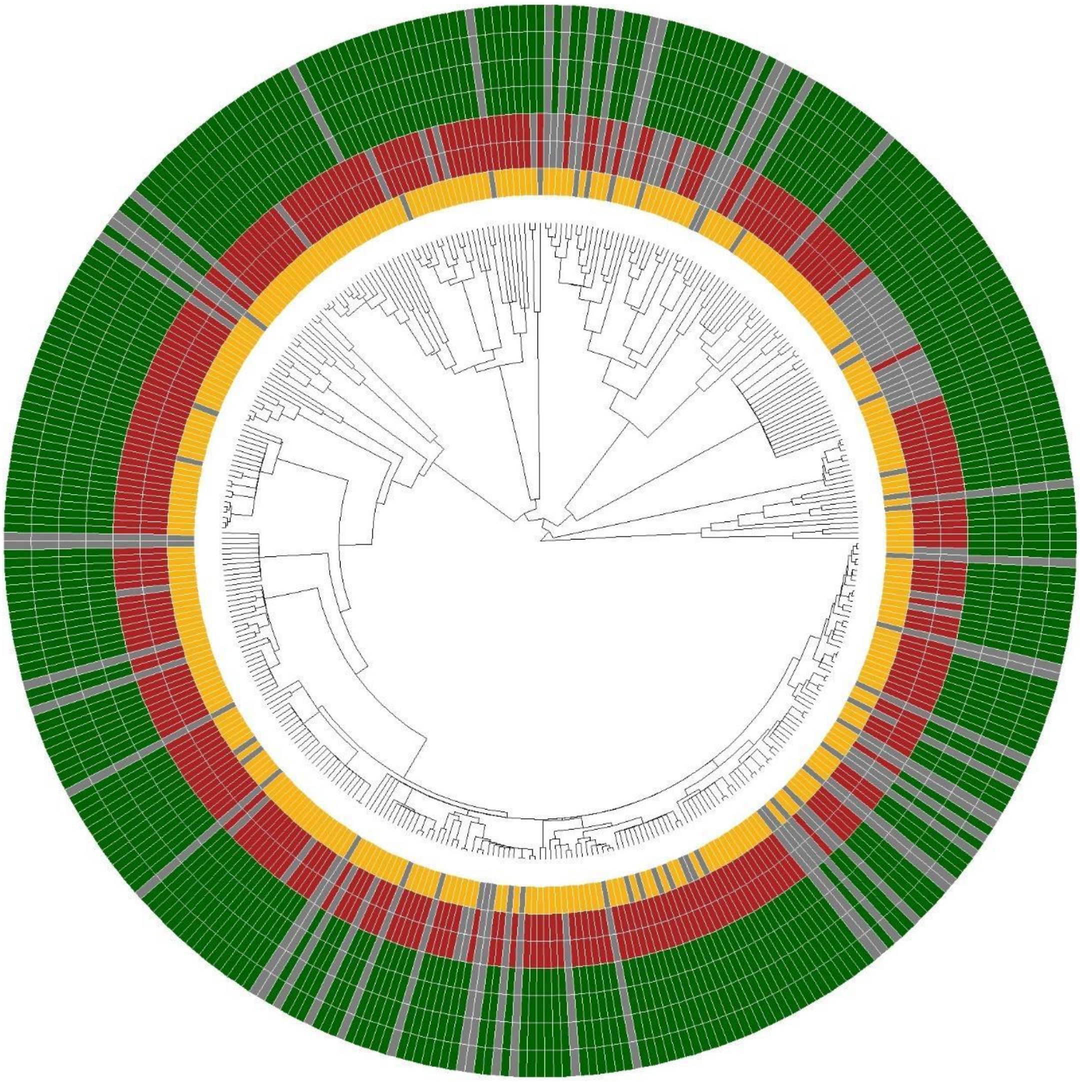

Fig S10. Distribution of missing traits (gray) in the squamate phylogeny. Body size (yellow), circadian activity (red), and habitat (green). See Table S3 for phylogenetic signal metric. Missingness in circadian activity is slightly clumped, while body size and habitat data are missing mostly at random, with amphisbaenids lacking most data.

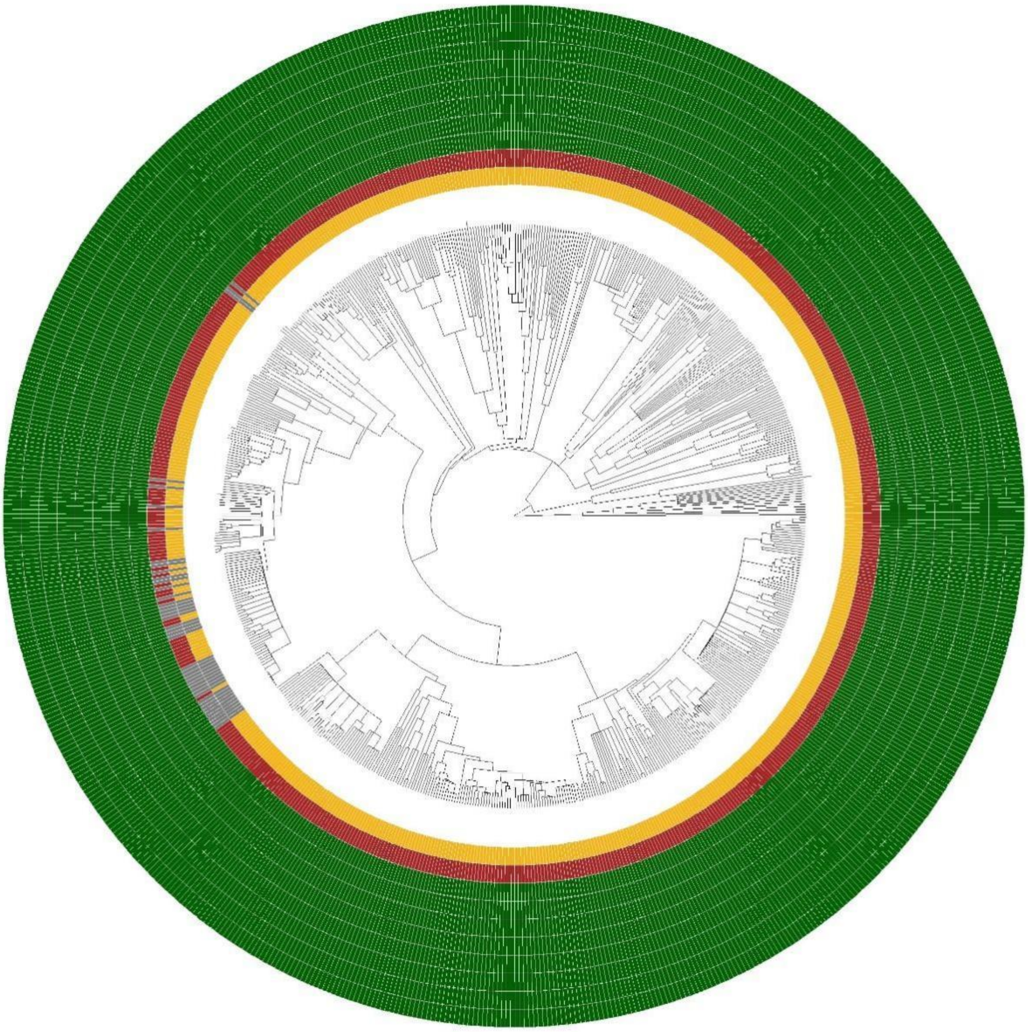

Fig S11. Distribution of missing traits (gray) in the bird phylogeny. Body size (yellow), circadian activity (red), and habitat (green). See Table S3 for phylogenetic signal metric. Missingness in body size and circadian activity are only slightly clumped. Habitat data are complete for all species.

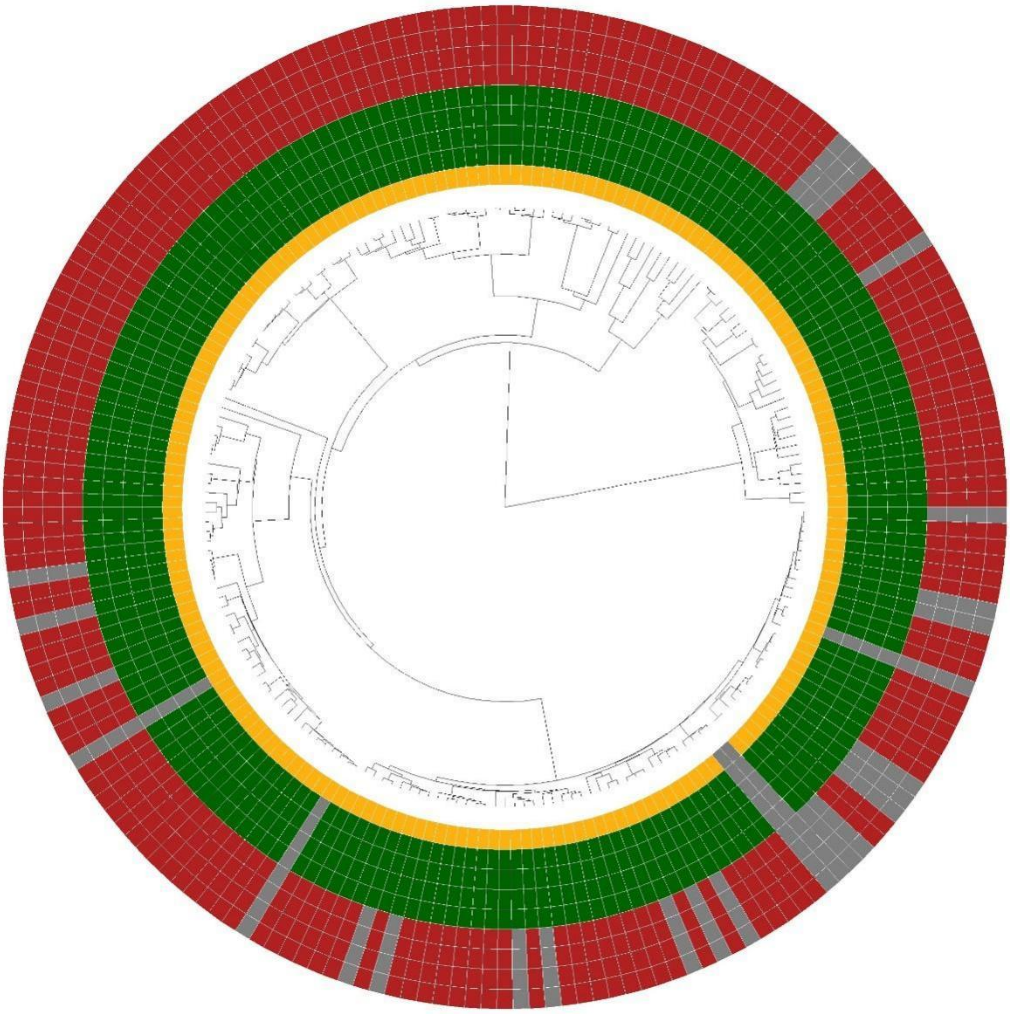

Fig S12. Distribution of missing traits (gray) in the mammal phylogeny. Body size (yellow), circadian activity (red), and habitat (green). See Table S3 for phylogenetic signal metric. Missingness in body size seems to be highly clumped, but the amount of missing data is low. Missingness is random in the other two traits.

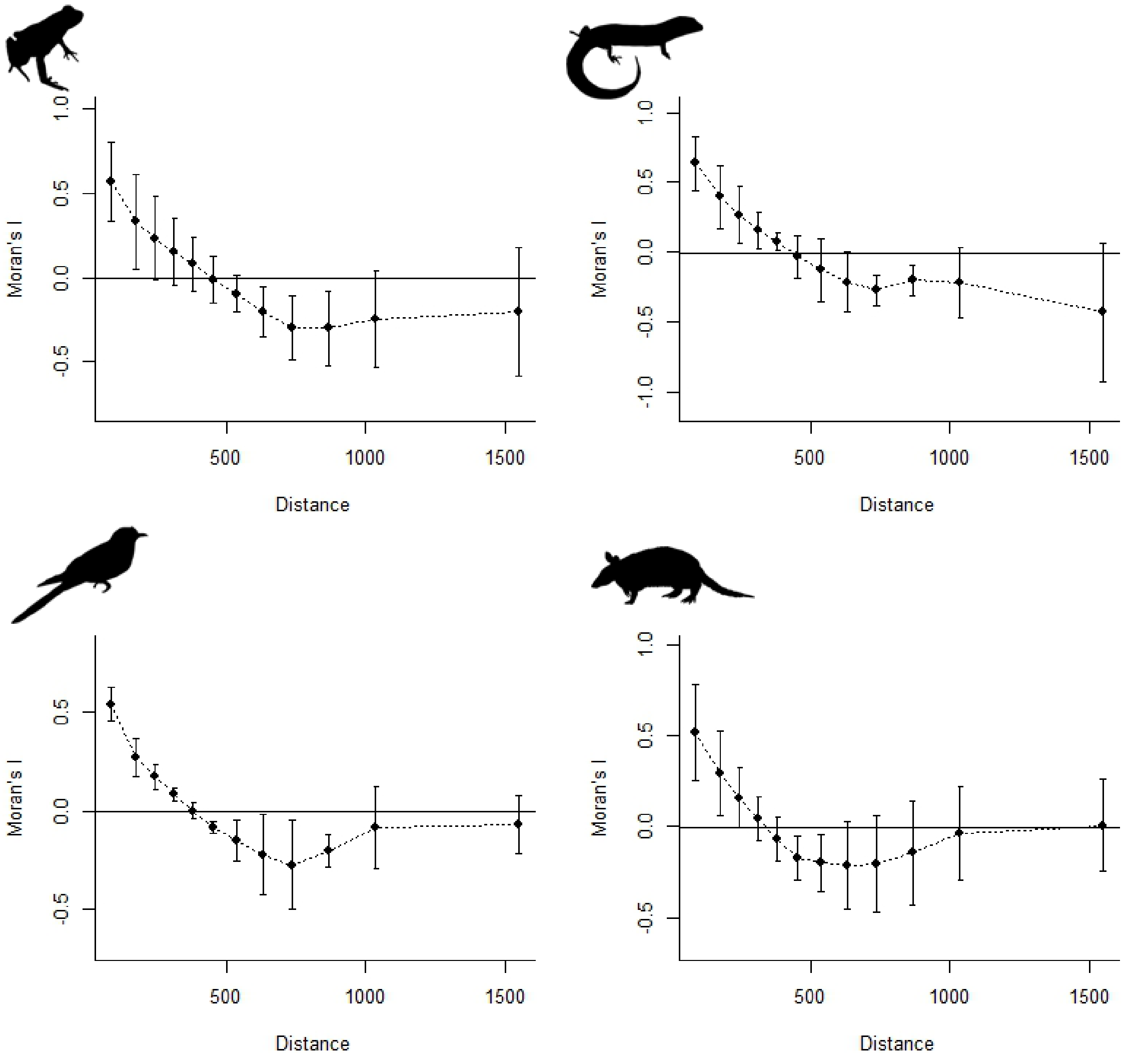

Fig S13. Spatial correlogram with Moran's *I* of the residuals of the best Generalized Least Square (GLS) models used in the structural equation models.

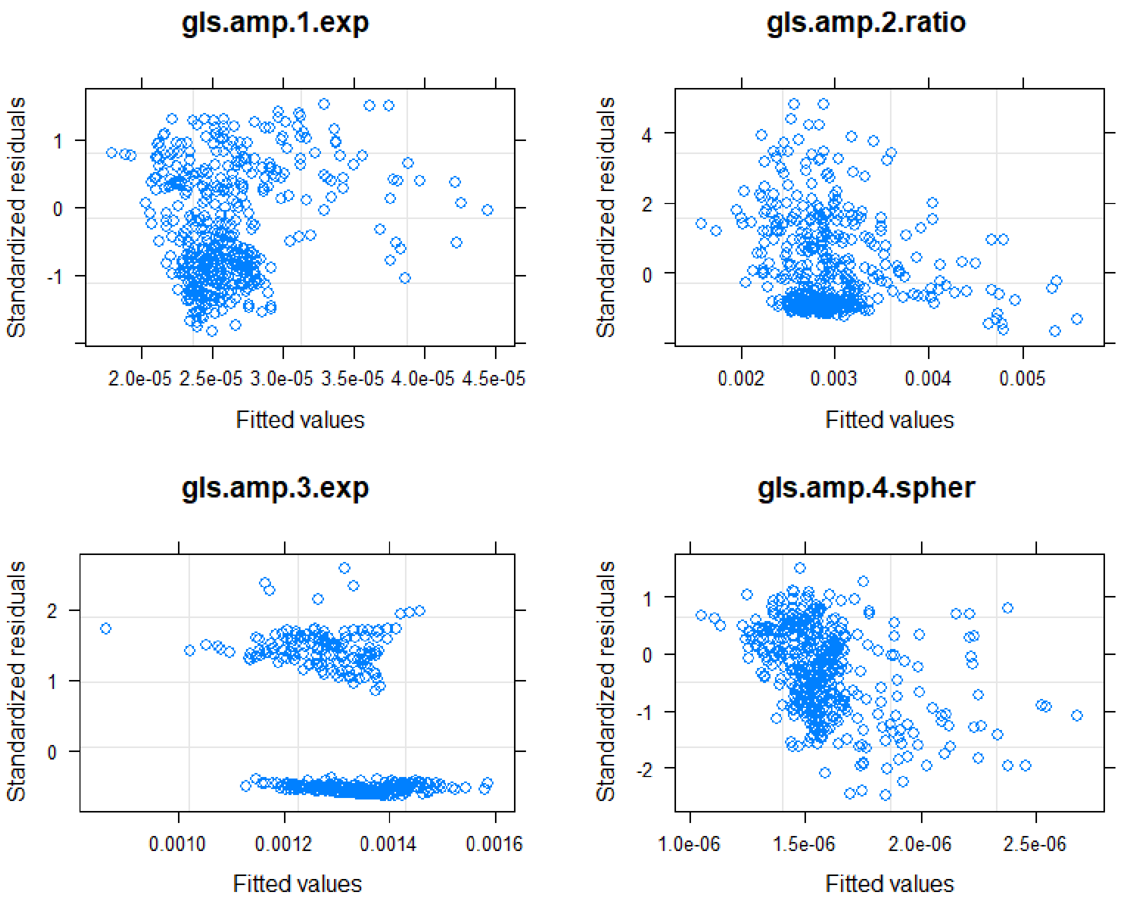

Fig. S14. Residual diagnosis for each of the four best GLS models included in the SEM for amphibians. Plots show the fitted vs. residuals for the best correlation structure, from the five tested (exponential, Gaussian, linear, ratio, and spherical), used in final GLS models.

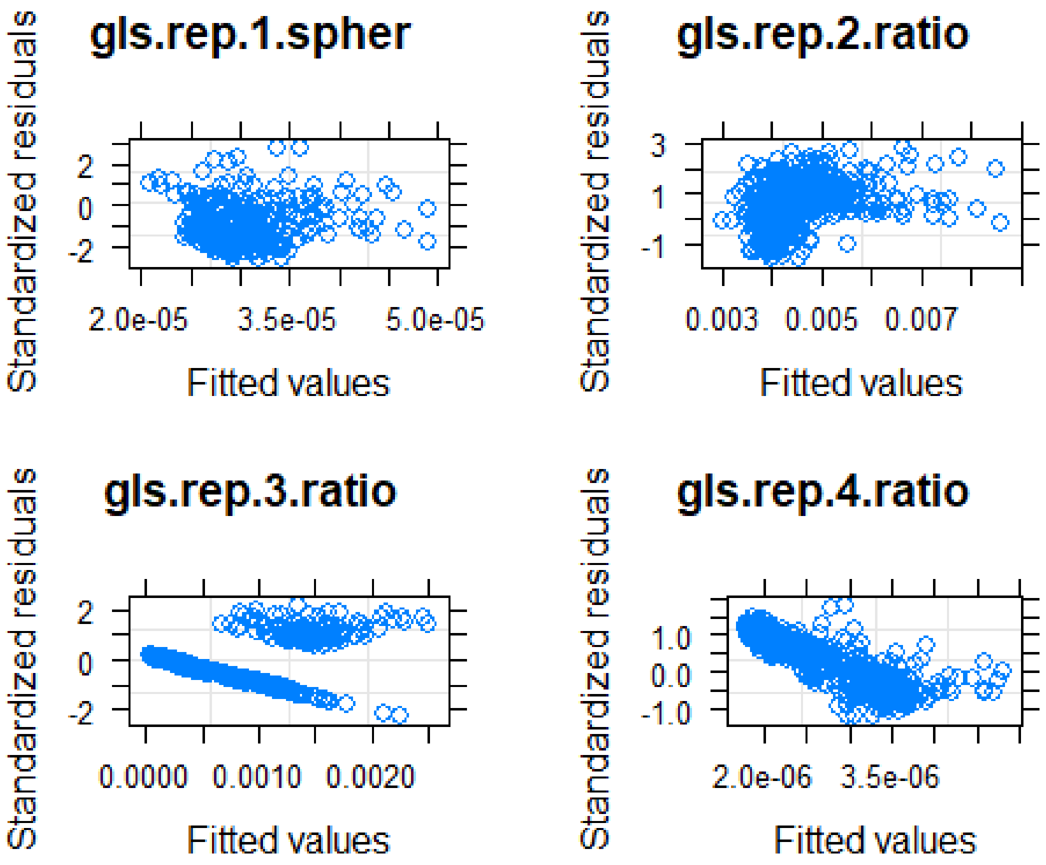

Fig. S15. Residual diagnosis for each of the four best GLS models included in the SEM for squamates. Plots show the fitted vs. residuals for the best correlation structure, from the five tested (exponential, Gaussian, linear, ratio, and spherical), used in final GLS models.

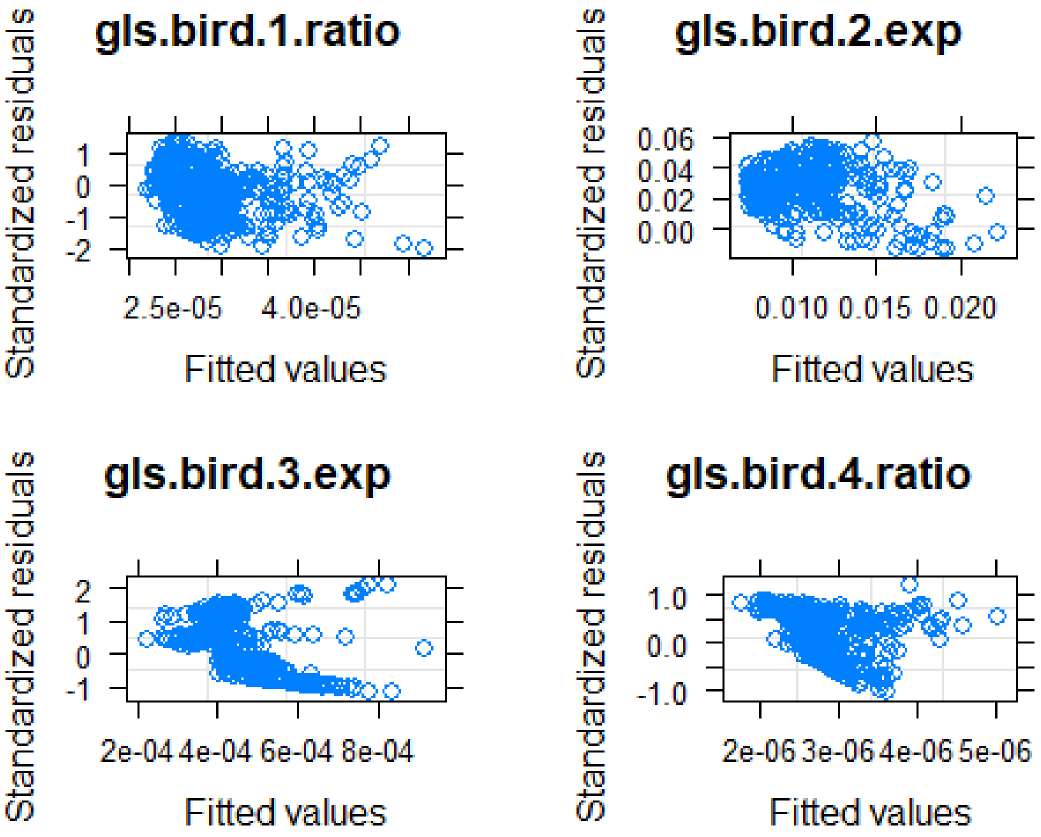

Fig. S16. Residual diagnosis for each of the four best GLS models included in the SEM for birds. Plots show the fitted vs. residuals for the best correlation structure, from the five tested (exponential, Gaussian, linear, ratio, and spherical), used in final GLS models.

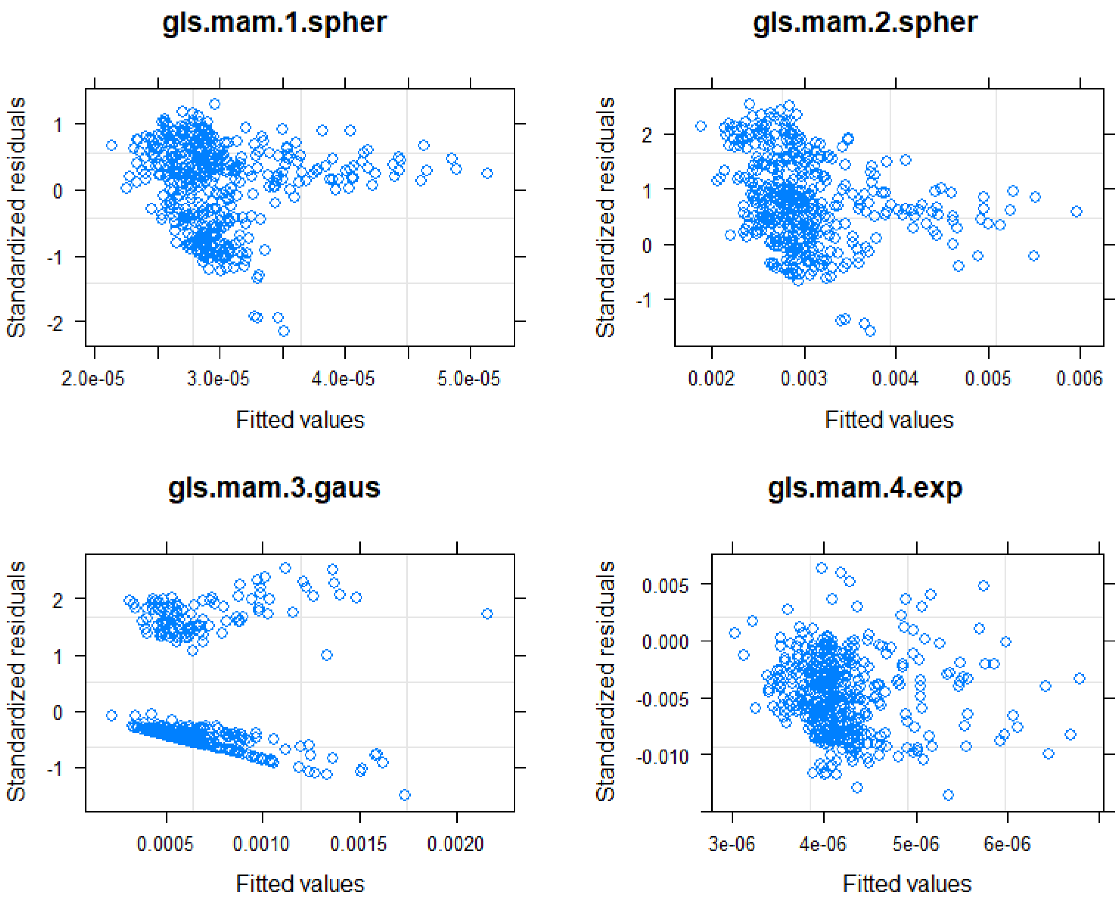

Fig. S17. Residual diagnosis for each of the four best GLS models included in the SEM for mammals. Plots show the fitted vs. residuals for the best correlation structure, from the five tested (exponential, Gaussian, linear, ratio, and spherical), used in final GLS models.

Tables

Table S1. Functional traits used to calculate functional dispersion (FDis), showing variable type and its ecological interpretation.

Traits	Group	Variable type	Ecological interpretation	Reference
Maximum body size (mm)	Anura/ Squamates	Continuous	Correlated with various ecological characteristics that impact fitness	Peters (1986)
Maximum body mass (g)	Birds/ Mammals			
Activity period	Anura	Dummy (Crepuscular, diurnal, nocturnal)	Time dimension. Affects foraging patterns in endotherms, and is related to desiccation risk in ectotherms	Kronfeld-Schor et al, (2001)
	Squamates	Dummy (Nocturnal or Diurnal)		
	Birds	Binary (Nocturnal or not)		
	Mammals	Dummy (Cathemeral, crepuscular, diurnal, nocturnal)		
Habitat	Anura	Dummy (Fossorial, terrestrial, aquatic, and arboreal)	Spatial dimension. The habitat in which a species is mostly found, which strongly influences species performance in the environment. Proxy for ecological specialization.	Oliveira and Scheffers (2018)
	Squamates	Dummy (Fossorial, terrestrial, aquatic, and arboreal)		
	Birds	Fuzzy/Binary (Foraging strategy understory, canopy, ground, mid high, aerial/Pelagic specialist)		
	Mammals	Dummy (Fossorial, ground dwelling, above ground dwelling, aquatic)		

Table S2. Pairwise spatial congruence between the harmonized (harm, species with traits only) and complete dataset (full, only species present in the tree) for species richness and Assemblage Age (AA). High correlation values indicate that the two datasets do not differ in terms of spatial patterns. Tjøstheim correlation coefficients above 0.46 are significant (*). As diversification rate also depends on ancestral range reconstruction, we used the complete dataset for calculating DR and assemblage age.

Amphibia	rich_harm	aa_harm
rich_full	0.891	-
aa_full	-	0.375
Squamates		
rich_full	0.848	-
aa_full	-	0.344
Birds		
rich_full	0.886	
aa_full	-	0.001
Mammals		
rich_full	0.838	-
aa_full	-	0.037

Table S3. Phylogenetic signal (Fritz' *D* statistic) for the distribution of missing traits in the phylogeny of each tetrapod group. *D* values close to 1, and significant, indicate that the trait is randomly distributed in the phylogeny, while those close to 0 indicate the trait is clumped, as it would be expected under a threshold model following a Brownian Motion model (Fritz & Purvis 2010). P(D>0) = *P value* for the difference from random distribution; P(D<1) = *P value* for departure from Brownian Motion.

	Frogs			**Squamates**			**Birds**			**Mammals**		
	D	***P(D>0)***	***P(D<1)***	***D***	***P(D>0)***	***P(D<1)***	***D***	***P(D>0)***	***P(D<1)***	***D***	***P(D>0)***	***P(D<1)***
Body Mass/Size	0.819	0.074	**0.044**	0.867	**0.021**	**0**	0.641	**0**	0.09	-1.389	**0.002**	0.838
Circadian activity	0.732	**0**	**0**	0.527	**0**	**0.001**	0.644	**0**	0.09	0.695	**0.001**	0
Habitat	0.354	**0.001**	0.352	0.793	**0.001**	**0**	1	**0**	**0**	0.719	**0.083**	0.081

Table S4. Continued

Harmonized dataset							
Amphibia	**LnL**	**numparams**	**d**	**e**	**j**	**AICc**	**Δ_AICc**
DEC+J	-1496.31	3	0.01	0.01	0.056827	2998.688	0
DEC	-1502.18	2	0.01	0.01	0	3008.387	9.699699629
Squamata							
DEC+J	-744.104	3	0.010753	0.001504372	0.205873	1494.301	0
DEC	-792.253	2	0.021318	0.014404208	0	1588.553	94.25132368
Birds							
DEC+J	-1664.56	3	0.002788	1.00E-12	0.041223	3335.166	0
DEC	-1900.67	2	0.01	0.01	0	3805.36	470.1946061
Mammals							
DEC+J	-468.508	3	0.037485	0.012229513	1.00E-05	943.1644	0
DEC	-483.756	2	0.031028	0.012878324	0	971.5862	28.42185226

Table S5. Model selection procedure used to choose the spatial correlation structure (corExp, corGaus, corLin, corRatio and corSpher) used in Generalized Least Squares (GLS) models and their respective degree of freedom (Df). Correlation structures were used to control for the spatial autocorrelation in model residuals *. Values represent Akaike information criterion (AIC). Bold values are the best-fit models entered in the Structural Equation Models (SEM).

Taxa	**Models**	**corExp**	**corGaus**	**corLin**	**corRatio**	**corSpher**	**Df**
Anura	fdis_amp ~ climate_amp + Elevation + Productivity + dr_amp + aa_amp	**-11401.88**	-11342.63	-11398.76	-11385.89	-11400.07	9
	rich_amp ~ climate_amp + Elevation + Productivity + dr_amp + aa_amp	-5802.490	-5797.746	-5801.138	**-5829.383**	-5803.619	9
	aa_amp ~ climate_amp + Elevation + Productivity	**-4529.912**	-4517.432	-4483.155	-4525.924	-4524.018	7
	dr_amp ~ aa_amp + climate_amp + Elevation + Productivity	-13167.47	-13156.05	-13166.82	-13166.09	**-13169.12**	8
Squamata	fdis_squa ~ climate_squa + Elevation + Productivity + dr_squa + aa_squa	-11253.72	-11213.58	-11253.72	-11244.02	**-11254.44**	9
	rich_squa ~ climate_squa + Elevation + Productivity + dr_squa + aa_squa	-6300.788	-6270.393	-6202.370	-6285.531	**-6301.763**	9
	aa_squa ~ climate_squa + Elevation + Productivity	-5229.741	-5229.955	-5226.806	**-5236.125**	-5229.712	7
	dr_squa ~ aa_squa + climate_squa + Elevation + Productivity	-12653.77	-12639.71	-12652.68	-12648.75	**-12657.02**	8

Table S5. Continued

Taxa	Models	corExp	corGaus	corLin	corRatio	corSpher	Df
Birds	fdis_birds ~ climate_birds + Elevation + Productivity + dr_birds + aa_birds	-11639.85	-11643.98	-11639.83	**-11657.59**	-11634.85	9
	rich_birds ~ climate_birds + Elevation + Productivity + dr_birds + aa_birds	-5314.605	-5332.195	-5314.605	**-5351.533**	-5315.251	9
	aa_birds ~ climate_birds + Elevation + Productivity	**-5869.470**	-5849.643	-5864.742	-5867.418	-5866.394	7
	dr_birds ~ aa_birds + climate_birds + Elevation + Productivity	-12852.42	-12838.82	-12852.42	-12848.76	**-12852.95**	8
Mammals	fdis_mammals ~ climate_mammals + Elevation + Productivity + dr_mammals + aa_mammals	**-11001.61**	-10975.20	-11001.61	-10992.68	-11001.61	9
	rich_mammals ~ climate_mammals + Elevation + Productivity + dr_mammals + aa_mammals	-6533.813	-6496.721	-6533.416	-6519.618	**-6534.631**	9
	aa_mammals ~ climate_mammals + Elevation + Productivity	-4717.570	-4718.390	-4676.348	-4717.584	**-4721.649**	7
	dr_birds ~ aa_birds + climate_birds + Elevation + Productivity	**-12087.83**	-12071.86	-12087.83	-12085.71	-12087.83	8

Effects of climatic niche on the rate of body size evolution in terrestrial vertebrates

Matheus de Toledo Moroti[1,2], Fernando R. Da Silva[3], Diogo B. Provete[2,4]*

[1] Pós-Graduação em Ecologia e Conservação, Instituto de Biociências, Universidade Federal do Mato Grosso do Sul, Campo Grande, Mato Grosso do Sul, Brazil.

[2] Instituto de Biociências, Universidade Federal do Mato Grosso do Sul, Campo Grande, Mato Grosso do Sul, 79002-970, Brazil.

[3] Laboratório de Ecologia Teórica: Integrando Tempo, Biologia e Espaço (LET.IT.BE), Departamento de Ciências Ambientais, Universidade Federal de São Carlos, Sorocaba, São Paulo, Brazil

[4] Gothenburg Global Biodiversity Centre, Box 100, S-405 30, Göteborg, Sweden.

*Corresponding author: diogo.provete@ufms.br

Data Availability Statement

All data and associated R scripts are available at https://github.com/mmoroti/vertebrates_evolution

Abstract

Several factors determine phenotypic variation at macroevolutionary scales. While the Red Queen Hypothesis highlights the importance of biotic factors, such as competition, in the divergence of traits between species, the "Court Jester Hypothesis" highlights the influence of abiotic factors, such as the climate niche. Studies indicate that the evolution of the climate niche can have a strong impact on the phenotypic variation of species. However, these issues have been evaluated on a global scale or using specific lineages, while little is known about how the climatic niche can influence the phenotypic evolutionary rates of different communities in the same geographic template. In addition, no study has yet analyzed how the climatic niche of vertebrates with different thermal tolerances affects the evolution of body size. Here, we estimated the rate of body size evolution for ectotherms (frogs and squamates) and endotherms (birds and non-volant mammals) that occur in the Atlantic Forest, a climatically and historically complex biome. Then, we tested how these rates are affected by their climatic niche. We found that terrestrial vertebrates show idiosyncratic patterns of body size evolution through time. Furthermore, we found high heterogeneity in evolutionary rates within each group in the Atlantic Forest, with lineages showing accelerations and other decelerations. Our results suggest that different selective pressures act on each group, leading to unique patterns of changes in body size over time. However, there is no statistically significant relationship between the rates of phenotypic evolution and the climatic niche of species, but the width had a greater influence on the variation of rates than the niche position. Our study represents the first step in understanding the evolutionary patterns of phenotypic evolution in vertebrates.

Keywords: Body mass, Functional traits, Tetrapods, Macroevolution, Red Queen Hypothesis,

Introduction

Several factors determine phenotypic variation on macroevolutionary scales (Harmon, 2017). From the tradition of paleobiology, the influence of biotic factors on trait evolutionary rates and lineage diversification has been called the "Red Queen Hypothesis" (Van Valen, 1973), while the influence of abiotic factors "Court Jester Hypothesis" (Barnosky, 1999). Much emphasis has been given to biotic interactions, such as competition (e.g. Drury et al, 2016; Drury et al, 2018), as being the main determinants of the divergence of ecologically relevant characters between species at micro and macroevolutionary scales (reviewed in Hembry and Weber, 2020). Conversely, other studies point out that the climatic niche can also influence the diversification and variation of traits (Lawson and Weir, 2014; Clavel and Morlon 2017, Luzuriaga-Aveiga and Weir 2019; Barreto et al, 2023a). The climatic niche is the set of climatic conditions to which populations of a species are subject throughout their geographic distribution (Budic and Dormann 2015). Usually, this measure is used to project the physiological tolerance limits of a species (Bozinovic et al, 2011) in the multidimensional climate space and to investigate its influence on the spatial distribution of species and range limits (Gaston, 2003). Interestingly, high rates of climatic niche evolution seem to promote speciation, as demonstrated for salamander lineages (Kozak and Wiens, 2010), *Anolis* lizards (Velasco et al, 2016), birds (Cooney et al, 2016; Barreto et al, 2023a), and Gentianaceae (Matuszak et al, 2016). Therefore, assuming that diversification rates of species are correlated with phenotypic rates evolution (see Rabosky and Adams, 2012, Rabosky et al, 2013, Barreto et al, 2023a), it is possible that the evolution of the climatic niche also has a strong influence on the phenotypic variation of species (Lawson and Weir, 2014).

The evolutionary rate of a trait is the speed with which it evolves along the phylogeny, that is, its variance through the time. In general, these issues have been evaluated on a global scale or using specific lineages (e.g. Luzuriaga-Aveiga and Weir 2019; Huang et al, 2022; Barreto et al, 2023a), while little is known about how the climatic niche can influence the phenotypic evolutionary rates of different communities in the same geographic template. For example, there is a marked difference between the North (historically warmer and more stable) and the South Atlantic Forest (colder and more unstable; Carnaval et al, 2014), which may contribute to selecting species with life history traits more adapted to each region. Ecological gradients seem to be involved in the speciation of *Rhinella crucifer* frogs in the Atlantic Forest (Thomé et al, 2010) and in the intraspecific divergence of birds and mammals on a global scale (Botero et al, 2014). Likewise, the ecological differentiation of Neotropical birds may accelerate trait evolution, but does not seem to affect species diversification (Luzuriaga-Aveiga and Weir, 2019). Specifically, elevation difference is associated with faster divergence in bird calls, as well as morphological traits that contribute to reproductive isolation (Luzuriaga-Aveiga and Weir, 2019). However, no study has yet analyzed how the climatic niche of vertebrates with distinct dispersal abilities and thermal tolerance affects the evolution of ecologically relevant traits such as body.

The body size of a species is often used to differentiate species (Peters, 1986). In addition, it is also a proxy for other ecologically important variables, such as metabolic rates and susceptibility to dehydration, which may restrict the dispersal and colonization capacity of certain lineages (Rolland et al, 2018; Gouveia et al, 2019). Endotherms (birds and non-volant mammals), for example, have significantly lower rates of body temperature evolution than ectotherms (amphibians and squamates; Moreira et al, 2021). Thus, endotherms and ectotherms are expected to have different thermal tolerances, triggering different evolutionary responses to climatic conditions (Rolland et al, 2018). According to Bergmann's rule, selection favors larger body sizes in colder climates, such as higher latitudes and elevations (e.g. Pincheira-Donoso, 2010). However, this evidence seems to be more supported in endotherms (Meiri, 2011; Olson et al, 2009; Pincheira-Donoso, 2010), while there are still divergences of its effect on ectotherms (Pincheira-Donoso & Meiri, 2013; Slavenko et al, 2019; Womack & Bell, 2020). In addition, there is also a relationship between rainfall seasonality and body size of frogs, in which species develop larger body sizes in climates where there is less precipitation (Johnson et al, 2023).

Here we tested how the climatic niche of terrestrial vertebrates (amphibians, squamates, birds and non-volant mammals) occuring in the Atlantic Forest, a climatically and historically complex biome, affects body size evolution. We address the following questions: 1) Is there a similar pattern in the evolutionary trajectories of ectotherms and endotherms? 2) Does the climatic niche of a species dictate the speed of phenotypic evolution? We expect that climate gradients over space and time are important in differentiating the body size evolution of endotherms and ectotherms. Thus, we expect to find more similar evolutionary trends between ectotherms, when compared to endotherms, since physiological restrictions can be important evolutionary drivers in these animals (Rolland et al, 2018; Gouveia et al, 2019).

Materials and methods

Phylogeny

The Maximum Clade Credibility Tree (MCCT) topology of Jetz & Pyron (2018), which includes 7,239 amphibian species, was used for frogs. The fully-sampled consensus tree by Tonini et al (2016), encompassing 9,754 squamate species. For mammals, we utilized the fully-sampled tree provided by Upham et al (2019) with 4,175 species. For birds, since a consensus tree was not available, we followed the approach of Rubolini et al (2015) and generated 10,000 posterior trees for the 9,993 bird species using the 'Hackett' backbone proposed by Jetz et al (2012). Subsequently, we constructed a maximum clade credibility tree (MCCT) using the *DendroPy* and *Sumtrees* (Sukumaran and Holder, 2010) packages in Python 3.9.13 (Van Rossum and Drake, 2009).

Trait data

We obtained data on body size for frogs, and body mass for squamates, birds, and mammals for all species included in the respective phylogenies above from the following sources: i) amphiBIO (Oliveira et al, 2017) and Vasconcelos et al (2019) for frogs; ii) Guedes et al (2023) for squamates; iii) AVONET (Tobias et al, 2022) for birds; and iv) Elton Traits (Wilman et al, 2014) for mammals, complemented with PanTHERIA (Jones et al, 2009) and Phylacine (Faurby et al, 2018). Afterwards, we pruned the respective phylogenies using the R package *picante* (Kembel et al, 2010) to only include species to which we have trait data. However, we excluded 786 amphibian species (~11%), 268 squamate species (~3%), and 322 mammal species (~8%) from further analysis, as they did not have available phylogenetic information in the phylogenies.Furthermore, 1,400 amphibian (~21%) and 82 mammalian (~2%) species had no body size/body mass data available. Therefore, we imputed trait data for these species.

We used phylogenetic imputation methods that perform well for macroecological studies. In addition, our data have adequate assumptions because they consist of continuous variables (body mass and body size) and represent <25% of the database (Johnson et al, 2021). Firstly, we fitted alternative evolutionary models (Brownian motion, Ornstein-Uhlenbeck, and Early Burst) to body size/body mass using the *geiger* R package (Pennell et al, 2014) for 5,053 species for amphibians and 3,771 species for mammals. The best fit model was Ornstein-

Uhlenbeck (OU) for both groups. After that, we used this model to conduct data imputation in the *RPhyloPars* package (Goolsby et al, 2017). For birds and squamates, this procedure was not necessary, as all species that have available body mass data were present in the respective trees. Thus, our final dataset contained 6,453 amphibians, 9,487 squamates, 9,993 birds, and 3853 non-flying mammal species. Our final dataset corresponds to ~75% of amphibian richness (8,646 species in Frost, 2023), ~82% of reptiles (11,549 species in Uetz, 2021), ~91% of birds (10,906 species in Billerman et al, 2022), and ~76% of mammals (5,084 species, excluding Chiroptera in Upham, 2023) known to occur in the world.

Rate of phenotypic evolution

To estimate the rate evolution of body size (Frogs) and body mass (Squamates, mammals and birds) of vertebrates occurring in the Atlantic Forest, we used a two-step procedure. First, we used trait data for all species sampled in the most comprehensive tree available in the literature for each group. Then, we retrieved the rate estimated only for the species occurring in the Atlantic Forest from these global trees. We adopted this approach because the Atlantic Forest species pool did not evolve independently of other sister species that may occur in other biogeographical formations (Drury et al, 2016; Drury et al, 2018; Drury et al, 2021). In addition, through simulation work, it was found that larger (≥ 450 points) and more complete (≥ 60%) phylogenetic trees are more suitable for analysis of diversification rates (Mynard et al, 2023).

We estimated rates of phenotypic evolution using BAMM v.2.5.0 (Bayesian analysis of macroevolutionary mixture; Rabosky et al, 2014). BAMM has some advantages in comparison with other methods (e.g. Cooney and Thomas, 2021; Barreto et al, 2023a). For example, it allows the modeling of evolutionary rates over time and between clades, detecting the heterogeneity. Furthermore, it is able to detect evolutionary innovations, rate shifts, and diversity dependency in phylogenetic trees. In addition, it is computationally efficient, allowing us to deal with large sets of phylogenetic data. Firstly, we used the 'BAMMtools' R package (Rabosky et al, 2014) to create a batch file, including priors and other parameter estimates for each group separately set the rate of change before $\gamma = 1$ and sampled models every 1,000 generations for a total of 12 million generations for amphibians and birds, 45 million generations for squamates, and 10 million generations for mammals. We used a burn-in of 25% of generations for all groups. The number of generations and burn-in used to estimate the evolutionary rates of the traits varied and were chosen based on visual inspection of the log-likelihood of the MCMC output and the effective sample sizes ($\geq$ 200). Afterwards, we extracted the rates from the posterior distribution to obtain the phenotypic rate for each species using the *getTipRates* function and *plotRateThroughTime* function to visualize the rate of evolution through the time. Although this is not a hypothesis testing approach, exploratory approaches can generate new insights into the phylogenetic natural history of clades (Uyeda et al, 2018)

Species composition of the study extent

Similarly to the first chapter, using the *letsR* package (Vilela and Villalobos, 2015) in R, we obtained presence-absence matrices separately for each group of vertebrates by overlaying polygons on a 10x10 Km grid with 0.5º cells, totaling 432 communities (or cell grids). We considered a species to be present in a cell if at least 50% of the species' polygon covered the cell. We used the consensus extent of the Atlantic Forest proposed by Muylaert et al (2018) to determine species occurrence in the domain. We obtained extent-of-occurrence data for amphibians from IUCN (2021) and complemented it with shapefiles from Vasconcelos et al (2019). Occurrence data for squamates was sourced from Roll et al (2017), while bird occurrence data was extracted from BirdLife (2015), and mammals from IUCN (2021). Our species pool comprised native and non-migrating species across the entire Atlantic Forest. In total, our presence-absence matrices included 518 frog species, 402 squamates, 815 birds, and 236 mammals.

Finally, we extracted the rates of phenotypic evolution for each species estimated with BAMM for the species present in those presence-absence matrices. However, 54 species of frogs (~10%), 34 species of squamates (~9%), 120 birds (~15%), and 42 mammals (~14%) were not sampled in their respectives phylogenies and are not included in further analysis. Our final dataset corresponds to ~89% of amphibian richness (707 species), ~91% of squamates (492 species), ~68% of birds (1,025 species), and ~74% of mammals (262 species) known to occur in the Atlantic Forest (Figueiredo et al, 2021).

Climatic niche

We used PALEO-PGEM-Series, a global dataset that provides spatio-temporal

(1° × 1°) information on climate variables dating to 5 Myr, to extract bioclimatic variables at a 1 kyr resolution (Barreto et al, 2023b). This dataset offers detailed climate data and is derived from emulations performed with an atmosphere-ocean general circulation model. In our study, we focused only on data from the past 5 Myr (Plio-Pleistocene). We collected this data because we assume that the phenotypic evolution of species occurred over time, being more influenced by past climates than present ones. For this reason, we collected the oldest spatially explicit climate data in the literature to our knowledge. By incorporating this database, we can use it as a proxy to evaluate the past climatic niche and its influence on evolutionary rates (Barreto et al, 2023b). This enables us to investigate the relationship between species evolution and past climate conditions, contributing to a better understanding of the connections between biodiversity and climate. This is particularly valuable for studying the macroevolutionary processes of species, as these processes occur over extended periods of time. For comparative purposes, we also used the present climate data from CHELSA (0.5° × 0.5°; Brun et al, 2022), which corresponds to the mean between 1981–2010. In order to obtain the climatic variables for the study geographical extent, we used the *raster* package (Hijmans and van Etten, 2015) in R and extracted the bioclimatic mean for each grid cell.

Factors such as temperature, precipitation, humidity, and seasonality can directly affect morphological, physiological, and behavioral aspects of organisms (Luzuriaga-Aveiga and Weir, 2019; Drury et al, 2021; Huang et al, 2022; Barreto et al, 2023). Thus, variations in climatic variables throughout space can influence trait evolution, such as body size and growth rate (e.g. Huang et al, 2022). For this reason, we have chosen six bioclimatic variables that potentially impact the rates of trait evolution in vertebrates. Furthermore, we chose the six bioclimatic variables that were present in both datasets: Mean annual air temperature (BIO1), Temperature Seasonality (BIO4), Temperature Annual Range (BIO7), Mean Temperature of Coldest Quarter (BIO11), Precipitation Seasonality (BIO15), and Precipitation of Driest Quarter (BIO17). Afterwards, we extracted the mean of each climate variable for the grid used to make the composition matrix. To identify and handle potential multicollinearity between variables, we calculated the Variation Inflation Factor (VIF) in the *usdm* R package (Naimi et al, 2014). Variables whose VIF values > 3 were excluded from further analysis. Specifically, we excluded Temperature Seasonality (BIO04), Temperature Annual Range (BIO07), and Mean Temperature of Coldest Quarter (BIO11) from the past data (PALEO-PGEM-Series) and Mean annual air temperature (BIO01) and Mean Temperature of Coldest Quarter (BIO11) from present data (CHELSA).

With the selected climate data, we calculated the climatic niche mean and breath for the past and present. We represented the breadth and position of the species' climatic niche using the Outlying Mean Index (OMI). The OMI analysis is a constrained ordination technique specifically developed to model linear and nonlinear species-environment relationships and it is useful to build multidimensional climatic volumes (Dolédec et al, 2000). Thus, it is possible to obtain insights into the tolerance (Tol) and the centrality (OMI) of the species' niche, distinguishing between generalist taxa that tolerate a wide range of environmental conditions and specialist ones that are limited to specific climatic conditions. Analysis was conducted in the *ade4* package (Dray and Dufour, 2007) in the R software. As climatic variables have different measurement units, the 'scale' and 'center' arguments of the ‘dudi.pca’ function were set to 'True' to standardize the scale (Legendre and Galagher, 2001).

Statistical analysis

To test the influence of the species' climatic niche on the rate of phenotypic evolution (rate_phenotipic_evolution ~ OMI_present + OMI_past + Tol_present + Tol_past), we used Phylogenetic Generalized Least Squares (PGLS) models for each group separately. This analysis consists of Generalized Linear Models (GLS) that incorporate a covariance matrix describing the phylogenetic relationships between the studied species. Specifically, we fitted the model using REML, while also estimating Pagel’s lambda parameter to control for phylogenetic autocorrelation in the residuals (Revell, 2010). Analysis was conducted in the *nlme* R package (Pinheiro et al, 2017). We calculated the coefficients of determination (R^2) using the *rr2* package in R (Ives and Li, 2018). (Figure 1). Diagnostics was conducted by visually inspecting the fitted vs. residual plot (Figure S1). Residuals of all models had homogeneity of variance.

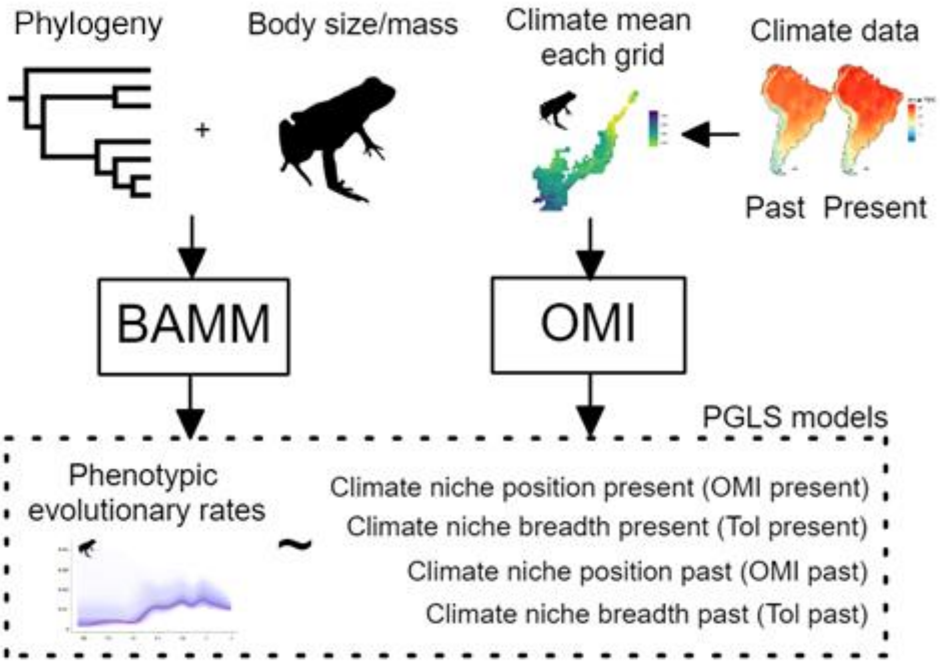

Figure 1. Schematic model of the methodology used. First, we chose the most comprehensive species tree known for each terrestrial vertebrate group, as well as using the respective broader databases with amphibian body size, and body mass of squamates, birds and mammals. After that, we estimate the evolutionary rates for each group using BAMM (Bayesian analysis of macroevolutionary mixture; Rabosky et al, 2014) and then extract these rates for each species to obtain the phenotypic evolutionary rate. To access the climatic niche of each species, we consulted two temporal-spatially explicit climate databases (Present in CHELSA database in Brun et al, 2022 and past PALEO-PGEM-Series in Barreto et al, 2023b). We extract the mean of each climate variable for the grid used to make the species composition matrix of vertebrates in Atlantic Forest. After that, we extract niche indices for past and present data. We chose to represent the breadth and position of the species' climatic niche using the Outlying Mean Index (OMI). Finally, to test the influence of the species' climatic niche on the rate of phenotypic evolution (rate_phenotipic_evolution ~ OMI_present + OMI_past + Tol_present + Tol_past), we employed a Phylogenetic Analysis of Generalized Least Squares (PGLS).

Results

The world's terrestrial vertebrates exhibit idiosyncratic patterns in their respective evolutionary rates of body size and body mass through time (Figure 2). The rate through time plot of amphibians shows a peak from 200 Myr then the rate is practically stationary onwards. There is also a small drop from 50 Myr onwards. In squamates, evolutionary rates are more stationary over time when compared to other groups, with a recent exponential peak, in the 60Myr. There is only a small increase before 50 Myr and another exponential increase more recently. In birds, there are two peaks: the first one close to 80 Myr, and another soon after 50 Myr. After these peaks, the rate of evolution of bird body mass shows a declining trend. In mammals, there is a declining trend in the rate through time.

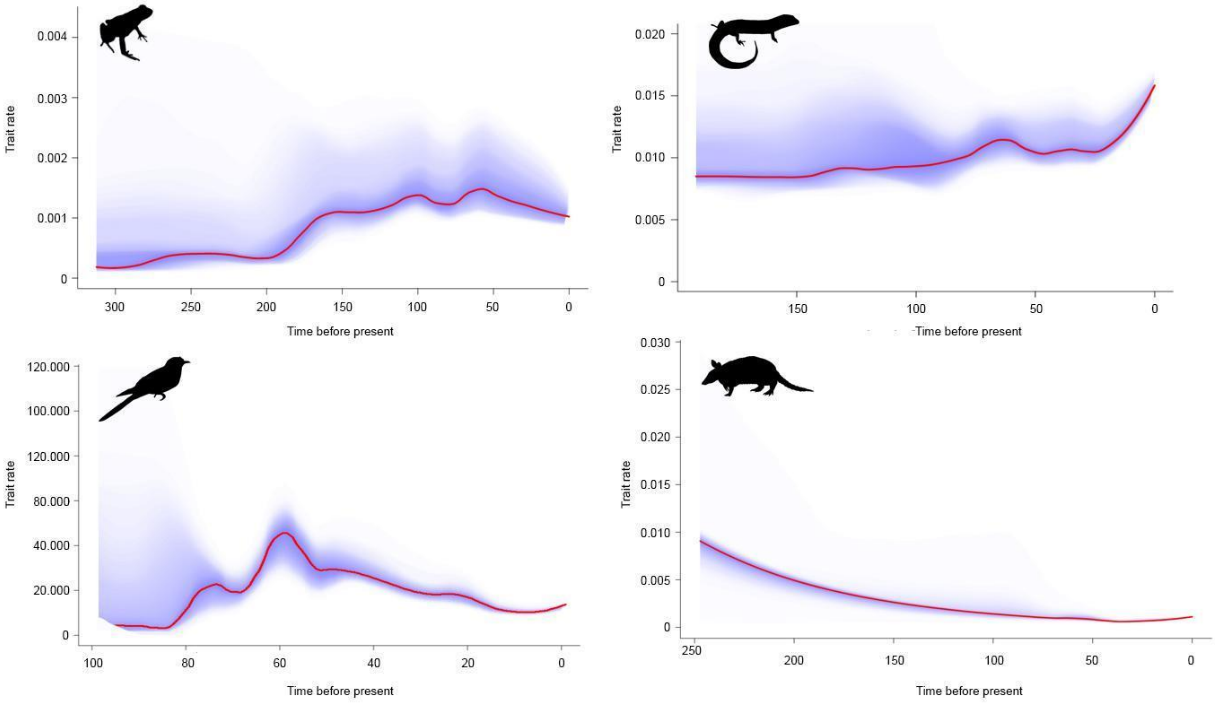

Figure 2. Rate evolution of body size (amphibians) and body mass (squamates, birds and mammals) through-time trajectories for terrestrial vertebrates. Trait rate indicates the evolution rates of body size/body mass for the broader tree known, indicating the trend of adaptive radiation of vertebrates in the world. The blue density shading illustrates the relative probability of a rate at any point in time and the red line indicates the evolutionary trajectory of body size/body mass.

We found high heterogeneity in the evolutionary rates within each group occurring in the Atlantic Forest (Figure 3). In amphibians, most species had higher rates. However, the highest rates were in *Bokermannohyla* treefrogs (Hylidae) and in *Leptodactylus* frogs (Leptodactylidae). In Bufonidae, those of the genus *Dendrophryniscus* and *Melanophryniscus* had lower rates, while *Rhinella* had higher rates. Likewise, brachycephalid frogs had lower rates of body size evolution. In squamates, rates differed between lizards, amphisbaenians, and snakes. Lizards had the lowest rates of body mass compared to other groups. Amphisbaenians on the other hand had high rates. In snakes, this pattern is more distributed, with *Dipsas* snakes (Dipsadinae) and *Liotyphlops* (Anomalepididae) with lower rates, and Boidae and Pseudoboinae with higher rates. In birds, rates were concentrated in only a few lineages, such as Tinamiformes, Galliformes, and Accipitriformes, with the highest ones in ducks, geese, and other waterfowl species. Other lineages, such as hummingbirds, generally had lower evolutionary rates for body mass. In mammals, there were more species with intermediate evolutionary rates. However, primates in general had lower rates, as well as the Tayassuidae wild pigs and tapir (*Tapirus terrestris*). Conversely, the highest evolutionary rates were in Felidae, *Cryptonanus* opossums, and some lineage-specific species.

We found more restricted climatic niche spaces in ectotherms (amphibians R2 = 0.93; squamates R2 = 0.35) when compared to endotherms (birds R2 = 0.93; mammals R2 = 0.93) (Figure 4). However, we found no significant relationship between species niche position or niche breadth on evolutionary rate of body size/mass in the species pool from the Atlantic Forest (Figure 5). Furthermore, niche breadth had a greater influence on evolutionary rate than niche position. The confidence interval overlaps positive and negative values, indicating that there is a high variation in rates across all vertebrate groups, but lower in amphibians. Still, there is a marked difference between amphibians and other vertebrates. While the niche breath for present climate data of amphibians negatively influenced the evolutionary rate, for the other groups it was the opposite. We also found opposite effects when comparing past and present climate data. There was a positive effect of present niche breadth on evolutionary rate, but a negative effect of past climate. In addition, past climate data showed negative coefficients in all groups, with the exception of niche position (OMI) in amphibians. This means that the effect of evolutionary rate depends on the time scale of the data and can affect the conclusions of how climate impacts on phenotypic rate evolution.

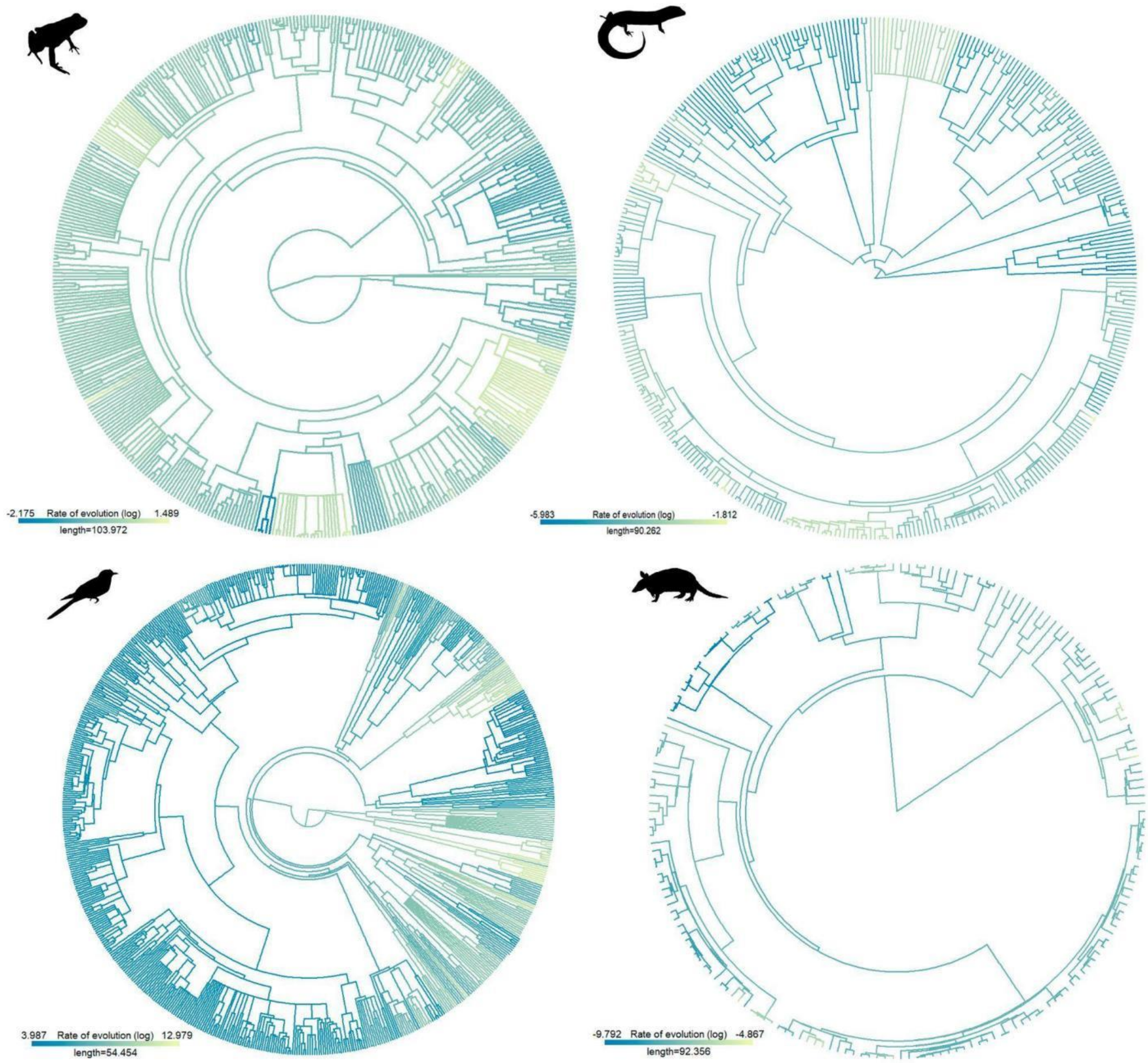

Figure 3. Evolution dynamics of body size and body mass of terrestrial vertebrates that occur in the Atlantic Forest domain. Warmer colors (yellow) denote faster rates of trait evolution, cold colors (blue) indicate slower rates. In general, it is possible to note that the faster evolutionary rates are more concentrated and distributed among the ectotherm lineages when compared to the endotherms. Trees with tip labels are available in supplementary material.

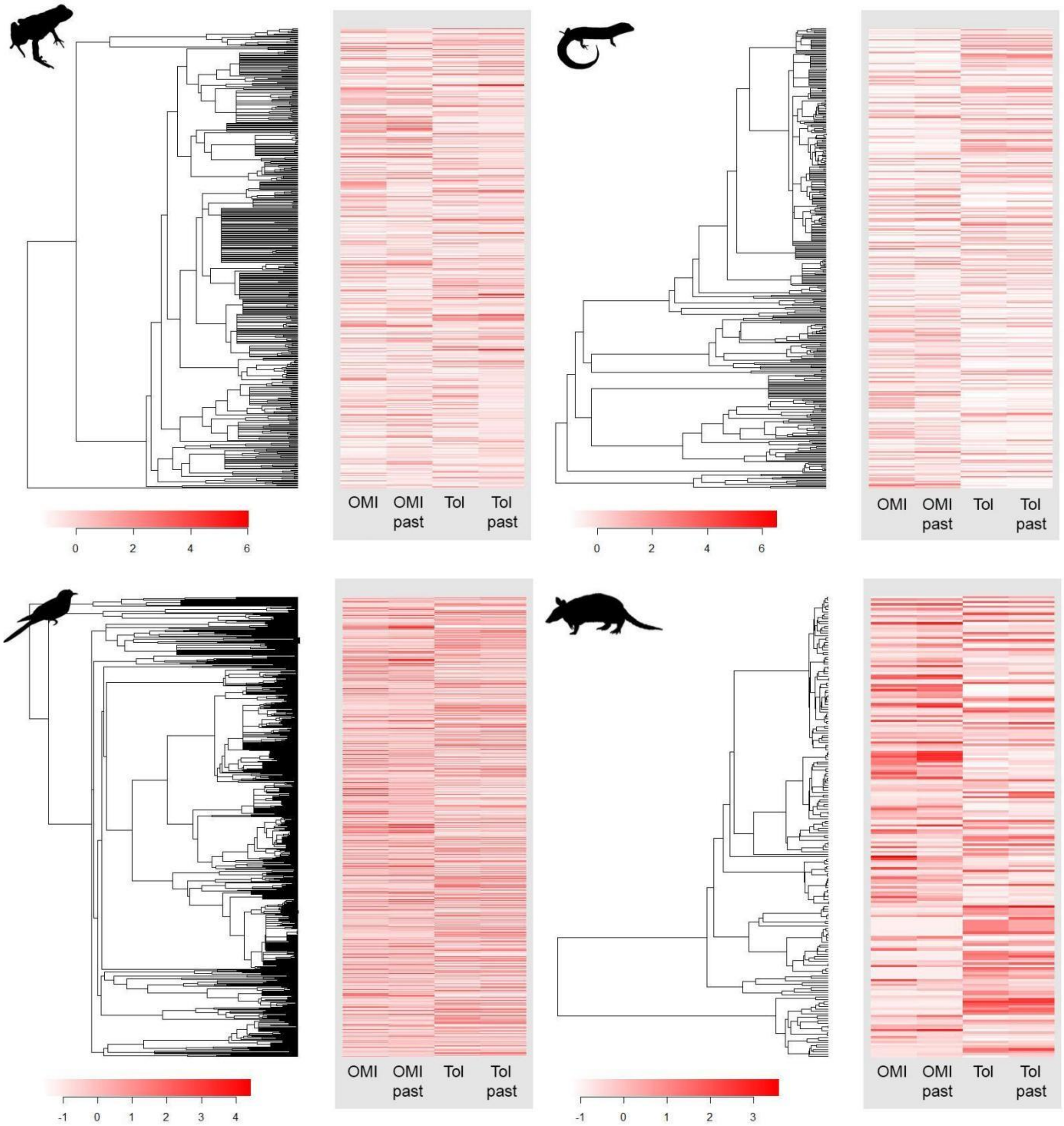

Figure 4. Climatic niche mean (OMI and OMI past) and niche breadth (Tol and Tol past) for the past and present data. Lower values (lighter tones) indicate more specialized taxa, in which case they are limited to specific climatic conditions. Higher values (reddish tones) indicate generalist taxa, those that tolerate a wide range of environmental conditions.

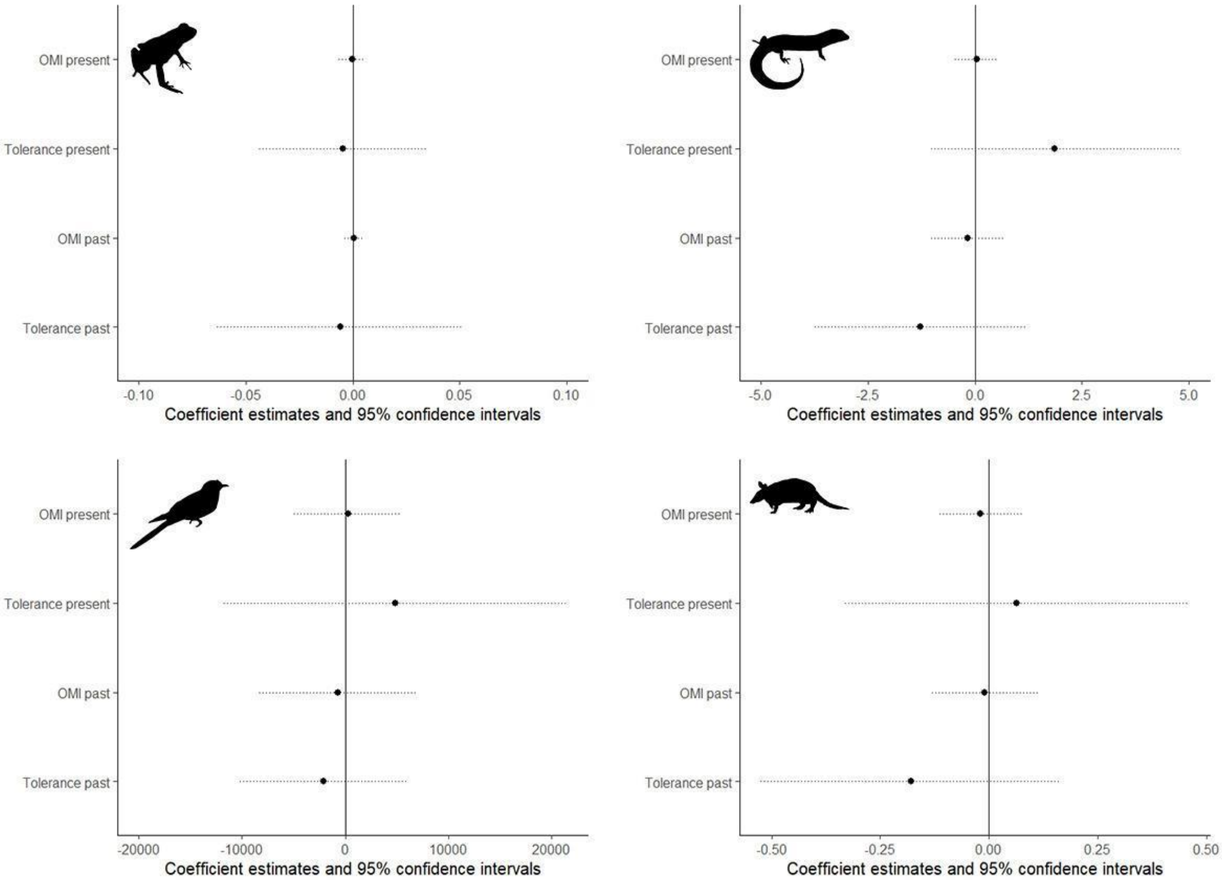

Figure 5. Phylogenetic Analysis of Generalized Least Squares (PGLS) of each group of vertebrates from the Atlantic Forest and the respective coefficients (black dots) and confidence intervals (dashed line). Specifically, we model climatic variables that represent the past and present climatic niche of terrestrial vertebrates, and what their effects are on the evolution of body size. Although no relationship tested was significant ($P > 0.05$), it is possible to observe that the breadth of the climatic niche has a greater effect on all vertebrate groups when compared to the position of the niche. OMI represents the position of the climatic niche in the present (OMI present) and in the past (OMI past), that is, the centrality of the climatic space in which the species occurs. Likewise, the climatic niche breadth is represented in the present (Tolerance present) and in the past (Tolerance past).

Discussion

We found distinct patterns in the temporal trends of the phenotypic rate evolution for terrestrial vertebrates. Still, we did not observe a marked difference between ectotherms and endotherms. These idiosyncratic patterns may indicate that different adaptive processes are operating in each group. Likewise, the same idiocratic pattern happens in the Atlantic Forest species pool. For example, there is a deceleration of the evolutionary rate in small amphibians species (e.g., *Dendrophryniscus* spp., Brachycephalidae), while in mammals there seems to be a deceleration in larger species (e.g., Primates and *Tapirus terrestris*). In addittion, we found no statistically significant relationship between climatic niche and rate of evolution of body size. However, the climatic niche breadth was more important than niche position to explain variations in evolutionary rates. This suggests that each group may have experienced distinct selective pressures, resulting in unique patterns of changes in body size through time (e.g., Luzuriaga-Aveiga and Weir, 2019; Drury et al, 2021). Our findings represent the first step to unravel the importance of climate on the rate of phenotypic evolution in vertebrates, especially for understanding the complex evolutionary history of the Atlantic Forest and its high biodiversity.

Contrary to our expectation, there was no marked difference between the temporal trends of endotherms and ectotherms. Furthermore, we found that the world's terrestrial vertebrates exhibit idiosyncratic patterns in their respective phenotypic evolutionary trajectories. Therefore, it is possible that terrestrial vertebrates are subject to different selective pressures that act differently on the body size evolution of each group (e.g., Moreira et al, 2021; Johnson et al, 2023). For example, an increase in the diversification rate occurred in birds from about 50 Myr ago to the present (Jetz et al, 2012). Conversely, when we evaluate the rates of body size evolution over time for birds, a deceleration happens at approximately the same period (~50 Myr). Although our results do not allow clarifying the mechanisms that influenced this pattern, a prominent decline in the body mass of modern birds is recognized in several taxa (Kiat et al, 2021), which may be related to the flight performance (Dececchi and Larsson, 2013; Puttick et al, 2014). Indeed, it is expected that fluctuations in the phenotypic rate evolution are related to the exploration of new adaptive zones for each group (e.g., Barreto et al, 2023a). Similarly, physiological constraints influence the body size of amphibians orders differently. For example, caecilians have larger body sizes in arid areas, while anurans are more subject to seasonality of precipitation and temperature (Johnson et al, 2023). In this context, biotic (Hembry and Weber 2020) and abiotic (Lawson and Weir, 2014; Clavel and Morlon, 2017;

Luzuriaga-Aveiga and Weir, 2019) pressures over time act in different ways in each group of vertebrates.

We found high heterogeneity in evolutionary rates within each group of Atlantic Forest vertebrates, with some lineages showing accelerations in the phenotypic rate evolution and others a deceleration. We found a pattern of high evolutionary rates in lineages of water and land birds, such as ducks, geese, and chickens. In snakes, we found higher rates in large species, such as those from the Boidae family, and decelerations in rates in snakes from the Typhlopoidea that have fossorial habits and are one of the smallest species in the regional pool. The bromeliad-toads *Dendrophryniscus* have small body sizes (Botelho et al, 2023), with low evolutionary rates of body size. While the cane toad (*Rhinella* spp.) is a large, terrestrial species and had high evolutionary rates. It is possible that the variation in evolutionary rates in this way are associated with specific adaptations to the ecological niche that these species occupy (Luzuriaga-Aveiga and Weir, 2019; Drury et al, 2021; Huang et al, 2022). Species like *Dendrophryniscus* spp. because they occupy bromeliads they need to have smaller body sizes to use this site, so it is possible that body size has changed little over time. For example, in Neotropical birds, the difference in habitat use can accelerate the evolution of song, an important attribute for sexual selection (Luzuriaga-Aveiga and Weir, 2019). Likewise, the evolution of mammalian body size has been strongly influenced by habitat transitions, with only an indirect effect of past climate changes (Huang et al, 2022). Thus, it is possible that the presence of lower evolutionary rates in certain groups indicates specialized adaptations and a certain stability through time in their ecological niches. Therefore, the rates may be related to the diversity and occupation of particular ecological niches of each lineage (Simpson, 1953; Jetz et al, 2012; Drury et al, 2021). Although exploratory, our phylogenetic natural history approach (Uyeda et al, 2018) adds new evolutionary hypotheses to explain the body size evolution of terrestrial vertebrate communities in the Atlantic Forest. We will add new efforts to include other axes of the ecological niche of species in an attempt to elucidate the processes that drive evolutionary rates of body size in vertebrates and whether these are related to the occupation of new adaptive zones.

We found that the climatic niche is not a correlate for the body size evolutionary rates, which contradicts what is expected by the Court Jester hypothesis (Barnosky, 1999). In addition, endotherms had a greater number of species with wider climatic niches than ectotherms. This may be related to greater thermal tolerance in these groups and a greater dispersal ability than ectotherms (Buckley et al, 2012; Rolland et al, 2018). The lack of a significant relationship between species position and niche width with phenotypic evolutionary rates may indicate that other factors, such as different ecological niche axes (Drury et al, 2018; Huang et al, 2022) and/or constraints of each clade (Drury et al, 2021; Acevedo et al, 2022) may play a more important role in shaping the patterns observed for terrestrial vertebrates of the Atlantic Forest. However, there is a greater influence of the niche breadth on the evolutionary rate, than niche position. This suggests that species tolerance has a greater influence on variation in evolutionary rates in vertebrates (Qu & Wiens, 2020). A possible explanation for this pattern is that species with broader climatic niches may experience greater ecological opportunities and experience more selection pressures (e.g., Rolland et al, 2018; Acevedo et al, 2022). Thus, leading to greater variation in evolutionary responses in phenotypic traits. An example of this is that in terrestrial vertebrates, changes in the climatic niche occur faster in endotherms than in ectotherms (Rolland et al, 2018), which allows these animals to exploit a wider range of resources and habitats, which can lead to greater phenotypic variation and adaptive responses. As a result, they may experience lower rates of evolution in phenotypic traits because they are already adapted to their environment and faceless selective pressure for further body size modifications (Barreto et al, 2023a). Furthermore, these responses may vary within each vertebrate group and spatially (e.g. Drury et al, 2021). More studies are needed to unravel the macroevolutionary patterns of terrestrial vertebrates, especially in historically complex environments such as the Atlantic Forest.

Our study represents the first step in understanding the evolutionary patterns of phenotypic evolution in vertebrates. In general, vertebrates showed distinct evolutionary trends of body size, probably associated with specializations in their respective life histories. Furthermore, we did not find a relationship between the position and width of the climatic niche and their respective body size evolutionary rates. It is possible that other axes of the ecological niche, such as the spatial niche related to the habitat and/or the trophic niche, act more strongly on the evolutionary rates of vertebrate body size. These findings have important implications for our understanding of the drivers of evolutionary change in phenotypic rates and the factors that shape biodiversity patterns at regional scales. Still, future studies should be directed towards verifying the evolutionary trends within orders and in the main families of vertebrates, in an attempt to unravel the macroevolutionary patterns of size and body mass in terrestrial vertebrates.

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References

Acevedo, A.A., Palma, R.E., & Olalla-Tárraga, M.Á. (2022) Ecological and evolutionary trends of body size in *Pristimantis* frogs, the world's most diverse vertebrate genus. *Scientific Reports,* **12**(1), 18106.

Barnosky, A.D. (1999) Does evolution dance to the Red Queen or the Court Jester. *Journal of Vertebrate Paleontology,* **19**, 31A.

Barreto, E., Lim, M.C., Rojas, D., Dávalos, L.M., Wüest, R.O., Machac, A., & Graham, C.H. (2023a) Morphology and niche evolution influence hummingbird speciation rates. *Proceedings of the Royal Society B,* **290**(1997), 20221793.

Barreto, E., Holden, P.B., Edwards, N.R., & Rangel, T.F. (2023b) PALEO-PGEM-Series: A spatial time series of the global climate over the last 5 million years (Plio-Pleistocene). *Global Ecology and Biogeography,* **00**:1–12.

Bozinovic, F., Calosi, P., & Spicer, J.I. (2011) Physiological Correlates of Geographic Range in Animals. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 155–179.

Budic, L., & Dormann, C. (2015). Climatic niches in phylogenetic comparative studies: a review of challenges and approaches. *bioRxiv*.

Billerman, S.M., Keeney, B.K., Rodewald, P.G., & Schulenberg, T.S. (2022) Birds of the World (editors). Cornell Laboratory of Ornithology, Ithaca, NY, USA. https://birdsoftheworld.org/bow/home

Botelho, L.M., Barbosa, A.C.F., Prado, J.S., Pedrozo, M., Moroti, M.T., Toledo, L.F., & Muscat, E. (2023). Reproductive biology, tadpole description, and natural history of *Dendrophryniscus haddadi* (Anura: Bufonidae). *Journal of Natural History*, **57**(9-12), 596-607.

Botero, C.A., Dor, R., McCain, C.M., & Safran, R.J. (2014) Environmental harshness is positively correlated with intraspecific divergence in mammals and birds. *Molecular Ecology*, **23**, 259–268.

Brun, P., Zimmermann, N.E., Hari, C., Pellissier, L., & Karger, D.N. (2022) Global climate-related predictors at kilometer resolution for the past and future. Earth *System Science Data*, **14**(12), 5573–603.

Buckley, L.B., Hurlbert, A.H., & Jetz, W. (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, **21**, 873–885.

Carnaval, A.C., Waltari, E., Rodrigues, M.T., Rosauer, D., VanDerWal, J., Damasceno, R., Prates, I., Strangas, M., Spanos, Z., Rivera, D., Pie, M.R., Firkowski, C.R., Bornschein, M.R., Ribeiro, L.F., & Moritz, C. (2014) Prediction of phylogeographic endemism in an environmentally complex biome. *Proceedings of the Royal Society B*, **281**, 20141461.

Clavel, J., & Morlon, H. (2017) Accelerated body size evolution during cold climatic periods in the Cenozoic. *Proceedings of the National Academy of Sciences*, **114**(16), 4183–4188.

Cooney, C.R., Seddon, N., & Tobias, J.A. (2016) Widespread correlations between climatic niche evolution and species diversification in birds. *Journal of Animal Ecology*, **85**(4), 869–878.

Cooney, C.R., & Thomas, G.H. (2021). Heterogeneous relationships between rates of speciation and body size evolution across vertebrate clades. *Nature Ecology & Evolution*, **5**, 101–110.

Dececchi, T.A., & Larsson, H.C.E. (2013) Body and limb size dissociation at the origin of birds: uncoupling allometric constraints across a macroevolutionary transition. *Evolution*, **67**, 2741–2752.

Dolédec, S., Chessel, D., & Gimaret-Carpentier, C. (2000) Niche separation in community analysis: a new method. *Ecology*, **81**(10), 2914–2927.

Dray, S., & Dufour, A.B. (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, **22**, 1–20.

Drury, J., Clavel, J., Manceau, M., & Morlon, H. (2016) Estimating the effect of competition on trait evolution using maximum likelihood inference. *Systematic Biology*, **65**(4), 700–

710.

Drury, J.P., Tobias, J.A., Burns, K.J., Mason, N.A., Shultz, A.J., & Morlon, H. (2018) Contrasting impacts of competition on ecological and social trait evolution in songbirds. *PLoS Biology*, **16**(1), e2003563.

Drury, J.P., Clavel, J., Tobias, J.A., Rolland, J., Sheard, C., & Morlon, H. (2021). Tempo and mode of morphological evolution are decoupled from latitude in birds. *PLoS Biology*, **19**(8), e3001270.

Faurby, S., Davis, M., Pedersen, R. Ø., Schowanek, S. D., Antonelli, A., & Svenning, J. C. (2018) PHYLACINE 1.2: the phylogenetic atlas of mammal macroecology. *Ecology*, **99**(11), 2626.

Figueiredo, M.S.L., Weber, M.M., Brasileiro, C.A., Cerqueira, R., Grelle, C.E.V., Jenkins, C.N., Solidade, C.V., Thomé, M.T.C., Vale, M.M., & Lorini, M.L. (2021) Tetrapod Diversity in the Atlantic Forest: Maps and Gaps, pp. 185–204. In *The Atlantic Forest: History, Biodiversity, Threats and Opportunities of the Mega-diverse Forest*. Springer.

Frost, Darrel R. (2023) Amphibian Species of the World: an Online Reference. Version 6.2 (10/jun/2023). Electronic Database accessible at https://amphibiansoftheworld.amnh.org/index.php. American Museum of Natural History, New York, USA.

Gaston, K.J. (2003) The structure and dynamics of geographic ranges. Oxford University Press, New York.

Goolsby, E.W., Bruggeman, J., & Ané, C. (2017) Rphylopars: fast multivariate phylogenetic comparative methods for missing data and within-species variation. Methods in Ecology and *Evolution*, **8**(1), 22–27.

Gouveia, S.F., Bovo, R.P., Rubalcaba, J.G., Da Silva, F.R., Maciel, N.M., Andrade, D.V., & Martinez, P.A. (2019) Biophysical modeling of water economy can explain geographic gradient of body size in anurans. *The American Naturalist*, **193**(1), 51–58.

Guedes, J.J.M., Moura, M.R., & Diniz-Filho, J.A.F. (2023) Species out of sight: elucidating the determinants of research effort in global reptiles. *Ecography*, e06491.

Harmon, L. J. (2017) Macroevolutionary rate in the Losos, J.B. (2017) The Princeton guide to evolution. Princeton University Press.

Hembry, D. H., & Weber, M. G. (2020) Ecological interactions and macroevolution: a new field with old roots. Annual Review of Ecology, *Evolution, and Systematics*, **51**, 215–243.

Hijmans R.J. & van Etten, J. (2012) raster: Geographic analysis and modeling with raster data. R package version 2.0-12. http://CRAN.R-project.org/package=raster

Huang, S., Saarinen, J. J., Eyres, A., Eronen, J. T., & Fritz, S. A. (2022) Mammalian body size evolution was shaped by habitat transitions as an indirect effect of climate change. *Global Ecology and Biogeography*, **31**(12), 2463–2474.

IUCN (2021) The IUCN Red List of Threatened Species. Version 2019-1. http://www.iucnredlist.org. Downloaded on 1th March 2023.

Ives, A.R., & Li, D. (2018) rr2: An R package to calculate R2s for regression models. *The Journal of Open Source Software*, **3**(30), 1028.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... & Purvis, A. (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. *Ecology*, **90**(9), 2648–2648.

Johnson, T. F., Isaac, N. J., Paviolo, A., & González-Suárez, M. (2021) Handling missing values in trait data. *Global Ecology and Biogeography*, **30**(1), 51–62.

Johnson, J.V., Finn, C., Guirguis, J., Luke, E.B., Goodyear, L.P., Harvey, R.M., Ron S., & Pincheira-Donoso D. (2023) What drives the evolution of body size in ectotherms? A global analysis across the amphibian tree of life. *Global Ecology and Biogeography*, **00**, 1–12.

Jetz, W., Thomas, G.H., Joy, J. B., Hartmann, K., & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, **491**(7424), 444–448.

Jetz, W., & Pyron, R.A. (2018) The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature ecology & evolution*, **2**(5), 850–858.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology." *Bioinformatics*, **26**(11), 1463–1464.

Kiat, Y., Slavenko, A., & Sapir, N. (2021) Body mass and geographic distribution determined the evolution of the wing flight-feather molt strategy in the Neornithes lineage. *Scientific Reports*, **11**(1), 21573.

Kozak, K.H., & Wiens, J.J. (2010) Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, **13**, 1378–1389.

Lawson, A.M., & Weir, J.T. (2014) Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. *Ecology Letters*, **17**, 1427–1436.

Legendre, P., & Gallagher, E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.

Luzuriaga-Aveiga, V.E., & Weir, J.T. (2019) Elevational differentiation accelerates trait evolution but not speciation rates in Amazonian birds. *Ecology Letters*, **22**(4), 624–633.

Matuszak, S., Favre, A., Schnitzler, J., & Muellner-Riehl, A.N. (2016) Key innovations and climatic niche divergence as drivers of diversification in subtropical Gentianinae in southeastern and eastern Asia. *American Journal of Botany*, **103**, 899–911.

Meiri, S. (2011) Bergmann's rule: What's in a name? *Global Ecology and Biogeography*, **20**, 203–207.

Moreira, M. O., Qu, Y.F., & Wiens, J.J. (2021) Large-scale evolution of body temperatures in land vertebrates. *Evolution Letters*, **5**(5), 484–494.

Muylaert, R.L., Vancine, M.H., Bernardo, R., Oshima, J.E.F., Sobral-Souza, T., Tonetti, V.R., Niebuhr, B.B., & Ribeiro, M.C. (2018) Uma nota sobre os limites territoriais da Mata Atlântica. *Oecologia Australis*, **22**(3), 302–311.

Mynard, P., Algar, A.C., Lancaster, L.T., Bocedi, G., Fahri, F., Gubry-Rangin, C., Lupiyaningdyah, P., Nangoy, M., Osborne, O.G., Papadopulos, A.S. & Sudiana, I. M. (2023) Impact of Phylogenetic Tree Completeness and Mis-specification of Sampling Fractions on Trait Dependent Diversification Models. *Systematic Biology*, **72**(1), 106–119.

Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K., & Toxopeus, A.G. (2014) Where is positional uncertainty a problem for species distribution modelling?. *Ecography*, **37**(2), 191–203.

Oliveira, B. F., São-Pedro, V. A., Santos-Barrera, G., Penone, C., & Costa, G. C. (2017) AmphiBIO, a global database for amphibian ecological traits. *Scientific data*, **4**(1), 1-7.

Olson, V.A., Davies, R.G., Orme, C.D.L., Thomas, G.H., Meiri, S., Blackburn, T.M., Gaston, K.J., Owens, I.P.F., & Bennett, P.M. (2009) Global biogeography and ecology of body size in birds. *Ecology Letters*, **12**, 249–259.

Pennell, M.W., Jonathan M.E., Graham J.S., Joseph W.B., Josef C.U., Richard G.F., Michael E. A., & Luke J.H. (2014) "geiger": an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics,* **30**(15), 2216–2218.

Peters, R.H. (1986) The ecological implications of body size. Cambridge University Press, Cambridge.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017) Package ‘nlme’. Linear and nonlinear mixed effects models, **3**(1), 274.

Pincheira-Donoso, D. (2010) The balance between predictions and evidence and the search for universal macroecological patterns: Taking Bergmann's rule back to its endothermic origin. *Theory in Biosciences*, **129**, 247–253.

Pincheira-Donoso, D., & Meiri, S. (2013) An intercontinental analysis of climate-driven body size clines in reptiles: No support for patterns, no signals of processes. *Evolutionary Biology*, **40**, 562–578.

Puttick, M.N., Tomas, G.H., & Benton, M.J. (2014) High rates of evolution preceded the origin of birds. *Evolution*, **68**(5), 1497–1510.

Qu, Y.F., & Wiens, J.J. (2020) Higher temperatures lower rates of physiological and niche evolution. *Proceedings of the Royal Society B*, **287**(1931), 20200823.

Rabosky, D.L., & Adams, D.C. (2012) Rates of morphological evolution are correlated with species richness in salamanders. *Evolution*, **66**, 1807–1818.

Rabosky, D.L., Santini, F., Eastman, J., Smith, S.A., Sidlauskas, B., Chang, J., & Alfaro, M.E. (2013) Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nature Communications*, **4**, 1958.

Rabosky, D.L., Grundler, M., Anderson, C., Title, P., Shi, J.J., Brown, J.W., Huang, H., &

Larson, J.G. (2014) BAMM tools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in Ecology and Evolution*, **5**(7), 701–707.

Revell, L.J. (2010) Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, **1**(4), 319–329.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., ... & Meiri, S. (2017) The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology & Evolution*, **1**(11), 1677–1682.

Rolland, J., Silvestro, D., Schluter, D., Guisan, A., Broennimann, O., & Salamin, N. (2018) The impact of endothermy on the climatic niche evolution and the distribution of vertebrate diversity. *Nature Ecology and Evolution,* **2**, 459–464.

Rubolini, D., Liker, A., Garamszegi, L.Z., Møller, A.P., & Saino, N. (2015) Using the BirdTree.org website to obtain robust phylogenies for avian comparative studies: a primer. *Current Zoology,* **61**(6), 959–965.

Simpson, G.G. (1953) The Major Features of Evolution. Columbia University Press.

Slavenko, A., Feldman, A., Allison, A., Bauer, A.M., Böhm, M., Chirio, L., Colli, G.R., Das, I., Doan, T.M., LeBreton, M., Martins, M., Meirte, D., Nagy, Z.T., Nogueira, C., Pauwels, O.S.G., Pincheira-Donoso, D., Roll, U., Wagner, P., Wang, Y., & Meiri, S. (2019) Global patterns of body size evolution in squamate reptiles are not driven by climate. *Global Ecology & Biogeography*, **28**, 471–483.

Sukumaran, J., & Holder, M.T. (2010) DendroPy: a Python library for phylogenetic computing. *Bioinformatics*, **26**(12), 1569–1571.

Thomé, M.T.C., Zamudio, K.R., Giovanelli, J.G.R., Haddad, C.F.B., Baldissera Jr, F.V.A., & Alexandrino, J. (2010) Phylogeography of endemic toads and post-Pliocene persistence of the Brazilian Atlantic Forest. *Molecular Phylogenetics and Evolution,* **55**, 1018–1031.

Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J., Yang, J., Sayol, F., ... & Schleuning, M. (2022). AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters*, **25**(3), 581–597.

Tonini, J.F.R., Beard, K.H., Ferreira, R.B., Jetz, W., & Pyron, R.A. (2016) Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*, **204**, 23–31.

Uetz, P. (2021) The Reptile Database: Curating the biodiversity literature without funding. Biodiversity Information Science and Standards, 246.

Upham, N.S., Esselstyn, J.A., & Jetz, W. (2019) Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS biology*, **17**(12), e3000494.

Upham, N.S. (2023). Mammal Diversity Database (Version 1.11) (10/jun/2023). Zenodo. https://doi.org/10.5281/zenodo.7830771 DOI

Uyeda, J.C., Zenil-Ferguson, R., & Pennell, M.W. (2018) Rethinking phylogenetic comparative methods. *Systematic Biology*, **67**(6), 1091–1109.

Van Rossum, G., & Drake, F.L. (2009) Introduction to python 3: python documentation manual part 1. CreateSpace.

Van Valen, L. (1973) A new evolutionary law. *Evolutionary Theory*, **1**, 1–30.

Vasconcelos, T.S., Da Silva, F.R., Dos Santos, T.G., Prado, V.H., & Provete, D.B. (2019) Biogeographic patterns of South American anurans. Cham: Springer International Publishing.

Velasco, J.A., Martínez-Meyer, E., Flores-Villela, O., García, A., Algar, A.C., Köhler, G., & Daza, J.M. (2016) Climatic niche attributes and diversification in *Anolis* lizards. *Journal of Biogeography*, **43**, 134–144.

Vilela, B., & Villalobos, F. (2015) letsR: a new R package for data handling and analysis in macroecology. *Methods in Ecology and Evolution*, **6**(10), 1229–1234.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., & Jetz, W. (2014) EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, **95**(7), 2027–2027.

Womack, M.C., & Bell, R.C. (2020) Two-hundred million years of anuran body-size evolution in relation to geography, ecology and life history. *Journal of Evolutionary Biology*, **33**, 1417–1432.

Supplementary material

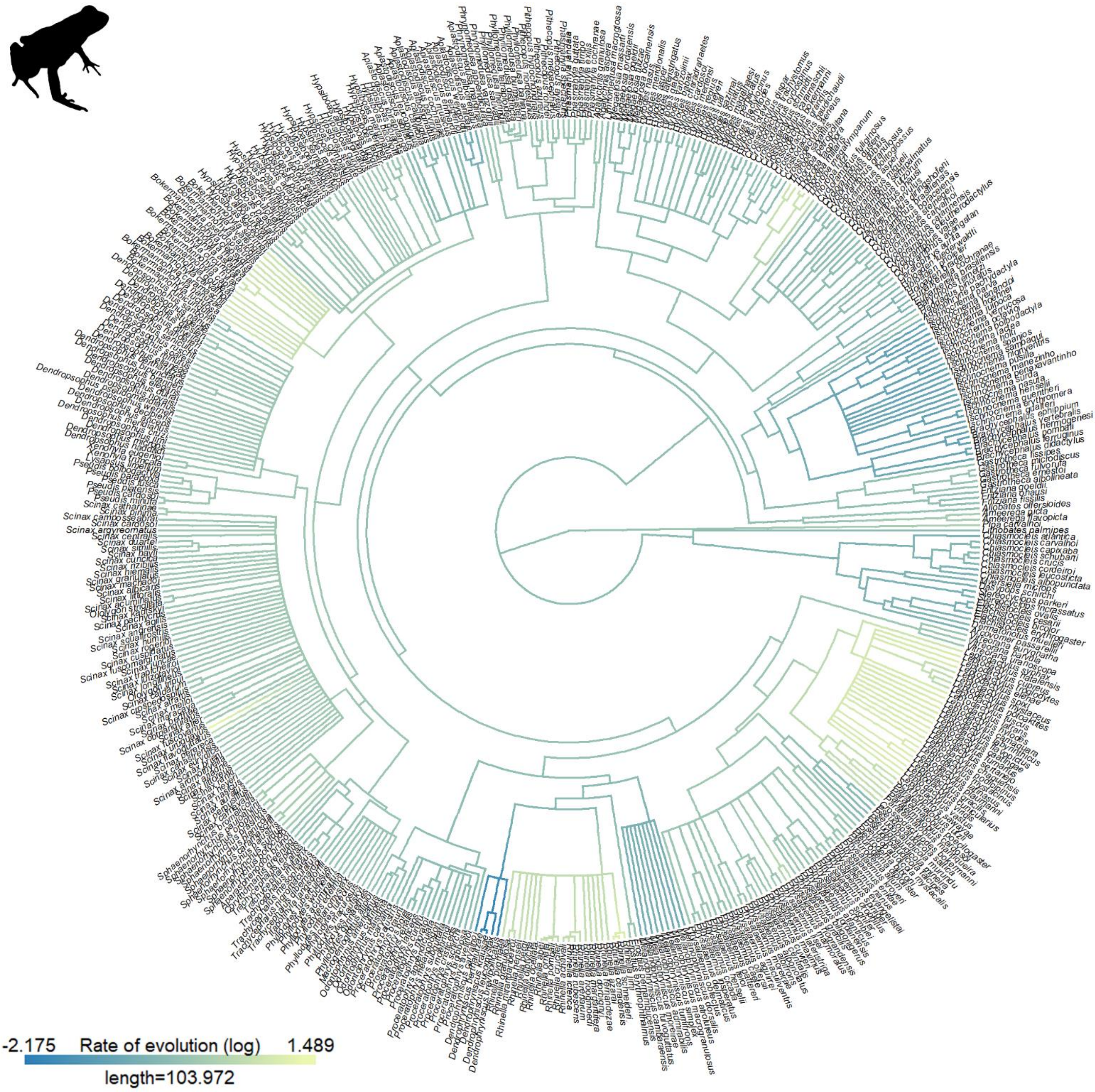

Figure S1. Evolution dynamics of body size of amphibians that occur in the Atlantic Forest domain. Warmer colors (yellow) denote faster rates of trait evolution, cold colors (blue) indicate slower rates.

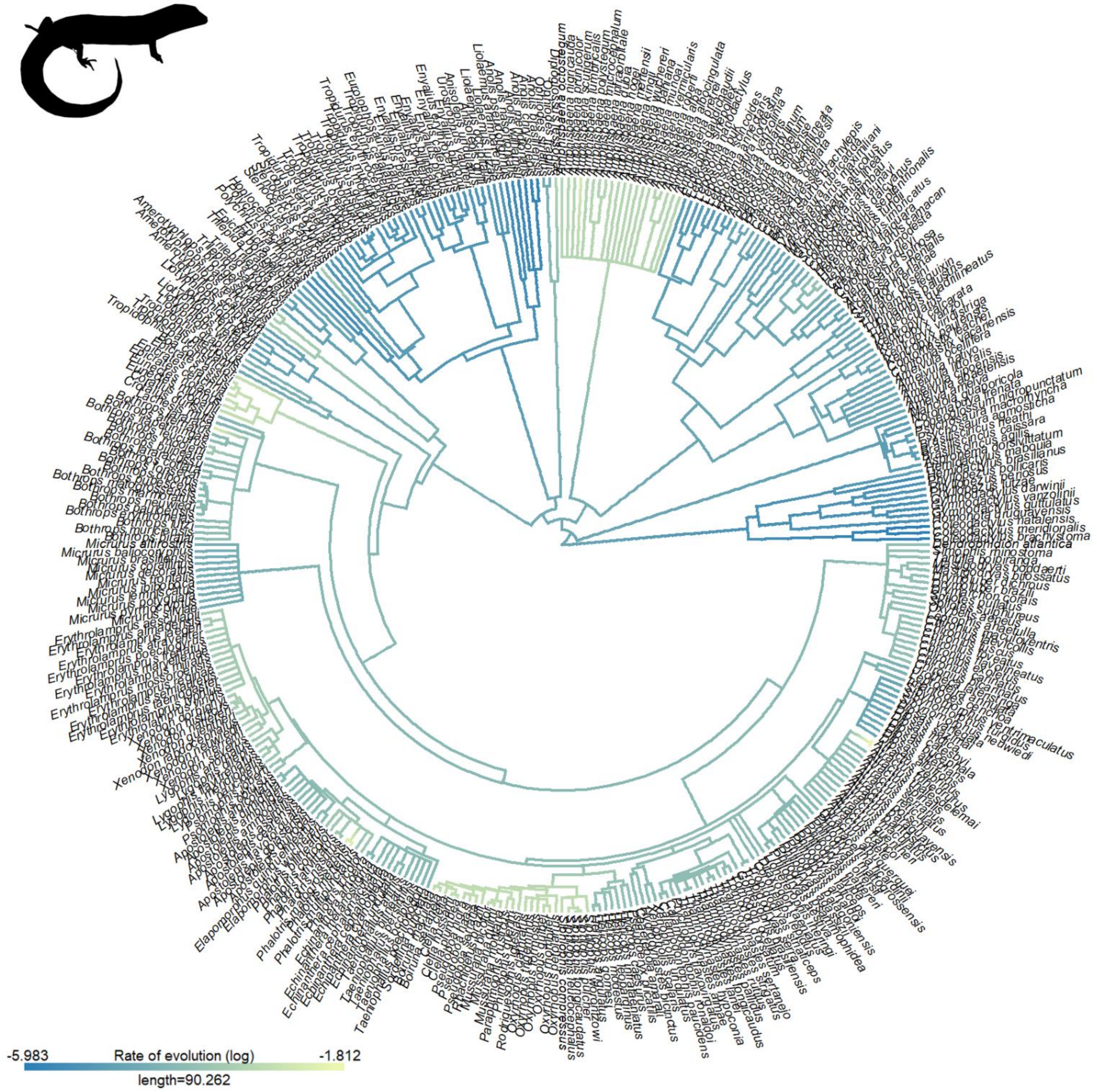

Figure S2. Evolution dynamics of body mass of squamates that occur in the Atlantic Forest domain. Warmer colors (yellow) denote faster rates of trait evolution, cold colors (blue) indicate slower rates.

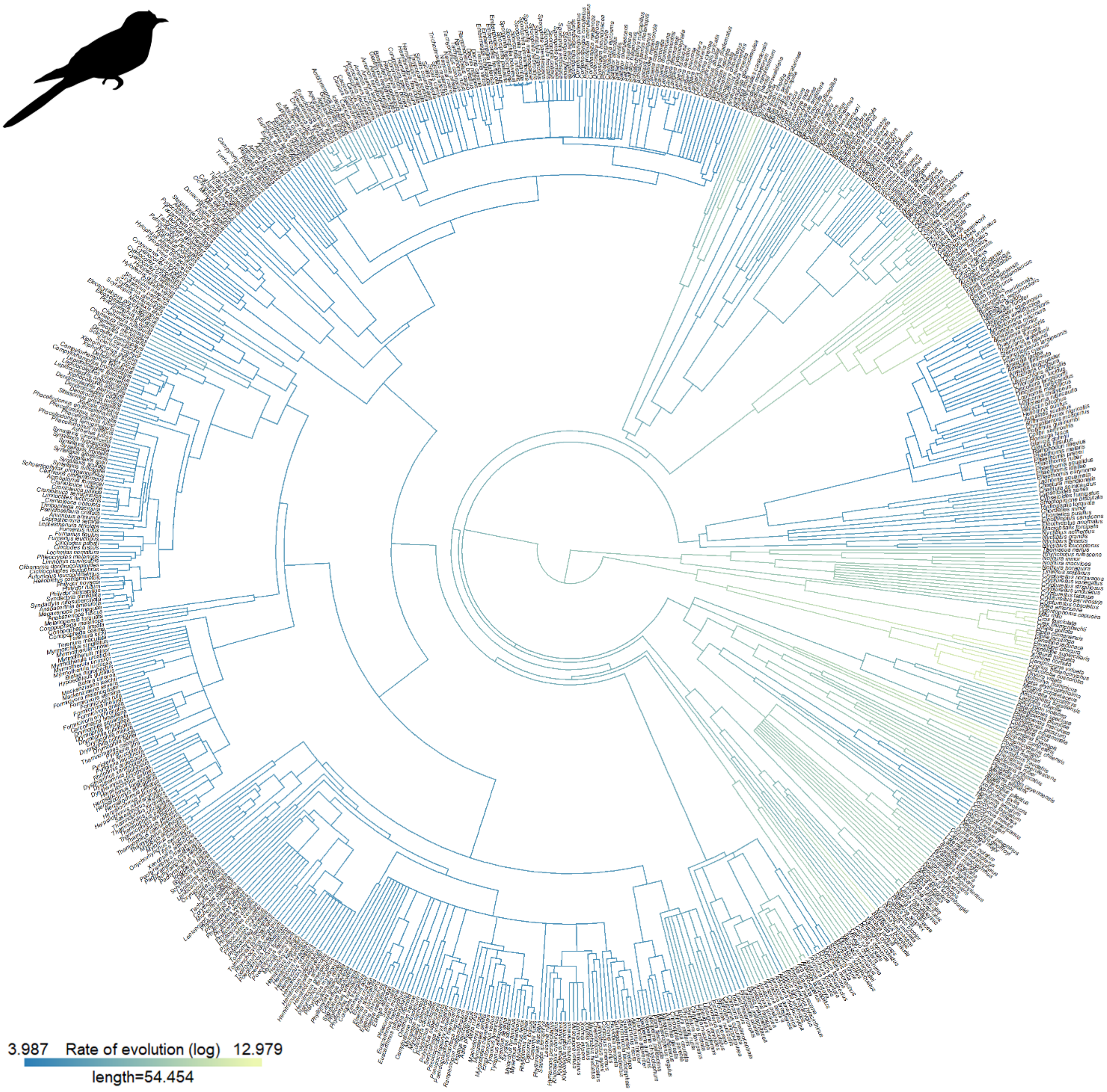

Figure S3. Evolution dynamics of body mass of birds that occur in the Atlantic Forest domain. Warmer colors (yellow) denote faster rates of trait evolution, cold colors (blue) indicate slower rates.

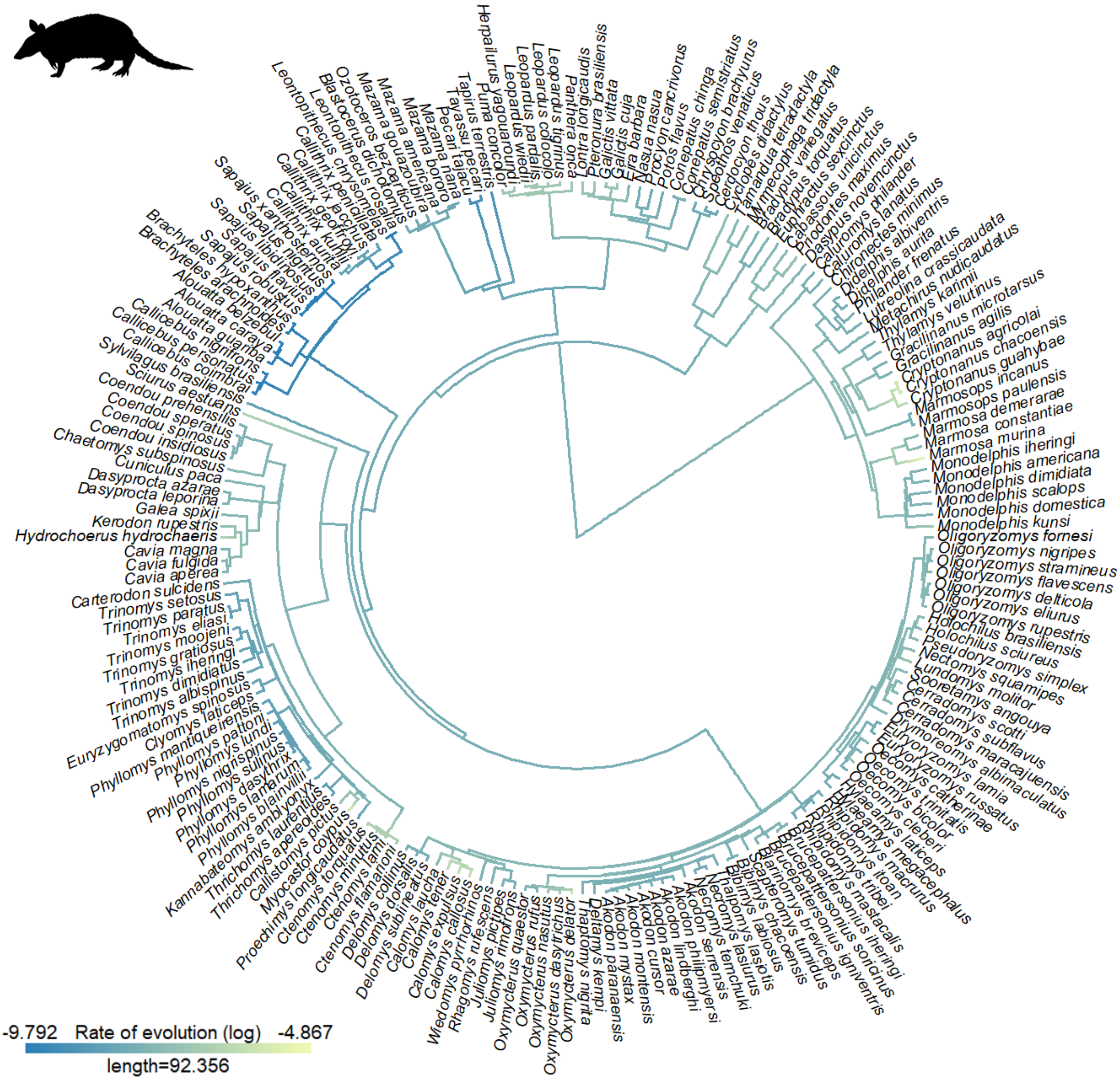

Figure S4. Evolution dynamics of body mass of mammals that occur in the Atlantic Forest domain. Warmer colors (yellow) denote faster rates of trait evolution, cold colors (blue) indicate slower rates.

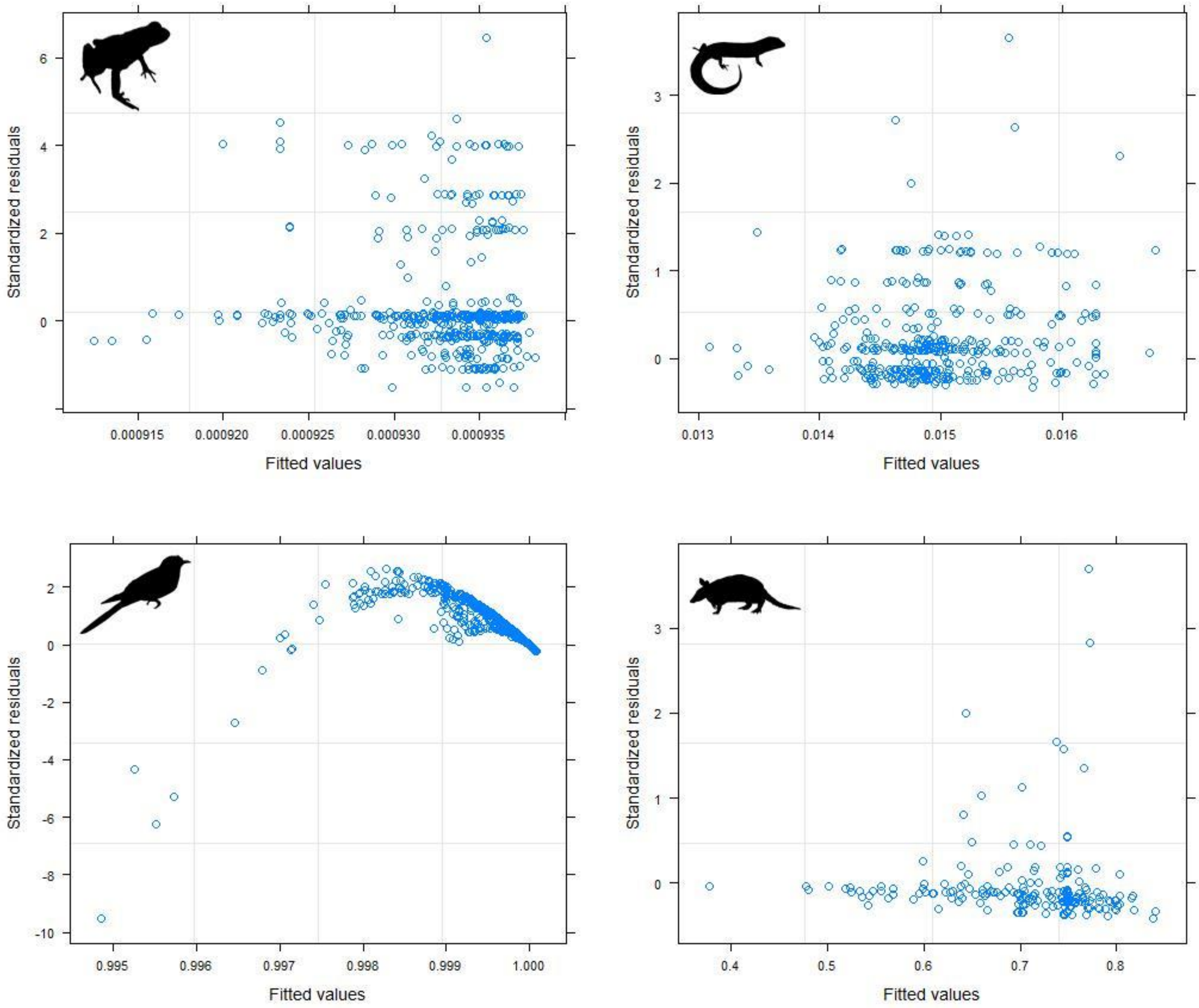

Figure S5. Diagnosis of the Phylogenetic Analysis of Generalized Least Squares (PGLS) model of each group of vertebrates from the Atlantic Forest.

Conclusão geral

- Ambas as dinâmicas de equilíbrio e não-equilíbrio atuam juntas para explicar a diversidade de espécies e de características de ectotérmicos e endotérmicos na Mata Atlântica.

- De uma maneira geral, os vertebrados possuem padrões de distribuição espacial idissioncráticos em relação a idade da comunidade, diversidade funcional (FDis) e das taxas de diversificação.

- Apenas a riqueza de espécies apresenta padrão de distribuição semelhante entre os endotérmicos, e destes com os sapos e squamatas. No entanto, não há um padrão congruente da riqueza entre os dois grupos de ectotérmicos.

- A riqueza de espécies e a diversidade de características têm os mesmos preditores nas linhagens de vertebrados terrestres, mas operam de maneira diferente no espaço.

- As trajetórias da taxa evolutiva do tamanho do corpo diferem entre os vertebrados, não havendo uma maior semelhança entre ectotérmicos e endotermos.

- Há uma alta heterogeneidade nas taxas evolutivas dentro de cada grupo de vertebrados da Mata Atlântica, com algumas linhagens apresentando acelerações na evolução fenotípica e outras desacelerando. É possível que as taxas estejam relacionadas a outros eixos do nicho ecológico das espécies, como o habitat.

- O nicho climático que uma espécie ocupa, especificamente a centralidade (posição) do nicho e sua amplitude, não ditam a taxa de evolução fenotípica de vertebrados terrestres da Mata Atlântica.

- Essas descobertas têm implicações para nossa compreensão dos impulsionadores de biodiversidade de vertebrados terrestres na Mata Atlântica, com destaque para a taxa de diversificação como um impulsionador da diversidade de características e da riqueza. Além disso, não encontramos evidências de que o nicho climático dos vertebrados terrestres cause mudanças evolutivas das taxas fenotípicas, seja o nicho climático passado ou do presente.