

UNIVERSIDADE FEDERAL DO AMAZONAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

**DIVERSIDADE DE ANUROS DA AMAZÔNIA: EXPLORANDO AS
LACUNAS DO CONHECIMENTO E OS PROCESSOS DE FORMAÇÃO
DAS COMUNIDADES**

Brena da Silva Gonçalves

Manaus

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Brena da Silva Gonçalves

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Zoologia, da Universidade Federal do Amazonas, como parte dos requisitos necessários à obtenção do título de Doutora em Zoologia.

Coorientador: Cristian de Sales Dambros

Orientadora: Fernanda de Pinho Werneck

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BRENA DA SILVA GONÇALVES

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RESUMO DA TESE

Esta tese aborda, de forma integrada, os padrões, processos e lacunas de conhecimento que moldam a diversidade de anfíbios anuros na Amazônia, combinando análises ecológicas, biogeográficas, síntese de dados e iniciativas de divulgação científica. O trabalho parte do reconhecimento de que a anurofauna amazônica, embora extremamente diversa, permanece limitada por déficits taxonômicos, geográficos e evolutivos que dificultam tanto a compreensão de sua história biológica quanto a proposição de estratégias de conservação eficazes. No Capítulo 1, são identificadas e quantificadas as principais lacunas de conhecimento sobre os anuros amazônicos. Os resultados mostram que grandes áreas da Amazônia seguem subamostradas, que a riqueza de anuros amazônicos documentada até o momento está aquém da riqueza real do bioma (sensu WWF) e que a escassez de dados genéticos compromete avaliações taxonômicas e biogeográficas. O capítulo destaca ainda regiões prioritárias para amostragem, a necessidade de abordagens integrativas de taxonomia e a importância de programas de monitoramento de longo prazo para avanços concretos no status de conhecimento sobre a biodiversidade de anuros amazônicos. O Capítulo 2 investiga os mecanismos que estruturam a diversidade beta — taxonômica, filogenética e funcional — ao longo da Amazônia, revelando uma hierarquia clara entre processos históricos e ecológicos. Em escalas amplas, o legado histórico das Áreas de Endemismo é o principal delimitador das grandes unidades biogeográficas; já ao longo de gradientes ambientais, fatores climáticos, especialmente a temperatura do trimestre mais úmido (BIO8), surgem como filtros ecológicos dominantes. Esses achados demonstram a interação multiescalar entre vicariância, seleção ambiental e sensibilidade fisiológica, e reforçam a vulnerabilidade dos anuros às mudanças climáticas. Os resultados ainda mostram que as beta-regiões identificadas para anfíbios diferem substancialmente dos esquemas biogeográficos clássicos, indicando que estratégias de conservação generalistas podem ser insuficientes para contemplar os diferentes eixos da diversidade deste grupo emblemático da megadiversidade amazônica. Complementarmente, a tese inclui produtos de divulgação e popularização científica, apresentados na forma de anexos, que sintetizam e comunicam temas centrais relacionados à biodiversidade e às ameaças climáticas aos grupos da herpetofauna. Entre eles estão um capítulo autorado no livro *Girinos do Brasil*, que reúne descrições inéditas e fotografias de girinos de todos os biomas brasileiros, e produção coautorada do livro *Emergência Climática e a Sociobiodiversidade*.

Amazônica, destinado a disseminar conhecimento sobre os impactos das mudanças climáticas na fauna amazônica. Esses materiais ampliam o alcance social da pesquisa e reforçam o compromisso com a educação ambiental e a comunicação científica. Em conjunto, os resultados desta tese fornecem um panorama abrangente sobre como déficits de conhecimento, processos históricos e filtros ambientais moldam a diversidade de anfíbios amazônicos. As análises e sínteses apresentadas oferecem bases científicas para aprimorar modelos biogeográficos, orientar prioridades de pesquisa e subsidiar ações de conservação urgentes diante do cenário de mudanças ambientais aceleradas.

Palavras-chave: Anuros, Amazônia, Lacunas do Conhecimento, Beta-diversidade.

ABSTRACT

This thesis comprehensively addresses the patterns, processes, and knowledge shortfalls that shape the diversity of anuran amphibians in the Amazon, integrating ecological and biogeographical analyses with data synthesis and science communication initiatives. The study stems from the recognition that the Amazonian anuran fauna, although extremely diverse, remains constrained by taxonomic, geographic, and evolutionary shortfalls that hinder both the understanding of its biological history and the development of effective conservation strategies. Chapter 1 identifies and quantifies the major knowledge gaps concerning Amazonian anurans. Results indicate that vast areas of the Amazon remain undersampled, that the anuran richness documented to date falls short of the biome's actual richness (*sensu* WWF), and that the scarcity of genetic data compromises taxonomic and biogeographical assessments. The chapter further highlights priority regions for sampling, the need for integrative taxonomic approaches, and the importance of long-term monitoring programs to achieve substantial improvements in the knowledge status of Amazonian anuran biodiversity. Chapter 2 investigates the mechanisms structuring beta-diversity—taxonomic, phylogenetic, and functional—across the Amazon, revealing a clear hierarchy between historical and ecological processes. At broad scales, the historical legacy of Areas of Endemism serves as the primary delimiter of large biogeographical units; conversely, along environmental gradients, climatic factors—particularly the Mean Temperature of Wettest Quarter (BIO8)—emerge as dominant ecological filters. These findings demonstrate the multiscale interaction between vicariance, environmental selection, and physiological sensitivity, reinforcing the vulnerability of anurans to climate change. Furthermore, the results show that the beta-regions identified for amphibians differ substantially from classic biogeographical schemes, suggesting that generalist conservation strategies may be insufficient to encompass the distinct diversity axes of this emblematic group of Amazonian megadiversity. Complementing these scientific chapters, the thesis includes science dissemination and popularization products, presented as appendices, which synthesize and communicate central themes related to biodiversity and climatic threats to herpetofauna. These include an authored chapter in the book *Girinos do Brasil*, comprising novel descriptions and photographs of tadpoles from all Brazilian biomes, and a co-authored contribution to the book *Emergência Climática e a Sociobiodiversidade Amazônica*, aimed at disseminating knowledge on the impacts of climate

change on Amazonian fauna. These materials expand the social reach of research and reinforce the commitment to environmental education and science communication. Collectively, the results of this thesis provide a comprehensive overview of how knowledge shortfalls, historical processes, and environmental filters shape the diversity of Amazonian amphibians. The presented analyses and syntheses offer a scientific basis to refine biogeographical models, guide research priorities, and inform urgent conservation actions in the face of rapid environmental change.

Key-words: Anurans, Amazon, Knowledge Gap, Beta-diversity.

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INTRODUÇÃO GERAL

A Amazônia destaca-se mundialmente como o maior remanescente de floresta tropical do mundo, sustentando aproximadamente 10% de toda a biodiversidade conhecida do planeta (Antonelli et al., 2018; Guayasamin et al., 2024). Essa vasta extensão é moldada por uma longa história paleoambiental e por acentuados gradientes físicos e geológicos, que resultam em uma alta heterogeneidade de ambientes – desde florestas de terra firme e alagáveis até áreas abertas de altitude, como os tepuis e os Andes, e ecossistemas exclusivos como campinas e lavrados (Vergara et al., 2022; Darela-Filho et al., 2024). Neste cenário, o sistema de drenagem assume protagonismo, atuando não apenas na gênese dessa diversidade de habitats (e.g. várzeas e igapós), mas como um elemento estruturante fundamental da paisagem amazônica. Essa complexidade ambiental sustenta uma riqueza ímpar, incluindo a maior diversidade de anfíbios anuros neotropicais (Guayasamin et al., 2024). No entanto, a exploração e o estudo de tal riqueza na Amazônia impõem grandes desafios logísticos, de acessibilidade e de investimento financeiro em pesquisa (Gonçalves et al., 2025; Carvalho et al., 2023). Tais barreiras levam à persistência e à criação de lacunas de conhecimento sobre as espécies e seus ambientes, limitando o potencial de estudos essenciais para a conservação. Infelizmente, muitas dessas espécies vêm sendo perdidas antes mesmo de serem catalogadas, devido ao aumento das pressões antropogênicas e às mudanças climáticas, que ameaçam a persistência da diversidade e a integridade dos ambientes (Silva Junior et al., 2021; Albert et al., 2023). Neste contexto de ameaça, identificar e mapear as lacunas de conhecimento é essencial para definir prioridades de pesquisa e planejar programas de conservação eficazes, especialmente para os anuros, um grupo altamente suscetível a essas mudanças.

A biodiversidade é um termo complexo que ultrapassa a riqueza de espécies (normalmente entendida como diversidade taxonômica), englobando outras dimensões e aspectos da diversidade biológica, como a diversidade filogenética (história evolutiva), funcional (papéis ecológicos), entre outros. O conhecimento atual sobre essa biodiversidade apresenta sérias lacunas (*shortfalls* ou *déficits*) que exigem abordagens integrativas para seu preenchimento (Hortal et al., 2015). Tais barreiras contribuem para a persistência dos sete *déficits* de conhecimento da biodiversidade descritos na literatura (Hortal et al., 2015). No contexto deste estudo, as lacunas mais críticas incluem a falta de conhecimento quanto a espécies catalogadas (Linnaean), mapas de distribuição

precisos (Wallacean), dados sobre atributos (Raunkiaeran), conhecimento sobre a história evolutiva (Darwinian) e sobre as tolerâncias abióticas/ambientais das espécies (Hutchinsonian). Essas incertezas são particularmente críticas para grupos megadiversos e pouco amostrados, como os anuros amazônicos, considerados os vertebrados mais sensíveis as mudanças climáticas e as pressões antrópicas (Pottier et al., 2025; Luedtke et al., 2023) por razões diversas, como sua relativa baixa mobilidade, pele permeável e forte dependência de microclimas (Duellman & Trueb, 1994). Além disso, a ampla presença de complexos de espécies crípticas em anuros no contexto amazônico (e. g. Bickford et al., 2007, Ortega-Andrade et al., 2015, Rodríguez et al., 2017, Ferrão et al., 2018, Carvalho et al., 2019, Lima et al., 2020, Mônico et al., 2024) e a carência de informações sobre distribuição e relações evolutivas reforçam a necessidade de abordagens integrativas que combinem dados ecológicos, filogenéticos e geográficos para o avanço do conhecimento quanto aos padrões de diversidade e processos geradores. Essas incertezas interconectadas afetam diretamente a capacidade de compreender os determinantes e preservar tanto as espécies quanto os ecossistemas amazônicos.

Para compreender a estruturação da biodiversidade, além da simples contagem de espécies (diversidade alfa), é necessário avaliar como a composição muda ao longo do espaço, ou seja, a diversidade beta (Whittaker, 1960). A teoria moderna indica que dois mecanismos principais são responsáveis pelas mudanças na composição, o aninhamento (*nestedness*) e a substituição (*turnover*) (Baselga, 2010). O aninhamento ocorre quando as espécies de uma comunidade local representam um subgrupo de uma comunidade regional mais rica, gerada por processos ordenados, como é o caso da exclusão competitiva e/ou colonização direcional (Si et al., 2016). Já a substituição pode ser gerada por dois processos principais. O primeiro, gerado pela seleção ambiental, é onde as espécies são filtradas de acordo com seus nichos ecológicos, criando comunidades distintas ao longo do gradiente ambiental. Já o segundo envolve restrições espaciais e históricas, causadas pela baixa capacidade de dispersão e presença de barreiras biogeográficas que promovem a divergência e especiação por vicariância, mesmo em ambientes similares (Baselga, 2010). No entanto, focar apenas na taxonomia é insuficiente para montar o quebra-cabeça completo sobre a biodiversidade, já que as outras facetas da diversidade podem trazer peças que faltam sobre os processos hierárquicos que realmente montaram e estruturam as comunidades locais ao longo do espaço e do tempo (Devictor et al., 2010; Rapacciuolo & Bolis, 2019).

A Amazônia é o palco ideal para testar a força e eventuais hierarquias desses processos em gerar e estruturar a diversidade biológica. Um dos debates centrais na biogeografia amazônica é a importância relativa entre o legado histórico (e.g., papel de grandes rios como barreiras vicariantes e geradoras de áreas de endemismo – AoEs) e os filtros ambientais contemporâneos (e.g., papel dos gradientes climáticos em estruturar a diversidade biológica em ecorregiões). Os anuros são organismos ideais para investigações nesse sentido, pois, como animais ectotérmicos, dependem diretamente da temperatura ambiental e da umidade para regular sua fisiologia e perda de água (Akat Çömden et al., 2023; Cao et al., 2024), fazendo deles altamente sensíveis a mudanças do ambiente e do clima (Amado et al., 2019; Anderson & Andrade, 2017). Além disso, possuem baixa capacidade de dispersão, o que os torna particularmente suscetíveis às restrições espaciais e barreiras históricas (Bredeweg et al., 2019), sendo, portanto, um grupo ideal para testar se os esquemas biogeográficos clássicos (em geral baseados em aves e primatas) se aplicam a organismos com baixa mobilidade. Contudo, a literatura atual apresenta resultados conflitantes e lacunas importantes, indicando que ainda não está claro como — e em que intensidade — esses processos moldam a diversidade beta dos anuros amazônicos, o que motiva a investigação alvo dessa tese de doutorado.

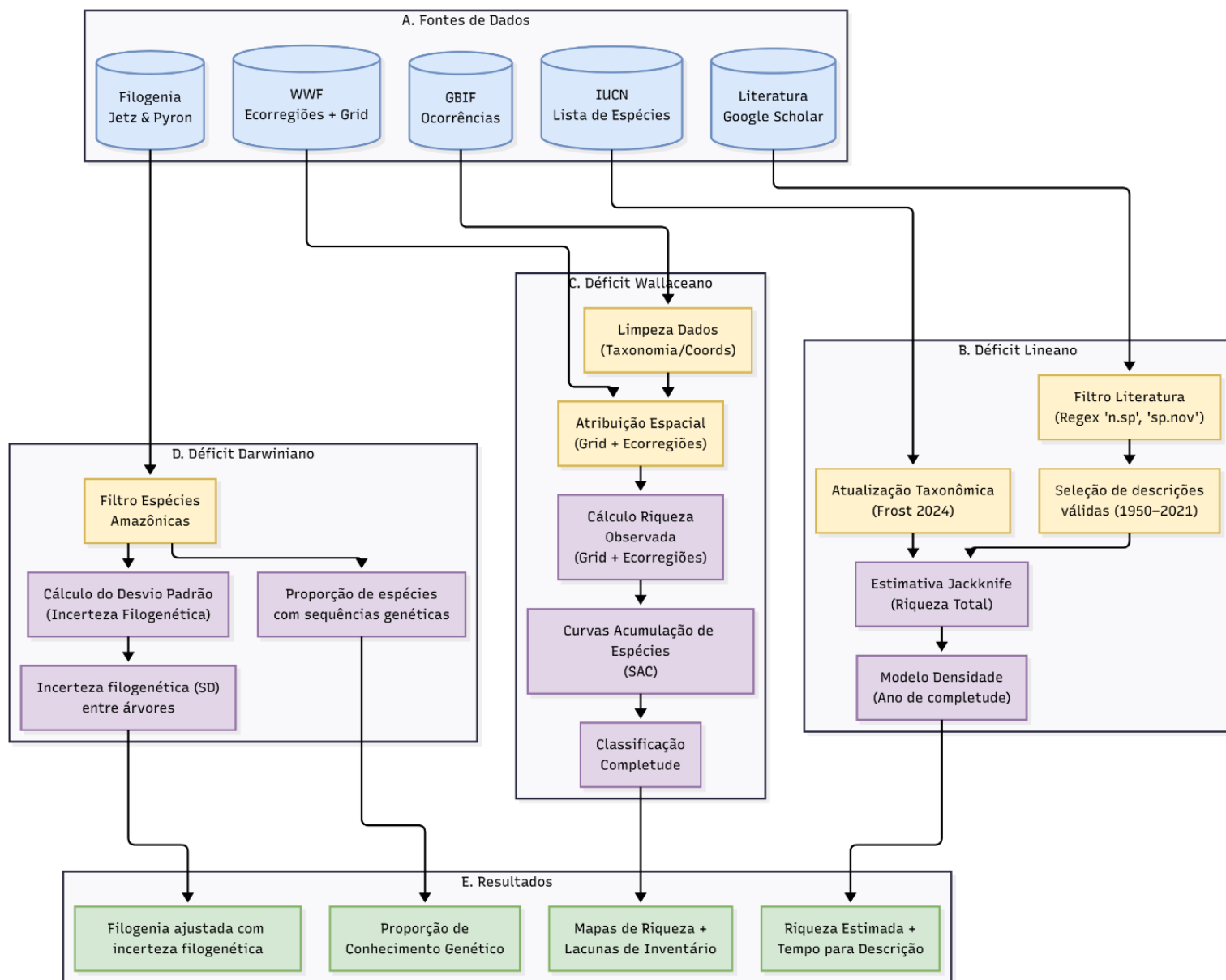
Diante dessas lacunas e da urgência da conservação, esta tese teve como objetivos gerais identificar e mapear as lacunas do conhecimento sobre anuros amazônicos e buscar compreender os determinantes que impulsionam e mantêm a diversidade do grupo na região. Para atingir esses objetivos gerais, a tese está estruturada em dois capítulos complementares em formato de artigos científicos. Paralelamente aos capítulos científicos, parte deste trabalho também envolveu iniciativas de divulgação e popularização científica relacionadas à herpetofauna amazônica, reforçando o compromisso com ciência aberta e com a ampliação do diálogo entre pesquisadores e sociedade. No Capítulo 1, mapeio e quantifico as incertezas taxonômicas, geográficas e evolutivas sobre a diversidade de anuros amazônicos e debato sobre áreas prioritárias para futuros esforços de coleta e pesquisa. No Capítulo 2, investigo a importância relativa de barreiras históricas e de filtros ambientais na estruturação da diversidade beta (taxonômica, filogenética e funcional) de anuros amazônicos, avaliando a congruência dos padrões recuperados com as AoEs propostas para a Amazônia e modelando a influência hierárquica de processos determinantes. Os resultados do primeiro capítulo oferecem as bases necessárias sobre o estado do conhecimento para que o segundo capítulo aborde de forma integrada os processos que moldam os padrões

biogeográficos da região. Por fim, a tese apresenta uma seção de anexos que contém produtos e resultados de esforços de divulgação e popularização científica sobre a diversidade de anfíbios anuros, desenvolvidos durante o período do doutorado como parte do compromisso com ciência aberta e engajamento social. Em síntese, esta tese busca fornecer um panorama biogeográfico mais preciso e fundamentado para os anuros e avançar na compreensão da hierarquia dos processos que moldam a biodiversidade amazônica, contribuindo para estratégias de conservação mais eficazes diante do cenário de rápidas mudanças ambientais.

Capítulo 1

Brena da Silva GONÇALVES, Cristian de Sales DAMBROS & Fernanda de P. WERNECK. Exploring Blind Spots in Amazonian Anuran Diversity: An Assessment of Research and Conservation Needs. Artigo publicado na revista *Acta Amazonica* em 2025. Disponível em: <http://dx.doi.org/10.1590/1809-4392202500072>.

Resumo Visual. Fluxograma metodológico para quantificação das lacunas de conhecimento sobre anuros amazônicos. (A) Integração de Dados: Compilação de registros de ocorrência, descrições taxonômicas e dados filogenéticos. (B–D) Análise de Lacunas: Avaliação dos três principais déficits de conhecimento: (B) Lineano (estimativa da riqueza real via curvas de descoberta); (C) Wallaceano (mapeamento da completude de inventários e vazios amostrais); e (D) Darwiniano (mensuração da disponibilidade de dados genéticos e incerteza filogenética). (E) Resultados: Consolidação dos mapas, estimativas e índices gerados para caracterizar a magnitude de cada déficit.



Exploring Blind Spots in Amazonian Anuran Diversity: An Assessment of Research and Conservation Needs

Abstract

Knowledge of Amazonian megadiversity remains underestimated due to the region's vast size, environmental heterogeneity, and inaccessibility. With increasing threats to the biome, it is crucial to map current knowledge before it is lost. This study addresses Linnean (species description), Wallacean (species distribution), and Darwinian (genetic knowledge) shortfalls for Amazonian anurans, quantifying what remains unknown. We reviewed species descriptions, analyzed occurrence data, and evaluated available genetic sequences and phylogenetic uncertainty. Species descriptions have grown over time, peaking around 2000. We estimate 1,525 species exist in Amazonia, but only 766 were found in species shapefiles and 810 in occurrence data. Richness was highest in northern and western Amazonia, while remote areas far from urban centers remain undersampled. Only two genes (mitochondrial 12S and 16S) have been sequenced for more than half of the known species and are available in open databases, while phylogenetic uncertainty predominates in most clades. Regions such as Gurupa Várzea and Cordillera Central Páramo are especially under-sampled. Our results show that taxonomic, distribution, and genetic shortfalls are complementary rather than overlapping, indicating that different regions and species groups require different research strategies. This study highlights major knowledge gaps and provides a framework to guide future efforts in taxonomy, biogeography, and evolutionary studies of Amazonian anurans, supporting conservation planning in one of the most diverse regions on Earth for one of the most diverse and threatened taxonomic groups.

Key-words: knowledge gaps, amazon, frogs, shortfalls, biodiversity

Explorando pontos cegos na diversidade de Anuros Amazônicos: Uma avaliação das Necessidades de Pesquisa e Conservação

Resumo

O conhecimento sobre a megadiversidade amazônica ainda é subestimado, devido ao vasto tamanho da região, à heterogeneidade ambiental e à sua difícil acessibilidade. Com as crescentes ameaças ao bioma, é fundamental mapear o conhecimento atual antes que seja perdido. Este estudo aborda as deficiências linneanas (descrição de espécies), wallaceanas (distribuição de espécies) e darwinianas (conhecimento genético) dos anuros amazônicos, quantificando o que permanece desconhecido. Revisamos as descrições de espécies, analisamos dados de ocorrência e avaliamos as sequências genéticas disponíveis, bem como a incerteza filogenética. As descrições aumentaram ao longo do tempo, com pico por volta de 2000. Estimamos que existam 1.525 espécies na Amazônia, mas apenas 766 foram encontradas em shapefiles de espécies e 810 em dados de ocorrência. A maior riqueza foi registrada nas porções norte e oeste da Amazônia, enquanto regiões remotas e distantes de centros urbanos permanecem subamostradas. Apenas dois genes mitocondriais (12S e 16S) foram sequenciados para mais da metade das espécies conhecidas e estão disponíveis em repositórios públicos, enquanto a incerteza filogenética predomina na maioria

dos clados. Regiões como Gurupa Várzea e Cordillera Central Páramo são particularmente pouco amostradas. Nossos resultados indicam que as deficiências taxonômicas, de distribuição e genéticas são complementares, e não sobrepostas, o que sugere que diferentes regiões e grupos de espécies demandam estratégias de pesquisa distintas. Este estudo destaca lacunas críticas de conhecimento e fornece uma base para orientar esforços futuros em taxonomia, biogeografia e estudos evolutivos de anuros amazônicos, contribuindo para o planejamento da conservação em uma das regiões mais biodiversas e para um dos grupos taxonômicos mais diversos e ameaçados do planeta.

Palavras-chave: lacunas de conhecimento, Amazônia, anuros, deficiências, biodiversidade

Introduction

Discovering and describing the planet's extant species remains a primary goal for many biologists and taxonomists. This is no easy task, and numerous challenges persist along the way. These include declining funding for basic research, taxonomic impediments, the systematic loss of natural habitats, and climate change (IUCN 2024). Such factors remove biological communities from the researchers' scope and can even lead to the extinction of many species before they are even known. As biodiversity conservation is a global priority for maintaining the environmental balance, ecosystem services, and human well-being (Joly et al. 2019), quantifying and identifying the current knowledge gaps in biodiversity may be key to defining future research priorities and effective conservation programs.

The Neotropics are widely recognized for harboring the greatest species richness on the planet. Located in northern South America, the Amazon is the largest tropical rainforest in the world and contains approximately 10% of all known biodiversity (Antonelli et al. 2018). The term Amazon can simultaneously refer to the Amazon River basin and the Amazonia biome (sensu WWF 2019). This biome covers about 40% of South America's territory and is shared by nine countries: Brazil, Peru, Colombia, Venezuela, Ecuador, Bolivia, Guyana, Suriname, and French Guiana (Vergara et al. 2022). Due to its vast extent and long paleoenvironmental history, the biome exhibits physical, chemical, and geological variations, which result in a range of distinct environments across the region, including different types of ecoregions, like forests, savannas, high-altitude areas, and wetlands (Igapó and Várzea) (Vergara et al. 2022, Darela-Filho et al. 2024). This environmental diversity enables biome to support the world's largest number of species of plants, birds, freshwater fish, insects, and anuran amphibians (Antonelli et al. 2018, Vergara et

al. 2022, Guayasamin et al. 2024). Estimates have shown that the species richness in the biome is even greater, and current richness estimates are likely largely underestimated (Camacho-Rozo and Urbina-Cardona 2024). However, not even such a rich environment remains unaffected by climate change and human activities (Albert et al. 2023). Climate change and anthropogenic pressures like deforestation are not spatially uniform across the Amazon — regions such as the "arc of deforestation" experience disproportionately high impacts (Silva Junior et al. 2021). These pressures may lead to local extinction, loss of phylogenetic diversity, phylogenetic endemism (Alves-Ferreira et al. 2025) or force species to shift their ranges in search of suitable habitats (Azevedo et al. 2024, Alves-Ferreira et al. 2025). Biological groups with limited mobility and habitat specificity may increase their extinction risks (Hof et al. 2011). Therefore, identifying knowledge shortfalls is essential for anticipating biodiversity responses to environmental change and for identifying potential climate refugia for conservation planning (Alves-Ferreira et al. 2025).

Biodiversity is a complex term and encompasses more than just species richness – it includes, for example, phylogenetic diversity (Faith 1992), functional traits (Cadotte et al. 2011), and ecological interactions (Tylianakis et al. 2008). Such facets demand integrative approaches to assess knowledge gaps (Hortal et al. 2015). Knowledge gaps (also named shortfalls or deficits) represent the difference between what has already been discovered (current knowledge) and the complete (ideal) knowledge of a taxonomic group at a given moment, usually in the present day (Hortal et al. 2015). These gaps include the need to adequately catalog species richness (Linnaean shortfall), map their geographic distributions (Wallacean shortfall), understand their evolutionary processes and phylogenetic relationships (Darwinian shortfall), investigate their functional traits and ecological roles (Raunkiaeran shortfall), and their abiotic tolerances (Hutchinsonian shortfall) (Hortal et al. 2015, Lees et al. 2020, IUCN 2024). These interconnected gaps directly affect our ability to understand the drivers and preserve both species and Amazonian ecosystems.

Anurans are the most endangered group of vertebrates, with approximately 40% of known species facing some level of threat (Anunciação et al. 2024, IUCN 2024). Due to biological characteristics, such as permeable skin, low mobility, and a biphasic life cycle, they are strongly dependent on water bodies and humid environments for their reproduction and survival (Duellman and Trueb 1994). Yet, this dependency varies among taxa, and some lineages exhibit reproductive adaptations which allow them to reproduce in less aquatic habitats, such as larvae with endotrophic

diet, direct development, and foam nest construction (Haddad and Prado 2005). Additionally, for species that are more dependent on water, the functional connectivity between aquatic and terrestrial habitats can be as critical as water availability itself. This makes them vulnerable to environmental shifts, like water pollution, contamination, pathogen exposure, habitat loss, and climate change (Luedtke et al. 2023). Thus, the conservation of anuran species is essential for sustaining ecosystem functioning, given their unique ecological roles. As keystone species, they regulate arthropod population, contribute to nutrient recycling in both aquatic and terrestrial ecosystems, and can act as ecological indicators (Duellman and Trueb 1994, Ceron et al. 2023). While some species may signal preserved and stable environmental conditions, other -especially disturbance-tolerance taxa- may indicate environmental degradation, depending on their ecological specialization. The Amazon environmental heterogeneity and abiotic conditions has fostered their extraordinary diversification, making them one of the richest groups in the biome (Frost 2024). Recently studies revealed the presence of cryptic species, which are morphologically similar and genetically distinct, and whose identification is hindered by the lack of phylogenetic studies (Ferrão et al. 2018, Rojas et al. 2018, Carvalho et al. 2019, Lima et al. 2020, Mônico et al. 2024), and the diversity of specialized reproductive modes (Haddad and Prado 2005, Nunes-de-Almeida et al. 2021). However, current knowledge about frogs is unevenly distributed, many species are known from very limited records, or are poorly ecological and evolutionary characterized, with historically underexplored regions throughout the Amazonia (Bickford et al. 2007, Camacho-Rozo and Urbina-Cardona 2024, Penhacek et al. 2024). Considering the accelerating habitat loss and climate change driven by anthropogenic pressures, studying this biological community is of utmost importance to identify these blind spots in knowledge gaps.

In such a context, this study aims to identify and map the Linnaean, Wallacean, and Darwinian gaps regarding Amazonian frogs, based on literature and available online data, so that we can highlight priority regions for future research and contribute to the understanding of one of the planet's most threatened biomes. Based on previous studies and accessibility patterns, we expected to find greater shortfalls in remote areas, with higher taxonomic and distribution knowledge concentrated around urban centers and well-studied regions (Hortal et al. 2015, Carvalho et al. 2023). In the context of increasing environmental change, understanding how many species occur, where their distribution and its limits, and what their relationship becomes crucial, especially for taxa with restricted ranges and low dispersal capacity, such as anurans.

Methods

Study area

We investigated shortfalls in biodiversity knowledge in the Amazonia rainforest, the largest tropical forest in the world, which encompasses nine countries (Bolivia, Brazil, Colombia, Ecuador, Guyana, French Guyana, Peru, Suriname, and Venezuela), and covers an area of seven million ha (Vergara et al. 2022). Although regional weather is broadly warm (average ~25°C) with mean precipitation of ~2,300mm/year (Fisch et al. 1998), the Amazon exhibits pronounced climatic heterogeneity, especially in temperature and precipitation seasonality across different regions, influenced by topography that is heterogeneous and includes areas from 0 to 100m a.s.l. to mountains higher than 3,000m a.s.l. (Hoorn et al. 2010, Flores et al. 2024). The Amazon biome also includes different vegetation types, from tropical forests (i.e., wet, mountain, and terra-firme) (Pires and Prance 1985) to open areas (i.e., white-sand savannas, mangroves, and tepuis) (Silva-Souza and Souza 2020).

Linnean deficit

To evaluate the Linnaean shortfall, we recorded the number of species currently occurring in the region, the number of available papers describing species over time, and estimated the complete number of species existing in the Amazonia. To determine the number of occurring species, we considered the anurans' shapefiles distributed in the Amazonia (IUCN 2024). First, we downloaded the species range shapefiles from the South American anurans, overlapped these with the Amazonia area shapefile (WWF 2019), and removed species that don't have distribution in the study area. Also, we only considered an 'Amazonian species' shapefiles with at least 50% of its distribution inside the Amazonian area. We removed the synonyms, checked, and updated the names following the Amphibian Species of the World (Frost 2024).

To compile studies about anuran species in the Amazonia region, we conducted a systematic literature search Google Scholar using the query '(anura OR anurans OR frogs OR sapos OR rãs OR pererecas) AND (Amazonia OR Amazon OR Amazônia OR Floresta Amazônica)', covering the period from 1700 to 2018. The starting point was chosen to include the first known species description from the region (Linnaeus 1758). We used the Zotero browser

extension to automatically retrieve 1,114 documents in PDF format, including articles, theses, dissertations, and books. We obtained 1,114 documents, including articles, thesis, dissertations, notes and books. To select only description papers, we applied a filtering script in R using regular expressions that searched for key terms such as “n.sp.”, “sp.nov.”, and “new.species” in the texts. This methodology didn’t count how many species were described in each paper, only if at least one species was. We excluded 824 documents that did not include new species descriptions, and our selection criteria focused on descriptions based on specimens collected in the Amazon biome. We narrowed our temporal analyses from 1950 to 2021 to compare them to actual and estimated species numbers. To estimate the complete number of species that have yet to be described and predict when this number might be reached, we extrapolated the current species count using the Jackknife richness estimator (Oksanen et al. 2024). Based on the time range covered by the previously surveyed papers, we selected 1700 as the start year and 2018 as the end year. This estimator uses the number of described species in this period as a sample and assumes that the annual descriptions result from homogeneous levels of sampling effort. The species curve can be extrapolated by considering different sampling effort values and accounting for heterogeneous sampling efforts. We used the *specpool* function of the *vegan* package, version 2.6-4 (Oksanen et al. 2024). Additionally, to determine the year in which the predicted number of species can be reached, we applied the adaptation of the density-dependent model proposed by Lu and He (2017) based on the work of Gotelli (2008):

$$N_t = K / [1 + (K / N_0 - 1) e^{(-rt)}]$$

Where K is the number of possibly existing species (calculated as the sum of Jack plus the number of species described before 1974), N is the number of species described over time (t), N₀ is the number of valid species described until t = 0, and r is the theoretical constant representing the rate of species description. We assessed the difference in sampling efforts by using multiple values for r (0.05, 0.1, 0.2, 0.3, 0.4, and 0.5), as proposed by Freitas et al. (2020).

Wallacean deficit

To assess the Wallacean shortfall, we used a different type of data to obtain the number of species in the Amazonia. We downloaded the occurrence of Anuran data available to the Amazon region from the Global Biodiversity Information Facility (GBIF 2024), and the 49 Amazonian

ecoregions shapefiles' from the World Wildlife Fund database (WWF 2019). The occurrence data (GBIF data) encompasses information from preserved specimens, publication observations, and biological collections. The ecoregion shapefiles were obtained from Olson et al. (2001), which classify ecoregions based on ecological, vegetation, and biogeographical characteristics. These ecoregions encompass diverse environments such as floodplain forests, *terra firme* rainforests, and white-sand savannahs. We applied two filtering procedures to process the occurrence data. First, we removed duplicated latitude, longitude, species names, and points with no species name. Second, we reviewed and updated the nomenclature according to Frost (2024), the most up-to-date nomenclature, and excluded instances where nomenclature could not be corrected or was incorrectly identified. At the end, we added a column corresponding to their respective ecoregions to the occurrence data. We adopted a two-scale approach to better characterize the Wallacean shortfall in Amazonia. First, we used a 1x1° grid over the entire biome to provide a broad overview of species richness and sampling completeness across space. Second, we analyzed the same information by ecoregions to account for environmental and biogeographic heterogeneity across the Amazon. This dual-scale framework allows for identifying both general patterns and more localized inventory gaps.

We checked if the occurrence points were localized inside the grid area and excluded those that were not. We utilized all unique occurrence points to calculate species richness per cell and ecoregion and to generate species accumulation curves (SAC). We employed accumulation curves as a proxy for assessing the deficit of inventories for cells and ecoregions. Cells or ecoregions with curves equal to or below 0.1 were considered well sampled (i.e. less than 10% of species still need to be described). SACs ranging from 0.1 to 0.5 were considered reasonably sampled, requiring additional sampling for completeness. Also, SACs above 0.5 were considered poor sampling and required great sampling effort.

Darwinian deficit

To assess the lack of knowledge regarding Amazonian anurans' phylogenetic relationships, we employed two approaches: (i) identify the proportion of species with genetic sequences sequenced and accessible at open databases and (ii) identify and quantify the positioning uncertainty in the phylogeny. To determine the proportion of sequences, we used the matrix provided in the supplementary material of Jetz and Pyron (2018), counting only the sequences for

anuran species recorded in the Amazonia, and then comparing this count to the estimated total number of species. To identify the phylogenetic uncertainty, we first selected a sample of 100 phylogenies from the 10.000 posterior distribution trees of Jetz and Pyron (2018). Subsequently, we computed the distance between all tip pairs from each phylogeny using *cophenetic.phylo* function of the *ape* package (Paradis and Schliep 2019). We excluded from the matrix the non-amazonian species distances, which did not match with our species list (using occurrence data). Therefore, we calculated the standard deviation (sd) from the trees using the distance matrix, as a proxy of the uncertain phylogenetic position of the species. Therefore, higher values of sd mean more uncertainty of the species relations between the compared trees, and lower values correspond to high certainty in the phylogenetic relations between species. All the analyses were done in the R software (R Core Team 2024).

Results

Linnean deficit

From the 1,114 published articles about Amazonian anurans that we analyzed, only 131 were recovered as species description papers. The first of such articles was published in 1758 (Linnaeus 1758). We did not recover papers for most of the years before 1850, but we recovered at least one article for almost all the subsequent years (Figure 1A). The average number of articles describing species of Amazonia anurans per year increased over time, starting with an average of 2 articles in the early 1800s and reaching 7.5 around 2000, and the highest number was 49 in 2007 (Figure 1A).

When we compared the data over the years, we noticed some discrepancies between the data downloaded and the description papers filtered. The number of species described followed a gradual increase pattern until approximately 1960 when the cumulative number of species described turned into an exponential curve (Figure 1B), with a decrease of the increment around 2000, with stagnation and decrease in 2021. A similar pattern of increase was found for the papers but in a short period. The number of studies about anurans increased slowly around 1980. After 2000 the increase was exponential with no signal of stagnation (Figure 1B). However, the number of descriptive studies gradually increased after 2000, reaching 131 papers (Figure 1B).

Based on the IUCN species shapefiles, we identified 766 species of anurans with their ranges currently distributed in the Amazonia, while our estimation suggests there could be around 1,525 anurans species in the region (jack1 = 1525.872). When we project this result into the future, we estimate that we will achieve this species number between 2030 (best-case scenario of sampling efforts; $r = 0.5$) and 2100 (worst-case scenario; $r = 0.05$). However, under the assumption of maintaining the current trajectory (scenario with $r = 0.1$), this number may be reached by 2070 (Figure 2).

Wallacean deficit

After filtering the occurrence data from GBIF, we obtained 35,498 occurrence points for 1,224 species of anurans distributed in the Amazon region, of which 27,018 were unique occurrences. These occurrences show a clear clustering pattern in the western, southwestern, central, and northeastern areas of Amazonia, particularly in Ecuador, Colombia, the Guianas, and near large urban centers in Brazil (Figure 3A). These clusters coincide with regions of higher inferred species richness, with the highest richness recorded in extreme western Amazonia, where a single cell reached 181 species. The average richness per cell was 10 species (Figure 3B), and the richness gradient aligns with the west-to-east decline observed in other studies. From the 918 cells analyzed, SACs could not be calculated for 486 cells (52.94%) due to insufficient sampling. Among the remaining cells, 249 (27.12%) were classified as poorly sampled, 153 (16.66%) as reasonably sampled, and only 30 (3.26%) as well-sampled (Figure 3C). The well-sampled cells are concentrated in the western and northern regions, consistent with the richness pattern observed. These findings highlight the uneven sampling effort across Amazonia and a correlation between sampling effort and inferred richness, emphasizing the need for further sampling efforts in less-explored regions.

The two most recorded anuran species in Amazonia are responsible for almost 10% of the total occurrences: *Rhinella marina* Linnaeus, 1758 (4.58%) and *Rhinella margaritifera* Laurenti, 1768 (4.52%). Summed, the ten more common species correspond to 15% of the occurrences (Table 1, Figure 4). The most recorded families are Bufonidae (*Rhinella* genus), Hylidae (*Scinax*, *Osteocephalus*, *Boana*, and *Trachycephalus* genera), Aromobatidae (*Allobates* genus), and Leptodactylidae (*Adenomera* and *Leptodactylus* genera; Table 1).

We found a mean of 96.8 species for the 40 ecoregions calculated. The richest ecoregion was the Eastern Cordillera Real Montane Forests, in western Amazonia, with 343 species (Figure 5A), followed by the Southwestern Amazonia Moist Forests with 284 species. The Gurupa Várzea is the least rich ecoregion with only 2 species registered (Figure 5A), followed by the Cordillera Central Páramo with 3 species. Despite the localization of these low-richness areas it is possible to visualize a richness pattern across the Amazonia, with higher richness regions concentrated in the west and poorer regions in the east (Figure 5A).

From the 49 ecoregions, SACs could be calculated for 40 (81.63%). Among these, 11 ecoregions (22.45%) were considered well-sampled (depicted in dark purple; Figure 5B), while 24 (48.98%) were reasonably sampled (depicted in purple). Only five ecoregions (10.20%) were poorly sampled (depicted in yellow and green; Figure 5B). The most well-sampled ecoregion was the Guianan Lowland Moist Forests ($SAC = 0.007$; Figure 5B), followed by Napo Moist Forest. Conversely, the Gurupa Várzea ($SAC = 1.00$) and Cordillera Central Páramo ($SAC = 1.00$) were the poorest sampled (Figure 5B). Following the richness pattern, the most well-sampled ecoregions are concentrated in the western part of the Amazon, except for the Guianan Lowland Moist Forests in the northeast. In contrast, the Gurupa Várzea, the most poorly sampled ecoregion (depicted in yellow, $SAC = 1.00$), is situated close to the well-sampled areas, highlighting a poorly explored or underrepresented area in the data.

Darwinian deficit

As expected, the most abundant sequences in data repositories are for the mitochondrial genes 16S and 12S (Figure 6), available for more than 500 of the currently recognized species, even though this estimate does not correspond to one-third of the estimated richness. The genes RAG1 (nuclear) and cytb (mitochondrial) were the next most frequent sequences in data repositories, sequenced for around 200 species. The less sequenced are the SLC8A3 and BDCF genes, known for less than 50 species (Figure 6).

After randomization and filtering, we retained 100 trees and adjusted for the 1,024 species distributed across 15 families. The standard deviation (sd) values ranged from 0 to 33.48 among clades. It is observed that uncertainty tends to vary within clades, with some terminal species showing lower variation compared to basal species. Considering variation by family, the mean SD values ranged from 3.16 to 28.91 (Figure 7, Table 2). Pipidae showed the highest phylogenetic

uncertainty (5 species, mean sd = 28.91), while Allophrynidae had the lowest value (2 species, mean sd = 3.16). There was a predominance of variation in species' positions within clades for most families (Figure 7). Despite encompassing widely recognized species complexes, more speciose families exhibited varied uncertainty values. For instance, the family Craugastoridae (268 species), which includes the genus *Pristimantis* – known for being one of the most challenging genera to identify – showed a mean sd value of 11.10, approximately one-third of the highest value observed for Pipidae (Table 2). Additionally, some families, such as Phyllomedusidae and Dendrobatidae, exhibit a more heterogeneous distribution, suggesting additional complexity in the phylogenetic placement of their species.

Discussion

Although amphibians are relatively well-studied on a global scale, significant knowledge gaps persist in regions with high species richness and limited sampling, such as the Amazonia. In our study, we assessed the extent of these gaps by evaluating taxonomy, distribution, and phylogenetic knowledge of Amazonian anurans. We estimate that approximately 50.22% of the species remain undescribed, and show that species records are spatially clustered around urban centers, large rivers, and easily accessible locations. In addition, our analysis revealed considerable uncertainty regarding the phylogenetic positioning and the availability of genetic data, entangling the understanding of Amazonian biodiversity distribution and its origins and evolutionary history.

The exponential growth in the number of species description publications reported here corresponds with trends observed for amphibians in Brazil (Guerra et al. 2020), South America (Vasconcelos et al. 2019), and globally (Frachea et al. 2024). Two major increases occurred: one in the early 20th century, and the second and largest occurred from the 2000s onwards, with the strengthening of scientific research and the expansion of post-graduation programs in Brazil and other Amazonian countries (CAPES 2024). This expansion enabled greater access to advanced molecular techniques, including integrative taxonomy (Schlick-Steiner et al. 2010). Applying these new methods accelerated the identification of previously undescribed species and revealed cryptic speciation through DNA sequence divergence, a process that traditional taxonomic approaches alone cannot achieve as efficiently (Moraes et al. 2017, Kok et al. 2018, Mônico et al. 2024). In addition to academic training and access to molecular tools, strengthening biodiversity

research in the Amazon also depends on expanding long-term monitoring programs based on permanent sampling sites, consolidating the management of protected areas through science-based actions, and improving biodiversity assessments associated with infrastructure licensing processes (Costa et al. 2015, Bergallo et al. 2023). Such efforts are fundamental not only to accelerate species descriptions but also to refine our understanding of species distributions, which remains one of the major challenges for Amazonian biodiversity.

Despite this recent history of capacity building (e.g., investment increase and training of new taxonomists) and the number of described species, we estimate that, at the current rate and research landscape, it would still take approximately 50 years to describe all Amazonian anuran species. The slow pace at which new species are described may be due to the difficulty in obtaining all necessary information about new species (holotypes, paratypes, and occurrence points) and accurately delineating the distribution area of known species. These challenges are primarily due to limited financial resources aimed at fulfilling specific gaps, logistical problems, and even a shortage of taxonomists (Drew 2011, Löbl et al. 2023). Therefore, there is a need to expand taxonomist training and increase financial investment at steady rates specifically to sample new areas. Knowing and describing species becomes urgent in the current climate change scenario and habitat destruction that directly threatens biodiversity even before it is fully understood (Löbl et al. 2023, Liu et al. 2024). Our results suggest that, despite the current number of universities and research institutes in the Amazonian region, specific policies, establishment of cross-countries research networks and investments are crucial for accelerating taxonomic studies within these institutions.

In addition to the large number of amazonian anuran species yet to be described, the known distribution of species has not been evenly recorded across the biome, with a significant concentration of records and studies around major urban centers, areas near large rivers, and roads. Many species have narrow ranges, often restricted to specific ecoregions or interfluves, while few are considered broadly distributed. Conversely, there are also cases where species initially thought to have narrow distributions, such as *Cruziohyla craspedopus*, were later found to be widely distributed as sampling expanded (Bitar et al. 2015). This highlights the critical role of detectability and sampling effort in shaping our current understanding of species distributions. These findings are consistent with distribution patterns observed in other taxonomic groups such as bats, angiosperms, arthropods, and birds (Oliveira et al. 2016, Santos et al. 2020). This suggests that the

species distribution knowledge is more challenging than the taxonomic deficit (Lees et al. 2020). It depends on refining information for already known species and delineating occurrence areas for undescribed species. Even for well-known and widely distributed species, conducting studies in remote areas can lead to the identification of cryptic species (species complexes) that were originally recognized under a single name (Guerra et al. 2020, Rainha et al. 2021, Frachea et al. 2024), as seen in some species of the genera *Allobates* (Lima et al. 2020), *Pristimantis* (Ortega-Andrade et al. 2015, Mônico et al. 2024), and *Anomaloglossus* (Vacher et al. 2017).

According to our criteria, only 3.26% of the cells and 22.43% of the ecoregions were considered well-sampled, while 43.78% of the cells and 58.78% of the ecoregions were poorly to reasonably sampled. This pattern aligns with recent analyses highlighting persistent invasive sampling gaps across the Amazon, which are driven by a combination of logistical barriers, financial limitations, and spatial biases (Carvalho et al. 2023). In Amazonia, the primary limiting factor for biological studies is low financial investment, which in 2010 was estimated to amount to only US\$ 0.01 per hectare (Magnusson et al. 2013). Expeditions to remote areas are extremely expensive, logistically challenging, and require extensive planning and execution periods (Moraes et al. 2017, Carvalho et al. 2023, FAPESP 2024). Even when expeditions are feasible, the detection of anurans can be difficult depending on the habitat, due to their small size, restricted geographic distribution, and morphological and behavioral traits (Barnett et al. 2023, Guedes et al. 2024). Additionally, it is important to note that, as with any analysis based on presence-only data, the absence of a species in a given cell does not necessarily represent a true absence but may reflect limited detectability or sampling effort. Therefore, the patterns of species richness and distribution described here are likely to capture a combination of biological reality and the spatial heterogeneity of sampling effort across the Amazon. Many species are active only during specific reproductive periods or times of the day and exhibit camouflage strategies that hinder their detection (Rojas 2017). Hence, expeditions to sample remote areas can provide previously unknown information about local and regional diversity (Metcalf et al. 2020, Moraes et al. 2022). Therefore, coordinated efforts among researchers, funding agencies, and governments are essential to expand knowledge about biodiversity and species distribution in the Amazon.

The Darwinian shortfall adds a further layer of complexity to biodiversity research. We found that only two genes (12S and 16S) are available for more than half of the known species, a similar result previously found by Mayer et al. (2019). The absence of molecular data limits our

understanding of biodiversity in several ways. First, it underestimates the genetic diversity present in populations. Second, it hinders the discovery of cryptic species, which are more appropriately detectable by sampling multiple genes and explicit use of species delimitation approaches (Rodríguez et al. 2017). Lastly, many genetic differences may be missed by simpler methodologies, making it necessary to employ more robust approaches (e.g., multilocus, genomic-level datasets or integrative taxonomy) to avoid species overlapping and establish a more solid foundation for taxonomic classification (Wiens 2007). Given our results on phylogenetic uncertainty, it is likely that the absence or incomplete sampling of genes is responsible for the inconsistent positioning of some taxa in the phylogeny. The lack of molecular data, combined with issues like misidentification, convergent traits, sequencing errors, and limited analytical methods, makes it harder to determine the correct position of species in the phylogeny (Wiens 2007, Rangel et al. 2015, Som 2015, Coates et al. 2018, Rancilhac et al. 2024). Our results show that the absence of molecular data occurs for more than half of the estimated species, even considering the most common genes, and such absences may reflect low confidence in the phylogenetic position of many Amazonian species. Maintaining the Darwinian shortfall directly impacts the conservation and management of species and their environments. Undetected species may lack the necessary protection, and genetically distinct populations could be mismanaged as a single group, raising their extinction risks (Coates et al. 2018). This gap will only be minimized with significant efforts and investments to collect as much molecular data as possible and to use approaches that account for the complexity of the biology of this group.

In summary, the combined knowledge gaps we identified across taxonomy, distribution, and molecular data reveal critical biodiversity blind spots for Amazonian anurans — regions, taxonomic groups, and gene datasets that remain underrepresented and require targeted research efforts. Notably, ecoregions such as Gurupa Várzea and Cordillera Central Páramo, families like Pipidae or Telmatobiidae, and nuclear genes and genomic datasets exemplify these blind spots and should be prioritized in future studies to guide conservation and fill persistent shortfalls.

Conclusion

Our study consolidated multiple data sources to assess the current knowledge deficits and highlight future research priorities about Amazonian anurans. Our key findings reveal that many regions within the biome are significantly under-sampled, the number of documented species is

low relative to the estimated species richness of the area, and the lack of genetic information, along with other knowledge gaps, could have direct consequences for the conservation of both the biome and its species. Based on these results, we recommend further research on Amazonian amphibians focused on expanding sampling efforts in underexplored regions, implementing integrative taxonomic approaches to identify cryptic species, and prioritizing genetic studies to address molecular knowledge gaps. Additionally, the identification of conservation priority areas and the establishment of long-term monitoring programs are essential for mitigating threats to the biome and its amphibian diversity.

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Figure 1. A) Historical trend in the number of publications of Amazonian anurans from 1700 to 2021. This graph illustrates a steady increase in research output, with notable peaks in recent decades. B) Temporal trends of the Linnean shortfalls for Amazonian anurans, with the cumulative number of species described (black line) following IUCN shapefiles, number of articles studying anurans from Amazonia (red line), and cumulative number of articles describing Amazonian anurans (green line). See text for methodology details.

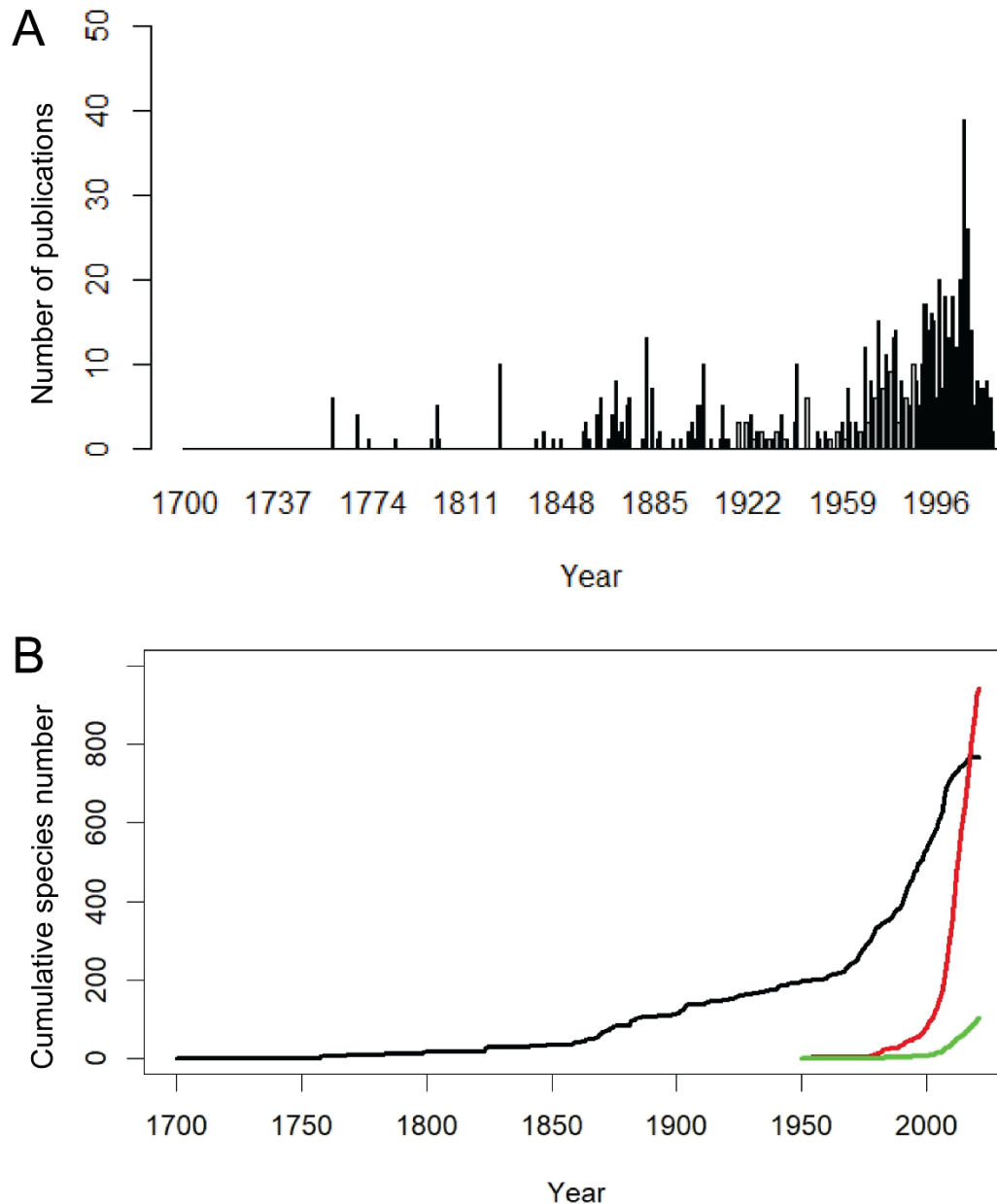


Figure 2. Richness estimation of Amazonian anurans using six different values of sampling effort, lower effort corresponds to $r = 0.05$ (red line) and higher effort to $r = 0.5$ (yellow line).

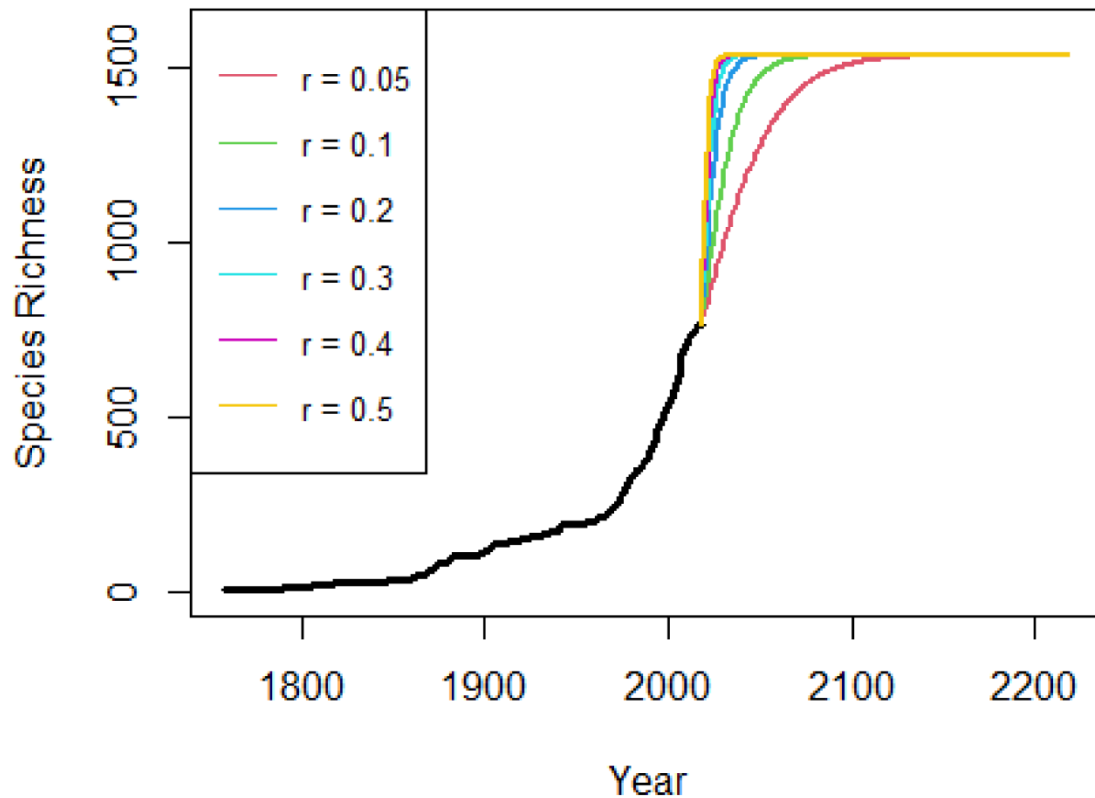
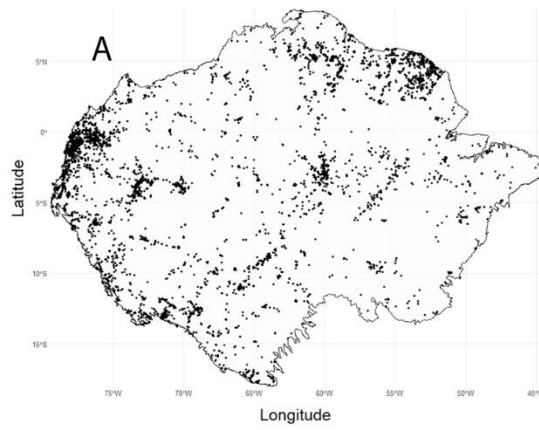
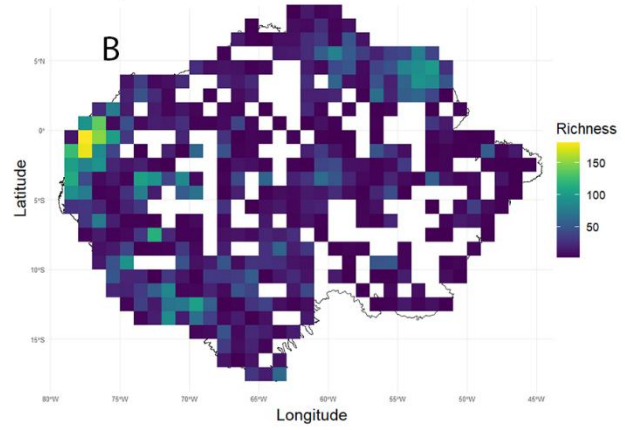


Figure 3. A) Geographic distribution of unique anuran species occurrences in the Amazon. Black dots represent occurrence locations, with a higher density of records in the northern and western regions. B) Anuran species richness distribution in the Amazon. The map shows species richness by grid cells, with colors ranging from blue to yellow, indicating increasing richness (scale on the right). Higher species concentrations are found in the western Amazon, while central and eastern areas show lower richness or lack of data. C) Inventory completeness distribution in the Amazon. The map highlights the accumulation species curves (SACs) by grid cells, with blue to yellow colors indicating an increasing need for inventories in yellow areas (scale on the right). Poorly sampled cells are scattered throughout the Amazon, while well-sampled cells are mainly in the northern and western regions.

Unique occurrences distribution



Species richness distribution



Inventory deficit

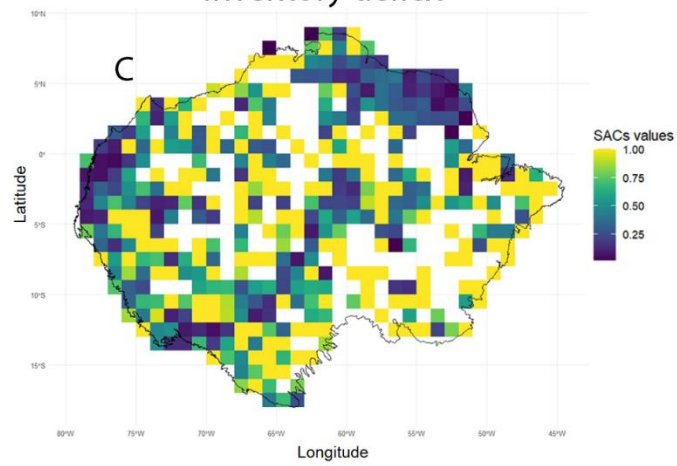


Figure 4. The ten most common species registered. A – *Rhinella marina*, B – *Rhinella margaritifera*, C – *Scinax ruber*, D – *Osteocephalus taurinus*, E – *Boana boans*, F – *Boana lanciformis*, G – *Allobates femoralis*, H – *Trachycephalus typhonius*, I – *Adenenomera andreae*, J – *Leptodactylus pentadactylus*. Picture credits: A/B/C/D/H/J – Lywouty Nascimento; E/I – Lucas Rosado; F – Jordana Guimarães; G – Igor Yuri Fernandes.

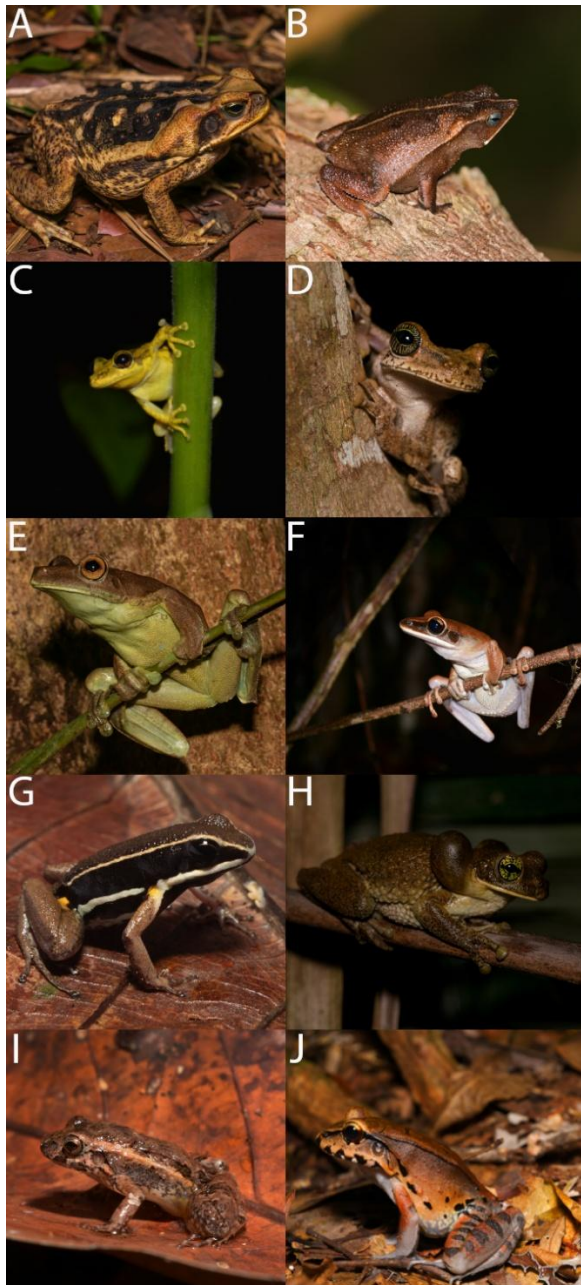


Figure 5. A) Species richness distribution per ecoregion based on the occurrence data. The letters correspond to an ecoregion. A - Eastern Cordillera Real Montane Forests, B - Southwestern Amazonia Moist Forests, C - Gurupa Várzea, and D – Cordillera Central Páramo. B) Inventory Deficit in Amazonian Ecoregions. The map displays the standardized inventory completeness (SAC) values across Amazonian ecoregions, representing sampling coverage. SAC values are shown with a color gradient from purple to yellow, where lighter tones (yellow) indicate lower completeness (higher inventory deficit) and thus a greater need for additional inventories, while darker tones (purple) represent better-sampled areas. The letters indicate the two most and last rich ecoregions: A - Guianan Lowland Moist Forests, B - Napo Moist Forest, C - Gurupa Várzea and D - Cordillera Central Páramo.

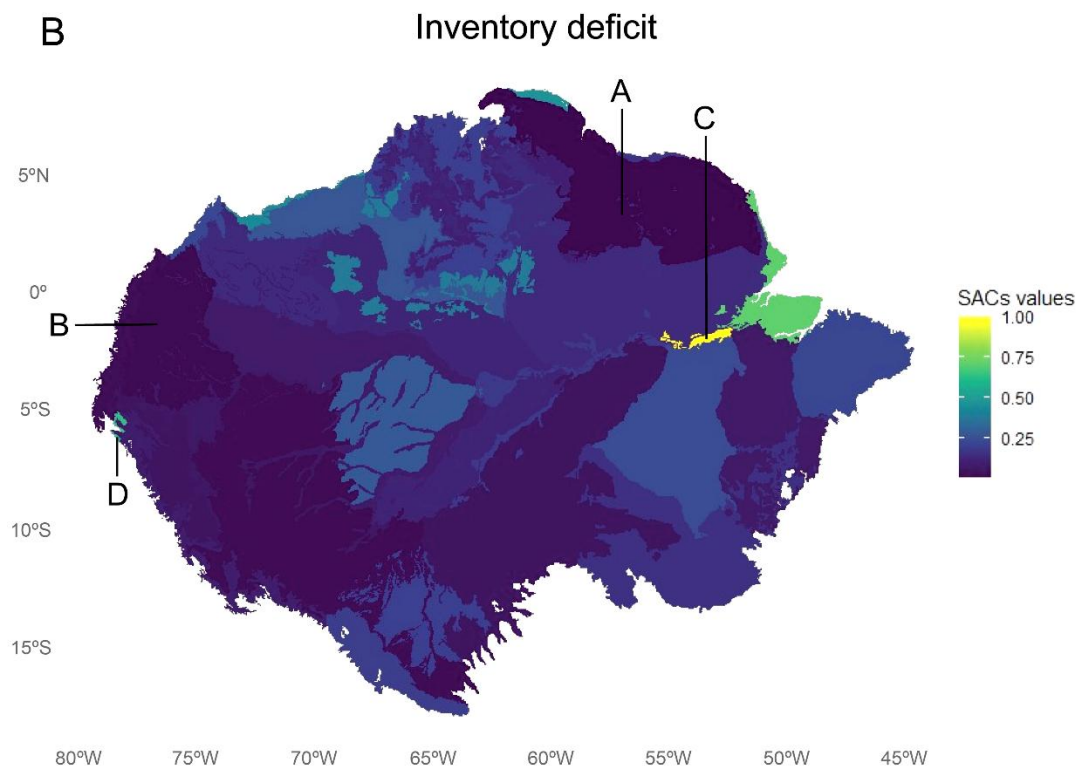
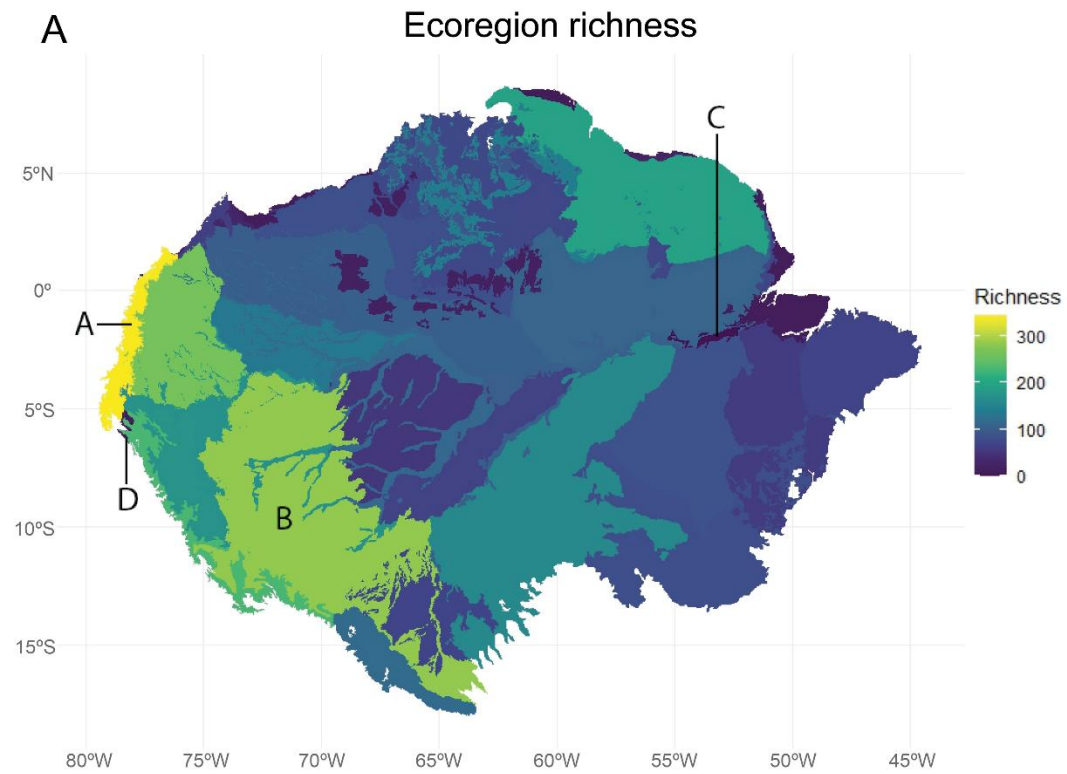


Figure 6. Bar chart showing the number of species for available sequences of mitochondrial and nuclear genes. The bars are ordered in descending order, with 'Estimated' and 'Known' (for species) at the top, followed by genes such as X16S, X12S, RAG1, cytb, among others.

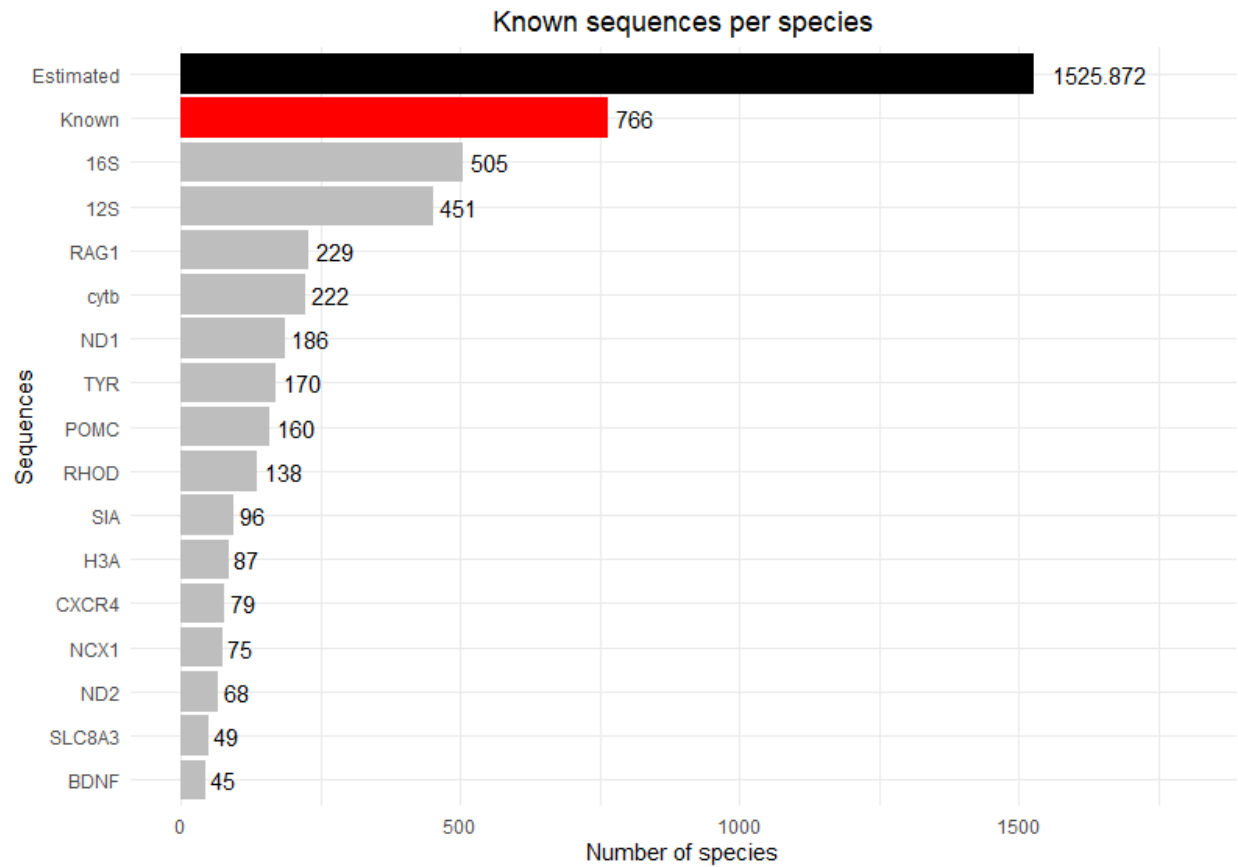


Figure 7. Phylogenetic trees show the variation in phylogenetic uncertainty among anuran species in the Amazon. The outer ring represents the mean standard deviation (SD) values of phylogenetic uncertainty for each species, with colors ranging from yellow (lower uncertainty) to dark purple (higher uncertainty). Families are labeled around the perimeter of the tree.

Phylogenetic uncertainty of anuran species

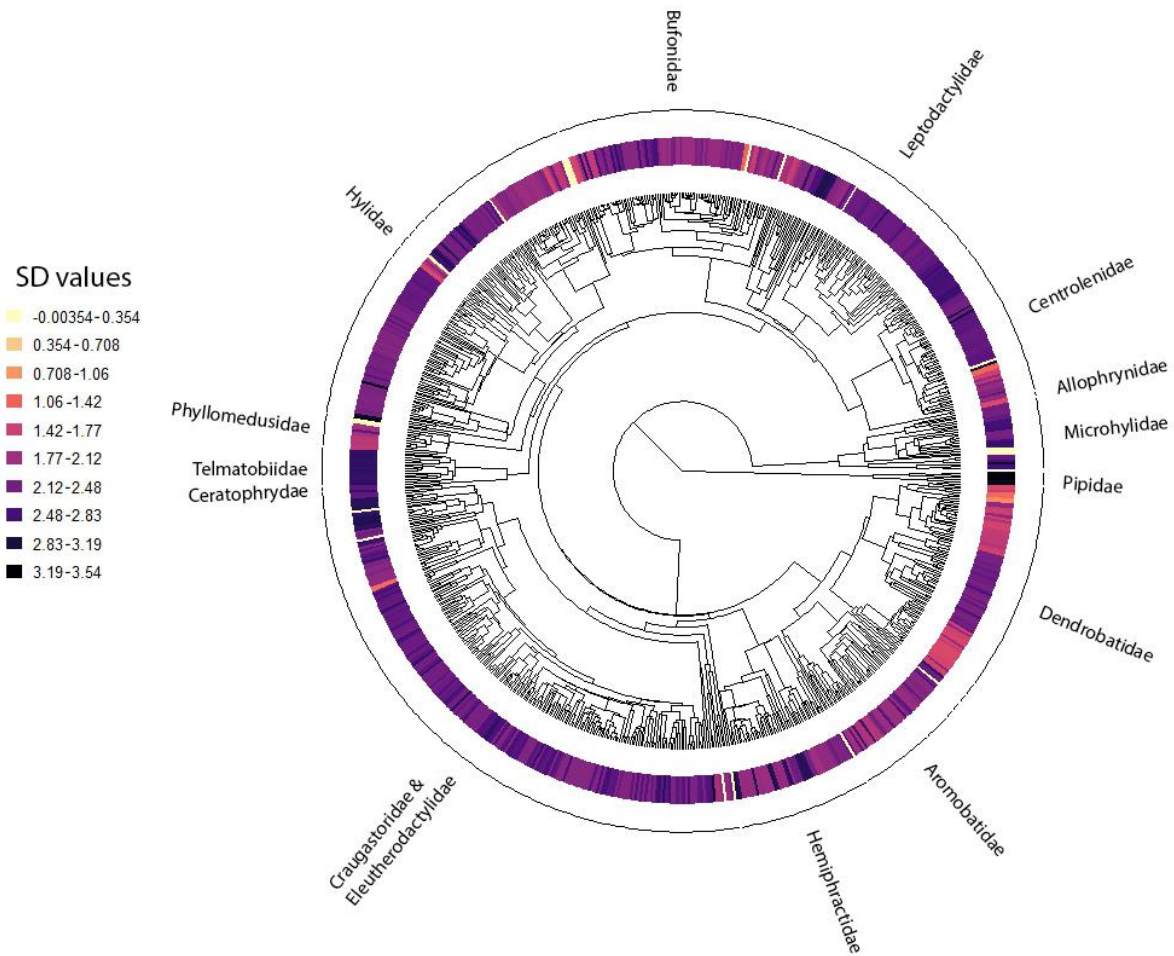


Table 1. The top ten most common species registered in our data and their respective record amounts.

Species name	Family	Occurrence records
<i>Rhinella marina</i>	Bufonidae	1322
<i>Rhinella margaritifera</i>	Bufonidae	1305
<i>Scinax ruber</i>	Hylidae	956
<i>Osteocephalus taurinus</i>	Hylidae	648
<i>Boana boans</i>	Hylidae	461
<i>Boana lanciformis</i>	Hylidae	409
<i>Allobates femoralis</i>	Aromobatidae	390
<i>Trachycephalus typhonius</i>	Hylidae	383
<i>Adenomera andreae</i>	Leptodactylidae	376
<i>Leptodactylus pentadactylus</i>	Leptodactylidae	363

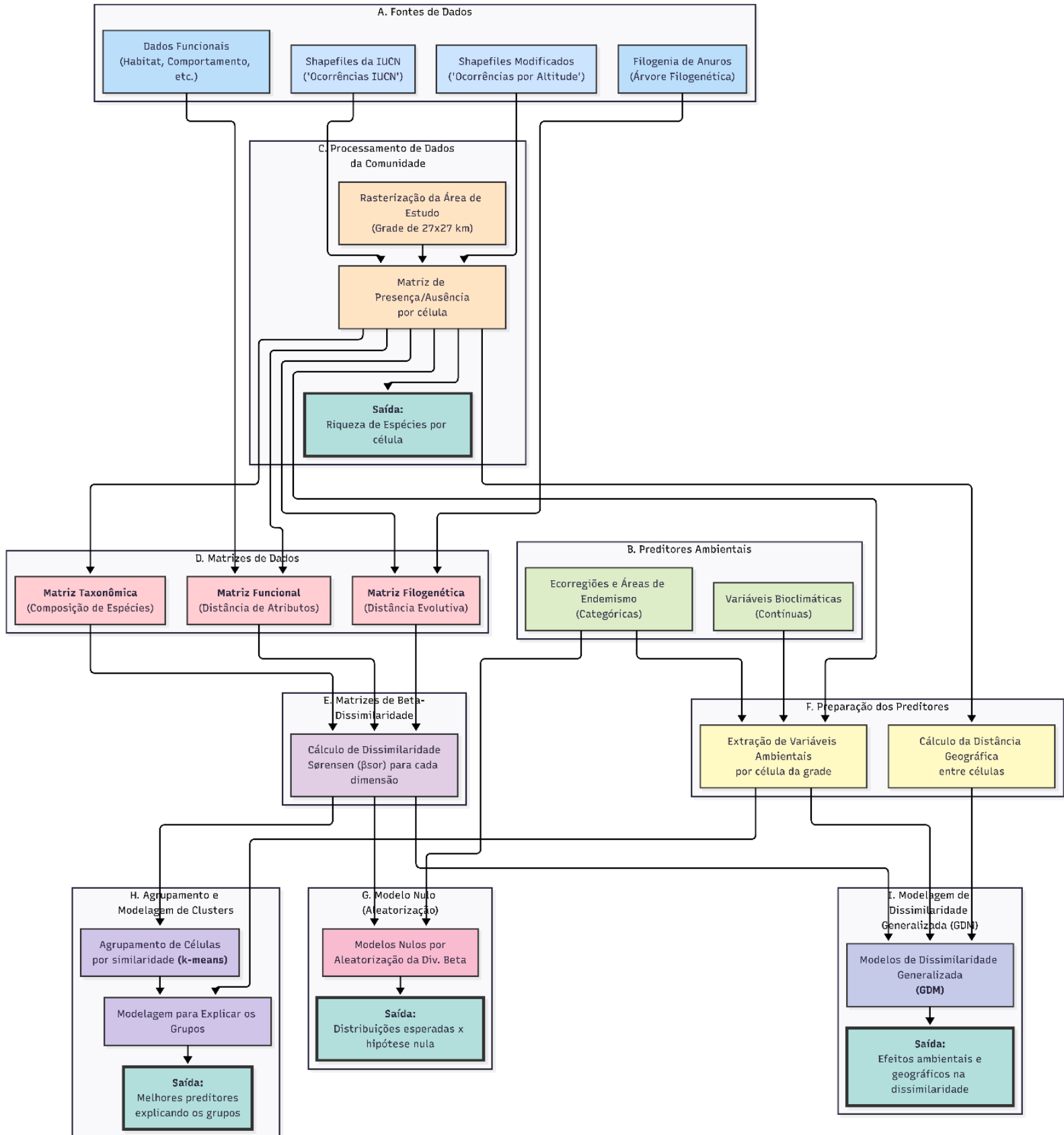
Table 2. Summary of species richness and phylogenetic uncertainty (SD) across anuran families. The table lists the number of species and the mean standard deviation (SD) of phylogenetic uncertainty for each family included in the study. Families with fewer species, such as Pipidae (5 species), exhibited the highest SD values (28.92). Conversely, families with many species, such as Craugastoridae (268 species), showed moderate uncertainty (mean SD = 11.10). The family with the lowest phylogenetic uncertainty was Allophrynidae (2 species, mean SD = 3.17).

Family	Species number	SD
Pipidae	5	28.91805
Telmatobiidae	16	17.18807
Ceratophryidae	2	11.6809
Microhylidae	36	11.19286
Craugastoridae	268	11.103
Centrolenidae	59	10.76937
Leptodactylidae	86	10.4335
Hemiphractidae	54	10.13657
Hylidae	213	9.13767
Aromobatidae	59	8.020893
Bufonidae	100	7.95004
Dendrobatidae	91	6.434303
Eleutherodactylidae	8	5.947633
Phyllomedusidae	23	4.768688
Allophrynidae	2	3.167011

Capítulo 2

Brena da Silva GONÇALVES, Caterina PENONE, Josué A. R. AZEVEDO, Gabriel C. COSTA & Fernanda P. WERNECK. Historical and environmental gradients have a combined but hierarchical role on structuring components of Amazonia anurans beta-diversity. Submetido à revista *Global Ecology and Biogeography*.

Resumo Visual. Estrutura analítica da diversidade beta. (A–C) Integração de mapas refinados, atributos funcionais e filogenia. (D–E) Cálculo do *turnover* taxonômico, funcional e filogenético. (F–I) Análises estatísticas via Modelos Nulos, Agrupamento (beta-regiões) e GDM (determinantes hierárquicos).



Historical and environmental gradients have a combined but hierarchical role on structuring components of Amazonia anurans beta-diversity

Short running title: Amazon Anuran β -diversity Drivers

Structured abstract

Aim. Beta-diversity measures variation in species composition between areas and is expected to reflect both environmental heterogeneity and historical barriers. In the Amazon, these factors jointly shape community structure. This study investigates the drivers of taxonomic, phylogenetic, and functional beta-diversity in Amazonian anurans, testing the relative importance of historical barriers, environmental filters, and geographic distance.

Location. Amazon Basin.

Time period. Contemporary.

Taxon. Anura (frogs and toads).

Methods. We used two distribution datasets: the original IUCN polygons (“IUCN occurrence”) and altitude-refined versions (“altitude occurrence”). We calculated turnover-based dissimilarity matrices for all three diversity facets and applied a hierarchical analytical framework: (1) K-means clustering to delineate major beta-regions; (2) Generalized Dissimilarity Modelling (GDM) to quantify the influence of climatic gradients and geographic distance on turnover; and (3) a formal hypothesis test comparing observed turnover to null expectations across site pairs classified by Area of Endemism (historical proxy) and Ecoregion (environmental proxy).

Results. We found a clear hierarchical structure in the drivers of anuran beta-diversity. The hypothesis test showed that historical and evolutionary processes associated with Areas of Endemism were the dominant force structuring communities, with a stronger effect than environmental filters (Ecoregions). This pattern held for taxonomic, phylogenetic, and functional turnover, suggesting strong niche conservatism. At the gradient scale, GDM revealed climate—particularly the Mean Temperature of the Wettest Quarter (BIO8)—as the main predictor of turnover, while geographic distance contributed negligibly.

Main conclusions. The biogeography of Amazonian anurans is primarily shaped by historical legacy (AoEs), with contemporary climatic gradients providing a secondary filtering effect. These results indicate that anuran communities are highly sensitive to climate and that their biogeographical patterns differ from those described for many other taxa. Together, these findings underscore the importance of incorporating both historical context and climatic sensitivity in conservation planning for Amazonian amphibians.

Key-words: Amazon, Anurans, Dissimilarity, Drivers, Macroecology, Metacommunities.

Introduction

The tropics are globally recognized for harboring the highest levels of species richness on Earth. Among them, the Amazonia stands out as the largest tropical forest and contains roughly 10% of all known biodiversity (Antonelli et al., 2018). Covering about 40% of South America, the Amazon biome is vast and heterogeneous, with marked physical, environmental, and geological gradients that give rise to a wide variety of ecosystems, including upland forests, savannas, montane areas, and seasonally flooded habitats (Darela-Filho et al., 2024; Vergara et al., 2022). This environmental diversity supports the greatest species richness of plants, birds, freshwater fishes, insects, and anuran amphibians (Antonelli et al., 2018; Guayasamin et al., 2024; Vergara et al., 2022).

The distribution of Amazonian species was shaped by an interplay of historical, environmental, and spatial processes that operate across evolutionary and ecological timescales (Guayasamin et al., 2024). The first is the historical-biogeographical legacy. Events such as the uplift of the Andes (Hoorn et al., 2010), the formation of lake systems (Pebas System), the change in the drainage system (Guayasamin et al., 2024; Hoorn et al., 2017), and climatic fluctuations (Haffer, 1969; Vanzolini & Williams, 1981) created opportunities for speciation. The formation of large rivers, specifically, is recognized as a powerful vicariance barrier for many groups (Cracraft, 1985; Haffer, 1969; Ribas et al., 2012). Resulting from these processes of isolation and evolution, the Amazonian biota was spatially structured into what we now recognize as 'Areas of Endemism' (AoEs), which represent spatial patterns of regions with unique evolutionary histories (Borges & Da Silva, 2012; Haffer, 1969). The second major driver is contemporary environmental selection. The vast heterogeneity of the basin generates strong climatic gradients (Rodrigues-Filho et al., 2024; Silva et al., 2019), as well as environmental gradients due to the diversity of environmental formations (Dinerstein et al., 2017; Perrigo et al., 2020). These gradients filter species based on their physiological tolerances, a process known as 'Isolation by Environment' (Wang & Bradburd, 2014; Wang & Summers, 2010), for which 'Ecoregions' are frequently used as a proxy (Dinerstein et al., 2017). Finally, species replacement can occur through simple dispersal limitation in space, generating the pattern known as 'Isolation by Distance' (Nekola & White, 1999). It is known that all these processes — historical, environmental, and spatial — can

act concomitantly or sequentially, further driving the extraordinary Amazonian diversity (Graco-Roza et al., 2022).

Understanding how this biodiversity is structured across the landscape requires examining not only alpha diversity (local species richness), but also beta-diversity, which captures how species composition changes from place to place. Beta-diversity provides essential insight into the processes that generate and maintain Amazonian biodiversity and helps reveal how environmental heterogeneity shapes biological communities (Whittaker, 1960). Beta-diversity can be partitioned into two distinct components: nestedness and turnover (Baselga, 2010). Nestedness occurs when the species in a local community are a subset of the species in a richer community (Ulrich & Gotelli, 2007), a pattern that emerges when species loss follows an orderly, non-random process, often driven by selective exclusion or directional colonization (Si et al., 2016). Turnover, on the other hand, is generated by two main sets of processes (Baselga, 2010; Qian et al., 2005). The first is environmental sorting, where species are filtered according to their ecological niche, producing distinct communities across environmental gradients. The second involves spatial and historical constraints, such as limited dispersal and biogeographical barriers that promote divergence and vicariant speciation, leading to species replacement even under similar environmental conditions (Cottenie, 2005; Dambros et al., 2020). Most analyses of beta-diversity assume that species are functionally equivalent and evolutionarily independent (Roa-Fuentes et al., 2019). However, relying solely on taxonomic identity overlooks the multidimensional nature of biodiversity, which also includes evolutionary history and functional traits. Ignoring these additional dimensions can obscure important ecological and evolutionary patterns and limit our understanding of community assembly processes (Díaz & Cabido, 2001; McGill et al., 2015; Roa-Fuentes et al., 2019). To overcome this limitation and gain a mechanistic understanding, it is essential to integrate multiple facets of diversity.

Phylogenetic beta-diversity ($P\beta$) measures the extent of the difference in the evolutionary relationships among communities (Graham & Fine, 2008), revealing whether communities are composed of closely or distantly related lineages. Functional beta-diversity ($F\beta$) quantifies differences in morphological, physiological, and ecological traits among communities (Petchey & Gaston, 2006), indicating variation in their ecological strategies and roles (Devictor et al., 2010). Although taxonomic, phylogenetic, and functional beta-diversity are often correlated, the patterns

of these diversity facets can be decoupled and reflect distinct ecological and evolutionary processes (Bender et al., 2017; Carvalho et al., 2020; Fluck et al., 2020; Heino & Tolonen, 2017; Li et al., 2021; Long et al., 2025; Mouillot et al., 2013; Prinzing et al., 2008). For example, a high taxonomic turnover may not correspond to a high turnover in ecological attributes or functions, a pattern known as functional redundancy (Casatti et al., 2015; Mouchet et al., 2010). Therefore, understanding how environmental filtering and historical constraints act on each of these facets is a fundamental step to unraveling the mechanisms behind the assembly of Amazonian communities.

Anuran amphibians provide an effective system for evaluating how these historical, environmental, and spatial drivers jointly structure community assembly. As ectothermic animals with permeable skin, they depend directly on environmental temperature and humidity to regulate their internal temperature and control water loss (Akat Çömden et al., 2023; Cao et al., 2024), making them highly sensitive to climatic and environmental gradients (Amado et al., 2019; Anderson & Andrade, 2017). Furthermore, they have low dispersal capacity (Bredeweg et al., 2019), which makes them particularly susceptible to spatial constraints and geographic barriers. Although recent studies have advanced our understanding of anuran biogeography in the Amazon, they reveal an incomplete picture due to conflicting results. Godinho & da Silva (2018) assessed how historical processes affect anuran taxonomic diversity and proposed seven bioregions that do not directly coincide with the classic AoEs. Moraes et al., (2016) tested the effects of flooded environments and rivers as barriers for anuran communities and found that only a small percentage of anurans were restricted by the Tapajós River, indicating that rivers may be permeable barriers for these communities. This differs from the findings of Dias-Terceiro et al., (2015), who identified a barrier effect of the Madeira River and environmental variables on the anuran community structure of the upper Madeira River. Together, these patterns highlight persistent gaps in our understanding of how species respond to historical isolation, environmental filtering, and spatial processes. Furthermore, it remains unclear whether the spatial patterns of taxonomic, phylogenetic, and functional beta-diversity are congruent with one another and align with the classic biogeographic frameworks historically proposed for the Amazon. Finally, the reliability of biogeographic inferences depends heavily on data quality. Macroecological analyses often rely on coarse distribution maps that may include unsuitable habitats — such as high-elevation areas for lowland species — introducing noise that can obscure true spatial patterns. Our study addresses

these gaps by evaluating the relative influence of these drivers within an integrative, multidimensional framework. Thus, we aim to answer the following questions: How are taxonomic, phylogenetic, and functional beta-diversity organized across the Amazon, and do these dimensions show congruence with one another and with historically proposed biogeographic regions? How do distribution data (raw vs. refined) influence the observed patterns? And principally, how do environmental, historical, and spatial processes determine the beta-diversity of Amazonian anurans?

To address this last question, we adapted the framework proposed by Penone et al. (2016) for the Amazon. In this framework, we used Areas of Endemism as proxies for historical and biogeographic barriers and Ecoregions as proxies for contemporary ecological conditions, generating four scenarios for taxonomic, phylogenetic, and functional beta-diversity across grid-cell pairs (Figure 1). First, when grid-cell pairs are in the same area of endemism and in the same ecoregion (Scenario C), we expect low beta-diversity across all facets because communities share similar environments and lack barriers that promote divergence (Fig.1C). Second, when grid-cell pairs share the same area of endemism and are in different ecoregions (Scenario A), we expect low taxonomic and phylogenetic beta-diversity, due to limited historical isolation, but high functional beta-diversity driven by environmental filtering and local adaptation (Fig.1A). Conversely, grid-cell pairs located in different areas of endemism but within the same ecoregion (Scenario D) should exhibit high taxonomic and phylogenetic beta-diversity, reflecting historical divergence, but low functional beta-diversity because similar environments impose comparable functional constraints (Fig.1D). Finally, cells that differ in both areas of endemism and ecoregion (Scenario B), are expected to show high beta-diversity across all facets, arising from the combined effects of historical isolation and environmental differentiation (Fig.1B). These predictions provide a clear framework for evaluating the processes governing the multidimensional structure of Amazonian anuran communities.

Methods

Data compilation

We compiled two presence–absence matrices to represent anuran species distributions across Amazonia. First, we delimited and then rasterized the Amazon region into 1,498 grid cells using the WWF (2019) shapefile and projected all spatial layers in an Albers Equal-Area coordinate system to minimize distortion. Each grid cell corresponds to a spatial resolution of approximately 27.8 km. Species occurrences were then assigned to cells by overlaying IUCN range polygons (IUCN, 2024), producing our baseline dataset, hereafter referred to as the “IUCN matrix.” Because IUCN range maps can overestimate species distributions, especially for taxa with imprecise limits or polygons extending into environmentally unsuitable areas, we generated a second dataset with some modifications on the original maps. In this refined dataset, we removed portions of species ranges falling outside their known elevational limits using updated information from Frost (2023), and AmphibiaWeb Database Search (2023). We refer to this filtered dataset as the “altitude matrix” or “altitude-refined data.” To ensure taxonomic consistency across both matrices, we excluded species absent from the most recent phylogeny (Jetz & Pyron, 2018) and standardized nomenclature following Frost (2023). After removing grid cells containing fewer than five species to minimize sampling artifacts and ensure analytical robustness, both matrices contained distributional data for 966 species.

We assessed evolutionary relationships using a subsample of 100 trees from the most comprehensive anuran phylogeny available (Jetz and Pyron 2018). These subsampling captures uncertainty in both topology and branch lengths, especially for species with imputed genetic placements. Each tree was pruned to retain only the species included in our dataset. For functional trait data, we used the most recent dataset of anuran traits provided by Moura et al., (2024). From this dataset, which integrates measurements from multiple sources and includes imputed values to improve completeness within taxonomic groups, we extracted trait records corresponding to our 966 focal species. We selected four traits representing different aspects of anuran biology and life history: two categorical traits, activity period (e.g., nocturnal, diurnal) and microhabitat (e.g., terrestrial), and two continuous traits, body length and body mass.

Predictor variables

Biogeographical and historical predictors

To test the influence of large-scale biogeographical patterns and historical barriers, we used two sets of categorical variables. First, we used ecoregions as a proxy for broad environmental characterization along gradients. Since ecoregions are explicitly defined by distinct vegetation formations, soil types, and habitat structure (Dinerstein et al., 2017), they effectively capture the environmental heterogeneity and structural complexity of habitats at the basin scale. The Amazon encompasses five bioregions that can be divided into 49 ecoregions (Dinerstein et al., 2017). To simplify interpretation and model complexity, we grouped the 49 ecoregions into 11 broader categories based on their main environmental formations (e.g., Beni savanna and Guianan savanna were grouped as Savanna) (Figure 2A). Second, as a proxy for the spatial patterns generated by historical barriers and evolutionary history, we used 7 recognized areas of endemism in Amazonia. These areas are traditionally recognized for birds in the Amazon lowlands (Cracraft, 1985; Da Silva et al., 2002; Haffer, 1969), with the addition of the Jaú region described by Borges and Da Silva (2012) (Figure 2B).

Climatic predictors

To test the effect of current climate conditions on the turnover patterns, we focused on climatic variables as these constitute the primary physiological filters for ectothermic organisms at macroecological scales (Buckley & Jetz, 2008). We downloaded 19 bioclimatic variables from WorldClim v2 (Fick & Hijmans, 2017), which were processed at our working grid resolution. To reduce multicollinearity among these variables, we applied the Variance Inflation Factor (VIF) procedure and excluded highly correlated predictors (Figure S1). We also removed variables considered uninformative for anuran distributions (Bio18 and 19) (Elith & Leathwick, 2009). The final set comprised six bioclimatic variables: four related to temperature (BIO2 - Mean Diurnal Range, BIO3 - Isothermality, BIO4 - Temperature Seasonality, BIO8 - Mean Temperature of Wettest Quarter) and two related to precipitation (BIO13 - Precipitation of Wettest Month and BIO14 - Precipitation of Driest Month).

Beta-diversity calculation

We assessed beta diversity by calculating the total pairwise dissimilarity between grid cells based on site-by-species presence-absence matrices. We used the Sørensen index (β_{sor}) framework proposed by Baselga (2010), implemented in the betapart R package (Baselga et al.,

2012), to partition this total dissimilarity into its two additive components: turnover (species replacement), measured by the Simpson dissimilarity index (β_{sim}), and nestedness-resultant dissimilarity (β_{sne}). For the subsequent analyses, we focused on the turnover component (β_{sim}), as this metric provides a measure of beta-diversity less dependent on species richness patterns (Baselga, 2012) and can be applied to taxonomic, functional, and phylogenetic dimensions (Weinstein et al., 2014). To ensure comparability between functional and phylogenetic turnover, we adopted a tree-based approach for the functional dimension, building a trait dendrogram that mimics the hierarchical structure of a phylogeny. First, we calculated Gower distances between species using two approaches: one considering all traits combined and another for each trait separately. Since categorical traits can disproportionately influence Gower distances (de Bello et al., 2021), we adjusted their contribution using the *gawdis* R package (De Bello et al., 2020), optimizing the trait weight by evaluating the correlation between the multiple-trait and single-trait Gower distances via Mantel tests. The correlations (Mantel r between 0.48 and 0.54) indicated a balanced contribution of all traits to the overall measure. Second, we used the adjusted Gower distances to generate a trait dendrogram through hierarchical clustering with the *fastcluster* package (Müllner, 2013), following a recent approach for beta-diversity analyses (Xu et al., 2023). To incorporate phylogenetic uncertainty, we calculated the phylogenetic dissimilarity matrix 100 times, once for each of the sampled phylogenies. We then summarized these 100 matrices by taking the cell-wise mean dissimilarity, resulting in a single phylogenetic dissimilarity matrix. Finally, we calculated the both trait and phylogenetic turnover based on the proportion of shared branch lengths between communities using the *phylobeta* function from the *phyloregion* R package (Daru et al., 2020), which is functionally equivalent to the phylogenetic turnover function in *betapart* but performs better with large datasets. To generate response variables for visualization and for the subsequent clustering analysis, we summarized the pairwise dissimilarity matrices. For each grid cell, we calculated the mean dissimilarity against all other cells in the study area. This metric represents the compositional (or phylogenetic/functional) uniqueness of each cell relative to the entire Amazon basin. We also calculated the standard deviation of pairwise dissimilarities for each cell to summarize the variability of beta-diversity values around the mean. We used the software R for all data compilation and analysis (R Core Team, 2024).

Hypothesis test: Testing the influence of biogeographical boundaries

We developed a framework analogous to that proposed by Penone et al., (2016) to test whether community turnover is primarily shaped by historical–biogeographic factors or by contemporary environmental conditions. For this, we employed two spatial classifications: areas of endemism (AoEs) representing the spatial patterns generated by biogeographic and evolutionary history, and ecoregions, representing current ecological and climatic processes. We classified each pair of grid cells into one of four pairwise classes: (A) same AoE, different ecoregion; (B) different AoE, different ecoregion; (C) same AoE, same ecoregion; and (D) different AoE, same ecoregion (Figure 1). For each class, we calculated the observed median turnover for the taxonomic, phylogenetic, and functional dimensions. Statistical significance was assessed by comparing observed medians against null distributions generated from 1000 randomizations of site pairs. We hypothesized that turnover would be significantly lower than the null expectation for pairs within the same classification (Class C) and significantly higher for pairs in both different classifications (Class B). Comparisons between classes A and D allowed us to evaluate the relative influence of historical barriers versus current environmental conditions. Specifically, based on our hypotheses (detailed in the Introduction), we expected that historical barriers (AoEs) would be dominant for taxonomic and phylogenetic turnover (predicting $D > A$), but that environmental filters (Ecoregions) would be dominant for functional turnover (predicting $A > D$).

Community Clustering Analysis / Identification of Beta-diversity Regions

To identify groups of sites with similar community composition, we applied k-means clustering to the site-by-site dissimilarity matrices derived from each facet of beta-diversity (taxonomic, phylogenetic, and functional) and from both datasets (IUCN matrix and altitude-refined matrix). The optimal number of clusters (k) was determined using the NbClust package (Charrad et al., 2012), testing values between 6 and 20 and selecting the best solution according to Krzanowski & Lai (KL) index. Each grid cell was thus assigned to a cluster for each facet, and the resulting classifications were mapped using the ggplot2 package (Wickham, 2016). To evaluate which factors best explained the formation of these compositional clusters, we fitted separate multinomial logistic regression models for each beta-diversity facet using Areas of Endemism, Ecoregions, and the selected bioclimatic variables as predictors using the nnet package (Ripley, 2009). Model selection was performed with the dredge function from the MuMIn package (Bartoń,

2010), testing all combinations of predictors and retaining those with $\Delta AICc < 2$. Relative predictor importance was calculated through model averaging based on Akaike weights.

Drivers of beta-diversity

To model the variation in turnover (taxonomic, phylogenetic, and functional) in response to geographic and environmental predictors, we used Generalized Dissimilarity Modeling (GDM) (Ferrier et al., 2007) implemented in the *gdm* R package (Fitzpatrick et al., 2015). We used the six selected climatic/environmental variables (WorldClim) and the geographic distance between paired cells as predictor variables. The analysis required three steps. First, to optimize the computational cost, we randomly selected a subset of 1000 cells for modeling. Second, we formatted the data using the *formatsitepair* function, which creates a table comprehending the biological dissimilarity, the environmental information for each variable, and the geographic coordinates of all the subset cells. Third, we performed a model selection to include only variables that significantly explain the dissimilarity, and we calculated their relative importance using the *gdm.varImp* function, which uses a backward elimination with 100 permutations. In the end, we adjusted the final GDM model to contain only the selected variables in the previous step for extracting and plotting the splines showing the response of the turnover in relation to each variable.

Results

For both occurrence matrices, the distribution of species richness was heterogeneous, with the highest diversity located in the western and central areas of Amazonia and decreasing towards the east (Figure 3). The west was the richest region, corresponding to the Napo and Inambari endemism areas and to the Moist Forest and Várzea ecoregions. In contrast to the high diversity observed in the west, richness progressively declined toward the ecotones, with the lowest values concentrated in the southeast (Cerrado ecotone) and the northwest (Llanos ecotone). The maximum number of species per cell was 125 (Figure 3A), while in the second matrix it was approximately 100 (Figure 3B). The difference in species richness per cell varies around 20 species between the matrices. The greatest differences in species richness values are spatially concentrated in the western and southwestern regions, but also in the northern part of the Amazon, which

includes the moist forest, savanna, and tepui ecoregions, as well as the Imeri and Guiana areas of endemism (Figure 3C). Conversely, the highest similarity in richness between the matrices was observed in ecotone regions, particularly at the northwestern region (corresponding to Campinarana and Imeri AoE), and in the southeastern region (corresponding to dry and moist forest ecoregions and Belém AoE). Given this overall geographical congruence and the greater biological accuracy of the altitude-refined data, we based all subsequent modeling analyses (clustering, hypothesis testing, and GDM) on the altitude-refined matrix. Detailed results from the IUCN matrix are available in the Supplementary Material.

Beta-diversity patterns

The taxonomic turnover values by cell ranged from 0.20-0.99, with a mean of 0.35 and SD = 0.14 (Table 1). The highest taxonomic turnover values occurred along the western and southwestern edges of Amazonia, especially near the Andes (Figure 4A), indicating that communities in these areas are compositionally distinct. Cells along the western margin showed taxonomic turnover values between 0.5 and 0.8, reflecting that these cells tend to have higher dissimilarity to the rest of the Amazon in pairwise comparisons. Similar high-turnover values were also observed in northern portions of the Guiana region. In contrast, cells located in central Amazonia exhibited lower turnover values (around 0.3), indicating more compositionally homogeneous communities (Figure 4A). Interestingly, turnover variability (SD) was higher in areas with lower taxonomic turnover and lower in areas with high turnover (Figure 4B).

The phylogenetic turnover across Amazonia ranged from 0.10 to 0.75, with a mean of 0.18 and SD = 0.07 (Table 1). Phylogenetic turnover was relatively homogeneous across most of the lowland Amazon (between 0.2 to 0.4), indicating that communities tend to share lineages that are not deeply divergent (Figure 4C). Relative to the taxonomic turnover, the phylogenetic structure of communities is more uniform across the basin. Higher phylogenetic turnover values (0.4-0.7) were concentrated near the Andes, the Guiana highlands (including tepui regions), and some ecotonal areas, where species assemblages include lineages that are more distantly related, resulting in greater phylogenetic heterogeneity (Figure 4C and D).

Functional beta-diversity ranged from 0.07 and 0.50, with a mean of 0.35 and SD = 0.14 (Table 1). Functional turnover exhibited a narrower range than both taxonomic and phylogenetic

turnover, indicating that communities tend to share similar trait compositions across most of Amazonia (Figure 4E). Even in areas with high taxonomic turnover (such as the western and southwestern), functional differences were relatively small, suggesting that distinct species often perform comparable ecological roles. This pattern is consistent with widespread functional redundancy in Amazonian anuran communities, where shifts in species composition do not necessarily translate into large shifts in trait structure (Figure 4E and F).

Hypothesis test: ecoregions and endemism areas

For the altitude-refined dataset, the hypothesis test clearly confirms our initial hypothesis. As expected, pairs of cells located within the same Area of Endemism and the same ecoregion (Class C) showed the lowest taxonomic turnover observed in the entire analysis (median = 0.162), substantially lower than the null expectation (median_null = 0.269, $p < 0.001$; Table 2). In contrast, pairs of cells belonging to different AoEs and different ecoregions (Class B) exhibited markedly higher turnover (median = 0.333), again significantly exceeding the null expectation ($p < 0.001$). Comparisons between the mixed classes further reinforced the stronger role of historical boundaries. Pairs of cells in the same AoE but within different ecoregions (Class A) showed lower turnover than expected by chance (observed = 0.227, null = 0.269, $p < 0.001$), whereas cells in different AoEs but within the same ecoregion (Class D) were only slightly below the null (observed = 0.262, null = 0.269, $p < 0.001$, Figure 6). Crucially, turnover in Class D remained consistently higher than in Class A, confirming that AoEs exert a stronger structuring effect on taxonomic communities than ecoregions (Figure 6A).

For the altitude-refined data, phylogenetic turnover closely followed the expected hierarchy among classes. As predicted, pairs of cells within the same AoE and ecoregion (Class C) exhibited the lowest turnover (observed median = 0.098), significantly below the null expectation (median_null = 0.153, $p = 0$). Cell pairs assigned to completely different AoEs and ecoregions (Class B) showed the opposite pattern, with substantially higher turnover than expected (observed = 0.181; median_null = 0.153, $p = 0$, Table 2). Likewise, turnover for cells located in different ecoregions but within the same AoE (Class A) was significantly lower than expected (observed = 0.128; median null = 0.153, $p = 0$), reinforcing the strong influence of historical boundaries. A notable deviation from the taxonomic results emerged for different AoE but same

ecoregion (Class D): turnover was significantly lower than the null expectation (observed = 0.152; median null = 0.153, $p = 0$). This indicates that when environmental conditions are held constant, AoE boundaries do not increase lineage turnover; instead, communities tend to be slightly more phylogenetically similar than expected by chance. This pattern suggests that shared environmental conditions may homogenize phylogenetic composition despite documented historical barriers (Figure 6B).

For functional dissimilarity, the altitude-refined dataset showed a clear pattern consistent with the structure observed for taxonomic and phylogenetic turnover. As expected, pairs of cells within the same area of endemism and the same ecoregion (Class C) exhibited substantially lower turnover than predicted by the null model (observed median = 0.089, null median = 0.140; Table 2). Conversely, pairs located in entirely different AoEs and ecoregions (Class B) showed markedly higher turnover (observed = 0.162, null = 0.140), confirming the expected contrast between fully congruent versus fully incongruent classifications. The mixed classes revealed the most informative deviations from the initial hypothesis. Functional turnover within the same AoE but across different ecoregions (Class A) was significantly lower than expected (observed = 0.118, null = 0.140), mirroring taxonomic and phylogenetic patterns. In contrast, turnover for cells located in different AoEs but sharing the same ecoregion (Class D) was only slightly lower than the null expectation (observed = 0.139, null = 0.140). Importantly, Class D turnover remained consistently higher than Class A. Together, these results indicate that, for functional traits, the historical structure represented by Areas of Endemism exerts a stronger influence on community similarity than environmental filtering defined by ecoregions, even after refining occurrence data by altitude.

Community clustering

For the altitude-refined dataset, the KL index indicated an optimal solution of 11 bioregions based on taxonomic turnover (Figure 7A). Despite being individually more extensive (e.g., clusters 3 and 5), these beta-regions showed a more fragmented spatial pattern compared to the IUCN-based results (Text S1, Figure S5A). This higher degree of fragmentation reflects the more disjunct distributions that emerge after applying the altitude filters. This pattern was particularly pronounced in the northern Amazon, where many species have altitudinal restricted ranges, involving bioregions 1, 9, 10, and 11 (Figure 7A). This indicates the existence of cells whose

species turnover pattern is drastically different from their immediate surroundings, yet highly similar to that of a geographically distant bioregion.

Clustering analysis of phylogenetic dissimilarity revealed spatial patterns similar to those observed for taxonomic turnover and identified 14 bioregions for the altitude-refined dataset (Figure 7B). These bioregions exhibited more fragmented boundaries than those derived from the IUCN-based data (Text S1, Figure S5B), a pattern consistent with the more disjunct nature of the altitude-filtered species distributions. As with the taxonomic turnover results, this fragmentation was most pronounced in the northern Amazon, where bioregions 1, 6, 9, and 10 formed an intricate mosaic (Figure 7B). This configuration indicates the existence of locations where phylogenetic turnover differs markedly from adjacent cells but resembles that of geographically distant bioregions. Notably, the observed patterns suggest that variation in phylogenetic turnover is driven primarily by differences in the tips and shallow branches of the phylogeny, rather than deeper evolutionary splits.

Using the altitude-filtered dataset, the clustering revealed 13 functional bioregions (Figure 7C). In contrast with the IUCN results, these bioregions were more irregular and spatially fragmented (Text S1, Figure S5C). The most drastic change was the westward expansion of bioregion 5 (equivalent to bioregion 3 in the IUCN results, Figure S5C), which extended from its central core into the western portion of the Amazon. Another major difference was the disjunct distribution of bioregion 12, whose core is located on the western margin but also includes cells in the northern Amazon. This long-distance functional similarity may reflect similar environmental filters operating in nonadjacent areas, selecting for comparable functional attributes despite geographic separation. As in the other facets, fragmentation was again more pronounced in the northern portion, resulting in a complex functional mosaic.

Modeling environmental gradients of turnover

The GDM models explained a substantial portion of turnover in anuran communities (Table 3). For the altitude-refined data, the models accounted for 31.1% of deviance in taxonomic turnover, 25.4% in phylogenetic turnover, and 16.8% in functional turnover. Across all dimensions, climatic variables were consistently the strongest predictors of beta-diversity. Geographic distance, although statistically significant, had a much smaller effect size, contributing

less than 1% of the explained deviance in every model (Table 3), indicating a weak or virtually absent isolation-by-distance pattern. Among climatic variables, Mean Temperature of Wettest Quarter (BIO8) emerged as the dominant predictor, explaining ~45% of the deviance in taxonomic turnover, ~37% in phylogenetic turnover, and ~24% in functional turnover. Other variables of secondary but consistent importance included Mean Diurnal Range (BIO2) and Precipitation of Wettest Month (BIO13). In contrast, Isothermality (BIO3) and Precipitation of Driest Month (BIO14) contributed minimally. These results indicate that steep temperature and precipitation gradients—particularly those associated with the Andean margin—are the primary drivers of anuran beta-diversity across Amazonia, while spatial distance plays only a minor role.

Discussion

By studying the factors that affect beta-diversity in the Amazon, we can begin to understand how such high anuran species diversity is generated and maintained in the region. Our study revealed a clear hierarchical pattern among the drivers of anuran beta-diversity in the Amazon. We demonstrated that: (1) historical biogeographical barriers (represented by Areas of Endemism) were the primary factor in delimiting large bioregions for all diversity components, overriding contemporary environmental conditions (represented by Ecoregions); (2) within these large regions, climatic gradients were the dominant drivers of turnover, while the influence of geographic distance was negligible; and (3) this pattern of historical dominance (Point 1) surprisingly held true not only for species composition and their lineages, but also for their functional attributes.

According to our hypothesis test, turnover for different AoE, same ecoregion (Class D) was consistently higher than for Class A (same AoE, different ecoregion), indicating that historical and evolutionary events were the primary drivers structuring Amazonian anuran beta-diversity. The most notable finding, however, was that historical processes also prevailed over environmental filtering in shaping functional diversity. This contradicts our initial hypothesis that environmental conditions (proxied by ecoregions) would be the dominant driver for this dimension. Instead, our results suggest that the analyzed functional attributes are likely constrained by phylogenetic history. This association among species, traits, and evolutionary history supports

the hypothesis of phylogenetic niche conservatism, where lineages tend to retain their ancestral attributes over time (Wiens et al., 2010; Wiens & Graham, 2005).

At the spatial level, the influence of these historical processes is also manifested in the congruence of our maps. Some of the beta-regions we identified were partially congruent with bioregions and areas of endemism proposed in previous studies. We identified a beta-region located in the Guiana Shield area that was consistently recovered across all analyzed metrics and partially matches the BR2 bioregion from Godinho & da Silva (2018) and the 'Guyanan Center' from Cracraft (1985). Another notable finding is the presence of two taxonomic beta-regions in the central Amazon whose boundary coincides with the Amazon River. This taxonomic pattern, also recovered in the work of Godinho & da Silva (2018), indicates that certain diversity metrics can be influenced by specific Amazonian rivers, acting as barriers. However, other studies have also highlighted that rivers may act as barriers depending on their characteristics and are not always barriers for all groups (Moraes et al., 2016; Santorelli et al., 2018), nor, in this case, for all diversity metrics. Our results also reveal regionalization patterns specific to anurans, which diverge significantly from the classic schemes based on birds (Cracraft, 1985; Haffer, 1969). These incongruencies are not surprising and reinforce that different taxonomic groups (e.g., birds vs. anurans), with their distinct dispersal capabilities and environmental sensitivities, have experienced unique biogeographical histories. Recent broad-scale assessments of Amazonian herpetofauna corroborate this distinctiveness, highlighting unique patterns of endemism and turnover driven by habitat heterogeneity across the basin (López-Rojas et al., 2025). Although delineation methods influence the results and may not apply to all taxa (Godinho & da Silva, 2018), our beta-regions, based on explicit turnover metrics, offer a novel biogeographical map fundamental for understanding the distribution and diversity of this group in Amazonia. Therefore, our work not only validates the importance of historical barriers for anurans but also provides a map of phylogenetic and functional bioregions for the group, demonstrating that this historical background restricts not only *which* species occur but also their ecological role.

Although historical barriers are the primary drivers of anuran beta-regions, the GDM analysis allowed us to quantify the relative importance of environmental gradients and geographic distance in structuring this diversity. Our models revealed two central findings. First, climatic gradients (temperature and precipitation) were the most important predictors of species turnover

for all diversity facets, particularly the Mean Temperature of Wettest Quarter (BIO8), followed by Mean Diurnal Range (BIO2), Temperature Seasonality (BIO4), and Precipitation of Wettest Month (BIO13). Second, in remarkable contrast to what is expected for many taxa at the Amazonian scale, geographic distance had a negligible contribution in all models. This result implies that species turnover is primarily driven by niche-based processes (environmental filtering) rather than neutral processes (dispersal limitation). In other words, climatic similarity predicts community composition better than spatial proximity. The strong positive influence of BIO8 is likely directly related to the physiology and reproductive cycle of Amazonian anurans. Because anurans are ectotherms, temperature and humidity are primary environmental filters for their persistence and activity. Ambient temperature affects organismal performance in acquiring energy, resources and interacting with other organisms, and can generate physiological stress if it exceeds thermal tolerances (Bennett, 1990; Buckley & Jetz, 2008). Furthermore, extreme temperatures negatively affect the availability of microclimates (Scheffers et al. 2014) and aquatic environments for reproduction (McMenamin et al., 2008). Simultaneously, environmental humidity is essential for thermoregulation and water balance, as anuran skin is highly permeable. Therefore, the interplay between temperature and humidity determines the availability of microhabitats for spawning (Haddad & Prado, 2005; Nunes-de-Almeida et al., 2021), restricts anuran mobility, and acts as a key limiting factor for species coexistence (Buckley & Jetz, 2008).

What becomes particularly notable is that while these climatic filters showed strong explanatory power, the influence of geographic distance was negligible, even for taxonomic turnover. Generally, it is expected for most biological communities, with increasing geographic and environmental distance, the similarity of these communities decreases (in this case, dissimilarity increases) (Nekola & White 1999). This pattern arises because dispersal limitations (Hubbell, 2001) and species-specific responses to the spatial structure of the environment (Cottenie, 2005) mean that increasing distance increases the probability of encountering barriers, hindering species occurrence along the gradient (Graco-Roza et al., 2022). This is especially true for anurans, which have physiological constraints and low dispersal capacity (Akat Çöm den et al., 2023; Smith & Green, 2005), and for which previous studies have found a significant effect of distance on anuran community similarity (Dalmolin et al., 2019; Neves et al., 2018; F. Silva et al., 2014). Our results also differed from those found for bats, shrews, and rodents (Monadjem et al., 2023) and for a wide range of animal and plant taxa (Dambros et al., 2020), but were consistent

with findings for diatoms, bryophytes, and macroinvertebrates (Astorga et al., 2012), and Amazonian lizards, which are also structured by the hierarchy of historical and environmental factors (Marques Peixoto et al., 2020). A plausible explanation for this near-absence of an isolation-by-distance signal is the strong geographic asymmetry in anuran turnover across Amazonia. Turnover is extremely high along the Andean margin but remains consistently low across most of the lowland Amazon basin. In this spatial configuration, short-distance comparisons near the Andes already encompass steep environmental gradients, driving high dissimilarity, while long-distance comparisons within the basin occur across relatively homogeneous environments. Consequently, the climatic signal overwhelms any gradual decay expected with distance, reinforcing the interpretation that anuran turnover is driven predominantly by Isolation by Environment (IBE) rather than Isolation by Distance (IBD) (Wang & Bradburd, 2014).

Another finding from our study was the decoupling of the diversity facets, where the magnitude of functional turnover was consistently lower than that of taxonomic turnover. It is known that high taxonomic diversity does not always reflect high functional or phylogenetic diversity (Devictor et al., 2010; Erdős et al., 2023; Wong et al., 2018). However, given the high diversity of environments and microhabitats in the Amazon, we hypothesized the opposite: that transitions between ecoregions would drive high functional turnover. Community assembly theory suggests that, at regional scales, strong environmental filters should promote niche differentiation among species to allow for coexistence (Cornwell et al., 2006; Diaz et al., 1998; Macarthur & Levins, 1967). However, our findings did not match this expectation. Contradicting this expectation, our findings revealed widespread functional redundancy. The low functional turnover, present even in areas with very high taxonomic turnover (e.g., the Andes region on the western edge), strongly suggests high functional redundancy in Amazonian anuran communities. This indicates that, although species identity changes drastically across space, the ecological attributes and functions they perform are conserved, with different species performing similar roles in the environment (Casatti et al., 2015; Mouchet et al., 2010). This suggests that while climatic gradients and barriers drive species replacement, the broad structural similarities of Amazonian habitats impose uniform selective pressures across the basin. Consequently, distinct species have evolved—or retained—convergent functional strategies to exploit these resources, leading to a saturation of functional space even where taxonomic turnover is high.

A methodological contribution of our work was demonstrating how the refinement of distribution data impacts the perception of biogeographical patterns. It is well-known that range maps, such as those from the IUCN, are recurrently criticized for overestimating species' areas of occurrence (Hughes et al., 2021; Hurlbert & Jetz, 2007; Rondinini et al., 2006; Sorte & Hawkins, 2007). However, they often remain the only standardized data source for large-scale analyses, especially in regions with significant sampling gaps (Ficetola et al., 2014), and filtering these maps with empirical data can make them much more realistic (Hughes et al. 2021). Our analysis with altitude-filtered data consistently revealed greater fragmentation of the beta-regions across all diversity metrics. This was particularly evident in the phylogenetic hypothesis test: where the raw IUCN data failed to detect a clear signal for Class D, the refined data revealed a statistically significant pattern. This suggests that the use of raw distribution maps can mask local heterogeneity and the realized distribution of species, thereby obscuring real biogeographical signals. Therefore, the addition of ecological filters, such as altitude and occurrence points, is a crucial step in making macroecological analyses more realistic, especially for organisms with low dispersal capacity, such as anurans.

In summary, our study provides a multifaceted framework for the drivers of anuran beta-diversity in the Amazon. We demonstrate that community structure is the result of processes acting at different scales: at a broad biogeographical scale, the historical legacy (Areas of Endemism) proved to be the main factor in delimiting the large beta-regions (outweighing the environmental proxy of Ecoregions); whereas at a continuous gradient scale, contemporary climatic factors act as the primary ecological filters, supplanting the effect of simple geographic distance. These results have direct and urgent implications for the conservation of Amazonian biodiversity. The fact that the beta-regions we delimited for anurans diverge significantly from the classic endemism schemes (based on birds) suggests that conservation strategies for the Amazon need to be taxon-specific, integrating different facets of diversity. Therefore, large-scale conservation planning would be more effective if it incorporated these different data sources, which are specific to amphibians and reflect their unique biogeographical patterns. Furthermore, the strong dominance of climatic factors (such as BIO8) in explaining turnover reveals a critical vulnerability. Our findings suggest that anuran communities, being physiologically sensitive, are intrinsically linked to current climatic gradients and, therefore, are particularly vulnerable to the impacts of climate change, making the protection of climatic refugia a priority. Finally, our work demonstrates the importance

of refining distribution data to reveal real biogeographical signals. Future studies, integrating genomic data to explicitly test vicariance processes and more detailed trait data, will be essential to deepen our understanding of how this extraordinary diversity evolved and how we can protect it.

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Table 1. **Minimum, maximum, mean, and standard deviation of taxonomic, phylogenetic, and functional beta diversity values across the Amazon from altitude-refined data.** Turnover values were derived from cell-level pairwise dissimilarities and summarize the overall magnitude and variability of each beta diversity dimension.

Beta-diversity components (Altitude)				
	min	max	mean	sd
Taxonomic turnover	0.207013	0.999747	0.325821	0.145734
Phylogenetic turnover	0.107385	0.750895	0.183648	0.077899
Functional turnover	0.073048	0.506845	0.155256	0.049712

Table 2. **Results of the hypothesis test evaluating the effects of Areas of Endemism (AoEs) and ecoregions on taxonomic, phylogenetic, and functional turnover for the altitude-refined dataset.** Classes represent combinations of AoE and ecoregion membership: A = same AoE, different ecoregion; B = different AoE, different ecoregion; C = same AoE, same ecoregion; D = different AoE, same ecoregion. For each class, the table reports the observed median turnover, the expected median under the null model, the number of cell pairs, and the direction of deviation relative to the null (“low” = lower than expected; “high” = higher than expected). Statistical significance is indicated by *p*-values obtained from 1,000 randomizations.

Class	Median null	Median observed	Pair number	P value	Diff type
Taxonomic turnover					
A	0.268657	0.227273	1813943	0	low
B	0.268657	0.333333	11412884	0	high
C	0.268657	0.162162	3708663	0	low
D	0.268657	0.261538	19654245	0	low
Phylogenetic turnover					
A	0.15338	0.127975	1813943	0	low
B	0.153386	0.181296	11412884	0	high
C	0.15338	0.09803	3708663	0	low
D	0.153381	0.151608	19654245	0	low
Functional turnover					
A	0.139709	0.118048	1813943	0	low
B	0.13971	0.162145	11412884	0	high
C	0.139721	0.088962	3708663	0	low
D	0.139723	0.139093	19654245	0	low

Table 3. **Deviance explained by the Generalized Dissimilarity Models (GDM) for the altitude-refined dataset across the taxonomic, phylogenetic, and functional dimensions of beta-diversity.** Values represent the percentage contribution of each predictor to the total deviance explained by the model. Asterisks indicate levels of statistical significance ($p < 0.1$; $p < 0.05$; $p < 0.01$); higher numbers of asterisks denote stronger significance.

Dimension	Explained variance	Geographic distance	bio_2	bio_3	bio_4	bio_8	bio_13	bio_14
Taxonomic	31.1%	0.4***	4.3***	—	9.4***	45.1***	3.7***	—
Phylogenetic	25.4%	0.6***	2.3***	0.5	5.5***	37.4***	5.8***	—
Functional	16.8%	0.4***	8.4***	—	7.4***	24.3***	9.3***	—

Figure 1. **Schematic of the four hypothesized scenarios for anuran beta diversity in the Amazon.** The diagram illustrates the predictions for taxonomic ($T\beta$), phylogenetic ($P\beta$), and functional ($F\beta$) turnover based on the combination of historical barriers (represented by Areas of Endemism - AoEs) and environmental filters (represented by Ecoregions). Ecoregion classifications are based on Dinerstein et al. (2017), while Areas of Endemism (AoEs) follow the delimitations by Haffer (1974, 1978), Cracraft (1985), Silva et al. (2002), and Borges & Silva (2012). Visual Key: The representation of boundaries varies to highlight the comparison in each scenario. In (A), the black outline represents a single Area of Endemism, containing different Ecoregions (colored areas). In (B), (C), and (D), the background/black outlines represent Ecoregions, while the colored shapes indicate Areas of Endemism. The 'X' markers denote the pair of sites compared in each case. (C) The baseline scenario (Same AoE, Same Ecoregion) represents high similarity, with low expected turnover for all facets. (A) In the scenario with a shared history but distinct environments (Same AoE, Different Ecoregions), we expect low $T\beta$ and $P\beta$ turnover (due to shared history), but high $F\beta$ turnover (due to local adaptation and environmental filtering). (D) Conversely, in similar environments but with separate evolutionary histories (Different AoEs, Same Ecoregion), we expect high $T\beta$ and $P\beta$ turnover (due to historical isolation/vicariance), but low $F\beta$ turnover (due to functional convergence). (B) Finally, in the total isolation scenario (Different AoEs, Different Ecoregions), we expect high turnover for all three facets, due to the combined effects of the historical and environmental drivers.

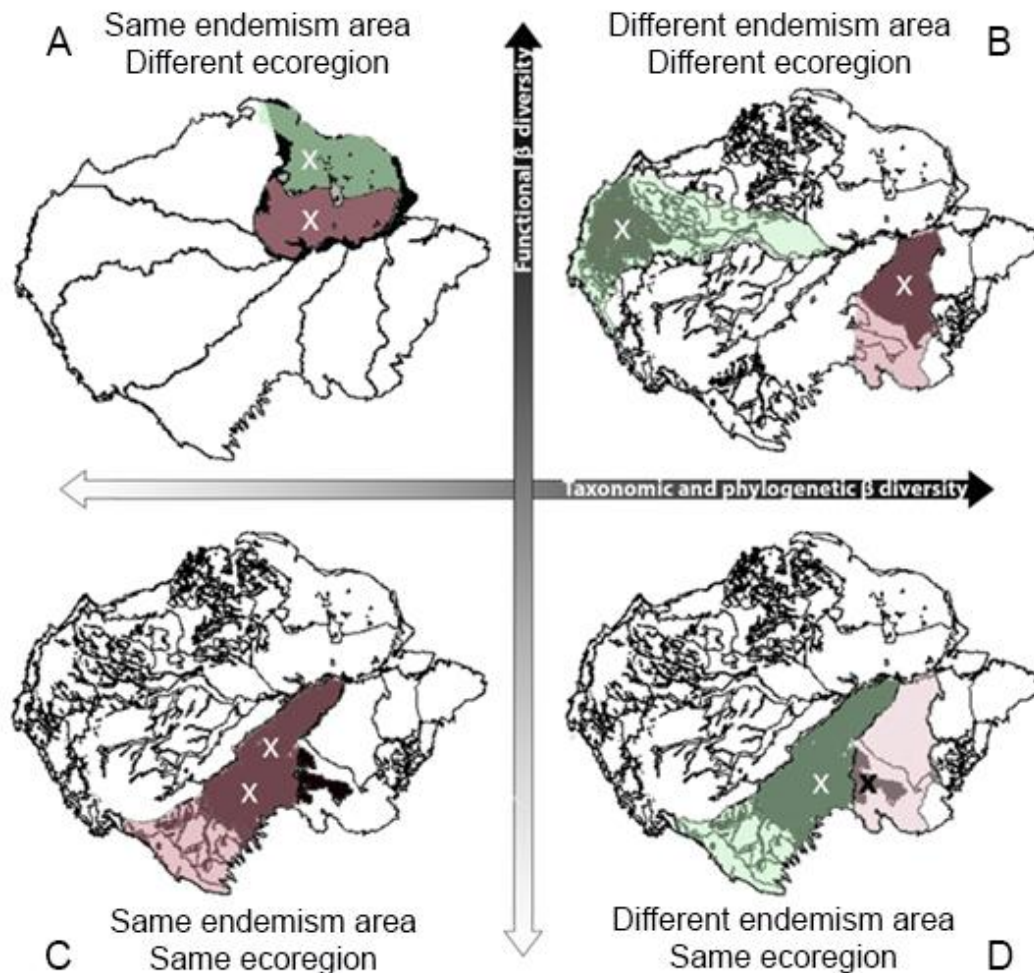


Figure 2. **Maps of the categorical predictors used as proxies for environmental and historical drivers.** (A) The 11 broad ecoregion categories, grouped from Dinerstein et al. (2017) and used as a proxy for environmental characterization. (B) The 7 recognized Areas of Endemism (AoEs) in the Amazon lowlands, used as a proxy for evolutionary history and biogeographical patterns of endemism (based on Haffer 1974; Cracraft 1985; Borges and Silva 2012).

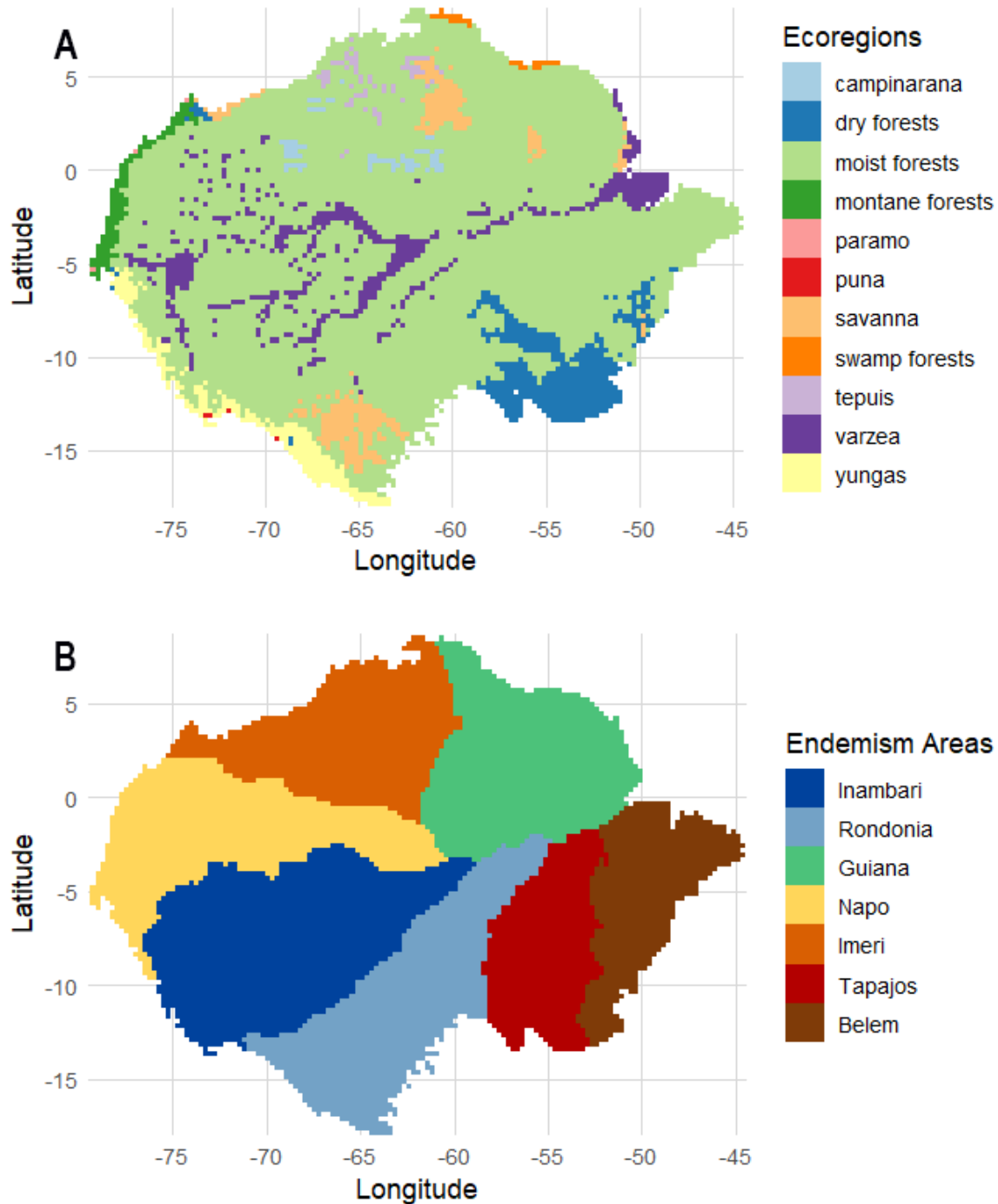


Figure 3. Comparison of anuran species richness distribution between raw IUCN range data and altitude-refined data. (A) Species richness calculated from raw IUCN range maps, showing a maximum of 125 species per cell. (B) Species richness calculated from the altitude-refined dataset, showing a maximum of approximately 100 species per cell. In both maps, color intensity represents the number of co-occurring species. (C) Absolute difference in species richness between the two matrices (Raw IUCN minus Altitude-refined data). Higher values (e.g., yellow and orange tones) indicate regions where the raw IUCN data significantly overestimated species richness, particularly along the western and northern Amazonian borders. Note: The black dotted lines and outlines (e.g., Guiana Shield, Andes) are included solely for geographical reference to facilitate the identification of major biogeographical structures, and they do not represent data boundaries used in the analyses.

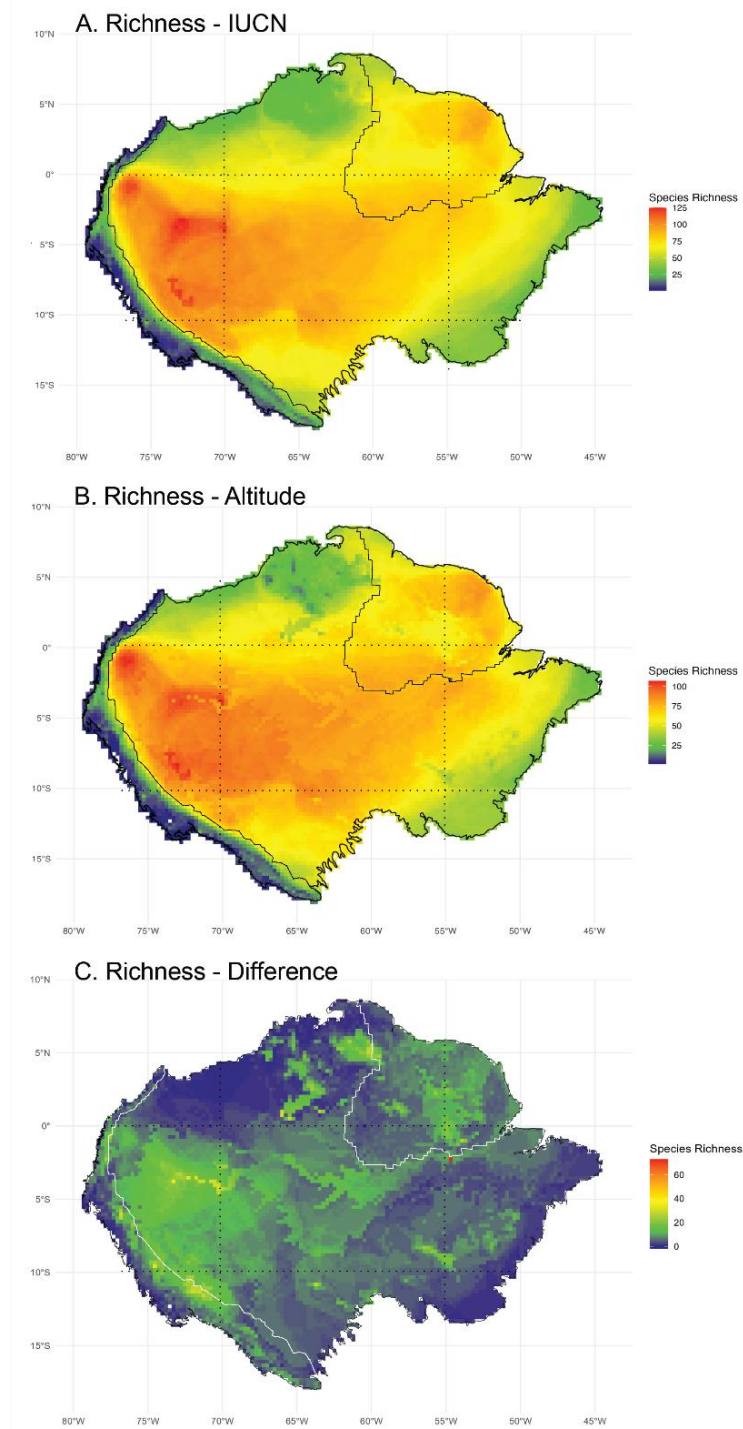


Figure 4. **Spatial patterns of taxonomic, phylogenetic, and functional beta diversity across Amazonia for altitude-refined data.** (A, C, E) Mean beta diversity per grid cell, representing its average dissimilarity relative to all other Amazonian cells. Higher mean values indicate communities that are compositionally more distinct from the rest of the biome. (B, D, F) Standard deviation of turnover values per cell, reflecting how consistently each cell differs from others—low SD indicates homogeneous dissimilarity across comparisons, while high SD indicates variable dissimilarity patterns.

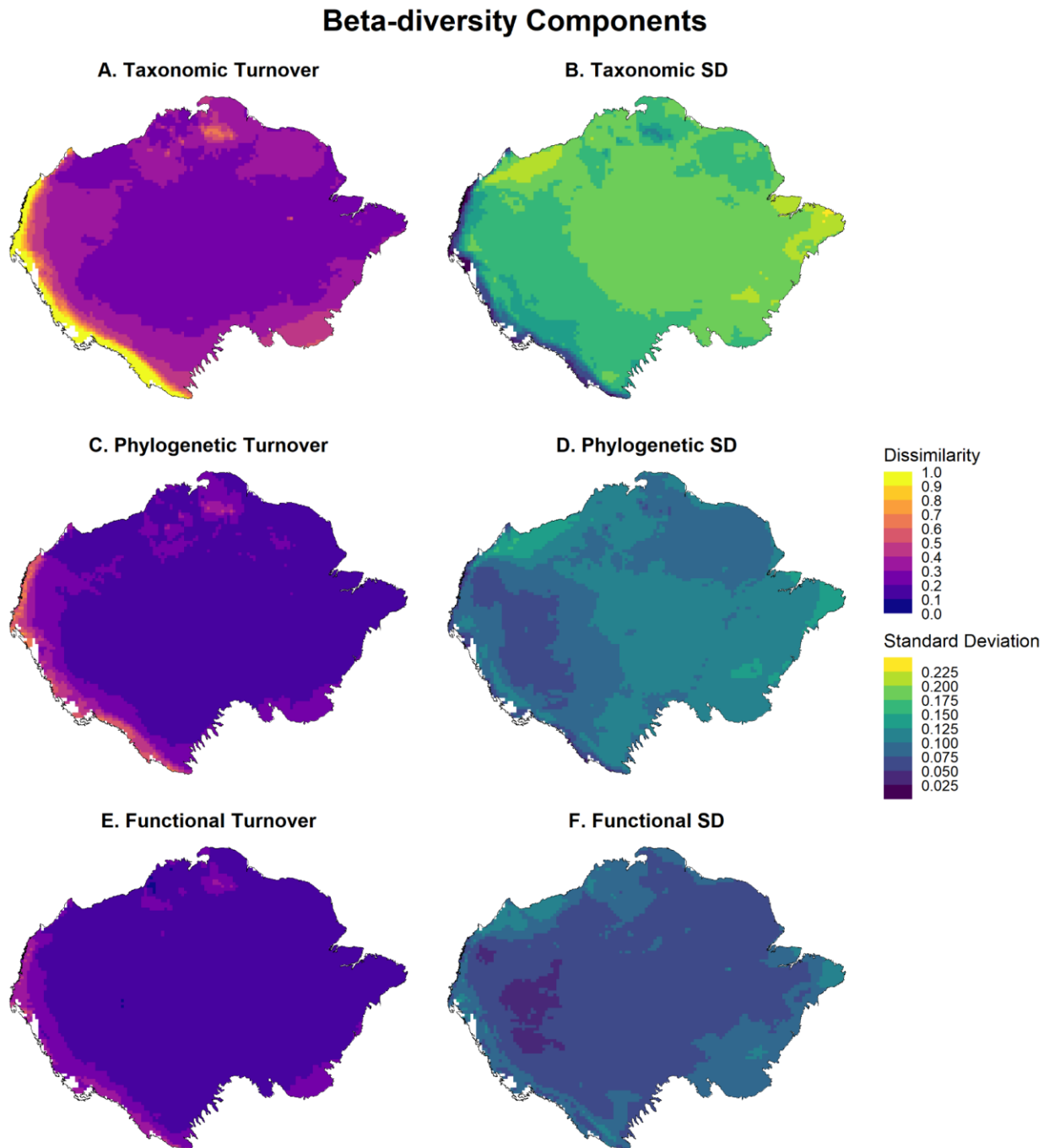


Figure 5. **Relationship between mean beta diversity and its variability (standard deviation) across Amazonian grid cells.** Each point represents a cell, showing how turnover magnitude (y-axis) relates to the dispersion of pairwise dissimilarities (x-axis). The red line represents the fitted linear model illustrating the overall trend. Higher SD values indicate cells with more heterogeneous pairwise comparisons, whereas lower SD values reflect more consistent turnover across comparisons.

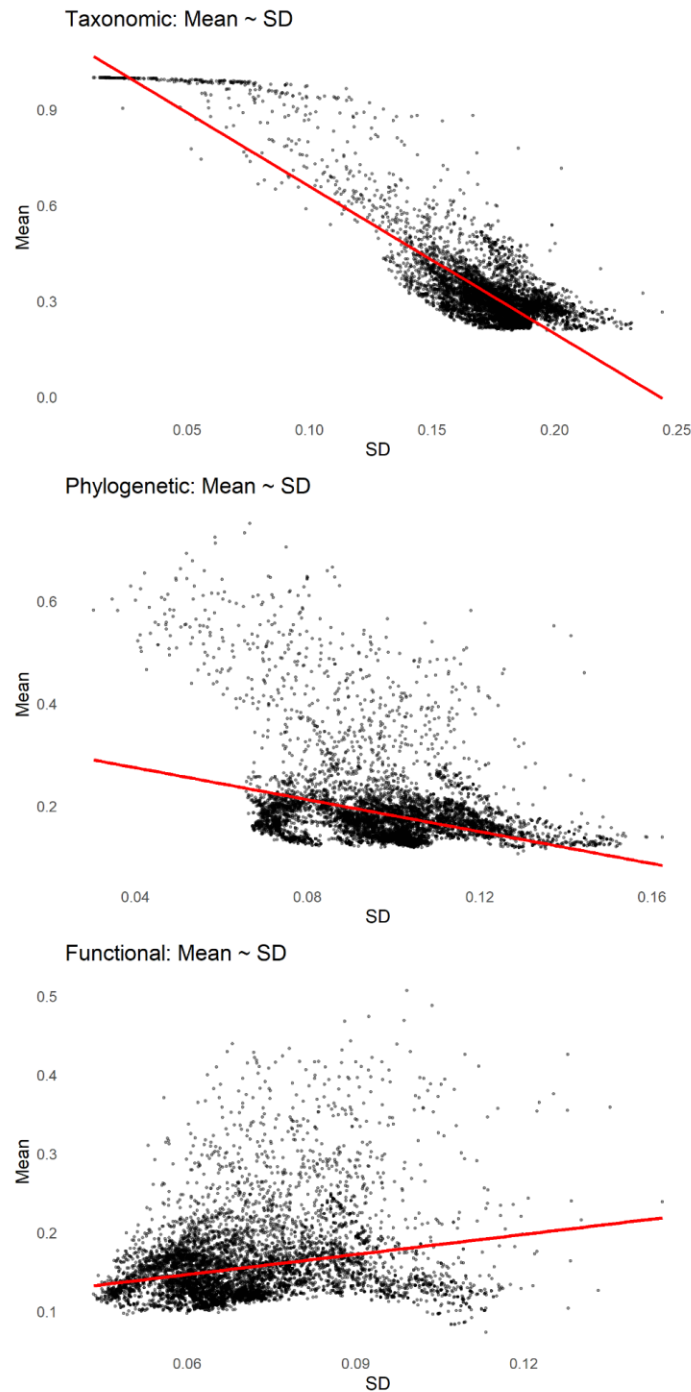


Figure 6. **Null distributions of median turnover compared to observed values for each diversity facet.** (A) Taxonomic turnover, (B) Phylogenetic turnover, and (C) Functional turnover. Each panel shows the null distribution (solid curve) generated from 1,000 randomizations, with the observed median turnover indicated by the dashed vertical line.

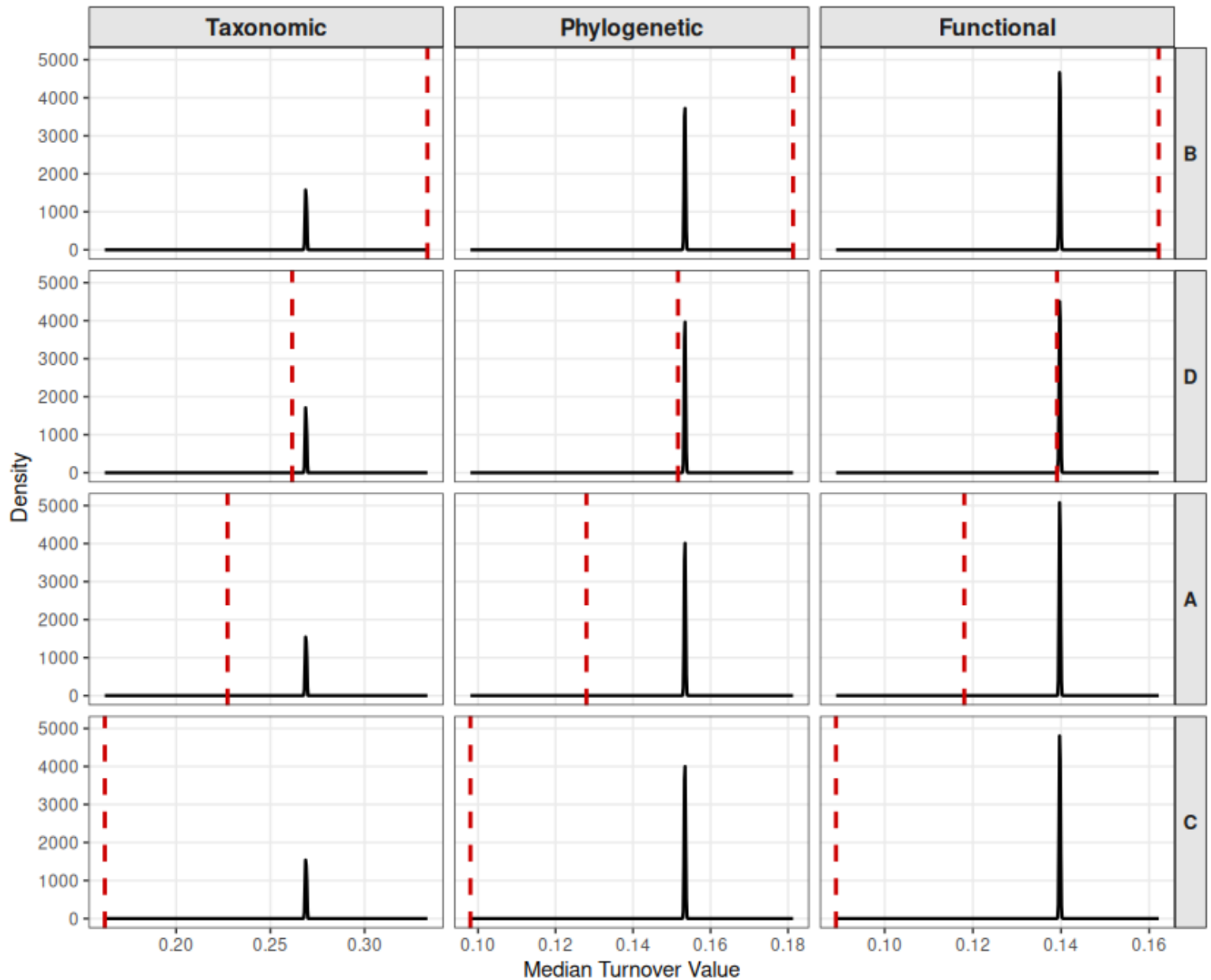
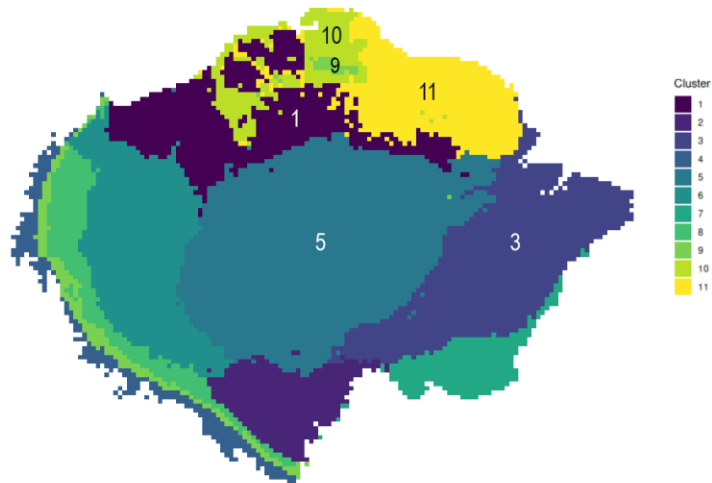
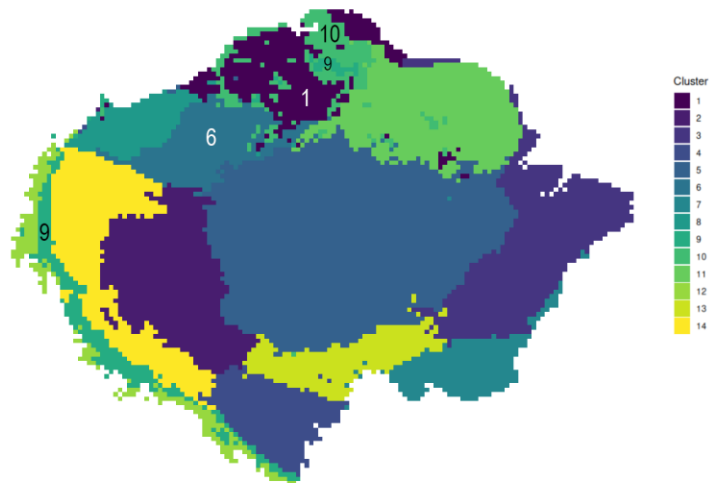


Figure 7. **Bioregionalization of Amazonian anuran communities based on the altitude-refined dataset.** Maps show the k-means clustering results for (A) taxonomic, (B) phylogenetic, and (C) functional turnover. The optimal number of clusters for each facet was identified using the Krzanowski & Lai (KL) index. Each grid cell is assigned to a cluster representing groups of sites with similar community composition. The cluster numbers (indicated in the legend and overlaid on the maps) correspond to the specific beta-regions discussed in the text.

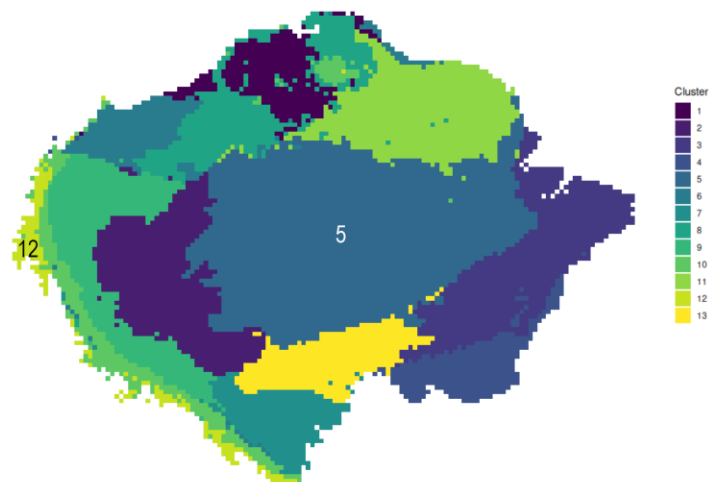
A. Taxonomic clustering



B. Phylogenetic clustering



C. Functional clustering



Supporting information

Text 1 (Results of IUCN-based dataset)

Hypothesis test: ecoregions and areas of endemism

Results from the IUCN-based dataset were fully consistent with the general patterns described for the altitude-refined data (Table S2). As in the refined dataset, taxonomic turnover was lowest for pairs of cells sharing both the same AoE and the same ecoregion (Class C; observed = 0.229, null = 0.417, $p < 0.001$), and highest for cells in different AoEs and different ecoregions (Class B; observed = 0.504, $p < 0.001$). The mixed classes also followed the same hierarchical structure. Turnover for cells in different ecoregions but within the same AoE (Class A) was lower than expected (observed = 0.333, null = 0.417, $p < 0.001$), whereas turnover for cells in different AoEs but the same ecoregion (Class D) was only slightly below the null (observed = 0.410, $p < 0.001$). As in the altitude-refined results, Class D consistently showed higher turnover than Class A, highlighting the stronger effect of historical barriers.

The IUCN-based results broadly mirrored the structure described for the altitude-refined dataset. Turnover was significantly lower than expected in Class C (observed = 0.090; null = 0.161, $p = 0$), and significantly higher in Class B (observed = 0.192; null = 0.161, $p = 0$), matching the predicted contrast between fully matched and fully mismatched classifications. Turnover in Class A was also significantly lower than the null expectation (observed = 0.124; null = 0.161, $p = 0$), similarly reinforcing the importance of AoE boundaries. However, as in the altitude-refined dataset, Class D again diverged from expectations. Here, turnover did not differ significantly from the null (observed = 0.161; $p = 0.288$), indicating a neutral effect of AoE boundaries when ecoregions are held constant. Taken together, both datasets show a consistent pattern for Class D: historical boundaries do not increase phylogenetic turnover in environmentally similar regions, although the altitude-refined data suggest slight homogenization whereas the IUCN data indicate neutrality.

The IUCN-based results were fully consistent with the general pattern described for the altitude-refined dataset, though with slightly different magnitudes (Table S2). As in the refined dataset, pairs of cells within the same AoE and ecoregion (Class C) showed significantly lower functional turnover than expected (observed = 0.080, null = 0.143), whereas pairs in entirely different classifications (Class B) exhibited markedly higher turnover (observed = 0.168, null = 0.143). Similarly, mixed classes followed the same hierarchy observed in the altitude-refined results. Turnover in Class A (same AoE, different ecoregion) was substantially lower than expected (observed = 0.115, null = 0.143), whereas Class D (different AoE, same ecoregion) showed only a slight but significant increase relative to the null (observed = 0.144, null = 0.143). As in the main dataset, Class D remained higher than Class A, reinforcing the stronger influence of AoEs over ecoregions in shaping functional turnover.

Community clustering

The optimal number of clusters, determined using the Krzanowski & Lai (KL) index, identified 17 beta-diversity regions when clustering taxonomic dissimilarity from the IUCN-based range maps (Figure S4). These bioregions were characterized by the formation of large, contiguous blocks with a low degree of fragmentation. An exception was the northern portion of the Amazon, where bioregions 9, 11, and 12 exhibited a more disjunct spatial pattern (Figure S4).

Clustering analysis of phylogenetic dissimilarity, which revealed spatial patterns similar to those observed for taxonomic turnover, identified 15 bioregions for the IUCN-based dataset (Figure S4). These bioregions formed mostly large and homogeneous spatial blocks, with well-defined boundaries and a low degree of fragmentation. This broad spatial coherence mirrors the patterns observed in the taxonomic clustering, indicating that the biogeographical processes shaping species turnover across the Amazon similarly affect the turnover of closely related evolutionary lineages rather than deeper phylogenetic splits. An exception to this otherwise contiguous pattern occurred in the northern Amazon, where bioregion 12 formed a mosaic interspersed with cells from bioregions 1 and 4 (Figure S4). Such a configuration highlights localized areas in which phylogenetic turnover deviates sharply from surrounding cells, despite the overall large-scale homogeneity.

Clustering analysis of functional dissimilarity identified 14 bioregions for the IUCN-based models (Figure S4). For the IUCN data, the macro-structure of the bioregions is consistent with taxonomic and phylogenetic results, consisting of large contiguous blocks with low fragmentation. The fragmentation is observed in the northern region, with bioregions 1, 11 and 12. This congruence suggests that the spatial organization of functional turnover parallels that of species and lineage turnover at the macro-scale.

Modeling environmental gradients of turnover

Patterns observed for the IUCN-based GDM models closely mirrored those described for the altitude-refined dataset (Table S3). The models explained 31.3% of deviance in taxonomic turnover, 21.8% in phylogenetic turnover, and 16% in functional turnover. As in the refined dataset, climatic variables overwhelmingly dominated model contributions, while geographic distance—though statistically significant—accounted for less than 1% of the explained deviance. BIO8 was again the single most influential predictor across dimensions, followed by BIO2 and BIO13. The only minor deviation from the altitude-refined results was a small contribution of BIO14 (1.1%) to functional turnover. Overall, the IUCN dataset reproduced the same general pattern: climatic gradients, rather than geographic distance, are the main determinants of anuran beta-diversity, reinforcing the robustness of the results presented in the main text.

Supplementary tables

Table S1. **Minimum, maximum, mean, and standard deviation of taxonomic, phylogenetic, and functional beta diversity values across the Amazon from IUCN-based data.** Turnover values were derived from cell-level pairwise dissimilarities and summarize the overall magnitude and variability of each beta diversity dimension.

Beta-diversity components (IUCN)				
	min	max	mean	sd
Taxonomic turnover	0.205235	0.999671	0.33834	0.149876
Phylogenetic turnover	0.113915	0.761463	0.189506	0.079424
Functional turnover	0.100448	0.476136	0.158787	0.048849

Table S2. **Results of the hypothesis test evaluating the effects of Areas of Endemism (AoEs) and ecoregions on taxonomic, phylogenetic, and functional turnover for the IUCN-based dataset.** Classes represent combinations of AoE and ecoregion membership: A = same AoE, different ecoregion; B = different AoE, different ecoregion; C = same AoE, same ecoregion; D = different AoE, same ecoregion. For each class, the table reports the observed median turnover, the expected median under the null model, the number of cell pairs, and the direction of deviation relative to the null (“low” = lower than expected; “high” = higher than expected). Statistical significance is indicated by p-values obtained from 1,000 randomizations.

Class	Median null	Median observed	Pair number	P value	Diff type
Taxonomic turnover					
A	0.333333333	0.416666667	1881274	0	low
B	0.504	0.416666667	11747736	0	high
C	0.228571429	0.416666667	3722092	0	low
D	0.409836066	0.416666667	19702034	0	low
Phylogenetic turnover					
A	0.124309186	0.160858307	1881274	0	low
B	0.192294539	0.160856746	11747736	0	high
C	0.090296015	0.160867425	3722092	0	low
D	0.161046929	0.160856039	19702034	0.288	Not different
Functional turnover					
A	0.114579763	0.1433592	1881274	0	low
B	0.167535152	0.143334352	11747736	0	high
C	0.079812014	0.143335104	3722092	0	low
D	0.143690847	0.143343388	19702034	0.01	high

Table S3. **Deviance explained by the Generalized Dissimilarity Models (GDM) for the IUCN-based dataset across the taxonomic, phylogenetic, and functional dimensions of beta-diversity.** Values represent the percentage contribution of each predictor to the total deviance explained by the model. Asterisks indicate levels of statistical significance ($p < 0.1$; $p < 0.05$; $p < 0.01$); higher numbers of asterisks denote stronger significance.

Dimension	Explained variance	Geographic distance	bio_2	bio_3	bio_4	bio_8	bio_13	bio_14
Taxonomic	31.3%	0.3***	6.9***	–	4.1***	45.3***	6.1***	–
Phylogenetic	21.8%	–	2.8***	–	2.3*	42.5***	5.7***	0.7
Functional	16.0%	–	10.3***	–	1.5*	28.7***	6.3***	1.1*

Supplementary figures

Figure S1. **Pearson correlation matrix of the 19 bioclimatic variables from WorldClim v2.** The plot visualizes the pairwise correlation coefficients (r) used to assess multicollinearity. The color indicates the direction of the correlation (e.g., blue for positive, red for negative), while the intensity of the color is proportional to the magnitude of the correlation (values closer to $|1|$). Blank spaces indicate non-significant correlations. This analysis was used to identify and exclude highly correlated variables from the final models.

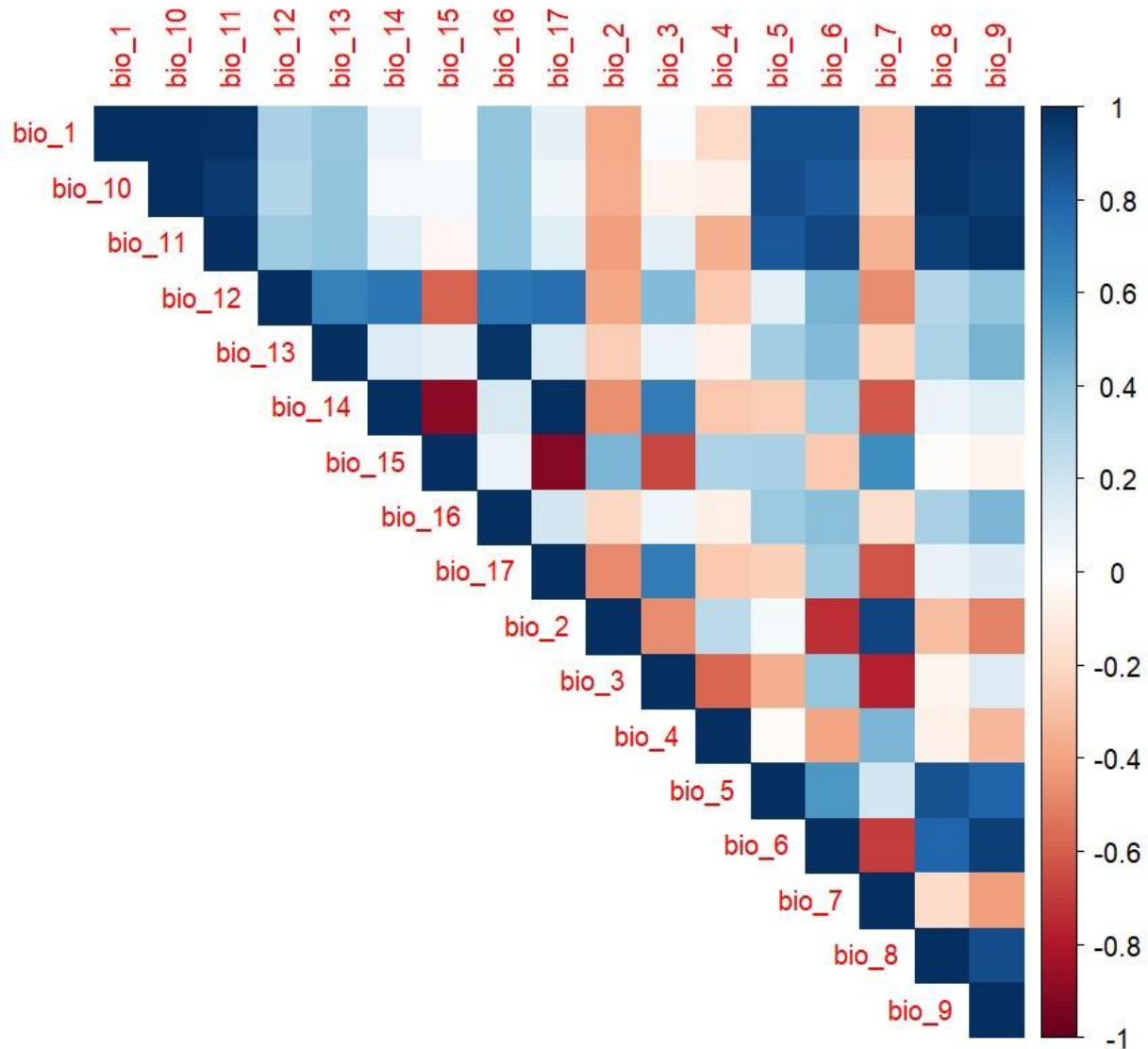


Figure S2. **Spatial patterns of taxonomic, phylogenetic, and functional beta diversity across Amazonia for IUCN-based data.** (A, C, E) Mean beta diversity per grid cell, representing its average dissimilarity relative to all other Amazonian cells. Higher mean values indicate communities that are compositionally more distinct from the rest of the biome. (B, D, F) Standard deviation of turnover values per cell, reflecting how consistently each cell differs from others—low SD indicates homogeneous dissimilarity across comparisons, while high SD indicates variable dissimilarity patterns.

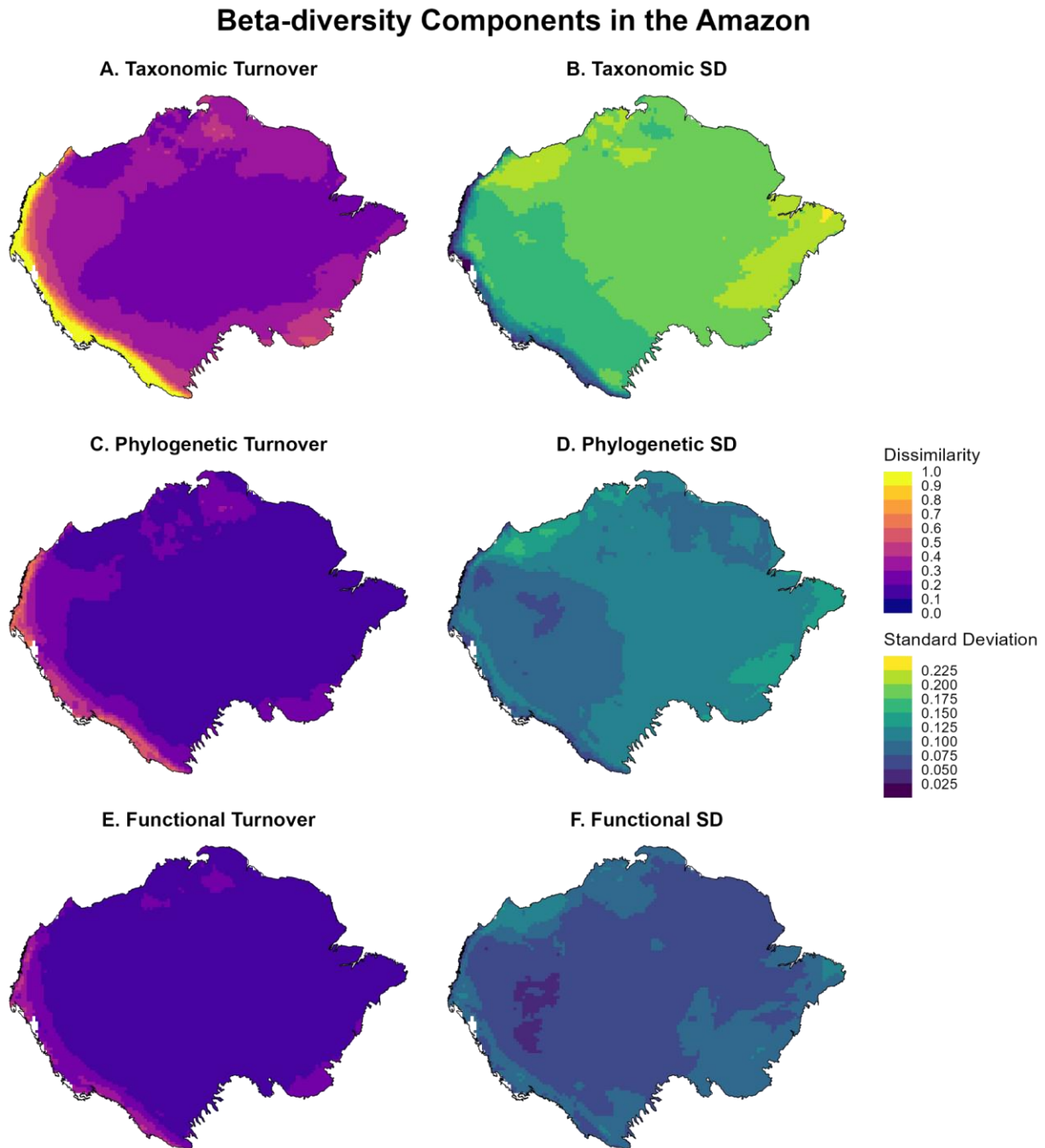


Fig S3. Relationship between mean beta diversity and its variability (standard deviation) across Amazonian grid cells for IUCN-data. Each point represents a cell, showing how turnover magnitude (y-axis) relates to the dispersion of pairwise dissimilarities (x-axis). The red line represents the fitted linear model illustrating the overall trend. Higher SD values indicate cells with more heterogeneous pairwise comparisons, whereas lower SD values reflect more consistent turnover across comparisons.

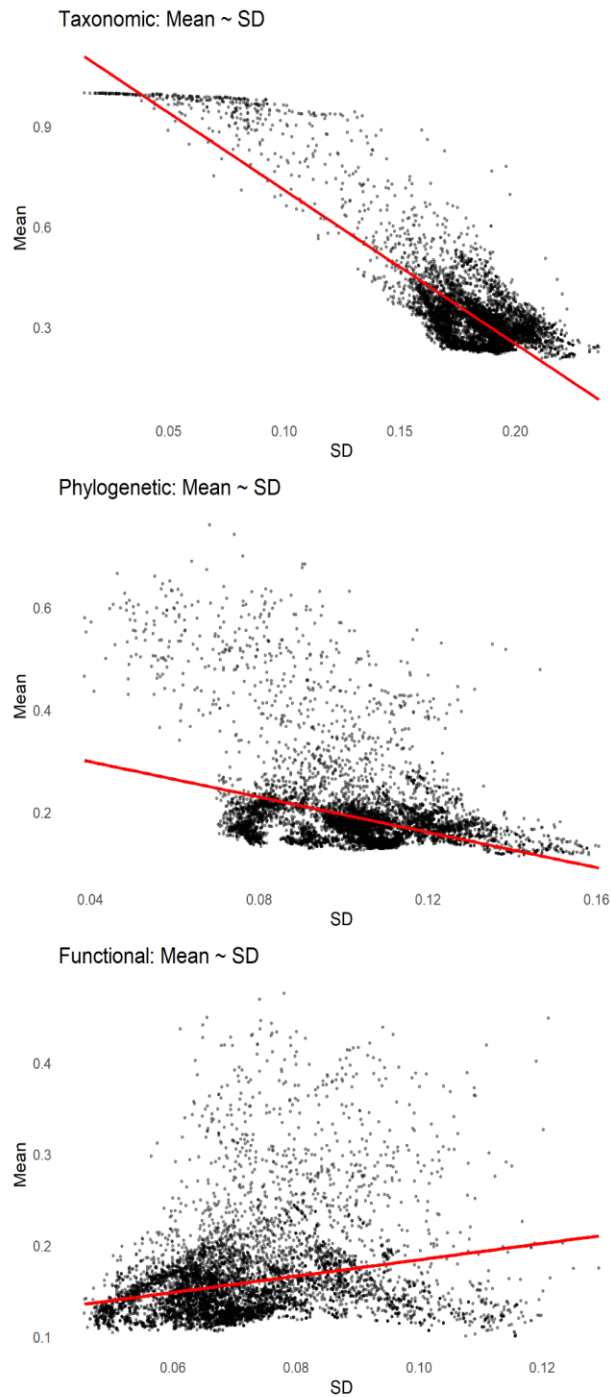


Figure S4. Results of the Hypothesis Test: Observed Turnover vs. Null Expectations for IUCN dataset. The figure presents the results of the formal hypothesis test, comparing the observed median turnover against the null distribution for three facets of anuran beta-diversity across four pairwise scenarios. Columns represent beta diversity facets (Taxonomic, Phylogenetic, Functional), and rows represent the Classes (A, B, C, D). The black density curve represents the null distribution, generated by 1,000 randomizations of site pairs. The red dashed vertical line indicates the observed median turnover for that specific geographic class.

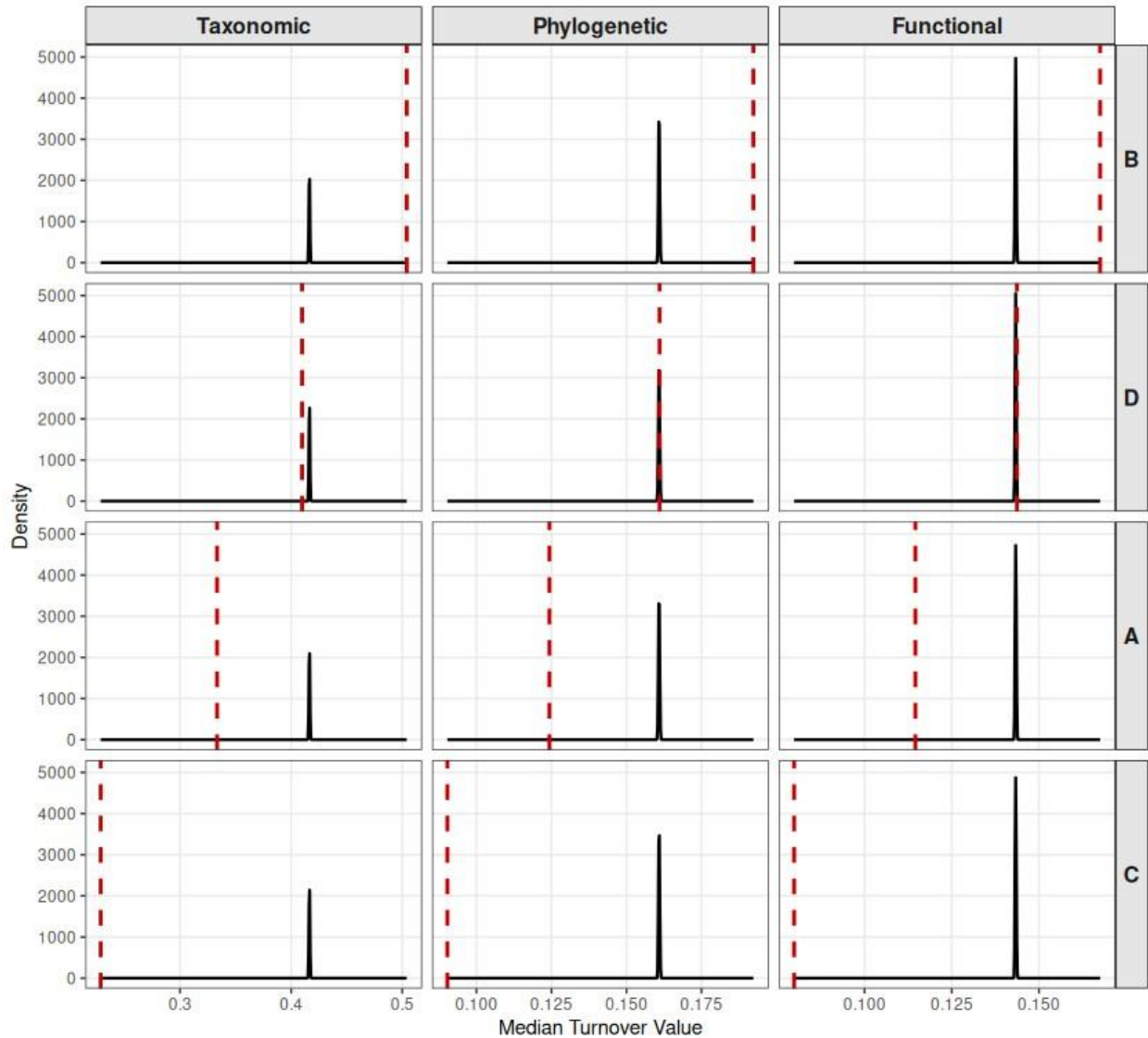
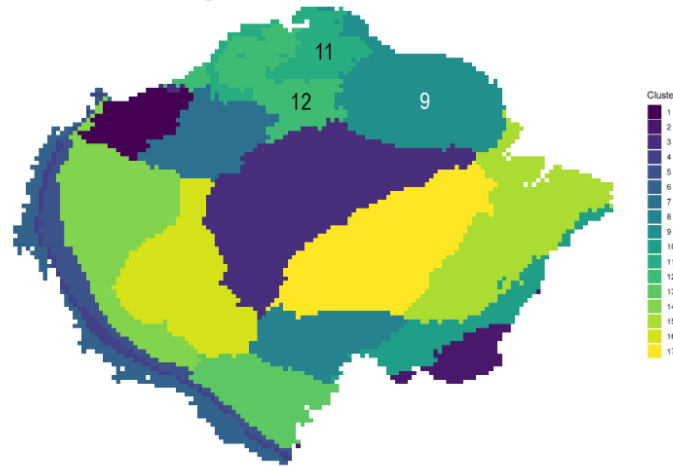
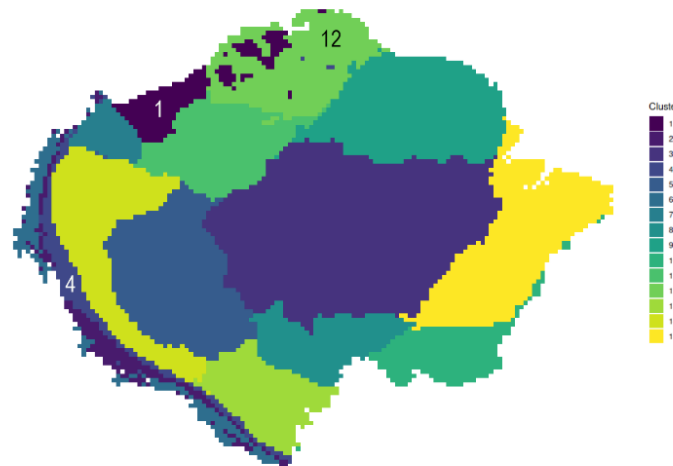


Figure S5. **Bioregionalization of Amazonian anuran communities based on the IUCN dataset.** Maps show the k-means clustering results for (A) taxonomic, (B) phylogenetic, and (C) functional turnover. The optimal number of clusters for each facet was identified using the Krzanowski & Lai (KL) index. Each grid cell is assigned to a cluster representing groups of sites with similar community composition. The cluster numbers (indicated in the legend and overlaid on the maps) correspond to the specific beta-regions discussed in the text.

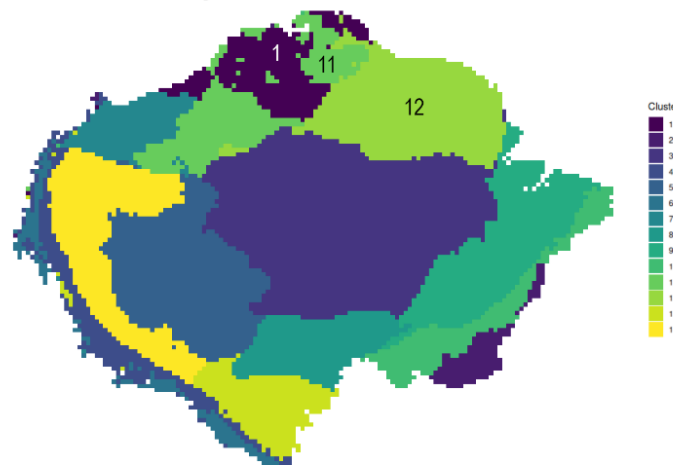
A. Taxonomic clustering



B. Phylogenetic clustering



C. Functional clustering



CONCLUSÃO GERAL

Esta tese teve como propósito central ampliar o conhecimento sobre a diversidade de anfíbios anuros amazônicos sob três perspectivas complementares: (1) identificar e quantificar lacunas taxonômicas, geográficas e evolutivas que limitam nosso entendimento sobre o grupo; (2) avaliar os processos históricos e ambientais que estruturam a diversidade beta em múltiplas facetas e (3) promover a divulgação e popularização científica sobre a diversidade de anuros amazônicos e ameaças enfrentadas. Juntos, os dois capítulos apresentados como artigos científicos publicados ou em processo de revisão revelam um quadro abrangente sobre como o conhecimento disponível, bem como os padrões biogeográficos subjacentes, moldam nossa capacidade de compreender e conservar a fauna de anuros na maior floresta tropical do mundo.

No Capítulo 1, demonstrei que a biodiversidade anurofaunística da Amazônia permanece severamente subdocumentada. A combinação de déficits de conhecimento taxonômico, geográfico e genético é tamanha que compromete tanto a inferência de padrões biogeográficos quanto o estabelecimento de prioridades efetivas de conservação. Regiões inteiras mostram-se subamostradas, e a ausência de dados genéticos e filogenéticos dificulta a resolução de complexos de espécies crípticas e a avaliação de suas relações evolutivas. Esses resultados evidenciam a necessidade urgente de ampliar expedições científicas, em especial com amostragem em regiões remotas, promover abordagens integrativas de taxonomia e estabelecer programas de monitoramento de longo prazo. O artigo também apresenta temas prioritários onde o avanço do conhecimento pode gerar impacto imediato, tanto para ciência básica quanto para políticas de conservação.

O Capítulo 2 complementa essa perspectiva ao revelar a hierarquia dos processos que moldam a diversidade beta de anuros, ou seja, os padrões de dissimilaridade da composição ao longo da Amazônia. Mostrei que, em escala biogeográfica ampla, o legado histórico associado à formação de Áreas de Endemismo é o principal responsável pela delimitação das grandes unidades de substituição de diversidade, superando a influência das ecorregiões tradicionais. Em contraste, ao longo de gradientes ambientais, fatores climáticos — especialmente a temperatura do trimestre mais úmido (BIO8) — são os filtros ecológicos dominantes, enquanto a distância geográfica (vista como um efeito neutro) desempenha um papel secundário, indicando que processos de seleção ambiental são também responsáveis por moldar a diversidade de anuros amazônicos. Esses resultados oferecem uma visão integrada na qual processos históricos e ambientais interagem em diferentes escalas para estruturar comunidades, reforçando a importância de abordagens hierárquicas em biogeografia. Além disso, o uso de dados de distribuição refinados por altitude revelou padrões que permaneciam ocultos em abordagens mais tradicionais, destacando a importância de melhorar a qualidade das bases de ocorrência para inferências biogeográficas mais robustas.

Além dos avanços científicos propriamente ditos, esta tese também gerou produtos de divulgação e popularização científica que buscaram aproximar o conhecimento sobre os anuros

amazônicos do público mais amplo. Esses materiais — apresentados como anexos — foram desenvolvidos ao longo do doutorado com o objetivo de comunicar, de forma acessível, a importância ecológica do grupo, as ameaças que enfrenta e a relevância das pesquisas realizadas. Embora não constituam o foco central da tese, tais iniciativas reforçam o compromisso com ciência aberta, formação de público e ampliação do impacto social das pesquisas em biodiversidade.

Tomados em conjunto, os achados desta tese demonstram que o avanço na compreensão da biogeografia de anuros amazônicos depende simultaneamente de preencher lacunas fundamentais de conhecimento e de empregar modelos que reconheçam a natureza multiescalas dos processos evolutivos e ecológicos. Do ponto de vista da conservação, os resultados ressaltam que a fauna de anuros — altamente sensível a condições climáticas — está particularmente vulnerável às mudanças ambientais globais, intensificando a necessidade de proteger tanto refúgios climáticos quanto regiões historicamente singulares. As beta-regiões identificadas aqui, divergentes dos esquemas clássicos baseados em outros vertebrados (aves e primatas), também revelam que estratégias generalistas de conservação podem ser ineficazes e que planejamentos devem considerar especificidades fisiológicas, ecológicas e evolutivas de cada grupo biológico.

Em sumário, esta tese reforça o papel central da Amazônia como laboratório natural para compreender como processos históricos e ambientais interagem para gerar e manter a biodiversidade de grupos emblemáticos e mega diversos, como anfíbios anuros. Futuras pesquisas que integrem dados genômicos, informações funcionais mais detalhadas e séries temporais de longo prazo serão essenciais para aprofundar o entendimento das linhagens anuros e para garantir que sua conservação acompanhe o ritmo acelerado das mudanças climáticas e ambientais. Assim, este trabalho representa um passo importante em direção a um mapa biogeográfico mais preciso para os anuros amazônicos e fornece bases científicas para ações de conservação mais eficazes e específicas ao grupo.

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ANEXOS

Anexo 1 — Livro *Girinos do Brasil*

Título: *Girinos do Brasil*

Ano: 2024

Editora: Anolis Books

Formato: Livro impresso, 826 páginas

Autores:

Denise de C. Rossa-Feres (Editora), Luis C. Schiesari, **Marcelo Menin**, Luiz N. Weber, Tiago Gomes dos Santos, Renan Nunes Costa, Caio Vinicius de Mira-Mendes, Franco L. de Souza, **Brena da Silva Gonçalves**, Tiago L. Pezzuti, Marcos Dubeux, Flora Acuña Juncá, Gilda V. de Andrade, Danusy Lopes Santos, Danilo Silva Ruas, Katiuce de O. da Rocha Picheli Thomé, Michel Varajão Garey, Darlene da Silva Gonçalves, Mirco Solé, Carlos Eduardo Conte, Edvaldo M. da Silva Neto, Paulo Cascon, Tami Mott e Fausto Nomura.

Descrição do conteúdo:

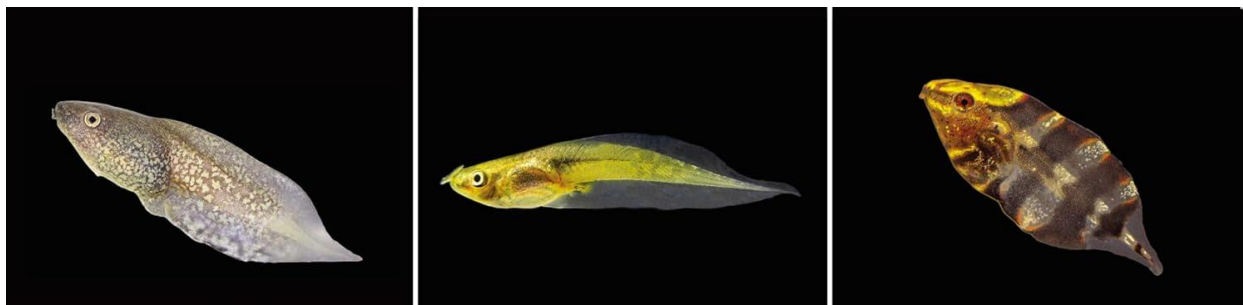
Girinos do Brasil é uma obra inédita e amplamente ilustrada que reúne informações detalhadas sobre a história natural dos girinos de sapos, rãs e pererecas dos seis biomas brasileiros. Após capítulos introdutórios sobre biologia, métodos de coleta, registro fotográfico e caracterização morfológica geral, o livro apresenta pranchas fotográficas individuais de 367 espécies, acompanhadas de ícones descritivos de bioma, habitat e micro-habitat.

O volume reúne, de forma sem precedentes, dados essenciais para pesquisas em sistemática, ecologia, etologia e biologia da conservação, ao mesmo tempo em que se destaca pela alta qualidade visual, combinando fotografia profissional, design gráfico cuidadoso e pinturas a óleo de Tiago Gomes dos Santos. Além do valor acadêmico, a obra busca também sensibilizar o público para a urgência da conservação dos anfíbios brasileiros e dos ambientes dos quais dependem.

Disponibilidade:

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GIRINOS do BRASIL

DENISE DE C. ROSSA-FERES
Editora



Aromobatidae (Allobatinae)

Allobates sumtuosus (Morales, 2002)

Comprimento total $22,72 \pm 1,74$ mm (20,36 - 26,14 mm, n = 8, estágio 36; Reserva Florestal Adolfo Ducke, Manaus, AM; LCS 529, 552). Corpo ovoide em vista dorsal, com comprimento (33%) e largura (58%) intermediários; deprimido (46%) em vista lateral. Focinho inclinado em vista lateral. Disco oral anteroventral, sem emarginações; borda recortada formando uma fileira de papilas marginais unisseriada, com interrupção anterior; papilas marginais triangulares e grandes, papilas submarginais ausentes. Fórmula dentária 2(2)/3(1), P1=P2=P3; cobertura queratinizada da maxila com espessura estreita em formato de arco, mandíbula estreita em formato de U. Narinas pequenas (12%), circulares, sem apófises e posicionadas dorsalmente. Olhos grandes (30%), dorsais. Espiráculo sinistro, com comprimento e largura intermediários, formato cilíndrico e parede centripeta livre e curta, posterodorsalmente direcionado e com abertura no terço posterior do corpo; comprimento correspondendo a 13% do comprimento do corpo e largura correspondendo a 18% da altura do corpo. Tubo anal dextral e aderido à nadadeira ventral. Cauda de comprimento intermediário, correspondendo a 67% do comprimento total e com extremidade afilada; musculatura caudal de largura intermediária correspondendo a 44% da largura do corpo. Nadadeira dorsal baixa, com 50% da altura da musculatura caudal, iniciando na junção corpo-cauda com inclinação suave e contorno paralelo ao eixo longitudinal da cauda por um curto trecho e então se elevando com inclinação média, formando contorno em arco amplo; nadadeira ventral baixa, com 35% da altura da musculatura caudal e contorno em arco amplo. Linha lateral evidente.

Amazônia



Caatinga



Cerrado



Pantanal



Pampa

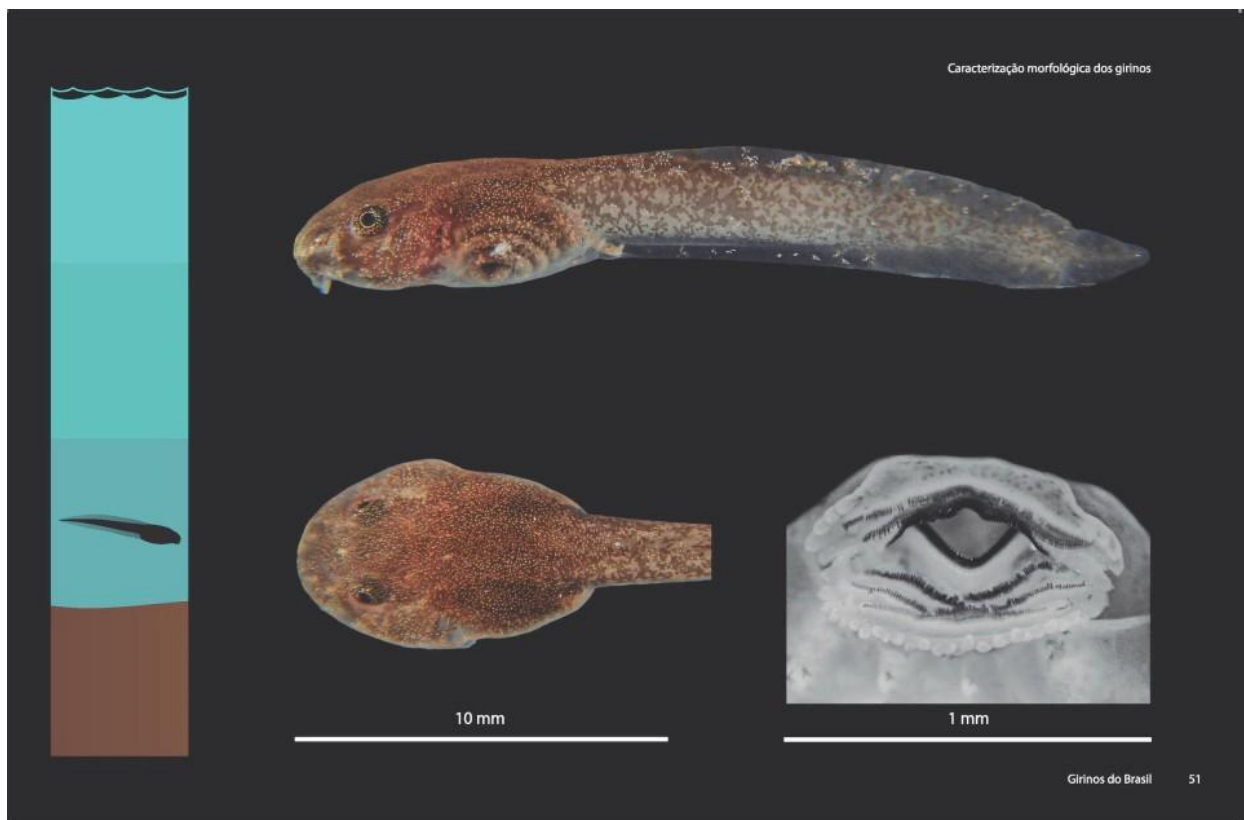


Mata Atlântica



Área de Transição





GIRINOS do BRASIL

Neste livro inédito e ricamente ilustrado, o leitor encontrará informações da história natural de uma ampla diversidade de girinos de sapos, rãs e pererecas de todos os seis biomas brasileiros. A partir de uma descrição básica da biologia, dos métodos de coleta e registro fotográfico, e da caracterização morfológica de girinos de forma geral, são apresentadas pranchas fotográficas individuais de nada menos que 367 espécies acompanhadas de ícones descritivos do bioma, habitat e micro-habitat de ocorrência. O volume e variedade de informação reunida, sem precedentes, deverá atrair novos estudantes e pesquisadores fomentando avanços em campos como sistemática, ecologia, etologia e biologia da conservação. O design gráfico e a qualidade das fotografias, bem como as pinturas a óleo de autoria de Tiago Gomes dos Santos, tornam o livro uma obra de grande qualidade visual e com potencial para inspirar o público em geral, sensibilizando para a urgência na conservação dos anfíbios brasileiros, e dos habitats e biomas dos quais dependem.



Anexo 2 — Livro *Emergência Climática e a Sociobiodiversidade Amazônica*

Título completo:

Emergência Climática e a Sociobiodiversidade Amazônica

Autores: Fernanda P. Werneck, Jordana Guimarães Ferreira, Ana Paula Vieira de Oliveira, André Yves, Brena da Silva Gonçalves, Eliza Ribeiro Costa, Erasmo Andrade, Josué A. R. Azevedo, Leandro J. C. L. Moraes, Lucas Rosado Mendonça, Pedro Paulo Goulart Tauci, Raíssa Rainha, Felipe Zanusso.

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Resumo do conteúdo:

Este livro apresenta, em linguagem clara e visualmente acessível, os principais conceitos, evidências científicas e desafios relacionados aos impactos das mudanças climáticas sobre a sociobiodiversidade amazônica. A obra integra resultados produzidos pelo projeto BioClimAmazônia e pelo Laboratório de Ecologia e Evolução de Vertebrados (LEEVI/INPA), reunindo informações sobre ecologia, história evolutiva, vulnerabilidade climática e conservação da herpetofauna amazônica. Além de explicar mecanismos que tornam anfíbios e répteis particularmente sensíveis às alterações ambientais, o livro discute riscos atuais, projeções futuras e o papel de políticas públicas embasadas em ciência. Produzido para estudantes, educadores, gestores e público geral, o material reforça a importância da comunicação científica e da educação ambiental no enfrentamento da desinformação, no fortalecimento da cidadania socioambiental e na promoção de ações de conservação diante das emergências climáticas globais.

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EMERGÊNCIA CLIMÁTICA E A SOCIOBIODIVERSIDADE AMAZÔNICA

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CAPÍTULO 3 O BRASIL E SUA MEGABIODIVERSIDADE

Como mencionado, as condições ambientais de um determinado local, constituídas a partir de processos naturais que ocorreram ao longo de centenas de milhões (até bilhões!) de anos de história da Terra explicam a evolução e a existência de um conjunto de espécies em uma determinada região. Por outro lado, os processos socioculturais que evoluíram ao longo de centenas de milhares de anos de história da vida humana também contribuíram para moldar as populações naturais através de processos como a domesticação de espécies.

O Brasil, por exemplo, é considerado um dos países mais biodiversos do planeta, conhecido como parte do grupo de países megadiversos. Nosso território abrange diferentes biomas e ecossistemas, como a Floresta Amazônica, o Pantanal, a Mata Atlântica, o Pampa, o Cerrado e a Caatinga, além de ambientes costeiros e marinhos.



AMAZÔNIA - IMPORTÂNCIA ECOSSISTÊMICA E AMEAÇAS AO BIOMA MAIS BIODIVERSO DO MUNDO

A Amazônia, considerada a maior floresta tropical úmida do mundo, contribui enormemente para a riqueza de espécies encontradas no Brasil. Esse bioma, que é compartilhado entre o Brasil e mais oito países, ocupa quase metade do território brasileiro (49,29%), e está presente nos Estados do Acre, Amapá, Amazonas, Pará, Roraima, Rondônia, Mato Grosso, Maranhão e Tocantins.

Na Amazônia estão a maior diversidade de espécies do planeta, o maior patrimônio genético, a maior bacia hidrográfica, a maior floresta tropical úmida e um quinto (1/5) de toda água doce do planeta. A Amazônia produz metade da sua própria chuva, pelo processo de reciclagem de água, e transporta essa água pelos "rios voadores" para o Sul-Sudeste do Brasil.

As estimativas recentes dos cientistas quanto ao número de espécies que a Amazônia abriga são impressionantes: cerca de 50.000 plantas vasculares, pelo menos 2.406 peixes na Bacia Amazônica, 427 anfíbios, 371 répteis, 1.300 aves e 425 mamíferos, números ainda nitidamente subestimados.

Devido às suas dimensões continentais e altíssima biodiversidade, a Floresta Amazônica fornece inúmeros serviços ecossistêmicos que contribuem para a manutenção da vida do planeta. Dentre os principais, destacam-se a atuação da floresta como fonte de diversidade biológica que fornece as bases de inúmeros serviços, como polinização; sequestro de carbono que, associado aos recursos hídricos, promove a formação dos rios voadores, contribuindo com chuvas em outras regiões do país e regulação climática regional e global; fornecimento de alimentos e recursos naturais; turismo e recreação; novidades evolutivas envolvidas nos processos de especiação e também no enfrentamento de condições climáticas desafiantes pelas populações naturais. De acordo com o trabalho "Valorização da preservação da floresta tropical na Amazônia" (traduzido do inglês), o valor desses benefícios é estimado em 317 bilhões de dólares anuais.



O VALOR DA FLORESTA EM PÉ

De acordo com estudo publicado em 2023 pelo Banco Mundial, intitulado "Equilíbrio delicado para a Amazônia Legal Brasileira: um memorando econômico", reconhecer o valor excepcional das florestas naturais da Amazônia Legal é fundamental para frear sua destruição. O Brasil é responsável por cerca de um terço do desmatamento tropical no mundo todo, principalmente devido à pecuária. A Amazônia Legal, mais especificamente a região conhecida como "Arco do Desmatamento", concentra as maiores taxas de desmatamento, em sua maioria ilegal. Além disso, a Floresta Amazônica corre o risco de atingir o ponto de inflexão, em que as mudanças climáticas, combinadas com o elevado desmatamento, resultarão em transformação e perda permanente de grandes extensões de

floresta tropical. Embora os pontos de inflexão sigam cercados de incertezas, inclusive em relação a quando serão atingidos, suas consequências seriam catastróficas. Desde 2000, três quartos da floresta tropical já perderam sua capacidade de regeneração e adaptação.

Se uma Amazônia preservada dos impactos das mudanças climáticas parecia, até recentemente, uma possibilidade, ainda que distante, os eventos de 2023 e 2024 — como a seca extrema dos rios, registros de incêndios florestais e alta mortalidade de animais — evidenciam que as mudanças climáticas já são uma realidade na região. Sem ações urgentes de enfrentamento e mitigação, catástrofes ambientais e sociais ainda mais graves podem estar próximas.

