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INFLUÊNCIA DE FATORES HISTÓRICOS E CONTEMPORÂNEOS NA REGIONALIZAÇÃO BIOGEOGRÁFICA DE AVES DA MATA ATLÂNTICA

São José do Rio Preto
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Dissertação apresentada à Universidade Estadual Paulista (Unesp), Instituto de Biociências, Letras e Ciências Exatas, São José do Rio Preto, para obtenção do título de Mestre(a) em Biodiversidade.

Orientador: Prof. Dr. Fernando Rodrigues da Silva

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IMPACTO POTENCIAL DESTA PESQUISA

A pesquisa desenvolvida neste mestrado contribui de forma relevante para a compreensão dos padrões e processos históricos e contemporâneos que moldam a biodiversidade da Mata Atlântica, um dos biomas mais ameaçados e ricos em espécies endêmicas do planeta. Ao integrar dados filogenéticos e de distribuição de aves em uma abordagem inovadora de regionalização biogeográfica, este estudo oferece subsídios técnicos e científicos para o planejamento de estratégias mais eficazes de conservação da biodiversidade, com especial atenção a espécies microendêmicas. Os resultados obtidos têm potencial de aplicação em políticas públicas ambientais nos âmbitos local, regional e nacional, além de dialogarem com agendas internacionais de preservação de *hotspots* de biodiversidade e enfrentamento das mudanças climáticas. O trabalho também contribui para o fortalecimento da ciência brasileira e da formação de recursos humanos qualificados em biodiversidade, ecologia e biogeografia, incentivando a colaboração internacional e a inserção de jovens cientistas em redes de pesquisa.

POTENTIAL IMPACT OF THIS RESEARCH

The research developed in this master's project makes a significant contribution to understanding the historical and contemporary patterns and processes that shape biodiversity in the Atlantic Forest – one of the world's most threatened and species-rich biomes. By integrating phylogenetic and distributional data for birds using an innovative biogeographic regionalization approach, this study provides technical and scientific support for more effective biodiversity conservation planning, with particular attention to microendemic species. The findings have potential applications in environmental policy at local, regional, and national levels, and contribute to global agendas focused on biodiversity hotspot conservation and climate change mitigation. Furthermore, the project strengthens Brazilian science and the training of qualified professionals in biodiversity, ecology, and biogeography, promoting international collaboration and the inclusion of early-career researchers in academic networks.

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UNESP – campus de Rio Claro

Aos meus pais, que me deram asas
ensinaram-me a ler os ventos
a enfrentar tempestades sem perder o rumo.
Se hoje voo longe, é porque me deram ninho
todo um céu infinito
e a certeza de sempre poder voltar.

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“Para ser grande, sê inteiro: nada
Teu exagera ou exclui.
Sê todo em cada coisa. Põe quanto és
No mínimo que fazes.”

(PESSOA, 1998, p. 315).

RESUMO

Compreender a estrutura biogeográfica das espécies é fundamental para a conservação da biodiversidade, especialmente em paisagens altamente diversas e fragmentadas. Neste estudo, integramos dados de distribuição e filogenia por meio de uma abordagem baseada em redes para delimitar biorregiões para aves na Mata Atlântica, um dos principais *hotspots* de biodiversidade globais. Nossa análise foi baseada em uma matriz de grades de 50x50 km, construída a partir de mapas de distribuição e dados filogenéticos de 867 espécies de aves não marinhas registradas no domínio. Ao aumentar o parâmetro de força da raridade (RSt), avaliamos a influência das espécies de distribuição restrita na formação das biorregiões. Além disso, identificamos zonas de transição entre biorregiões e aplicamos modelos espaciais autorregressivos (SAR) para investigar como heterogeneidade climática, topografia e barreiras fluviais moldaram os limites biogeográficos. Identificamos cinco principais regiões biorregiões (BRs) congruentes com áreas de endemismo previamente descritas para aves e outros táxons: BR1 (Florestas de Araucária), BR2 (Litoral da Bahia e Serra do Mar), BR3 (Alto Paraná), BR4 (Centro de Endemismo de Pernambuco) e BR5 (Diamantina). As fronteiras biogeográficas foram influenciadas principalmente por heterogeneidade climática, gradientes de precipitação e variação altitudinal. Zonas de transição entre as biorregiões evidenciaram conexões históricas. A incorporação de dados filogenéticos revelou novos padrões, especialmente sob altos valores de RSt, nos quais espécies de distribuição restrita reforçaram os limites das biorregiões. Embora as variáveis ambientais tenham influenciado a formação das biorregiões, apenas uma pequena fração da variação pôde ser explicada por estes correlatos (1 – 9%), sugerindo o papel de outros processos ecológicos e evolutivos. Nossos resultados reforçam, portanto, a importância de integrar dados taxonômicos e filogenéticos para capturar com maior precisão os processos históricos e contemporâneos da regionalização biogeográfica. Biorregiões com alta concentração de espécies microendêmicas devem ser priorizadas para conservação, pois abrigam linhagens evolutivas insubstituíveis, mas permanecem altamente vulneráveis à perda de hábitat. O número atual de áreas protegidas na Mata Atlântica é claramente insuficiente para garantir a manutenção da diversidade de aves, especialmente em zonas de transição, que desempenham um papel essencial na conectividade da paisagem e na persistência das espécies diante de mudanças ambientais. Estudos futuros devem adotar abordagens multi-táxon e multi-escala, integrando dados ecológicos, geográficos e genômicos para aprimorar estratégias de conservação em *hotspots* de biodiversidade.

Palavras–chave: Biorregionalização; Diversificação; Avifauna; Florestas Tropicais; América do Sul.

ABSTRACT

Understanding species biogeographic structure is crucial for biodiversity conservation, particularly in highly diverse and fragmented landscapes. Here, we integrate species distribution and phylogenetic data using a network-based approach to delineate biogeographic regions for birds in the Atlantic Forest, an important global biodiversity hotspot. Our analysis is based on a 50x50km grid matrix built on occurrence range maps and phylogenetic data of 867 non-marine avian species occurring within the domain. By increasing the rarity strength parameter (RSt), we assessed the influence of range-restricted species in shaping biogeographical regions. Therefore, we highlighted transition zones between bioregions and applied spatial autoregressive (SAR) models to evaluate how climatic heterogeneity, topography and riverine barriers shaped biogeographic boundaries. We identified five main biogeographic regions (BRs) aligned with areas of endemism reported for birds and other taxa: BR1 (Araucaria Forests), BR2 (Coastal Bahia and Serra do Mar), BR3 (Alto Paraná), BR4 (Pernambuco Centre of Endemism) and BR5 (Diamantina). The boundaries between bioregions were primarily shaped by climatic heterogeneity, precipitation gradients and altitude variation. Transition zones between bioregions highlighted deep historical connections. Incorporating phylogenetic data revealed novel patterns, particularly under high RSt values, where range-restricted species strengthened biogeographic boundaries. While influencing bioregion delineation, environmental variables explained only a small portion of variation (1 – 9%), suggesting the role of additional evolutionary and ecological processes. Our findings highlight the importance of integrating phylogenetic and taxonomic data to capture both historical and contemporary drivers of bioregionalization. Bioregions with a high number of microendemic species should be prioritized for conservation, as they harbour irreplaceable evolutionary lineages yet remain highly vulnerable to habitat loss. The current number of protected areas in the Atlantic Forest is insufficient to maintain bird diversity, particularly in transition zones, which play a crucial role in maintaining connectivity and species persistence in response to environmental change. Future research should adopt multi-taxon and multi-scale approaches, integrating ecological, geographic and genomic data to refine conservation planning in biodiversity hotspots.

Keywords: Bioregionalization; Diversification; Avifauna; Tropical forests; South America.

SUMÁRIO

1. INTRODUÇÃO

Em linhas gerais, a regionalização biogeográfica pode ser definida como um sistema de organização da biodiversidade em unidades espaciais que apresentam uma composição de espécies semelhantes, refletindo a influência de fatores históricos e contemporâneos, como interações bióticas, variações geológicas e mudanças climáticas (Kreft & Jetz, 2010; Rueda et al. 2010; Holt et al. 2013; Morrone, 2018). Desde o século XIX, pesquisadores vêm subdividindo áreas geográficas com base na fauna e flora, buscando compreender os mecanismos que estruturam os padrões espaciais da biodiversidade (Sclater, 1858; Wallace, 1876; Olson et al. 2001; Whittaker et al. 2013). No entanto, grande parte desses estudos desconsiderou a história evolutiva dos táxons coocorrentes. Nos últimos anos, a crescente disponibilidade de dados filogenéticos para diferentes grupos biológicos (e.g., Jetz et al. 2012; Smith & Brown, 2018; Upham et al. 2019; McTavish et al. 2024) e os avanços em métodos analíticos (Daru et al. 2015; Edler et al. 2023) consolidaram a regionalização filogenética como uma abordagem promissora para investigar a evolução espacial e temporal da biota. Ao incorporar relações evolutivas, essa metodologia permite delimitações biogeográficas mais robustas, fornecendo uma visão mais precisa sobre a formação histórica da biodiversidade (Goldberg et al. 2011; Holt et al. 2013; Daru et al. 2015; Carta et al. 2022). No entanto, apesar desses avanços, abordagens metodológicas que integrem dados taxonômicos e filogenéticos ainda são escassas, especialmente em escalas regionais e locais nos trópicos, onde se concentram diversos *hotspots* de biodiversidade (Myers et al. 2000).

Dentre esses *hotspots*, a Mata Atlântica se sobressai como a segunda maior floresta tropical da América do Sul e uma das regiões neotropicais com maiores índices de riqueza e endemismo de espécies de vertebrados (Ribeiro et al. 2011; Figueiredo et al. 2021), com destaque para a avifauna: são aproximadamente 893 espécies de aves vivendo dentro de seus limites, sendo que aproximadamente 220 são consideradas endêmicas ao domínio (Silva et al. 2004; Vale et al. 2018; Hasui et al. 2018). Estudos de regionalização biogeográfica para diferentes táxons indicam uma diferenciação histórica entre as porções norte, central e sul do bioma, cada uma abrigando comunidades biológicas distintas (Galindo-Leal & Câmara, 2003; Cabanne et al. 2008; Carnaval et al. 2009). Dada a necessidade urgente de proteger espécies de distribuição restrita em um cenário de fragmentação florestal e perda de hábitat (Ribeiro et al. 2009; Vancine et al. 2024), pesquisadores têm concentrado esforços na identificação de áreas de endemismo para espécies florestais, a fim de aprimorar ações de conservação nessas regiões-chave (Silva et al. 2004; Cabanne et al. 2008; Chaves et al. 2014; Cabanne et al. 2016; Carvalho

et al. 2017; Araujo et al. 2024). Estudos apontam que fatores ambientais, como oscilações climáticas passadas, heterogeneidade climática contemporânea e variação altitudinal, influenciam esses padrões em diferentes escalas temporais e espaciais, bem como nas respostas evolutivas das espécies (Batalha-Filho et al. 2013; Cabanne et al. 2016; da Silva et al. 2024). Apesar das variações observadas, a congruência entre biorregiões delimitadas para a avifauna como um todo e as áreas de endemismo definidas para grupos menores sugere que abordagens distintas podem ser complementares, considerando que processos evolutivos geram respostas em múltiplas escalas (Banks-Leite et al. 2024). A interação entre fatores ambientais diversos e processos históricos em escalas temporais e espaciais distintas exige metodologias mais robustas para a identificação e compreensão dos padrões biogeográficos, especialmente em comunidades complexas como a avifauna da Mata Atlântica (Dantas et al. 2011; Batalha-Filho et al. 2013; Carvalho et al. 2017; Oliveira et al. 2017).

Com base nesse contexto, aplicamos uma abordagem de análise de redes integrando dados de distribuição e informação filogenética para delimitar regiões biogeográficas taxonômicas e filogenéticas da avifauna da Mata Atlântica. Além disso, para avaliar o papel de espécies de distribuição restrita na regionalização, simulamos cenários ajustando o peso dessas espécies na delimitação das biorregiões. A partir desses resultados, investigamos quais fatores históricos e contemporâneos melhor explicam os limites entre as regiões identificadas por meio das abordagens taxonômica e filogenética. Formulamos as seguintes hipóteses: (i) as biorregiões derivadas de dados filogenéticos apresentarão padrões divergentes daqueles previamente descritos com base apenas na distribuição das espécies, pois a filogenia captura a história evolutiva além das faixas de distribuição atuais (Daru et al. 2017); (ii) o número, a forma e a composição das biorregiões variarão de acordo com o peso atribuído às espécies de distribuição restrita; (iii) os fatores explicativos (gradientes climáticos históricos e contemporâneos, variações topográficas e barreiras fluviais) que influenciam os limites biogeográficos diferirão entre as abordagens taxonômica e filogenética: enquanto as fronteiras filogenéticas podem estar mais associadas a fatores históricos (e.g., estabilidade paleoclimática), as fronteiras taxonômicas refletirão gradientes ambientais contemporâneos (Daru et al. 2017; Antonelli et al. 2018). Ao testar essas hipóteses, buscamos gerar novos insights sobre os processos que moldam os padrões atuais de diversidade de aves na Mata Atlântica, contribuindo para um entendimento mais amplo da formação histórica da biodiversidade e fornecendo subsídios científicos para orientar estratégias de conservação.

2. UNVEILING BIOGEOGRAPHIC PATTERNS OF ATLANTIC FOREST BIRDS: A NETWORK-BASED APPROACH INTEGRATING SPECIES DISTRIBUTION AND PHYLOGENETICS

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UNVEILING BIOGEOGRAPHIC PATTERNS OF ATLANTIC FOREST BIRDS: A NETWORK-BASED APPROACH INTEGRATING SPECIES DISTRIBUTION AND PHYLOGENETICS

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ABSTRACT

Aim

This study aims to integrate species distribution and phylogenetic data using a network-based approach to delineate biogeographic regions for Atlantic Forest birds, assessing how past and contemporary variables shape biogeographic boundaries and evaluating the role of range-restricted species in the regionalization process.

Location

Atlantic Forest, South America.

Time period

Contemporary, with reference to historical processes.

Major taxa studied

Non-marine bird species occurring within the Atlantic Forest domain (867 species).

Methods

We used a combination of taxon-specific occurrence data and phylogenetic information to delineate bioregions through a network-based approach applied to the software *Infomap Bioregions* v. 2.0. To assess the influence of range-restricted birds in shaping biogeographical regions, we simulated different scenarios by increasing the weight of narrowly distributed species in the analysis (Rarity Strength parameter). We also identified transition zones between different bioregions. Finally, to evaluate the role of present-day and past climatic heterogeneity, topography and riverine barriers in shaping biogeographic boundaries in each scenario, we built spatial autoregressive (SAR) models using Generalized Linear Mixed Models (GLMM) with spatially autocorrelated errors.

Results

We identified five main biogeographic regions (BRs) closely aligned with previously reported areas of endemism for birds and other taxa within the Atlantic Forest: BR1 (Araucaria Forests), BR2 (Coastal Bahia and Serra do Mar), BR3 (Alto Paraná), BR4 (Pernambuco Centre of Endemism) and BR5 (Diamantina). Bioregionalization was primarily influenced by climatic heterogeneity, precipitation gradients and altitude variation. Transition zones between bioregions highlighted historical connectivity. Incorporating phylogenetic data revealed novel patterns, particularly under high RSt values, where range-restricted species strengthened biogeographic boundaries. While influencing bioregion delineation, environmental variables explained only a small portion of variation, suggesting the role of additional evolutionary and ecological processes.

Main conclusions

Our findings highlight the importance of integrating phylogenetic and taxonomic data to capture both historical and contemporary drivers of bioregionalization. Bioregions with high concentrations of microendemic species should be prioritized for conservation, as they harbour irreplaceable evolutionary lineages yet remain highly vulnerable to habitat loss. Current protected areas are insufficient, particularly in transition zones, which play a crucial role in maintaining connectivity and species persistence in response to environmental change. Future research should adopt multi-taxon and multi-scale approaches, integrating ecological, spatial and genomic data to refine conservation planning in biodiversity hotspots worldwide.

Keywords: Bioregionalization; Diversification; Avifauna; Tropical forests; South America.

INTRODUCTION

Biogeographic regionalization is generally defined as an organising method that provides spatial representations of biodiversity into groups sharing similar species composition in response to historical and contemporary factors, such as biotic interactions, and geological and climatic variations (Kreft & Jetz, 2010; Rueda et al. 2010; Holt et al. 2013; Morrone, 2018). While biogeographic regions for terrestrial animals and plants have been studied since the 19th century (Sclater, 1858; Wallace, 1876; Olson et al. 2001), many of these studies have ignored the evolutionary history of co-occurring taxa. Over the past decade, the growing availability of phylogenetic data across diverse biological groups (*e.g.*, Jetz et al. 2012; Smith & Brown, 2018; Upham et al. 2019; McTavish et al. 2024) and advancements in analytical methods (Daru et al. 2020; Edler et al. 2023) have positioned phylogenetic regionalization as a powerful tool for understanding the spatial and temporal evolution of biota. By incorporating evolutionary relationships, this approach refines the delineation of biogeographic units, offering a more robust perspective on the historical assembly of biodiversity (Goldberg et al. 2011; Holt et al. 2013; Daru et al. 2015; Carta et al. 2022). However, despite these advances, methodological frameworks integrating both taxonomic and phylogenetic data remain scarce, particularly at regional and local scales in the Neotropics where several global biodiversity hotspots are located (Myers et al. 2000).

Here, we built an integrative biogeographic regionalization scheme for the Atlantic Forest bird community, using a network analysis approach that integrates distribution data and phylogenetic information of the species. The Atlantic Forest is the second-largest tropical forest in South America and one of the neotropical biodiversity hotspots with the greatest species richness (Ribeiro et al. 2011; Figueiredo et al. 2021). Regionalization studies for several Atlantic Forest taxa suggest a historical differentiation among the northern, central and southern portions of the domain, with distinct biological communities occupying each region (Galindo-Leal & Câmara, 2003; Cabanne et al. 2008; Carnaval et al. 2009). Considering the urge for protecting range-restricted species in a scenario of forest fragmentation and habitat loss in the Atlantic Forest (Ribeiro et al. 2009; Vancine et al. 2024), researchers have been focusing on identifying areas of endemism for forest-dependent species to enhance conservation actions in those key areas (Silva et al. 2004; Cabanne et al. 2008; Chaves et al. 2014; Cabanne et al. 2016; Carvalho et al. 2017; Araujo et al. 2024). These studies have shown that environmental factors, such as past climatic events, present climatic heterogeneity and altitude variability, have been influencing those patterns at different levels, depending on temporal and spatial scales, as well

as individual species evolutionary responses (Batalha-Filho et al. 2013; Cabanne et al. 2016; da Silva et al. 2024). Despite this variation, the congruence between biogeographic regions for the entire avian community and the areas of endemism formed by a smaller group of species suggest that different approaches might benefit from looking through each other's lens, considering that evolutionary processes generate cross-scale responses (Banks-Leite et al. 2024). Given the broad environmental heterogeneity and the interaction of countless processes at different temporal and spatial scales, identifying patterns and understanding the processes that generate them demands an even more robust methodological framework, especially when dealing with complexly diverse communities such as the avifauna of the Atlantic Forest (Dantas et al. 2011; Batalha-Filho et al. 2013; Carvalho et al. 2017; Oliveira et al. 2017).

Based on this context, we applied a network analysis approach integrating species distribution data and phylogenetic information to delimit taxonomic and phylogenetic biogeographic regions for Atlantic Forest birds. Additionally, to assess the role of range-restricted species in regionalization, we simulated scenarios adjusting their weight in bioregion delimitation. Using these results, we examined which historical and contemporary factors best explain the position of the boundaries between regions identified via taxonomic and phylogenetic-based approaches. We formulated the following hypotheses: (i) Bioregions derived from phylogenetic data will show convergence with previously identified areas of endemism based on species distribution data, as the integration of phylogenetic relationships should enhance the robustness of biogeographic delimitations and reinforce patterns already observed in the literature (Daru et al. 2017); (ii) The number, shape and composition of bioregions will vary with the weight assigned to range-restricted species; (iii) Consequently, the explanatory variables (historical and contemporary climatic gradients, topographic variations and river barriers) influencing biogeographic boundaries will between taxonomic and phylogenetic approaches: phylogenetic boundaries may align more strongly with historical factors (*e.g.*, paleoclimatic stability), while taxonomic boundaries reflect contemporary environmental gradients (Daru et al. 2017; Antonelli, 2017). By testing these hypotheses, we aim to generate insights into the processes shaping current patterns of bird diversity in the Atlantic Forest, contributing to a broader understanding of the biodiversity's historical assembly and providing science-based evidence to guide strategic conservation actions.

METHODS

Study area

The Atlantic Forest originally covered an area of approximately 1.6 million km², distributed along the Brazilian coast (92%) and smaller areas in the interior of Paraguay and Argentina (Galindo-Leal & Câmara, 2003; Ribeiro et al. 2009). Due to its extensive latitudinal, longitudinal, altitudinal, and soil-climatic gradients that generate a wide environmental heterogeneity, this domain can be defined as a diverse mosaic of habitats, characterized by complex boundaries with other ecosystems such as the Pampas, Bolivian Chaco, Pantanal, Cerrado, and Caatinga (Galindo-Leal & Câmara, 2003; Ribeiro et al. 2009; Ribeiro et al. 2011). The vegetation is characterized by humid forests (dense, open and mixed ombrophilous forests), dry formations (semideciduous and deciduous seasonal forests) and coastal vegetations (mangroves and restingas) (Costa, 1997; Silva & Casteleti, 2003; Joly et al. 2014). However, due to the intense process of forest degradation and fragmentation that has been affecting the region for more than five centuries, only about 9% of its original vegetation cover has been preserved, mostly in the form of small and isolated forest remnants (Ribeiro et al. 2009; de Lima et al. 2015; Vancine et al. 2024).

The boundaries of the Atlantic Forest have been historically discussed, and different geographic extensions were suggested according to political and environmental factors (Silva & Casteleti, 2003; Muylaert et al. 2018; Vancine et al. 2024). These variations stem from the complex nature of the biome, which presents connections with other ecosystems such as the Cerrado, Caatinga, Pampas and Chaco, as well as historical connectivity with the Amazon during past climatic fluctuations (Sobral-Souza et al. 2015; Muylaert et al. 2018). Given this complexity, different mapping approaches can either adopt a more inclusive or a more restrictive perspective. Here, we chose to work with a consensual map based on the Muylaert et al. (2018), that covers the territories of Brazil, Argentina, and Paraguay, with a total area equivalent to approximately 1.3 million km². This choice ensures that the analyses remain focused on regions where the Atlantic Forest is unanimously recognized, reducing uncertainties associated with transitional zones and historical range shifts. Although this delimitation does not encompass all ecotonal regions that may have played a role in past species dispersal and diversification, it provides a conservative and ecologically coherent framework for biogeographic analyses, enhancing comparability with other studies that adopt similar spatial criteria while maintaining a robust definition of the Atlantic Forest domain.

To process the analyses, we overlayed the Atlantic Forest area map with a grid of approximately 50x50 km area cells (equivalent to 0.5 degrees), covering latitudes from 3° to 30° S and longitudes from 35° to 60° W, resulting in 493 cells (Figure S1). Grid-based approaches provide a structured and standardized framework for analyzing species distributions, particularly in macroecological and biogeographic studies (Kreft & Jetz, 2010). The use of grid cells ensures spatial consistency, reducing the influence of sampling biases that often affect raw occurrence points (Cantú-Salazar & Gaston, 2013). Many species occurrence datasets are heterogeneous, with records clustered around well-surveyed areas while remaining sparse or absent in poorly sampled regions (Hurlbert & White, 2005; Ficetola et al. 2014). By aggregating species occurrences into equal-sized grid cells, our method mitigates the geographical bias inherent in point locality data while maintaining meaningful resolution for biogeographic delineation. These differences do not significantly change the ecological understanding of environmental factors influencing bird diversity at broad spatial scales (Aronsson et al. 2024).

Species distribution data and taxonomic standardization

To delineate biogeographic regions, we compiled a list of bird species occurring within the Atlantic Forest domain using a combination of species distribution maps and literature review, ensuring that the dataset accurately represented the avifauna of the region. Species selection was based on their geographic occurrence within the domain, regardless of habitat preference, meaning that our list was not restricted to forest specialists. We considered all non-marine bird species registered within the Atlantic Forest boundaries, excluding occasional or strictly marginal occurrences within the study area.

To establish a preliminary list, we extracted species range maps from BirdLife International (http://datazone.birdlife.org/species/requestdis) and overlaid them onto a 50x50 km grid covering the study area (Figure S1). Presence-absence within each grid cell was determined based on the centroid method: each species was recorded as present within a grid only if the cell's centroid fell within its range polygon. This approach mitigates the overestimation of occurrences in edge cells where only partial overlap with the range polygon might occur. The resulting presence-absence matrix assigned binary values (1 = presence, 0 = absence) to each species per grid cell, with centroid coordinates extracted to represent occurrence locations.

To refine this dataset, we conducted a literature review to incorporate newly described species and validate species occurrences in the domain. We compared our dataset to published

lists of Atlantic Forest birds (*e.g.*, Parker III et al. 1996; Moreira-Lima, 2013; Hasui et al. 2018; Vale et al. 2018) and consulted three major biodiversity databases: GBIF (http://www.gbif.org), and WikiAves (http://www.wikiaves.com.br). These databases provided occurrence records that were cross-referenced with our range-based approach to improve species selection accuracy. When species were not present in the range maps, we incorporated them manually using occurrence records from complementary databases. By overlaying these occurrence points onto our grid cells, we classified species as present or absent within each grid cell, ensuring that range-restricted and newly described species were not overlooked due to gaps in global distribution datasets. All spatial processing was conducted using the letsR package (Vilela & Villalobos, 2015) in R software v. 4.3.3 (R Core Team, 2023).

To ensure taxonomic consistency across analyses, we primarily followed the Clements Checklist v.2023 (Clements et al. 2023), as it is also the classification used in the phylogenetic dataset. However, we acknowledge that this taxonomy is more conservative than the one adopted by the Brazilian Committee on Ornithological Records (CBRO), which incorporates recent taxonomic revisions and is widely used by ornithologists (Pacheco et al. 2021). To address this discrepancy, we updated the dataset by incorporating species recognized by CBRO that were absent from Clements' classification. For example, species such as *Dendrocincla taunayi* (Pernambuco Woodcreeper), *Phaethornis margarettae* (Margaretta's Hermit), and *Pyriglena pernambucensis* (Pernambuco Fire-eye) are recognized as full species by CBRO but remain lumped as subspecies in Clements. In such cases, we aligned our dataset with CBRO to ensure taxonomic accuracy while maintaining consistency with the phylogenetic framework.

Biogeographic regionalization

We adopted an approach that integrates biogeographic and evolutionary perspectives to delineate biogeographic regions for the Atlantic Forest bird community (Edler et al. 2023). Network-based methods identify bioregions by organizing species distribution data into spatial grid cells, building a bipartite network where the links connect species to the grid cells in which they occur. In this network, communities are areas with more shared species within than across them, defining a bioregion (Vilhena & Antonelli, 2016; Edler et al. 2017). This approach overcomes the methodological problems of similarity clustering methods, as they recognize that species' occupation histories vary in form and, therefore, individual species have different contributions to biogeographic structure (Vilhena & Antonelli, 2016). Here, we first applied a method to identify taxon-specific regions based on species occurrence range maps and then incorporated phylogenetic information into the results. Additionally, recognizing the

importance of endemic and narrowly distributed species in revealing biogeographic patterns and guiding practical conservation efforts (Edler et al. 2023; Araujo et al. 2024), we simulated different scenarios increasing the weight of those species in the analysis.

i) Taxon-specific regionalization and rarity strength parameter

To delineate bioregions based on species occurrence data, we used a method that integrates cluster analysis and information network (Rosvall & Bergstrom, 2008; Vilhena & Antonelli, 2015; Bloomfield et al. 2017), implemented in the interactive online platform *Infomap Bioregions v. 2.0* (https://www.mapequation.org/bioregions2/; Edler et al. 2017; Edler et al. 2023). The software first compiles species distribution records into a matrix of geographic cells (grids). From these data, a bipartite network is generated that links species to grid cells, and this network is subsequently partitioned into bioregions using the *Infomap* algorithm (Figure S3). The results also highlight species with a higher frequency of occurrence within each bioregion – described as *indicative* species – according to their relative abundance in a specific bioregion. The score ($Is|r$) for species s in bioregion r is calculated as the ratio between the species' frequency in the region ($fs|r$) and its frequency across all regions (fs), $Is|r = fs|r / fs$. For instance, a score of 2 shows that a species is twice as frequent in a given bioregion as it is across the entire dataset (Edler et al. 2017).

We performed the analysis using the default settings of the application, modifying only the following parameters: (i) cell size range set to 0.5º (minimum and maximum) while disabling adaptive resolution to avoid hierarchical partitioning of the geographic space into progressively smaller grid cells, as our data source was distribution maps rather than point occurrences (Edler et al. 2017); (ii) the number of test repetitions (trials) was set to 1,000 to optimize clustering results; and (iii) the rarity strength (RSt), which ranged from 1.0 to 2.0, was adjusted to account for the influence of narrowly distributed species in the bioregion delineation, since range-restricted species reveal key biogeographic and evolutionary patterns (Quintero & Jetz, 2018) and often hold higher conservation value (Farooq et al. 2020). Consequently, we ran this step six times, generating six scenarios (c1–c6) based on the rarity strength value applied: s1) $RSt = 1.0$; s2) $RSt = 1.2$; s3) $RSt = 1.4$; s4) $RSt = 1.6$; s5) $RSt = 1.8$; and s6) $RSt = 2.0$. Here, we chose to keep RSt values ≤ 2.0 because excessively high weights (maximum = 3.0) fragmented bioregions into small and isolated areas, collapsing them into nested microrefugia (*e.g.*, single valleys) and reflecting fine-scale endemism patterns instead of broader evolutionary patterns.

ii) Regionalization integrating phylogenetic tree

We applied new features incorporated in the latest version of *Infomap Bioregions* to integrate phylogenetic data into the biogeographical regionalization analysis (Edler et al. 2023). To define bioregions not only based on shared species but also on shared evolutionary histories, we supplemented the species occurrence data from the previous analysis with a Maximum Clade Credibility (MCC) phylogenetic tree provided by McTavish et al. (2024), which includes 11,017 bird species. Since our study focused on a subset of species occurring in the Atlantic Forest, we pruned the original tree to retain only the species present in our dataset. This was performed using the *ape* (Paradis et al. 2004) and *phytools* (Revell, 2011) packages in R software v. 4.3.3 (R Core Team, 2024). Although we recognize that the inclusion of phylogenetic data depends on the completeness and resolution of available trees, which might overlook recent evolutionary events (Prum et al., 2015), this dataset is the most complete and up-to-date currently available, ensuring further reproducibility and comparison with other studies (McTavish et al. 2024).

Species absent from the MCC tree (*Formicivora paludicola*, *Formicivora littoralis* and *Dendrocincla taunayi*) were manually added to the tree to maintain phylogenetic consistency. As all the missing species had a well-established closest relative (Buzzetti et al. 2014; Firme & Raposo, 2011; Schultz et al. 2019), they were inserted as direct sister taxons to that species, preserving known evolutionary relationships. This allowed us to integrate all studied species into the phylogenetic framework while minimizing uncertainty in their evolutionary placement. Although the inclusion of missing taxa inevitably introduces some level of imprecision, this method ensures greater comparability with previous studies and maximizes the reproducibility of our findings using the most comprehensive and up-to-date phylogenetic dataset currently available (McTavish et al. 2024).

By incorporating distribution data into the phylogenetic tree on *Infomap Bioregions*, each ancestral node in the phylogeny is linked to the geographic grids where its descendant species are found. This process indirectly associates grids with species that share common ancestors within a specified evolutionary timeframe. As the phylogenetic tree is traversed over time, the method generates an interpolation between bioregions defined solely by distribution data and those defined by spatially segregated clades. This approach reveals evolutionarily distinct bioregions at different temporal scales. It also reduces biases arising from discrepancies in species delimitation and minimizes the risk of overfitting when dealing with sparse data,

where closely related but distinct species might otherwise be assigned to disconnected bioregions composed of only a few grids (Edler et al. 2023).

iii) Transition zones

To identify transition zones between the identified bioregions, *Infomap Bioregions v. 2.0* applies the participation coefficient, a network metric that measures how strongly each cell (node) connects with various bioregions (modules) (Edler et al. 2017; Edler et al. 2023). Each grid cell is then shaded with an opacity proportional to the fraction of species it shares with the same module, considering the connection strength to each species. To further enhance map detail, each cell's colour is blended with that of the second most connected bioregion, weighted according to the strength of those connections.

Correlates of biogeographic boundaries

Following Ficetola et al. (2017, 2021) and da Silva et al. (2024), we applied spatial autoregressive regression (SAR) models to evaluate the influence of historical and contemporary factors on the delineation of boundaries between the identified bioregions. These models allowed us to assess the extent to which a specific predictor variable might enhance the likelihood of a given grid representing a biogeographic boundary between regions. SAR models are spatially explicit, accounting for spatial autocorrelation by incorporating a neighbourhood matrix (or spatial proximity matrix). We used a 300 km neighbourhood – the minimum distance required to ensure grids within the same ecoregion remained connected. The SAR models were built using Generalized Linear Mixed Models (GLMM) with spatially autocorrelated errors. The dependent variable was a binary indicator of whether a grid is (1) or is not (0) in contact with a biogeographic boundary. The cell was considered on the boundary between bioregions if at least one adjacent cell (following the queen case of spatial contiguity) belonged to a different region. This step was performed using tools provided in the *raster* (Paradis et al. 2004), *terra* (Revell, 2011), *hglm* (Ronnegard et al. 2010), *sf* (Pebesma, 2018), *sp* (Pebesma & Bivand, 2005), *spdep* (Pebesma & Bivand, 2023) and *dplyr* (Wickham et al. 2023) packages in *R* software v. 4.3.3 (R Core Team, 2023). As independent variables, I considered four main factors (Figure S4):

i) Present-day climatic heterogeneity – To assess high spatial heterogeneity in present-day climate, we used the following climatic variables: (i) Mean Annual Temperature (bio1), (ii) Temperature Seasonality (bio4), (iii) Annual Precipitation (bio12), and (iv) Precipitation

Seasonality (bio15). These metrics not only provide a general overview of climatic patterns within the Atlantic Forest based on temperature and precipitation fluctuations but also represent key variables influencing species distribution concerning their physiological and ecological constraints (Giorgi et al. 2014; Oliveira-Silva et al. 2022). We extracted climatic data from *WorldClim v. 2.1* (https://www.worldclim.org/data/worldclim21.html) and adjusted it to resolutions compatible with the species' presence-absence matrices. Local climatic heterogeneity for each grid was calculated using the coefficient of variation (CV), comparing the grid of interest to its eight neighbouring grids. Higher heterogeneity values were observed for grids exhibiting climates significantly different from those of nearby cells (Ficetola et al. 2017; Ficetola et al. 2021).

ii) Past climate change velocity (late Quaternary) – To assess the role of historical climate change, we calculated the average rate of temperature change velocity during the Last Glacial Maximum (12.000 years ago) for each grid (Sandel et al. 2011; Ficetola et al. 2021).

iii) Orographic barriers – We assessed altitude variation by calculating the average elevation difference (mean absolute values derived from SRTM elevation data) between each grid and its eight neighbouring grids. Data was extracted from *WorldClim v. 2.1*. (https://www.worldclim.org/data/worldclim21.html).

iv) Riverine barriers – To investigate the influence of rivers on biogeographic regionalization, we utilized a grid-based Atlantic Forest layer categorized according to the distribution of major rivers within the region, referencing the Atlantic Forest hydrology map available in the *Agência Nacional de Águas* (ANA, 2012) spatial database (https://metadados.snirh.gov.br/geonetwork/srv/api/records/a01764d3-4742-4f7d-b867-01bf544dde6d). For each grid, we recorded the presence (1) or absence (0) of the four primary rivers intersecting the biogeographic boundaries between bioregions: *Doce*, *Jequitinhonha*, *Paraíba do Sul* and *São Francisco*.

All variables were log-transformed to mitigate skewness and enhance normality, followed by scaling and normalization (mean = 0, variance = 1). Pairwise Pearson's correlations among environmental variables were found to be less than 0.7 (Ficetola et al. 2021). We conducted this procedure separately for both taxonomic and phylogenetic-based results considering the six different scenarios to facilitate subsequent comparisons and associations.

To evaluate model fit, we calculated the difference (ΔAICc) in the conditional Akaike Information Criterion (AICc) between each SAR model and the corresponding null model,

which incorporates random spatial effects but excludes environmental variables. We then computed the evidence ratio (E) for the models by comparing those with environmental predictors to those with only random spatial effects. This is expressed as $E = wi / wj$, where *wi* represents the Akaike weight of the model that includes both environmental predictors and random spatial effects, and *wj* is the weight of the model that contains only random spatial effects. The evidence ratio provides empirical support for the model with environmental predictors in relation to the null model; specifically, models with *E* values greater than 10 indicate good support, while those with *E* values exceeding 100 demonstrate strong support (Burnham & Anderson, 2002).

RESULTS

Biogeographic regionalization

The number of bioregions and the position of their boundaries varied across different scenarios in both taxon-specific and phylogenetic bioregionalization schemes (Figure 1). In both cases, the number of bioregions increased in response to higher rarity strength (RSt) values. In the taxon-specific models (Figure 1a), increasing *RSt* from 1.0 to 2.0 resulted in progressively clearer and more distinct biogeographic regions from the outset. In contrast, the phylogenetic-based models (Figure 1b) exhibited less differentiation in earlier scenarios (s1 to s3), with more distinct bioregions emerging only from scenario 4 (*RSt* = 1.6), at which point the results began to align more closely with those observed in the taxon-specific analysis. We recognized as bioregions the areas composed of at least 10 grid cells, despite the designed boundaries between different regions. This threshold was established to balance spatial resolution with ecological relevance, ensuring that identified bioregions were not artifacts of fragmented or sparsely distributed occurrences. Previous studies in biogeography and macroecology have adopted similar approaches to define meaningful spatial units while avoiding over-segmentation due to small, isolated clusters (*e.g.* Vilhena & Antonelli, 2015; Ficetola et al., 2017). Additionally, using a minimum number of grid cells reduces the likelihood of defining bioregions based solely on outliers or transitional occurrences, which may not accurately reflect biogeographic structure (Laffan et al. 2016; Edler et al. 2023). This methodological decision ensures that bioregions are robust and biologically meaningful rather than statistical artifacts of the network partitioning process.

Therefore, we could identify five main bioregions (BRs) for birds within the Atlantic Forest: **BR1** – located in the extreme southern region, encompassing part of the mixed

Ombrophilous Forest; **BR2** – located to the east, encompassing the Serra do Mar and Mantiqueira mountains and a portion of the northern portion of the Atlantic Forest; **BR3** – located to the west, encompassing part of the Semideciduous Seasonal Forest; **BR4** – covers the extreme northern portion of the Atlantic Fores; **BR5** – extends from the extreme southern part of Bahia to the central part of Minas Gerais. According to this criterion, the three nested regions within the Serra do Mar (**NRs**) were not considered biogeographic regions. The five bioregions present congruencies with areas of endemism previously described for different taxa across the Atlantic Forest: Araucaria Forest (BR1), Bahia Coastal Forest (BR2), Alto Paraná (BR3), Pernambuco Area of Endemism (BR4) and Diamantina (BR5). We also identified transition zones between bioregions (Figure 2).

Regarding the species with the greatest relative presence in each bioregion (high score values), we observed that some bioregions presented a higher proportion of species recognized as Atlantic Forest endemics, according to expert assessments and literature records, while others included species with broader or transitional distributions. In BR1, species with a strong relative presence in this region, such as *Hemitriccus kaempferi*, *Formicivora acutirostris* and *Xanthopsar flavus*, are widely accepted as Atlantic Forest endemics. A similar pattern is observed in BR2, where species with the highest relative occurrence scores include Atlantic Forest endemics such as *Phylloscartes beckeri*, *Nemosia rourei, Thripophaga macroura* and *Pyriglena atra*. In BR4, the most representative species also align with known endemics, including *Phylloscartes ceciliae*, T*erenura sicki*, *Synallaxis infuscata*, and *Xiphorhynchus atlanticus*.

In contrast, in BR3 and BR5, several species with high relative occurrence scores are known to occur in transitional zones between the Atlantic Forest and neighboring biomes, such as the Cerrado and Caatinga. As a result, fewer strict Atlantic Forest endemic species are present in these regions. For instance, while *Campylopterus diamantinensis* and *Embernagra longicauda* were identified within these grids, both are recognized as endemics of the Espinhaço Range, a well-known transitional zone between the Cerrado, Caatinga, and Atlantic Forest domains. Given these considerations, we prioritized the interpretation of species with high occurrence scores that are consistently classified as part of the Atlantic Forest avifauna, reducing potential biases introduced by species with broad distributions across multiple biomes.

Correlates of biogeographic boundaries

For taxon-specific bioregions, spatially explicit models showed a strong fit to the data across all scenarios (ΔAICc > 8, evidence ratio (E) > 70; Figure 1, Table S1). Scenarios 5 and

6 yielded the best model fit, suggesting a robust correlation between environmental variables and biogeographic boundaries. The analysis revealed that the delineation of biogeographic boundaries is primarily influenced by present-day climatic heterogeneity and orographic barriers, with annual precipitation (p = 0.017 – 0.049), temperature seasonality (p = 0.018 – 0.052) and elevation heterogeneity (p = 0.035 – 0.050) emerging as key drivers. The results for phylogenetic-based bioregions were similar to the taxon-specific ones, except for the first three scenarios, for which no valid estimates could be generated to construct spatially explicit models due to the absence of valid boundaries. For the other three scenarios, spatially explicit models demonstrated strong model fit (ΔAICc > 8, evidence ratio (E) > 70; Figure 1, Table S1), especially Scenario 6. Annual precipitation (p = 0.019 – 0.049), temperature seasonality (p = 0.042 – 0.048) and elevation heterogeneity (p = 0.027 – 0.034) also showed up as the main boundary correlates. However, r^2 fixed for both taxon-specific (r^2 = 0.01 – 0.03) and phylogenetic models (r^2 = 0.04 – 0.09) were considerably low, suggesting that while the environmental variables contribute to bioregion delineation, they explain only a small proportion of the observed variation.

DISCUSSION

Our network-based biogeographic analysis revealed that taxon-specific bioregions align with areas of endemism reported for birds (Cracraft, 1985; Silva et al. 2004; Carvalho et al. 2017) and biogeographic regions identified for other taxa, such as non-volant mammals (Costa et al. 2000), frogs (Vasconcelos et al. 2014) and snakes (Moura et al. 2016; Barbo et al. 2020). This pattern emphasizes the dynamic interplay of historical and contemporary factors shaping biodiversity across the domain and reflects unique ecological and evolutionary processes (Carnaval et al. 2009; da Silva et al. 2024).

However, when incorporating phylogenetic data at lower rarity strength (RSt) values, we identified different patterns, suggesting that bioregionalization is highly dependent on how species relationships are weighted within the analysis. Lineages are broadly shared across bioregions, but distinct regionalization emerged only when increasing the RSt to prioritize range-restricted species with shorter phylogenetic branches (Daru et al. 2018; Edler et al. 2023). For example, under high RSt values (≥1.6), narrowly distributed taxa like *Phylloscartes beckeri* (BR2) and *Synallaxis infuscata* (BR4) – species with limited dispersal and recent divergence – strengthened boundaries, effectively transforming phylogenetic regionalization into patterns resembling taxonomic dissimilarity (Daru et al. 2017; Yusefi et al. 2019). This suggests that

weighting short-branched microendemics amplifies their spatial clustering, overriding deeper phylogenetic signals from widespread lineages. Such convergence between phylogenetic and taxonomic delineations mirrors findings in other fragmented systems, where fine-scale endemism drives regionalization more than evolutionary depth (Lavinia et al. 2019; Damasceno et al. 2021).

These findings also highlight the importance of carefully interpreting statistical classifications in bioregionalization frameworks. The *Infomap Bioregions* algorithm assigns a relative occurrence score to each species based on its spatial distribution across different grid cells (Edler et al. 2023). However, this score is derived solely from network structure, without considering species-specific ecological traits, historical biogeography, or habitat specialization. As a result, species with broad distributions – particularly those inhabiting transition zones – may receive high scores even if they are not strictly associated with a given bioregion. This likely explains why some species typically associated with the Cerrado or Caatinga, such as *Campylopterus diamantinensis* and *Embernagra longicauda*, were classified as highly frequent in BR3 and BR5. These species are known to occur predominantly in the Espinhaço Range, a transitional area between the Atlantic Forest and adjacent biomes. While the statistical classification does not contradict this biogeographic reality, it underscores the need to distinguish network-driven patterns from well-established ecological and evolutionary knowledge.

Notably, in bioregions such as BR1 and BR2, the species with the highest scores were more consistently aligned with known Atlantic Forest endemics. This is likely because these regions contain a higher proportion of species that are strongly associated with the biome, reducing the statistical influence of widespread taxa. For instance, *Hemitriccus kaempferi, Formicivora acutirostris* and *Xanthopsar flavus* in BR1, as well as *Phylloscartes beckeri, Nemosia rourei* and *Pyriglena atra* in BR2, exhibit both high relative occurrence scores and well-established endemism within the Atlantic Forest. Given these patterns, our interpretation prioritized species with high occurrence scores that are also recognized in the literature as Atlantic Forest taxa, ensuring that statistical outputs align with biologically meaningful bioregionalization.

By integrating network-based and phylogenetic approaches, while considering bird ecology and natural history, our framework effectively captures the multifaceted nature of biogeographic structuring in the Atlantic Forest. Unlike clustering methods that rely solely on species co-occurrence, our approach incorporates lineage relationships, allowing the detection

of evolutionary signals even in fragmented or discontinuous distributions (Edler et al. 2023). This is particularly relevant in highly degraded landscapes, where historical connectivity has been disrupted by anthropogenic changes (Haddad et al. 2015; Pizo & Tonetti, 2020). However, the sensitivity of phylogenetic biogeographic methods to parameter adjustments underscores the importance of integrating multiple analytical approaches to achieve a robust understanding of species distribution and evolutionary history.

Narrow-range bird species

Previous phylogenetic analyses suggest that shared evolutionary histories, particularly among clades that diversified during different geological periods, contribute to biogeographic structure (Carnaval et al. 2009; Rull, 2011). In contrast, the lack of clear phylogenetic patterns in earlier scenarios with low rarity strength values could indicate that widespread species with weaker phylogenetic signals obscure the deeper evolutionary imprints of range-restricted species in our analysis. By adjusting the weight for species with narrow distributions, we enhanced the resolution of bioregional boundaries, revealing nuanced patterns that reflect historical isolation and environmental specialization (Bloomfield et al. 2017). As RSt values increased, the spatial configuration of several bioregions changed and the number of distinct bioregions rose, reflecting the growing contribution of range-restricted species to the delineation of spatial boundaries. This effect was particularly pronounced in regions such as BR2 (Bahia Coastal Forest) and BR4 (Pernambuco Area of Endemism), where highly localized species reshaped biogeographic structures. The emergence of BR3 as a distinct bioregion in later scenarios further underscores the influence of evolutionary processes operating at different temporal and spatial scales, reinforcing the need to integrate both phylogenetic and distributional data in biogeographic studies (Batalha-Filho et al. 2013; Daru et al. 2018).

The identification of these regions aligns with previous research emphasizing the evolutionary importance of microendemic species in defining biodiversity hotspots (Cabanne et al. 2016; Araujo et al. 2024). These findings suggest that narrow-range species, often sensitive to environmental fluctuations, act as biogeographic markers, reflecting historical isolation and habitat specialization processes (Carvalho et al. 2017; Calatayud et al. 2019). It also indicates a scale-dependent interaction between ecological and evolutionary processes, where the relative importance of phylogeny becomes more pronounced at finer spatial or temporal scales (Daru et al. 2017; Smith & Brown, 2018; Antonelli, 2017; Carta et al. 2022).

Biogeographic boundaries and environmental correlates

The results of the spatially explicit models reinforce a biogeographic structure within the Atlantic Forest, as annual precipitation, temperature seasonality and elevation heterogeneity were found to be the main drivers of biogeographic boundaries for both taxon-specific and phylogenetic-based bioregions. This indicates that on a macroecological scale, present-day climatic heterogeneity and orographic barriers might play a major role in shaping the distribution of bird communities across the domain. The congruence between bioregions and areas of endemism highlights the intertwined roles of historical processes and contemporary environmental conditions in shaping the evolutionary biogeography of the Atlantic Forest and its avifauna. Climatic heterogeneity fosters a variety of ecological niches, which supports species with distinct physiological and ecological tolerances (Ficetola et al. 2017; Calatayud et al. 2019).

The identification of BR2 and BR4 as distinct bioregions is consistent with previous studies that emphasize the role of climatic heterogeneity in promoting species persistence and endemism (Rull, 2011; Carnaval et al. 2014). Topographic barriers such as the Serra do Mar, Serra da Mantiqueira and Espinhaço Range also emerged as critical determinants of biogeographic boundaries. These mountain ranges create elevation gradients that drive speciation by isolating populations and promoting ecological specialization (Dantas et al. 2011; Chaves et al. 2014; Costa et al., 2022). The endemism observed in BR2 may be attributed to the region's climatic stability and complex topography, which have promoted both speciation and the persistence of relict populations (Cabanne et al. 2008; Carnaval et al. 2009). This region is marked by high rainfall and topographical complexity, generating diverse microhabitats that promote speciation and endemism (Chaves et al. 2014; Araujo et al. 2024). Notable endemic species, such as *Phylloscartes beckeri*, *Tangara brasiliensis* and *Myrmotherula urosticta*, persist due to the region's climatic stability and rugged landscape, emphasizing the role of montane environments as biodiversity reservoirs (Chaves et al. 2014). On the other hand, BR4 stands out as a distinct bioregion in the northern portion of the Atlantic Forest due to its unique climatic conditions, isolated coastal forests, historical isolation and high concentration of range-restricted species (Araujo et al. 2023). This region encompasses a complex mosaic of forest types, including moist lowland forests and seasonal forests, which contribute to its high levels of avian endemism and consequent vulnerability to deforestation and habitat fragmentation (Araujo et al. 2023).

In contrast, the velocity of climatic changes during the late Quaternary did not show a significant correlation with biogeographic boundaries, highlighting that regional differentiation is not solely a product of past climatic events. Instead, contemporary climatic heterogeneity continues to influence species distributions across the domain. The same is observed for riverine barriers, which did not show a significant correlation with biogeographic boundaries, suggesting that rivers may play a secondary role in shaping avian distribution compared to climatic and topographic factors (Carvalho et al. 2017). However, the proportion of variation explained by the models including the environmental variables is considerably low when compared to the proportion of variation explained by random effects. The weak explanatory power might indicate that additional factors, such as species-specific ecological traits, dispersal limitations and unmeasured historical processes may be influencing biogeographic boundaries in ways not captured by present-day climatic and topographic variables (Cabanne et al. 2016; Pigot et al. 2016).

Moreover, evolutionary responses of Atlantic Forest bird populations to historical range shifts appear to vary considerably, which may account for the mixed evidence found in single-species studies on how past habitat changes influenced population evolution (Cabanne et al., 2016). Likely, each species adapted differently to forest dynamics based on factors such as their specific ecological traits and population histories (Machac, 2020; Tonetti et al. 2023). This aligns with findings from other tropical forests, where different species and communities exhibit diverse responses to environmental changes (Carnaval et al. 2014; Smith et al. 2014; da Silva et al. 2024). Such variability suggests that relying on biome-wide refugia models may not accurately capture the refugial patterns of individual species, supporting the view that species-specific refugia models are often more appropriate (Rull, 2011; Porto et al. 2013). It might influence our results, considering that past climatic conditions did not appear as a major boundary correlate.

Transition zones

Transition zones emerged prominently in our analysis, particularly in the Serra do Mar and Serra da Mantiqueira areas. This result may reflect the timing of species diversification influenced by past geological events and climatic oscillations (Calatayud et al. 2019; Morrone, 2024). Quaternary climatic fluctuations and forest fragmentation have driven cycles of expansion and contraction, promoting speciation and endemism within the Atlantic Forest (Cabanne et al. 2016; Carnaval et al. 2014). These processes are reflected in the evolutionary divergence of sister species across domains, such as *Xiphorhynchus fuscus*, which exhibits

phylogeographic splits between northern and southern populations (Cabanne et al. 2008). Additionally, the bioregions identified in our study suggest historical connectivity between the Atlantic and the Amazon forests, mediated by forest corridors during favourable climatic periods (Costa et al. 2003; Santos et al. 2007). This connection is evidenced by shared lineages and dispersal events in species like *Xiphorhynchus fuscus* and other Amazon-Atlantic taxa (Batalha-Filho et al. 2013; Ledo & Colli, 2017). These findings reinforce the idea that transition zones are not merely boundaries, but areas of active biotic interchange shaped by evolutionary and environmental processes (Ferro & Morrone, 2014; Morrone, 2018).

Bioregionalization frameworks and bird conservation in the Atlantic Forest

The identification of biogeographic regions and transition zones in the Atlantic Forest has significant implications for bird conservation, providing a spatially explicit framework for designing and managing protected areas. For instance, BR2 and BR4 host exceptional concentrations of microendemic species that are highly vulnerable to habitat loss, and whose survival hinges on targeted habitat protection (Araujo et al. 2024; Joly et al. 2014). However, as highlighted in Figure 3, current protected areas (PAs) remain insufficient to safeguard these hotspots under projected climate scenarios, as fragmentation and anthropogenic pressures exacerbate extinction risks (Tonetti et al. 2023; Vancine et al. 2024). Only ~110,000 km² (approximately 8% of the total area) is officially protected, and many protected areas are disproportionately distributed and disconnected, limiting their effectiveness in preventing species declines (WWF, 2017). Therefore, accounting for spatial, ecological and evolutionary factors when delineating priority areas would be a more effective strategy (Hoffmann, 2020; Araujo et al., 2024).

In this context, transition zones between the Atlantic Forest and other domains might act as ecological corridors, facilitating gene flow for climate-vulnerable species and mitigating the risk of local extinctions (Vale et al. 2018; Peixoto et al. 2020; Hoffmann, 2020; Yusefi, 2021). The protection of these connectivity areas is critical given the increasing fragmentation of the Atlantic Forest, which has already lost over 80% of its original vegetation cover (Joly et al. 2014; Vancine et al. 2024). Conservation planning that incorporates biogeographic data can ensure the establishment of protected areas that align with ecological boundaries rather than arbitrary administrative boundaries, improving their long-term effectiveness in safeguarding biodiversity (Myers et al. 2000; Whittaker & Ladle, 2011; Hoffmann, 2020).

Integrating phylogenetic data further strengthens conservation prioritization by identifying regions that harbour unique evolutionary lineages and phylogenetic diversity. For

instance, BR1 and BR4 stand out as phylogenetic hotspots, preserving not only high species richness but also deep evolutionary lineages (Farooq et al. 2020; Edler et al. 2023). This approach shifts focus from static species counts to dynamic metrics like phylogenetic diversity and endemism, addressing limitations of traditional conservation frameworks by focusing on protecting evolutionary processes that maintain ecosystem resilience and adaptive potential in the face of climate change (Tonetti et al. 2023; Joly et al. 2014). This is particularly relevant as the Atlantic Forest is projected to undergo further climatic shifts, which will likely alter species distributions and exacerbate extinction risks (Whittaker & Ladle, 2011; Yusefi, 2021).

On a broader perspective, future research should focus on adopting a multi-taxon approach to identify conservation priorities that extend beyond birds to other vertebrates and invertebrates, which may exhibit distinct biogeographic patterns due to differing dispersal capabilities and ecological requirements (Araujo et al. 2024; da Silva et al. 2024). Additionally, integrating ecological, spatial and genomic data could provide insights into past range shifts and inform adaptive conservation strategies under future climate scenarios (Bhakti et al. 2018; Damasceno et al. 2021). Expanding this framework beyond the Atlantic Forest to other biodiversity hotspots worldwide would further refine conservation strategies through comparative and evolutionary perspectives, ensuring that biogeographic and phylogenetic data contribute meaningfully to global biodiversity conservation efforts.

CONCLUSIONS

Our study advances the understanding of Atlantic Forest biogeography by integrating network-based and phylogenetic approaches to delineate bioregions and transition zones, revealing complex interactions between historical, ecological, and evolutionary processes. Taxon-specific bioregions align with known areas of endemism for birds and other taxa, underscoring the role of contemporary climatic heterogeneity and topographic barriers (*e.g.*, Serra do Mar) in shaping biodiversity patterns. However, incorporating phylogenetic data uncovered novel regionalization driven by microendemic species under high rarity strength (RSt) values, emphasizing the importance of prioritizing range-restricted taxa in biogeographic analyses. Transition zones, particularly in montane regions, emerged as critical corridors for biotic interchange, reflecting Pleistocene-driven diversification and historical connectivity with the Amazon.

For conservation, our findings highlight the urgency of expanding protected areas (PAs) in microendemic hotspots like BR2 (Bahia Coastal Forest) and BR4 (Pernambuco Area of

Endemism), where anthropogenic pressures threaten irreplaceable lineages such as *Phylloscartes beckeri* and *Synallaxis infuscata*. Align PAs with biogeographic boundaries rather than administrative limits and prioritize connectivity in transition zones will enhance resilience to climate change (Tonetti et al. 2023; Vancine et al. 2024). Integrating phylogenetic metrics into conservation planning – focusing on regions with high evolutionary distinctiveness – ensures the preservation of adaptive potential and ecosystem resilience (Edler et al., 2023; Araujo et al., 2024).

Future research should focus on multi-taxon frameworks to capture cross-system biodiversity dynamics (Araujo et al. 2024). Combining ecological, spatial and genomic data at different scales will clarify historical drivers of bioregion shifts and refine climate-adaptive strategies (Damasceno et al. 2021; Banks-Leite et al. 2024). Expanding this approach globally, particularly in fragmented *hotspots* like the Atlantic Forest, will strengthen conservation biogeography through comparative evolutionary insights (Whittaker & Ladle, 2011; Yusefi, 2021). By bridging ecological and evolutionary perspectives, our work provides a template for conserving the Atlantic Forest avian community and other hyperdiverse yet threatened ecosystems worldwide.

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FIGURES

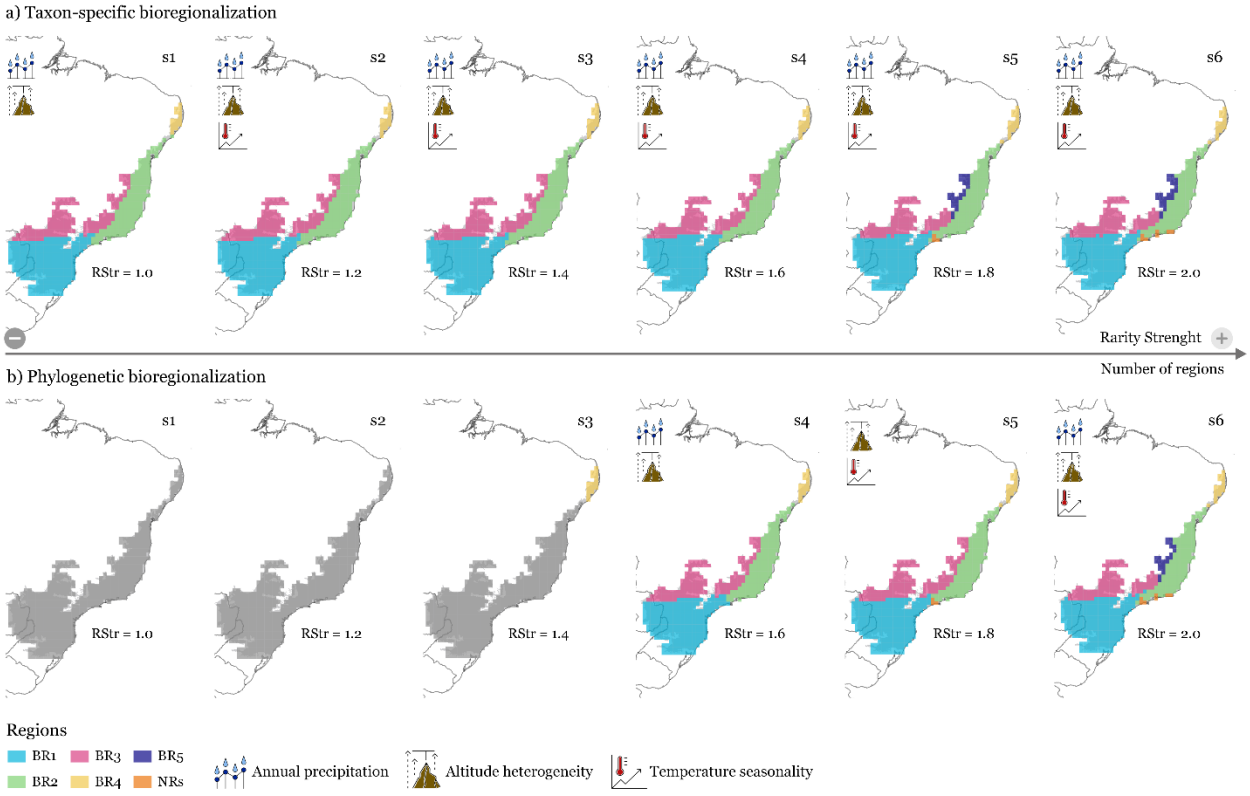

Figure 1. Biogeographic (BRs) and Nested (NRs) regions identified for birds in the Atlantic Forest. The results are categorized into six scenarios (s1–s6) according to the rarity strength (RSt) applied in the analysis. The environmental variables which showed a significative correlation to the delimitation of the boundaries between bioregions are also highlighted in each scenario. **(a)** Taxon-specific bioregions, based only on distribution data; **(b)** Phylogenetic bioregions, identified by incorporating a phylogenetic tree of the species into the analysis.

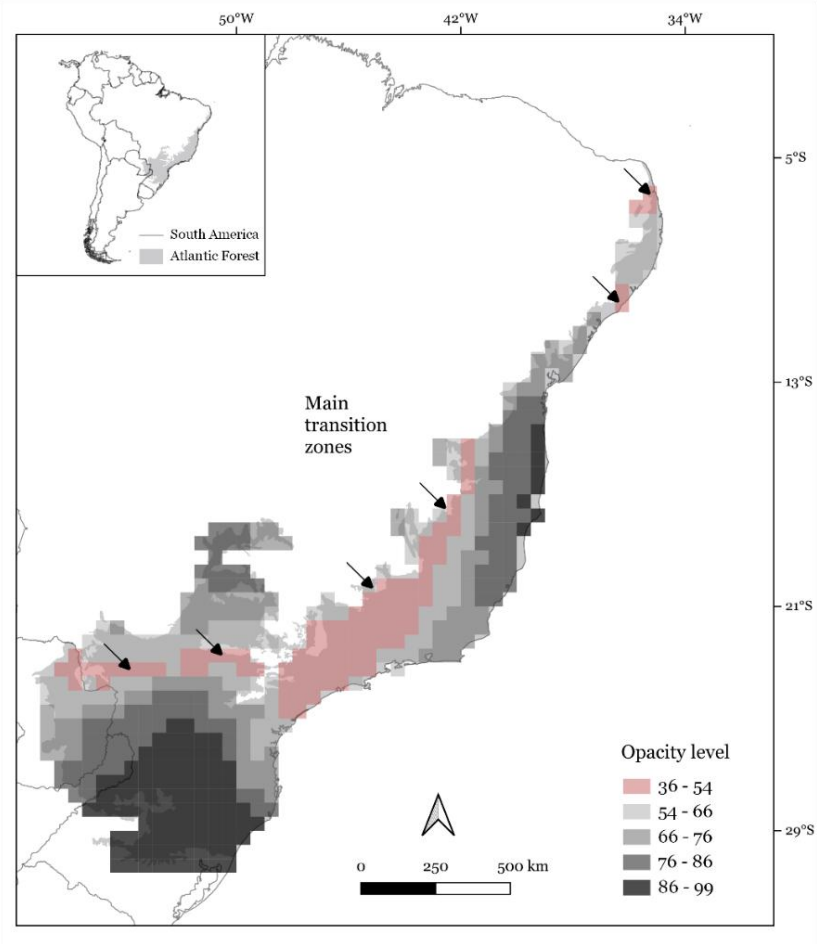

Figure 2. Transition zones between bioregions, identified in the *Infomap Bioregions 2.0*. (Edler et al. 2017; Edler et al. 2023). The transition zones are highlighted based on the participation coefficient, which quantifies the degree to which each node is connected to other modules. The opacity of each grid cell corresponds to the fraction of connected species that belong to the same module, weighted by the link strength of each species. Thus, areas with greater interpolation are represented by grids with lower opacity levels (lighter colours, highlighted in red), indicating a more transitional character, whereas grids with higher opacity (darker colours) levels suggest stronger affiliation to a specific bioregion.

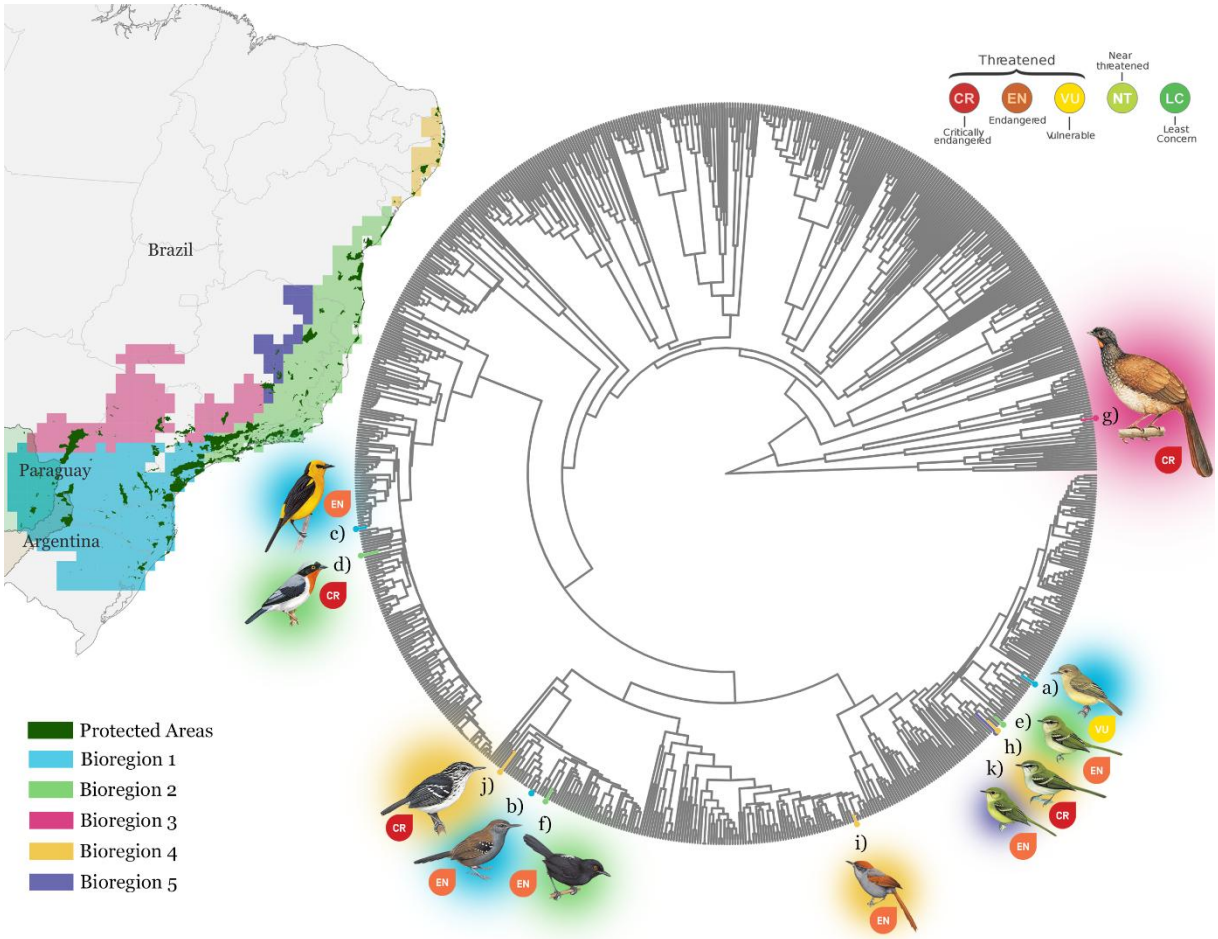

Figure 3. Biogeographic regionalization of Atlantic Forest birds integrating species distribution and phylogenetic data, highlighting some of the endemic, endangered species and their respective conservation status following IUCN criteria (IUCN, 2024). Each bioregion is represented by a distinct colour, as well as its related species: **Bioregion 1** (Blue) – Southern Atlantic Forest (Araucaria forests): **(a)** *Hemitriccus kaempferi*, **(b)** *Formicivora acutirostris* (male) and **(c)** *Xanthopsar flavus* (male); **Bioregion 2** (Green) – Serra do Mar and Central Atlantic Forest: **(d)** *Nemosia rourei*, **(e)** *Phylloscartes beckeri* and **(f)** *Pyriglena atra* (male); **Bioregion 3** (Pink) – Western Atlantic Forest (transition with Cerrado): **(g)** *Ortalis remota*; **Bioregion 4** (Yellow) – Northeastern Atlantic Forest (Pernambuco Area of Endemism): **(h)** *Phylloscartes ceciliae*, **(i)** *Synallaxis infuscata* and **(j)** *Terenura sicki* (male); **Bioregion 5** (Purple) – Diamantina: **(k)** *Phylloscartes roquettei*. Dark green polygons indicate existing Protected Areas within the domain (UNEP–WCMC & IUCN, 2025). Bird species illustrations retrieved from Birds of the World (2022).

SUPPLEMENTARY MATERIAL

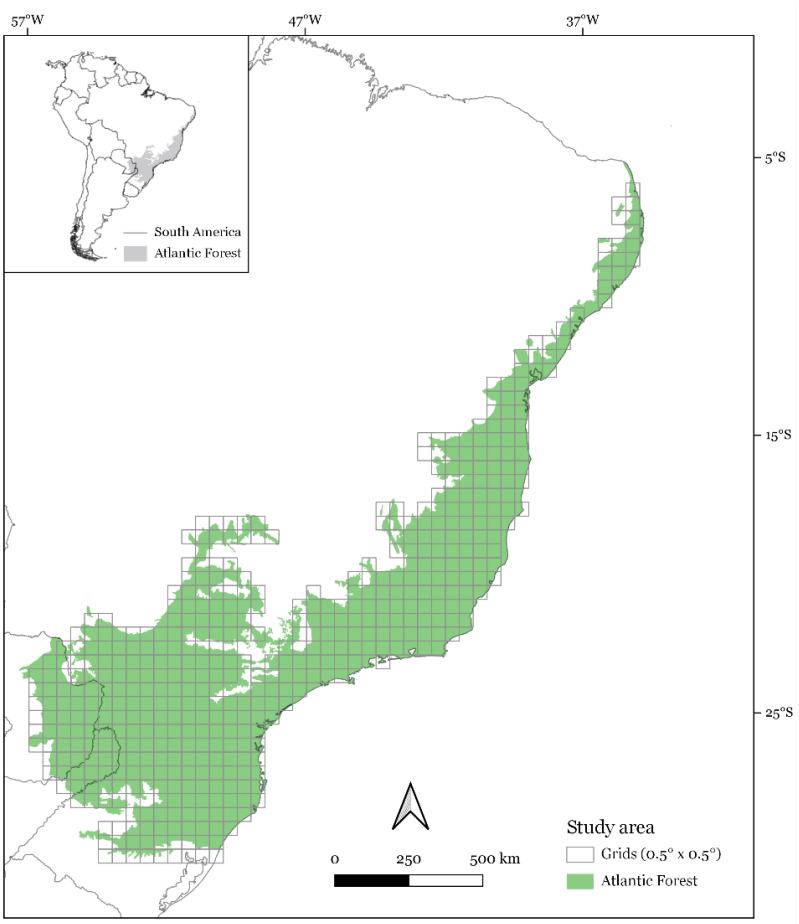

Figure S1. Map of the Atlantic Forest domain used as the reference for building the 50x50 km grid matrix applied in the biogeographic analyses. Delimitation adapted from the consensual limit proposed by Muylaert et al. (2018).

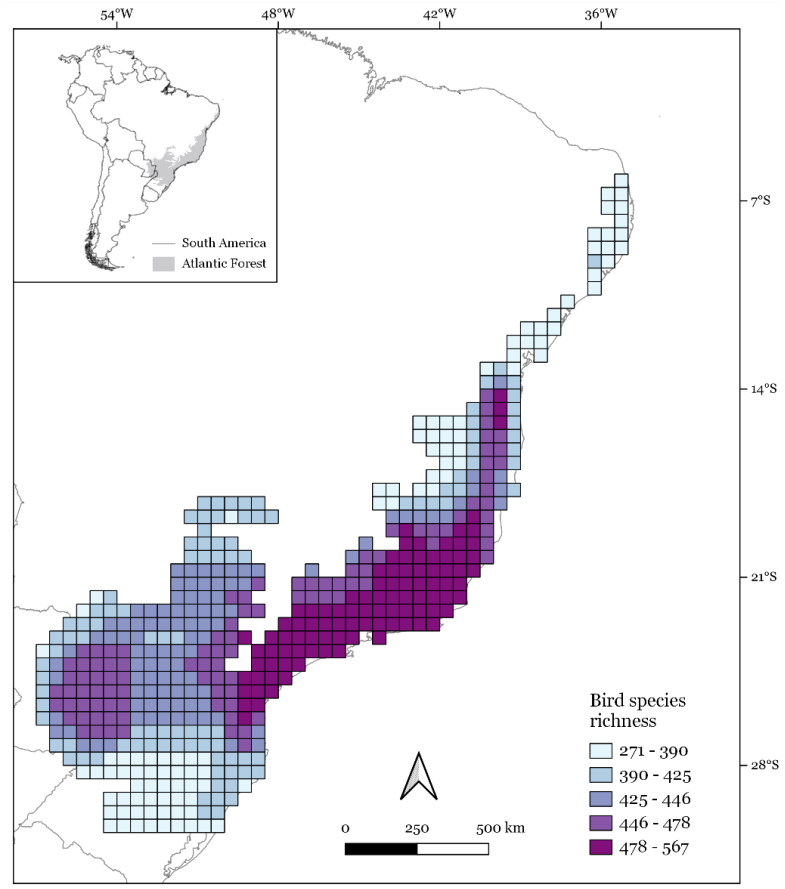

Figure S2. Geographical distribution pattern of bird species richness in the Atlantic Forest based on a matrix of grids at a resolution of 50x50km.

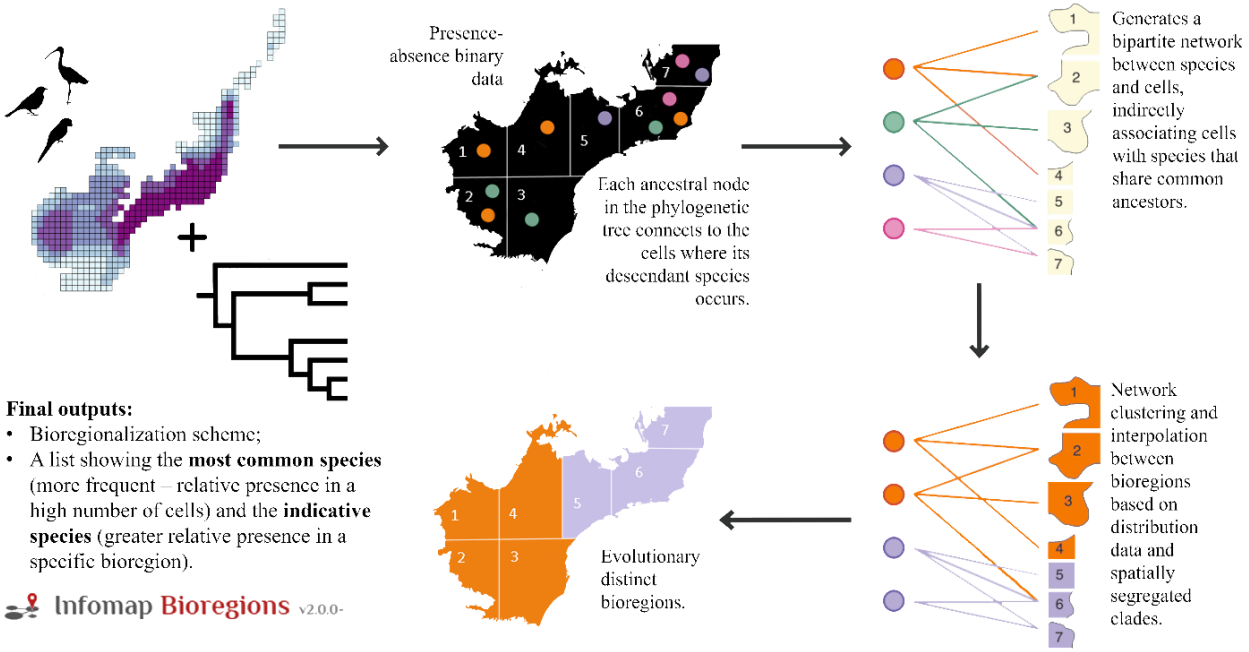

Figure S3. Step-by-step illustration of how *Infomap Bioregions* generates bioregions from species distribution data (adapted from Edler et al. 2017).

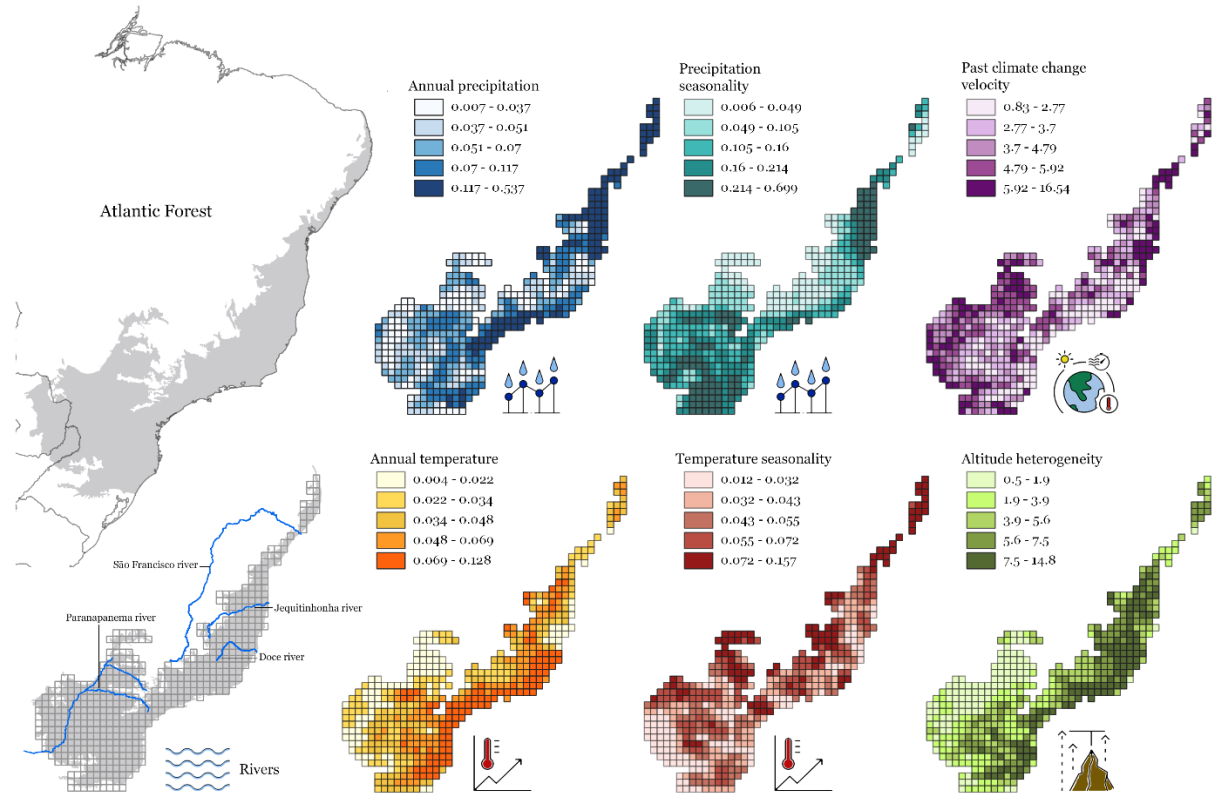

Figure S4. Spatial variation of six key environmental correlates of biogeographic boundaries within the Atlantic Forest. Each grid cell represents a 50x50km resolution unit.

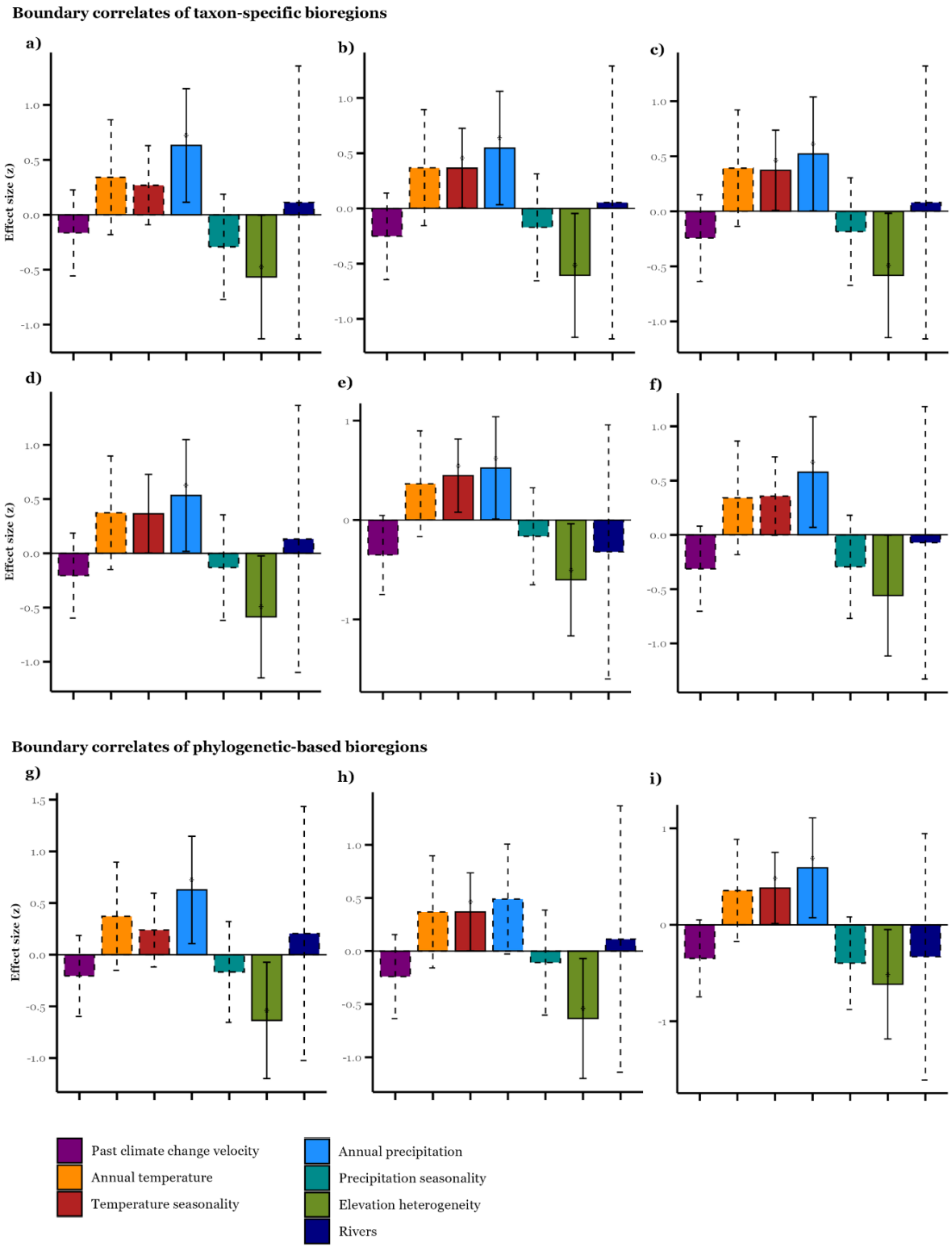

Figure S5. Relationships between environmental variables and the position of biogeographical boundaries of **(a)** taxon-specific and **(b)** phylogenetic-based models. Bars represent the effect sizes (from autoregressive regression models) of each variable in explaining the boundaries between bioregions in different scenarios (rarity strength values). Dashed lines indicate non-significant effects. Effect size was assessed using Fisher's z; error bars are 95% confidence intervals of z.

TABLE S1 – Results of the spatially explicit regression models (simultaneous binomial autoregressive models) evaluate the strength of relationships between the position of biogeographic boundaries among bioregions and potential environmental covariates. The model could not be calculated for the three first scenarios of the phylogenetic regionalization analysis, β = regression coefficients; *SE* = standard error; ΔAICc = difference in the conditional Akaike information criterion between each model and the corresponding model that includes spatial random effects but excludes environmental variables; *E* = evidence ratio of the model; r^2 = refers to the proportion of variation explained by the fixed terms of the model.

Taxon-specific bioregions					
Scenario	**Environmental variables**	***β***	**SE**	***t***	***p***
1 (*RSt* = 1.0)	Past climate change velocity	-0.1653	0.200	-0.825	0.410
	Annual precipitation	0.632	0.264	2.393	**0.017**
	Annual temperature	0.342	0.267	1.284	0.200
	Precipitation seasonality	-0.293	0.245	-1.194	0.233
	Temperature seasonality	0.269	0.184	1.463	0.144
	Elevation heterogeneity	-0.567	0.287	-1.977	**0.049**
	Rivers	0.112	0.634	0.176	0.860
		Model fit	**ΔcAIC** = 8.62	r^2 = 0.03	***E*** = 74.30
2 (*RSt* = 1.2)	Past climate change velocity	-0.252	0.200	-1.259	0.209
	Annual precipitation	0.547	0.262	2.089	**0.037**
	Annual temperature	0.369	0.26768	1.38	0.168
	Precipitation seasonality	-0.171	0.247	-0.691	0.490
	Temperature seasonality	0.365	0.184	1.977	**0.049**
	Elevation heterogeneity	-0.606	0.286	-2.119	**0.035**
	Rivers	0.054	0.630	0.085	0.932
		Model fit	**ΔcAIC** = 10.41	r^2 = 0.02	***E*** = 182.22
3 (*RSt* = 1.4)	Past climate change velocity	-0.243	0.201	-1.206	0.228
	Annual precipitation	0.521	0.264	1.974	**0.049**
	Annual temperature	0.392	0.270	1.453	0.147
	Precipitation seasonality	-0.184	0.249	-0.738	0.461
	Temperature seasonality	0.372	0.186	2.002	**0.046**
	Elevation heterogeneity	-0.583	0.288	-2.022	**0.044**
	Rivers	0.080	0.632	0.126	0.900
		Model fit	**ΔcAIC** = 10.07	r^2 = 0.02	***E*** = 153.38
4 (*RSt* = 1.6)	Past climate change velocity	-0.206	0.200	-1.03	0.304
	Annual precipitation	0.533	0.263	2.029	**0.043**
	Annual temperature	0.374	0.267	1.401	0.162
	Precipitation seasonality	-0.132	0.248	-0.533	0.594
	Temperature seasonality	0.365	0.185	1.97	**0.050**
	Elevation heterogeneity	-0.586	0.287	-2.046	**0.041**
	Rivers	0.132	0.628	0.209	0.834

		Model fit	**ΔcAIC** = 9.57	r^2 = 0.05	***E*** = 119.66
5 (*RSt* = 1.8)	Past climate change velocity	-0.352	0.203	-1.739	0.083
	Annual precipitation	0.524	0.263	1.992	**0.047**
	Annual temperature	0.365	0.271	1.344	0.180
	Precipitation seasonality	-0.164	0.249	-0.656	0.512
	Temperature seasonality	0.447	0.188	2.376	**0.018**
	Elevation heterogeneity	-0.602	0.288	-2.088	**0.037**
	Rivers	-0.321	0.652	-0.491	0.624
		Model fit	**ΔcAIC** = 13.51	r^2 = 0.02	***E*** = 858.88
6 (*RSt* = 2.0)	Past climate change velocity	-0.313	0.200	-1.569	0.117
	Annual precipitation	0.578	0.260	2.224	**0.027**
	Annual temperature	0.341	0.267	1.281	0.201
	Precipitation seasonality	-0.295	0.243	-1.216	0.225
	Temperature seasonality	0.357	0.184	1.946	0.052
	Elevation heterogeneity	-0.559	0.284	-1.97	**0.050**
	Rivers	-0.073	0.640	-0.114	0.910
		Model fit	**ΔcAIC** = 12.53	r^2 = 0.01	***E*** = 526.02

Phylogenetic bioregions					
Scenario	**Environmental variables**	***β***	**SE**	***t***	***p***
4 (*RSt* = 1.6)	Past climate change velocity	-0.206	0.200	-1.027	0.305
	Annual precipitation	0.627	0.265	2.363	**0.019**
	Annual temperature	0.372	0.267	1.394	0.164
	Precipitation seasonality	-0.167	0.249	-0.669	0.504
	Temperature seasonality	0.239	0.182	1.313	0.190
	Elevation heterogeneity	-0.636	0.287	-2.215	**0.027**
	Rivers	0.205	0.627	0.328	0.743
		Model fit	**ΔcAIC** = 8.93	r^2 = 0.09	***E*** = 87.12
5 (*RSt* = 1.8)	Past climate change velocity	-0.241	0.202	-1.195	0.233
	Annual precipitation	0.490	0.264	1.858	0.064
	Annual temperature	0.369	0.269	1.373	0.171
	Precipitation seasonality	-0.109	0.252	-0.432	0.666
	Temperature seasonality	0.369	0.187	1.98	**0.048**
	Elevation heterogeneity	-0.635	0.288	-2.209	**0.028**
	Rivers	0.113	0.640	0.177	0.860
		Model fit	**ΔcAIC** = 8.74	r^2 = 0.04	***E*** = 79.14
6 (*RSt* = 2.0)	Past climate change velocity	-0.348	0.203	-1.713	0.087
	Annual precipitation	0.591	0.264	2.24	**0.026**
	Annual temperature	0.356	0.270	1.317	0.189
	Precipitation seasonality	-0.398	0.245	-1.627	0.105
	Temperature seasonality	0.382	0.188	2.036	**0.042**
	Elevation heterogeneity	-0.616	0.289	-2.131	**0.034**
	Rivers	-0.332	0.652	-0.510	0.610
		Model fit	**ΔcAIC** = 15.07	r^2 = 0.04	***E*** = 1869.85

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3. CONSIDERAÇÕES FINAIS

Os resultados deste estudo contribuem para o avanço do conhecimento sobre a biogeografia da Mata Atlântica ao integrar abordagens baseadas em redes e filogenia na delimitação de biorregiões e zonas de transição. A forte congruência entre as biorregiões identificadas e as áreas de endemismo previamente descritas para aves e outros grupos taxonômicos reforça o papel da heterogeneidade climática e das barreiras topográficas na estruturação da biodiversidade do domínio. No entanto, a inclusão de dados filogenéticos revelou novos padrões, destacando a importância das espécies microendêmicas na delimitação de biorregiões, especialmente sob altos valores do parâmetro de força de raridade (RSt). Além disso, a identificação de zonas de transição, especialmente em áreas montanhosas e nos ecótonos com o Cerrado e a Caatinga, evidencia sua importância como corredores ecológicos e sua conexão histórica com outros domínios.

Do ponto de vista conservacionista, os resultados indicam que a atual rede de áreas protegidas (APs) na Mata Atlântica é insuficiente para garantir a preservação da diversidade de aves, especialmente em regiões de microendemismo como a BR2 (Florestas Costeiras da Bahia) e a BR4 (Centro de Endemismo de Pernambuco). A ampliação e melhor distribuição das APs, considerando as fronteiras biogeográficas em vez de limites administrativos, pode contribuir para a proteção de linhagens evolutivamente distintas e espécies vulneráveis, como *Phylloscartes beckeri* e *Synallaxis infuscata*. Além disso, a manutenção da conectividade entre biorregiões, especialmente nas zonas de transição, é essencial para garantir a persistência das espécies diante das mudanças ambientais.

Diante disso, recomenda-se que futuros estudos adotem abordagens multi-táxon e multi-escala, incorporando dados paleoecológicos e genômicos para aprofundar a compreensão dos processos evolutivos que moldam os padrões biogeográficos. Além de contribuir para a delimitação de regiões prioritárias para a conservação, a integração de múltiplas perspectivas biogeográficas pode subsidiar políticas públicas mais eficazes na proteção da biodiversidade, especialmente em *hotspots* fragmentados como a Mata Atlântica. Ao unir informações ecológicas e evolutivas, este estudo oferece um modelo aplicável não apenas à conservação da avifauna da Mata Atlântica, mas também a outros ecossistemas tropicais ameaçados.

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