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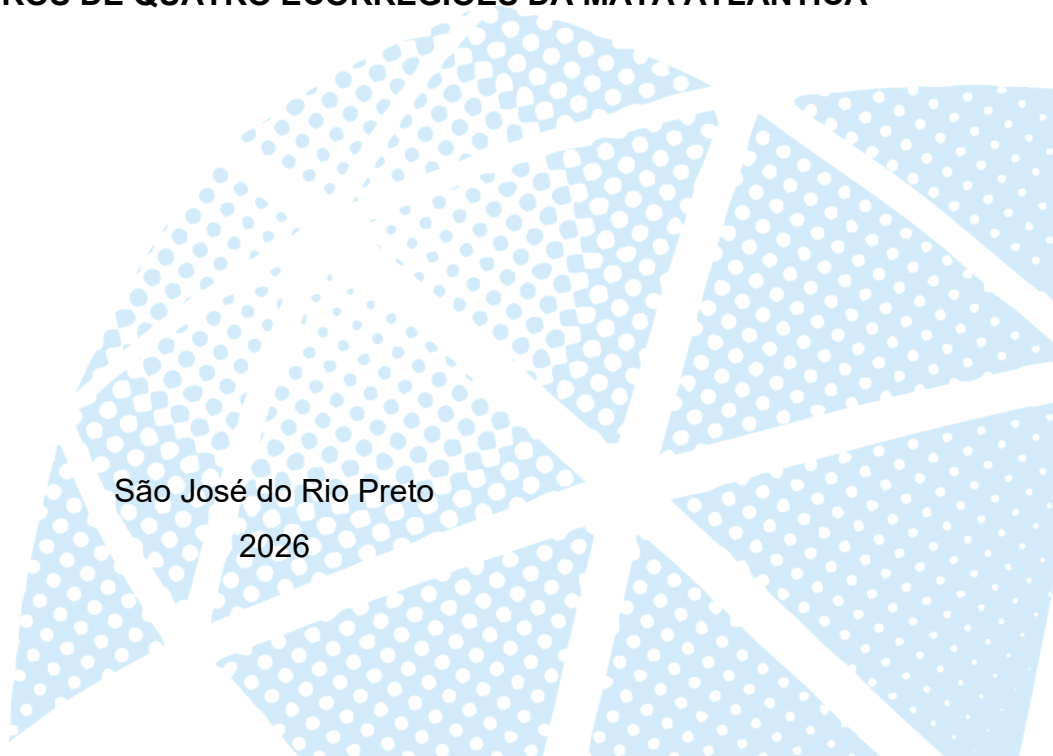
Ibilce - Instituto de Biociências, Letras e Ciências Exatas - Câmpus de São José do Rio Preto

ALEXANDRE POLETTINI NETO

O EFEITO DA PERDA FLORESTAL NA BIODIVERSIDADE TAXONÔMICA E FUNCIONAL DE ANUROS DE QUATRO ECORREGIÕES DA MATA ATLÂNTICA



São José do Rio Preto

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Tese apresentada à Universidade Estadual Paulista (UNESP), Ibilce – Instituto de Biociências, Letras e Ciências Exatas – Campus de São José do Rio Preto, para obtenção do título de Doutor em Biodiversidade – área de concentração: ecologia e comportamento.

Orientador(a): Prof. Dr. Fernando Rodrigues da Silva

Coorientador(a): Prof. Dr. Denise de Cerqueira Rossa-Feres

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IMPACTO SOCIAL

Os resultados desta pesquisa podem apoiar gestores ambientais e formuladores de políticas públicas na definição de estratégias mais eficazes para conservar a Mata Atlântica, indicando quais grupos de espécies são mais vulneráveis à perda florestal e quais regiões demandam maior prioridade para conservação e restauração (ODS 15).

SOCIAL IMPACT

The results of this study can support environmental managers and policymakers in developing more effective strategies for conserving the Atlantic Forest by identifying which species groups are most vulnerable to forest loss and which regions should be prioritized for conservation and restoration efforts (SDG 15).

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Instituto Nacional da Mata Atlântica

Dedico este doutorado aos meus pais Angela e Luiz e à minha avó Etelvina (*in memoriam*).

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Meu tapete é de folhas e galhos
Cipós e espinhos são meu escudo
Um chão de painas: meu céu

A sombra que aconchega
E a luz que multiplica os verdes:
Moram em mim cores que curam

Meu cheiro é de terra e água
E é no silêncio do caminhar das onças
Que surge a música feita de pássaros

Da aspereza dos troncos à sutileza das flores
Posso ser generosa ou hostil se preciso
Equilíbrio é minha arte: o balanço da existência

Uma rede intrincada me sustenta
Sou casa de feras e espíritos
A diversidade infinda de vida me faz bela

Sou mata, sou mãe
Sou guardiã da memória de eras
Sou Floresta

(Floresta - Alexandre Polettini Neto)

RESUMO

A perda florestal é um dos vetores mais predominantes da perda de biodiversidade. No entanto, ainda há pouca compreensão sobre como o impacto da perda florestal sobre a biodiversidade varia entre regiões com diferentes histórias biogeográficas e entre espécies com diferentes traços ecológicos. Neste estudo, integramos abordagens biogeográfica e de ecologia de paisagem para avaliar o efeito da perda florestal sobre espécies de anuros, especialistas ou generalistas, em quatro ecorregiões da Mata Atlântica. Compilamos dados de 168 estudos de comunidades de anuros realizados entre 1986 e 2024, abrangendo 330 paisagens e 299 espécies. As ocorrências foram organizadas espacialmente utilizando buffers com raio de 2,5 km ao redor dos locais de amostragem, e a perda florestal foi quantificada dentro de cada buffer utilizando mapas de cobertura do solo. Consideramos quatro ecorregiões da Mata Atlântica brasileira: Sudeste Interior, Sudeste Litorâneo, Nordeste Litorâneo e Sul. No primeiro capítulo, analisamos o efeito da perda florestal na riqueza de espécies de anuros especialistas de floresta, de áreas abertas e generalistas, investigando se esses efeitos eram consistentes entre as ecorregiões. Utilizamos um modelo linear misto generalizado multinominal e verificamos que os efeitos da perda florestal variam entre os grupos de uso de habitat, mas são consistentes entre as ecorregiões. Espécies especialistas de floresta responderam negativamente à perda florestal, enquanto a riqueza de espécies generalistas apresentou pequena redução e a riqueza de espécies de áreas abertas aumentou. Ao considerar conjuntamente o contexto ecorregional e a especialização de habitat, este estudo amplia a compreensão das respostas dos anuros à perda florestal e subsidia estratégias de conservação mais eficazes. No segundo capítulo, investigamos como a perda florestal afeta a diversidade funcional e traços específicos das comunidades de anuros nas quatro ecorregiões. Utilizamos modelos lineares generalizados para avaliar os efeitos da perda florestal sobre a riqueza funcional, a dispersão funcional e respostas específicas de traços, com foco no tamanho corporal e em características reprodutivas. A perda florestal reduziu consistentemente a dispersão funcional, indicando aumento da filtragem ambiental e convergência de traços em direção a estratégias generalistas. Em contraste, a riqueza funcional permaneceu inalterada, sugerindo dinâmicas compensatórias, nas quais perdas de espécies são compensadas pela substituição por espécies funcionalmente semelhantes. As respostas específicas de traços revelaram declínios em estratégias reprodutivas dependentes de floresta, como reprodução em riachos, oviposição em serapilheira e desenvolvimento direto, e aumentos em traços associados a ambientes abertos e mais secos, incluindo reprodução em corpos d'água temporários, ninhos de espuma e maior tamanho corporal. Essas respostas variaram entre as ecorregiões, com efeitos mais fortes nas ecorregiões costeiras e mais fracos ou ausentes nas ecorregiões Sul e Sudeste Interior, refletindo diferenças nas condições ambientais e na composição funcional dos pools regionais de espécies. Ao integrar diversidade funcional e respostas específicas de traços entre ecorregiões, nossos resultados mostram que a

perda florestal filtra estratégias ecológicas, embora sua intensidade dependa do contexto ecorregional, destacando a importância de considerar simultaneamente a variação biogeográfica e as respostas específicas de traços para compreender e prever os efeitos da perda florestal sobre a biodiversidade.

Palavras-chave: Anfíbios; Desmatamento; Quantidade de habitat; Perda de habitat; Especialização de habitat; Riqueza de espécies; Diversidade funcional; Regiões biogeográficas; Anura; Paisagem; Filtragem de atributos.

ABSTRACT

Forest loss is one of the most pervasive drivers of biodiversity loss. However, there is still limited understanding of how its impacts on biodiversity vary among regions with different biogeographic histories and species with distinct ecological traits. In this study, we integrated biogeographic and landscape ecology approaches to evaluate the effects of forest loss on specialist and generalist anuran species across four Atlantic Forest ecoregions. We compiled data from 168 anuran community studies conducted between 1986 and 2024, encompassing 330 landscapes and 299 species. Species occurrences were spatially organized using 2.5-km-radius buffers centered on sampling sites, and forest loss within each buffer was quantified using land-cover maps. We considered four Brazilian Atlantic Forest ecoregions: Southeast Inland, Southeast Coastal, Northeast Coastal, and Southern. In Chapter 1, we assessed the effects of forest loss on the species richness of forest specialists, open-area specialists, and generalist anurans, and investigated whether these effects were consistent across ecoregions. We fitted multinomial generalized linear mixed models and found that the effects of forest loss differed among habitat-use groups but were consistent across ecoregions. Forest specialist species exhibited strong declines in richness with increasing forest loss, whereas generalist species showed slight reductions and open-area specialist species increased in richness. By jointly considering ecoregional context and habitat specialization, this study provides a more refined understanding of anuran responses to forest loss and supports more effective conservation strategies to mitigate biodiversity decline. In Chapter 2, we investigated how forest loss affects the functional diversity and trait composition of anuran communities across the four Atlantic Forest ecoregions. We used generalized linear models to assess the effects of forest loss on functional richness, functional dispersion, and trait-specific responses, focusing on body size and reproductive traits. Forest loss consistently reduced functional dispersion, indicating increased environmental filtering and trait convergence toward generalist ecological strategies. In contrast, functional richness remained unchanged, suggesting compensatory dynamics in which species losses are offset by replacement with functionally similar species. Trait-specific analyses revealed declines in forest-dependent reproductive strategies, including stream breeding, leaf-litter oviposition, and direct development, together with increases in traits associated with open and drier environments, including reproduction in temporary water bodies, foam nests, and larger body size. These responses varied among ecoregions, with stronger effects in the coastal ecoregions and weaker or absent responses in the Southern and Southeast Inland ecoregions, reflecting differences in environmental conditions and the functional composition of regional species pools. By integrating functional diversity and trait-specific responses across ecoregions, our findings show that forest loss filters ecological strategies, although the magnitude of this process depends on the ecoregional context, highlighting the importance of considering both trait-specific responses and biogeographic variation to better understand and predict biodiversity responses to forest loss.

Keywords: Amphibians; Deforestation; Habitat amount; Habitat loss; Habitat specialization; Species richness; Functional diversity; Biogeographic regions; Anura; Landscape; Environmental filtering.

SUMÁRIO

1 INTRODUÇÃO

A perda de florestas é um dos principais fatores do declínio da biodiversidade (Watson et al., 2016; Betts et al., 2017; Barlow et al., 2018), afetando não apenas a riqueza de espécies, mas também a estrutura funcional das comunidades, com consequências diretas para o funcionamento dos ecossistemas (Flynn et al., 2011; Mori et al., 2018). No entanto, ainda é pouco explorado como esses impactos variam entre diferentes regiões biogeográficas de um mesmo bioma e entre espécies de um mesmo táxon que possuem diferentes características e adaptações ao ambiente.

Para entender essas variações, é fundamental considerar que a distribuição das espécies é influenciada por processos contemporâneos e históricos, que moldaram a diversificação, a composição e o tamanho dos pools regionais de espécies (Ricklefs, 1987; Benício et al., 2021; Jarzyna et al., 2025). Esses legados históricos também influenciam a forma como as espécies respondem às mudanças ambientais atuais, ao determinar não apenas quais espécies compõem os pools regionais, mas também as características ecológicas, funcionais e evolutivas que condicionam sua capacidade de persistir, colonizar e se adaptar a diferentes contextos ambientais (Carstensen et al., 2013; Weeks et al., 2016).

Nesse contexto, filtros ambientais, tanto históricos quanto contemporâneos, atuam selecionando espécies com determinados atributos, levando à persistência de algumas e à exclusão de outras (Newbold et al., 2018; Betts et al., 2019; Orme et al., 2019). Assim, comunidades de regiões com diferentes histórias climáticas e evolutivas podem apresentar respostas distintas à perda de florestas, o que torna essencial incorporar a dimensão biogeográfica na análise das respostas da biodiversidade às alterações antrópicas.

A Mata Atlântica brasileira constitui um sistema ideal para investigar essas questões devido a sua alta biodiversidade, heterogeneidade ambiental e complexa história climática e geológica (Ab'Saber, 1977; Carnaval & Moritz, 2008; Brown et al., 2020). Evidências sugerem que ecorregiões costeiras do sudeste e nordeste, mais estáveis climaticamente durante o Quaternário (último máximo glacial, ~21.000 anos atrás), atuaram como refúgios, favorecendo o acúmulo de espécies endêmicas e especializadas; enquanto que ecorregiões do sul e do interior do sudeste apresentaram um clima mais instável e seco, que atuou como um filtro ambiental para as espécies mais sensíveis, resultando em comunidades mais dominadas por

espécies generalistas (Carnaval et al., 2014; Turchetto-Zolet et al., 2013; Vasconcelos et al., 2014; Benício et al., 2021).

Apesar de ter perdido cerca de 77% de sua cobertura original (Vancine et al., 2024), a Mata Atlântica ainda mantém elevada diversidade biológica (Bogoni et al., 2024; Maurenza et al., 2025), sendo o bioma brasileiro com maior diversidade de anfíbios (719 espécies, sendo 504 endêmicas; Figueiredo et al., 2021). Os anfíbios constituem um grupo particularmente adequado para investigar os impactos da perda de habitat, devido à sua alta sensibilidade a mudanças ambientais, decorrente da pele permeável, dependência de micro-habitats úmidos, ciclos de vida complexos e baixa capacidade de dispersão (Urbina-Cardona et al., 2006; Almeida-Gomes et al., 2019). Além disso, apresentam ampla variação em traços ecológicos, incluindo modos reprodutivos, tamanho corporal e grau de especialização de habitat, que estão relacionados à tolerância ambiental e à persistência sob diferentes condições (Haddad et al., 2013).

Nesta pesquisa, no primeiro capítulo, investigamos como a perda florestal, em escala de paisagem, afeta a riqueza de espécies de anuros em diferentes ecorregiões da Mata Atlântica. Mais especificamente, analisamos as diferentes respostas de espécies especialistas de floresta, de área aberta e generalistas à perda florestal e verificamos se os padrões encontrados diferem entre as ecorregiões.

No segundo capítulo, investigamos como a perda florestal afeta a diversidade funcional das comunidades de anuros de diferentes ecorregiões da Mata Atlântica e, mais especificamente, quais traços específicos (incluindo modos reprodutivos e tamanho corporal) são positiva ou negativamente afetados pela perda florestal, verificando se os padrões encontrados são consistentes entre as ecorregiões.

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Habitat use modulates the effects of forest loss on anuran diversity across Atlantic Forest ecoregions

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Abstract

Aim. Forest loss is among the most pervasive drivers of biodiversity loss. However, there is little appreciation of how the impact of forest loss on biodiversity varies among regions with different biogeographical histories or among species with distinct suites of traits. Here, we integrate biogeographical, trait-based, and landscape ecological approaches to evaluate the direction and magnitude of forest loss on anuran species across four Atlantic Forest ecoregions. We predicted that the magnitude of change in species richness in response to forest loss would be attenuated in ecoregions that

have experienced high climatic variability from the Pleistocene to the present. We also predicted that species that rely on unique forest microhabitats for reproduction would be more susceptible to forest loss relative to generalist species or open-habitat specialists.

Location. Four ecoregions in the Atlantic Forest in Brazil: Southeast Inland, Southeast Coastal, Northeast Coastal, and Southern.

Time Period. From 1986 to 2023.

Methods. We compiled data from 168 studies spanning 330 landscapes and 299 anuran species. Species were classified into three groups defined by habitat use: forest specialists, open-habitat specialists, and generalists. Forest loss and species richness were quantified using standardized buffers at sampling sites and analyzed through multinomial generalized linear mixed models.

Results. We found that the effect of forest loss on anuran species richness varied among habitat-use groups, but these trait-dependent effects were consistent across ecoregions. Forest specialists responded negatively to forest loss, with mean declines of 68% of species (difference between the 5th and 90th percentiles of forest loss), while generalists showed only small reductions (21.5%) and open-area species increased on average (29.6%).

Main conclusions. By accounting for both ecoregional context and habitat specialization, this integrative approach provides a more nuanced understanding of anuran responses to forest loss and supports the development of more effective conservation frameworks to mitigate biodiversity declines.

Key-words Amphibians; Deforestation; Habitat amount; Habitat Loss; Habitat specialization; Species Richness

1. Introduction

Ecologists have traditionally focused on local and landscape-level factors to explain the impact of forest loss on various aspects of biodiversity (Tscharntke et al., 2012; Fletcher et al., 2023; Gonçalves-Souza et al., 2025). However, present-day species distributions are determined not only by contemporary local and landscape processes but also by past environmental change. History has also shaped diversification and left a lasting legacy of effects on the size and composition of the regional species pool (Ricklefs, 1987; Benício et al., 2021; Jarzyna et al., 2025). Environmental filtering acts on these regional species pools by imposing strong selective pressure on species traits. This process leads some species to go extinct, while others persist and respond to contemporary forest loss (Haddad et al., 2015; Newbold et al., 2018; Betts et al., 2019; Orme et al., 2019). For instance, species in regions historically impacted by glaciation tend to be less affected by contemporary landscape alterations, compared with species in regions that have been more stable over geological time (Betts et al., 2019). Thus, ignoring differences across regions when examining biodiversity responses to habitat loss can lead to confounding interpretation of local or landscape effects, when variation in community responses is actually moderated by historical processes.

While the spatial scale-dependence of biodiversity responses to forest loss is well-established (Fletcher et al., 2023), many studies assume that species turnover is driven solely by local ecological processes (e.g., habitat filtering), neglecting the role of historical processes in shaping local assemblages (Teng et al., 2020). This oversight is critical because historical processes determine which species are available to colonize local habitats (Carstensen et al., 2013; Weeks et al., 2016). An ecoregion is a large area defined by shared ecological characteristics assembled through time.

Ecoregions have distinct biogeographical and evolutionary histories, and support distinct species pools (Olson et al., 2001; Holt et al., 2013; da Silva et al., 2024). Consequently, because the responses of species can vary among populations and geographic areas, the impact of forest loss on biodiversity may differ among ecoregions (Banks-Leite et al., 2022). Because ecoregions incorporate evolutionary, historical, and ecological processes, they offer a valuable framework for integrating species- or region-specific effects of forest loss on biodiversity and can reveal why species in some regions are more sensitive to forest loss and help to refine conservation priorities (Olson et al., 2001; Orme et al., 2019).

Here, we combined biogeographic and trait-based approaches (i.e., the degree of specialization in habitat use) to investigate the effects of landscape-scale changes in forest cover on anuran diversity across ecoregions of the Brazilian Atlantic Forest. Despite losing approximately 77% of its original area to human activities (Vancine et al., 2024) and experiencing high biodiversity loss connected with forest loss (Bogoni et al., 2024; Maurenza et al., 2025), this region still harbors exceptional biodiversity (Figueiredo et al., 2021). This is attributed to variation in topography (ranging from sea level to 2000 m a.s.l.), high latitudinal and longitudinal extents, habitat heterogeneity, and complex climatic and geological history (Ab'Saber, 1977; Carnaval & Moritz, 2008; Brown et al., 2020). The persistence of refugia (humid forests) during the cooler and drier periods of the Quaternary may have contributed to the high endemism in the southeast and northeast coastal ecoregions (Carnaval & Moritz, 2008; Carnaval et al., 2014; Fig. 1), whereas regions that were less climatically stable (southeast inland and southern ecoregions) may have experienced extinction filtering of more sensitive species (Balmford, 1996; Turchetto-Zolet et al., 2013). These differences in biogeographic histories among ecoregions have led to differences in the regional

species pool and their functional composition (e.g., the proportion of habitat specialists vs. habitat generalists) (Vasconcelos et al., 2014; Benício et al., 2021; da Silva et al., 2024). Therefore, the magnitude of biodiversity loss due to forest loss likely differs among ecoregions; a hypothesis we test here.

To assess the impact of forest loss on species richness across four ecoregions of the Brazilian Atlantic Forest, we compiled data from 168 studies across 330 landscapes, totaling 299 anuran species (Fig. 1). Anurans, due to their narrow ecological niches, complex life cycles, physiological constraints, and high dispersal limitations, are highly vulnerable to forest loss (Almeida-Gomes et al., 2019). They exhibit a range of habitat uses, including forest specialists, open-area specialists, and generalists that utilize both habitat types (Haddad et al., 2013). While forest specialists are highly dependent on continuous forest patches, generalists and open-area species are often better able to exploit human-disturbed landscapes (da Silva & Rossa-Feres, 2007; da Silva et al., 2012a). Specifically, we asked: how do differences in biogeographical history and habitat specialization influence the effects of forest loss on species richness? Given differences in the regional species pools among ecoregions (da Silva et al., 2012a, 2014; Benício et al., 2021), we hypothesize that richness responses to forest loss will generally be negative. However, we expect weaker impacts of forest loss in ecoregions that historically experienced strong environmental filtering in the Pleistocene, because species in those ecoregions are less likely to be sensitive to contemporary environmental change, given their biogeographic history. Additionally, we hypothesize that anuran species that are forest specialists will be more affected by forest loss than generalists or open-area species (da Silva et al., 2012a; Müller et al., 2013). Therefore, in ecoregions where open-area

species dominate, the influence of forest loss on species richness may be less pronounced.

2. Methods

Study area

The Atlantic Forest is an ideal system in which to disentangle the relative contributions of contemporary and historical processes in structuring present-day species distribution patterns. Originally spanning approximately 1.3 million km², the Atlantic Forest has experienced extensive anthropogenic alteration (Vancine et al., 2024). Today, most forest fragments are small—typically less than 50 hectares—and only about 10% of fragments are located within officially designated protected areas (Vancine et al., 2024). Here, we adopted the four ecoregions of the Brazilian Atlantic Forest as defined for anuran communities based on an independent analysis of data separate from the dataset used in the current study (Vasconcelos et al., 2014; Fig. 1). These ecoregions exhibit strong spatial congruence with the distribution of major vegetation types and other taxa, which are largely determined by geomorphological features, including complex topography and riverine barriers, along with both paleoclimatic and current climatic regimes (e.g., Silva & Casteleti, 2003; Brown et al., 2020; Peres et al., 2021; da Silva et al., 2024). The ecoregions are characterized as follows (Fig. 1):

Southeast Coastal – This ecoregion is dominated by ombrophilous (evergreen) forests and spans a broad elevational gradient from 50 to 2,200 m a.s.l. It experiences high and evenly distributed precipitation throughout the year (2,000 to 3,600 mm) and mean annual temperatures between 22°C and 25°C (Oliveira-Filho & Fontes, 2000; Colombo & Joly, 2010). Climatic oscillations during the Quaternary suggest that

mountainous areas within this region functioned as climatic refugia (Carnaval & Moritz, 2008; Carnaval et al., 2014). This ecoregion supports the highest levels of anuran species richness and endemism, including many narrow-ranged taxa (Moroti et al., 2024), and the greatest proportion of forest specialists — 153 of 240 species (63.7%).

Northeast Coastal – This ecoregion encompasses both semi-deciduous and ombrophilous forests that occupy slopes of the coastal mountain range, with average elevations around 1,000 m a.s.l. It generally lacks a defined dry season and is characterized by higher temperatures and lower humidity relative to the Southeast Coastal Ecoregion (Vasconcelos et al., 2014; Vancine et al., 2018). Quaternary climatic reconstructions indicate that certain areas in the states of Bahia and Pernambuco served as climatic refugia. This ecoregion harbors the second highest levels of species richness and endemism (Moroti et al., 2024), as well a similar proportion of forest specialists than Southeast coastal ecoregion, 98 of 165 species (63.2%).

Southeast Inland – This ecoregion comprises seasonal semi-deciduous forests and transitional zones bordering the Cerrado biome, and occurs predominantly at elevations below 700 m a.s.l. It is characterized by a pronounced dry season lasting from 2 to 6 months (April to September), annual precipitation ranges between 1,500 and 2,000 mm, and mean annual temperatures range from 22°C to 25°C (Oliveira-Filho & Fontes, 2000; Colombo & Joly, 2010). Paleoclimatic evidence indicates that this region underwent significant climatic fluctuations during the Quaternary (Carnaval & Moritz, 2008; Carnaval et al., 2014). It supports the lowest anuran species richness among the ecoregions, with most species exhibiting wide distributions (Vasconcelos et al., 2011). It has the lowest proportion of forest specialists, 31 of 95 species (32.6%; Fig. 1).

Southern – This ecoregion is covered primarily by Mixed Ombrophilous Forest (i.e., Araucaria forest) and is located in the southern portion of the Atlantic Forest, extending northward to the Serra da Mantiqueira at approximately 20°S latitude at elevations above 500 m a.s.l.. It is characterized by tropical to subtropical humid climates without a pronounced dry season, annual precipitation between 1,400 and 2,200 mm, and mean annual temperatures ranging from 12°C to 18°C (Oliveira-Filho & Fontes, 2000; Colombo & Joly, 2010). Like the Southeast Inland Ecoregion, this region experienced marked climatic fluctuations during the Quaternary. It supports relatively low anuran species richness and has the second lowest proportion of forest specialists, 58 of 130 species (44.6%; Fig. 1).

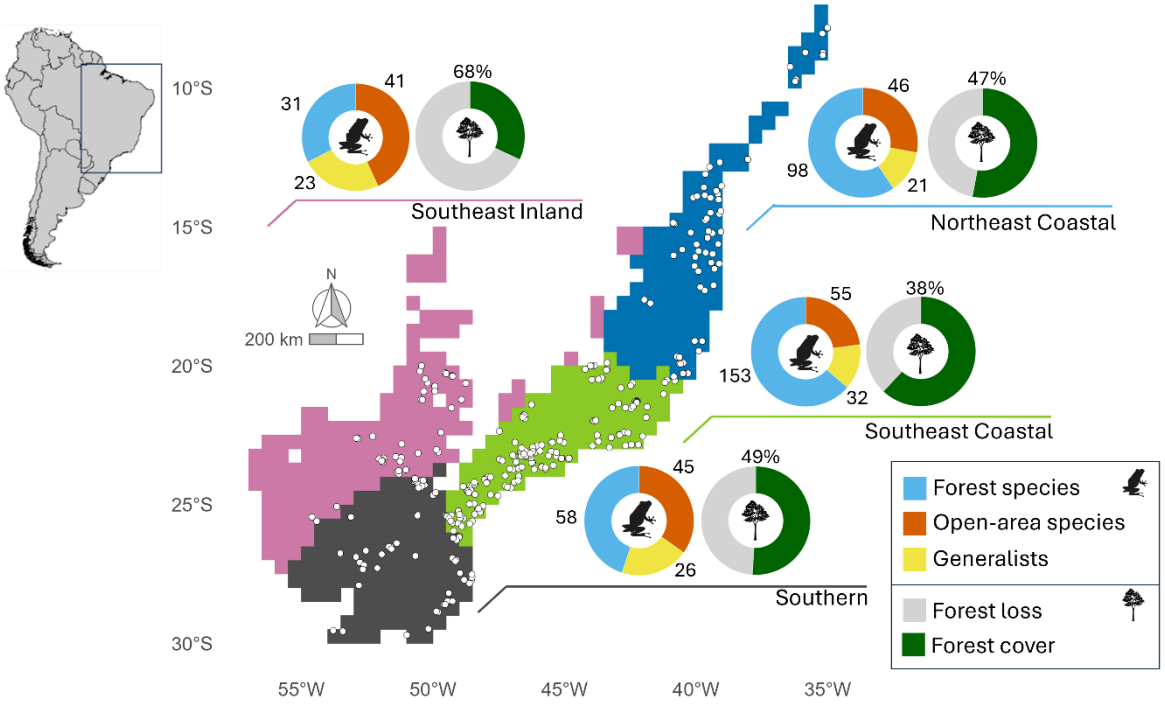

Figure 1. Sampling locations (white dots) across the ecoregions of the Atlantic Forest, Brazil (Southeast Inland = pink; Southeast Coastal = green; Northeast Coastal = blue; Southern = dark gray). The larger circles show, for each ecoregion, the species number of each habitat-use group, and the averages of forest loss (percentage) across the buffers.

Database compilation and filtering

We used data on anuran communities primarily from the most comprehensive and up-to-date database on amphibian occurrences in the Atlantic Forest compiled by Vancine et al. (2018). In addition, we expanded the dataset and incorporated records from 2018 to 2024 by conducting systematic literature searches using Google Scholar, Scopus, and Web of Science. These searches employed Boolean operators with relevant keywords and their portuguese equivalents: “amphibian*”, “anuran*”, “Atlantic Forest”, and “communit*” (Supplementary Material: Table S1).

To ensure data quality and spatial consistency with our landscape-scale analysis (2.5 km radius), we applied a rigorous set of inclusion criteria. To prevent undersampling and methodological biases, we excluded studies that: (1) utilized only pitfall traps as the sampling method; (2) had an overly narrow taxonomic scope (e.g., targeting only a few species rather than a whole community); (3) were conducted in overly restrictive habitats (e.g., a single stream, a single pond, surveying only bromeliads or open sandy forest such as “restinga”); (4) employed limited temporal effort (e.g., sampling only diurnally); or (5) failed to report essential methodological details (the study duration, the habitats sampled, or the sampling methods used). To address spatial inaccuracies and ensure precise landscape characterization, we excluded studies that: (6) used sampling locations external to the boundaries of the ecoregions or the Atlantic Forest biome; (7) lacked precise geographic coordinates (e.g., providing only a city name); (8) had coordinates representing a regional area exceeding a 2.5 km radius; (9) were conducted on small islands, or in coastal areas, where a 2.5 km buffer would be largely oceanic. Additionally, (10) for studies with multiple sampling locations within a 2.5 km radius, a single central coordinate was used to represent the study area, and, to mitigate temporal incongruence between biodiversity data and the landscape variable considered, we excluded studies (11) with

an excessively long sampling duration (>60 months), as the landscape in the final year may not reflect conditions present during the entire period, and the time of sampling effort was disproportionally longer.

Following these criteria, we retained 168 studies, from which 16 were conducted in the Southeast Inland Ecoregion, 85 studies in the Southeast Coastal, 34 studies in the Northeast Coastal, and 33 studies in the Southern Ecoregion. Taxonomic nomenclature was reviewed and standardized based on the most recent amphibian classification (Frost, 2024).

Forest cover and forest loss estimation

We calculated the percentage of forest cover from land cover maps available in the MapBiomas project (Collection 9.0; Souza Jr. et al., 2020). These maps provide land cover and land use data for the Atlantic Forest based on Landsat satellite images (30-meter accuracy, WGS84 projection) from 1985 to 2023. We extracted forest cover by using the 'terra' and 'raster' packages in R software, version 4.4.2 (Hijmans 2023a, 2023b; R Core Team, 2025). We reclassified pixels into forest and non-forest categories using a classification matrix. The Forest category (~28% of the biome area; MapBiomas, 2024) included forest formations, savanna woodlands, mangroves, and arboreal restinga. We did not consider herbaceous and shrubland vegetation (~2.5% of the biome area; MapBiomas, 2024), as we focused solely on forest loss impacts. We used the percentage of non-forest cover corresponding to the last year of each study considered in the analysis.

Around each sampling location, we created 2,500 m radius buffers and calculated the percentage of forest and non-forest area within them. Because the entire area was originally forest, forest loss was defined as the proportion of non-forest cover

within each buffer (see Pinho et al., 2024), based on data from the final year of each study. To address the non-independence among multiple sampling buffers from the same study and to align with our focus on differences among ecoregions, we aggregated the forest loss data by calculating the average forest loss across all buffers from that study.

To facilitate comparison across ecoregions, we standardized forest loss by centering and scaling values, across all sampling sites combined, using the ‘scale’ function from the ‘base’ R package (Becker et al., 1988; R Core Team, 2025).

Definition of habitat use

We defined the species’ habitat use based on Haddad et al. (2013) and additionally on specialized literature (Thomé & Brasileiro, 2007; Silva et al., 2008; Santoro & Brandão, 2014; de Mira-Mendes et al., 2018; Lourenço-de-Moraes et al., 2018, 2020; Neves et al., 2019; Potrich et al., 2020; Vaz-Silva, 2020). Species strictly dependent on closed-canopy environments for completing their life cycles were designated as “forest species”. These species are typically sensitive to habitat fragmentation and edge effects due to their dependence on specific microhabitats within forests — such as bromeliads and moist soil — for reproduction (Haddad & Prado, 2005; da Silva et al., 2012a; Almeida-Gomes et al., 2019). In contrast, “open-area species” are typically found in swamps and ponds surrounded by herbaceous or shrubby vegetation, including natural grasslands or anthropogenically altered environments such as pastures and croplands. These species often exhibit greater ecological plasticity and higher tolerance to environmental disturbance (da Silva & Rossa-Feres, 2007). Species that use both forested and open habitats were classified

as “generalists”, reflecting a broader ecological niche and potential resilience to landscape-level habitat heterogeneity.

Statistical analysis

We used a Generalized Linear Mixed Model (GLMM) that takes the Poisson log-linear approach to multinomial analysis (Baker, 1994; Lang, 1996; Guimarães, 2004; Zuur et al., 2009), with the response variable being the number of species per habitat-use grouping (forest species, open-area species or generalists) within each study. Fixed predictors included the categories of habitat use, ecoregions, scaled forest loss, and their two- and three-way interactions. We defined sampling effort as the multiplication of the number of habitat types sampled, months of study and sampling methods for each study as an additional fixed predictor to account for sample bias. A random effect was specified for study identity (reference number) to account for the dependence between richness estimates for forest, generalist, and open-area categories recorded within the same study. As Poisson GLMM models employ a log-link function, the interaction effects between habitat-use level and the other fixed predictors (ecoregion and forest loss) represent the log-odds that the relative frequencies of habitat-use groups vary across the other predictors in the model.

The model was fitted using the glmmTMB package (Mollie et al., 2017). We assessed the assumptions of normality, homogeneity of variances, and dispersion of residuals using the DHARMa package (Hartig, 2024). All analyses were carried out in R version 4.5.1 (R Core Team, 2025).

Results

The effects of forest loss on species richness varied significantly among the three categories of habitat association (interaction between forest loss and habitat use: $p < 0.001$, Table 1), and we found that the richness of each group varied across ecoregions (interaction between habitat use and ecoregions: $p < 0.001$, Table 1). We detected a significant overall effect of forest loss ($p < 0.001$, Table 1), but the interaction between forest loss and ecoregions, and the three-way interaction, were not significant ($p = 0.97$, $p = 0.76$, respectively, Table 1), indicating the effects of forest loss on species richness do not vary among ecoregions.

Forest species were the most negatively affected by forest loss (Figure 2). Generalists showed neutral responses (Figure 2). In contrast, species richness of open-habitat species tended to be highest in areas with the highest forest loss. These patterns were congruent across the four ecoregions (Figure 2).

Table 1. Analysis of Deviance table summarizing the effects of forest loss, ecoregion and species' habitat use on anuran species richness. Bolded values represent significant p values.

Predictors	**χ^2**	**df**	**p**
Sampling effort	17.50	1	**< 0.001**
Habitat-use	246.20	2	**< 0.001**
Forest loss	21.68	1	**< 0.001**
Ecoregions	3.16	3	0.36
Habitat use * Forest loss	184.76	2	**< 0.001**
Habitat use * Ecoregions	179.34	6	**< 0.001**

Forest loss * Ecoregions	0.22	3	0.97
Habitat use * Forest loss * Ecoregions	3.31	6	0.76

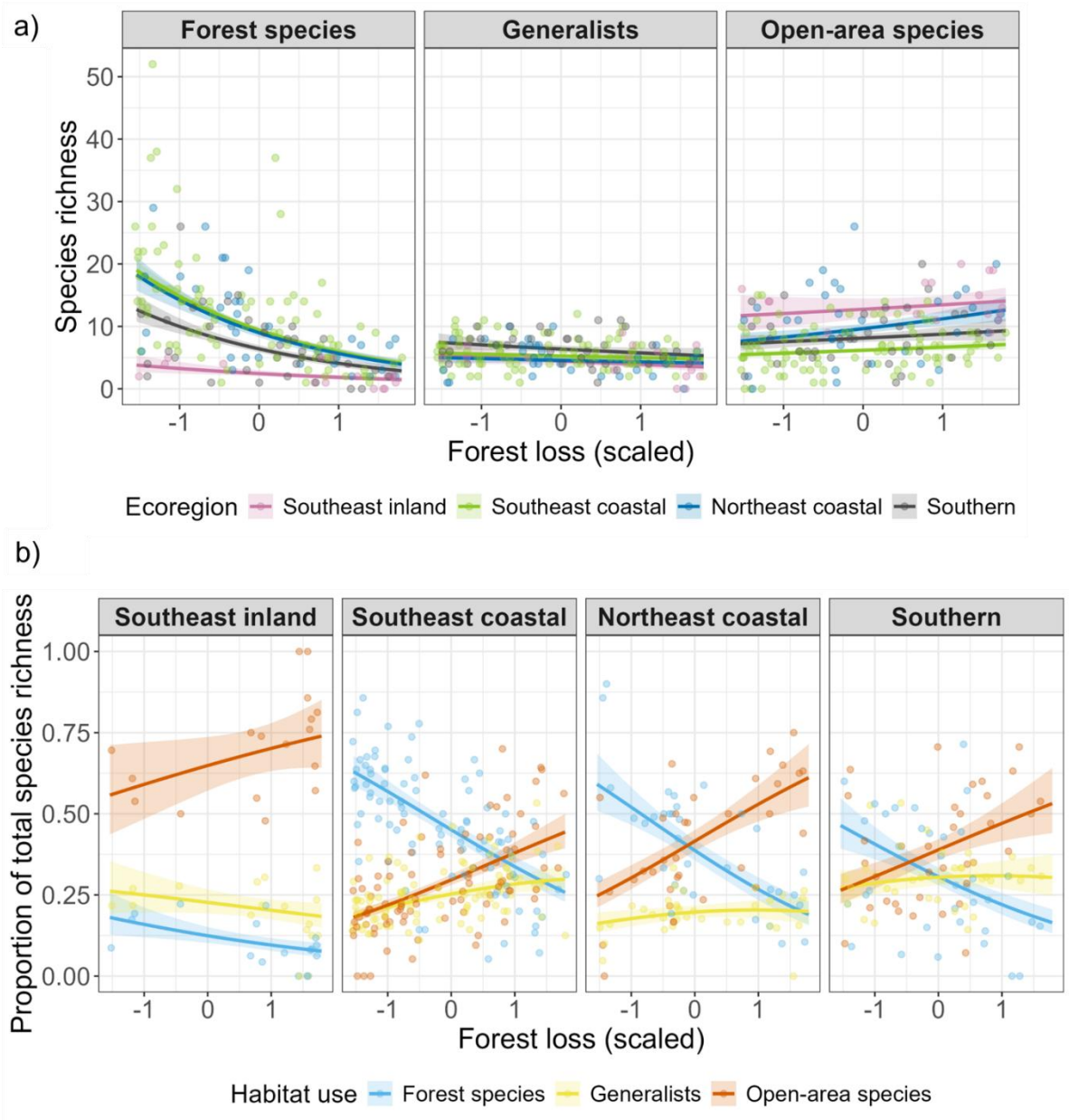

Figure 2. (a) Relationship between observed species richness of anurans in each habitat-use group versus standardized forest loss (centered and scaled) across four ecoregions in the Atlantic Forest of Brazil. Fitted lines represent the mean (± 1 S.E.) model-predicted estimates from a multinomial GLMM (Table 1). (b) The same data and model-predicted effects, re-plotted for ease of interpretation as proportion of total species richness against standardized forest

loss in each ecoregion. In (a) and (b) the forest loss interval (–1.5 to 1.5) corresponds to percentage forest loss of: Southeast inland (0–95.5%, average = 68%), Southeast coastal (0–97%, average = 38%), Northeast coastal (1–95%, average = 47%), and Southern (2–92%, average = 49%).

Discussion

The effects of forest loss on biodiversity have been extensively studied, but most studies have focused on local or landscape-level processes, often overlooking variation among ecoregions (Banks-Leite et al., 2022). We combined the biogeographic history of distinct regional species pools with trait-based perspectives to assess how forest loss shapes anuran diversity across Atlantic Forest ecoregions. At the biome scale, our findings reveal an overall effect of forest loss on anuran species richness, and its direction and magnitude varied across habitat-use groups. Forest specialists were the most negatively affected, whereas species richness of open-area species tended to be highest in areas with the highest forest loss, and generalists showed neutral responses to forest loss. These results indicate that species that are forest specialists are disproportionately vulnerable to deforestation, while open-area species are benefited. These patterns are, surprisingly, consistent across ecoregions, although ecoregions that harbor a higher number of forest species may be losing a greater absolute number of species with forest loss.

Previous studies have shown that sites in ecoregions with lower climatic variability during the Pleistocene and greater topographic complexity may have served as diversification hotspots for anuran species with specialized reproductive modes, due to reduced extinction rates and enhanced opportunities for speciation (da Silva et al., 2012a, 2014; Benício et al., 2021). Consequently, these ecoregions could support

many anuran species with narrow geographic ranges, making them particularly vulnerable to habitat loss (Staude et al., 2020). In contrast, the proportion of open-area species increased with forest loss. These results indicate two opposite consequences of deforestation for anuran diversity. It erodes forest assemblages but facilitates the expansion of open-area species. This trait-mediated shift in species composition—where disturbance-adapted species (also known as “winner species”) replace sensitive taxa (“loser species”)—has been demonstrated across animal and plant studies (Almeida-Gomes et al., 2019; Lourenço-de-Moraes et al., 2019; Pinho et al., 2024). Consequently, ecoregions dominated by forest specialists are expected to be more vulnerable to forest reduction than those characterized by widespread generalists or open-area species. By explicitly incorporating the biogeographic histories of regional species pools as well as variation in species’ habitat use, our study helps explain why simple measures of local habitat change often fail to predict biodiversity responses consistently across regions (Fahrig, 2013).

Our results indicate that forest loss exerts stronger negative impacts on forest species than on generalist or open-area species. One explanation for the strong negative response of forest species to deforestation is their dependence on specialized microhabitats and microclimatic conditions, such as phytotelmata, leaf litter, and pristine streams, which act as key ecological filters constraining their distribution (Henle et al., 2004; Urbina-Cardona et al., 2006; Almeida-Gomes, et al. 2019). Furthermore, habitat loss has been shown to reduce connectivity, forcing many amphibians with aquatic larvae to undertake risky breeding migrations through disturbed environments, which can lower survival rates of both adults and juveniles; this process is known as “habitat split” (Becker et al., 2007). By contrast, open-area species exhibit generalized reproductive strategies and desiccation-resistant traits,

including foam nests, burrowing, and explosive breeding (Haddad & Prado, 2005; da Silva et al., 2012a). It is important to emphasize, however, that even open-area species that benefit from deforested areas still depend on forests to some extent for shelter and foraging (da Silva and Rossa-Feres, 2007). In the Southeast Inland ecoregion, where open-area species are proportionally more abundant, previous studies have shown that the proximity of breeding sites to forests strongly influences species richness and abundance (da Silva et al., 2012a). Because responses vary across ecoregions and habitat use, we emphasize that integrating historical biogeographic data into conservation prioritization can help identify regions where forest loss will yield the greatest long-term losses of biodiversity based on trait-informed prioritization.

Integrating responses across local, landscape, and regional scales remains a challenge claimed by several studies (Newman et al., 2019; Chase, 2020; Teng et al., 2020). Reliable assessments of diversity change require knowledge of how many species were present within a given locality at a specific point in the past and how many persist there today. However, such information is rarely available beyond short-term studies at local or landscape scales. To minimize these biases, we employed an extensive set of criteria for data inclusion and incorporated sampling effort as a predictor in our models. Furthermore, we recognize that our dataset cannot capture the full complexity of multiscale processes. While deforestation is a dominant driver, other mechanisms at finer scales can strongly mediate anuran responses. For instance, patch isolation and connectivity, as well as edge effects, influence colonization–extinction dynamics (Teixido et al., 2021). Likewise, environmental descriptors reflecting the vegetation complexity in breeding ponds are key predictors of anuran diversity (da Silva et al., 2012b). Despite these constraints, by highlighting both the broad-scale impacts of deforestation and their interaction with traits such as

habitat use, our study provides a framework that can be refined in future work to incorporate additional drivers and better reconcile biodiversity patterns across scales.

Conclusions

Our results demonstrate that the negative impacts of forest loss on biodiversity are not uniform but vary in both strength and direction, particularly when species' habitat use is considered. Forest specialists were most strongly affected by forest loss, whereas open-area and generalist species exhibited positive and neutral associations with forest loss, respectively. These findings indicate that biogeographic history and evolutionary processes not only determine the size and composition of regional species pools (Ricklefs, 1987; Benício et al., 2021) but also mediate present-day biodiversity responses to landscape change through environmental filtering, which shapes the distribution of species traits across ecoregions.

Accordingly, we emphasize the importance of conservation strategies that integrate both broad-scale and ecoregion-specific perspectives. Incorporating trait-based approaches into conservation planning can help anticipate which ecoregions are most vulnerable, prioritizing the protection of unique assemblages, such as coastal forest specialists that experience the greatest loss due to deforestation. This approach also ensures that both specialist and generalist species across different ecoregions are accounted for in management decisions. More broadly, our study demonstrates that integrating biogeographic context with species' habitat use can reveal both general patterns and trait-based nuances of regional biodiversity changes, offering a framework for conservation in other biomes worldwide.

Data Availability Statement: All data supporting the findings of this study are openly available at Zenodo under DOI: https://doi.org/10.5281/zenodo.17753914

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Artigo ainda não submetido

Forest loss filters anuran traits and erodes functional dispersion across Atlantic Forest ecoregions

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Abstract

Forest loss is a major driver of biodiversity change, and its effects on functional diversity are increasingly well documented. However, how these effects vary across ecoregions and which functional traits are consistently filtered remain unclear. Here, we investigated how forest loss affects functional diversity and specifics traits of anuran communities across four ecoregions of the Brazilian Atlantic Forest.

We compiled data from anuran community studies conducted between 1983 and 2024, totaling 168 studies and 299 species. Species occurrences were spatially organized using buffers with a 2.5-km radius around sampling sites. We quantified forest loss within each buffer using land-cover maps. We then applied generalized linear models to assess the effects of forest loss on functional diversity, including functional richness (FRic) and functional dispersion (FDis), as well as on trait-specific responses, focusing on body size and reproductive traits.

Forest loss consistently reduced functional dispersion, indicating increased environmental filtering and trait convergence toward generalist strategies. In contrast, functional richness remained unchanged, suggesting compensatory dynamics in which species losses are offset by the replacement of taxa with similar ecological roles. Trait-specific responses revealed consistent declines in forest-dependent reproductive strategies, such as stream breeding, leaf-litter oviposition, and direct development, alongside increases in traits associated with open and drier environments, including pond breeding, foam nests, and larger body size.

Importantly, these responses varied across ecoregions, with stronger and more consistent effects in coastal ecoregions and weaker or absent responses in southeast inland and southern ecoregions, reflecting differences in environmental conditions and the functional composition of regional species pools.

By integrating functional diversity and trait-specific responses across ecoregions, our results show that forest loss consistently filters ecological strategies while its strength depends on ecoregional context. This highlights the importance of considering both trait-specific responses and biogeographical variation to better understand and predict biodiversity responses to forest loss.

Key words: Functional diversity, Habitat loss, Biogeographic regions, Anura, Landscape, Trait filtering

Introduction

Forest loss is one of the main drivers of biodiversity decline worldwide (Watson et al. 2016, Betts et al. 2017, Barlow et al. 2018), affecting not only species richness but also the functional structure of ecological communities, with critical consequences for ecosystem functioning (Flynn et al. 2011, Mori et al. 2018). Despite numerous studies investigating the effects of environmental change on functional diversity across multiple taxa (e.g. Matuoka et al. 2020, Luza et al. 2023, Pinho et al. 2025), the consistency of these effects across ecoregions and the underlying trait-specific responses remain underexplored.

In tropical forests such as the Atlantic Forest, forest loss reshapes landscapes by modifying habitat configuration and imposing both biotic and abiotic filters on ecological communities, thereby acting as a strong environmental filter on species persistence (e.g. Ewers & Banks-Leite 2013). Amphibians are particularly sensitive to these changes due to their permeable skin and strong dependence on moist microhabitats, making them a model group for understanding how environmental filtering operates on functional traits (da Silva et al. 2012, Urbina-Cardona et al. 2006).

Functional diversity (FD) provides a useful framework to address these changes by focusing on species traits linked to ecological strategies and roles (Violle et al. 2007, Tilman et al. 1997). A growing body of research has shown that trait diversity is associated with key ecological processes (Cadotte et al. 2011, Gagic et al. 2015), supporting the use of FD metrics to assess the impacts of land-use change (Villéger et

al. 2008, Flynn et al. 2009) and enabling the identification of which ecological strategies persist or are lost under environmental change (Tabarelli et al. 2012, Filgueiras et al. 2021, Pinho et al. 2025)

Species responses depend on characteristics such as habitat specialization and dispersal capacity (Pandit et al. 2009), and disturbance often disproportionately affects species with more specialized habitat requirements (Clavel et al. 2011). In amphibians, variation in morphology, physiology, and reproductive traits is closely linked to habitat use and environmental tolerance, directly influencing species ability to persist under different conditions (Liu et al. 2021).

Importantly, the effects of forest loss on biodiversity are not uniform across space. Species pools vary among ecoregions due to differences in geological history, evolutionary processes, and environmental conditions (Ricklefs 1987, Cornell & Harrison 2013). Communities within the same biogeographic region may share historical and climatic constraints, yet differ markedly from those in other regions, leading to variation in both species composition and functional trait distributions (Carstensen et al. 2013, Lessard et al. 2012). Consequently, species from different ecoregions may respond differently to similar environmental gradients (Prado & Rossa-Feres, 2014, Provete et al. 2014), resulting in spatially heterogeneous patterns of functional change.

Overall, losses in forest cover at landscape scales have been shown to alter multiple dimensions of functional diversity, including functional richness and dispersion, with important consequences for ecosystem processes in tropical systems (Hatfield et al. 2018). However, because some ecological functions are more resilient than others, it remains essential to identify which components of functional diversity are most sensitive to forest loss. A trait-based, regionally explicit approach is therefore crucial to understanding how anthropogenic disturbances affect community assembly and how these effects vary across biogeographically structured species pools.

Here, we investigate how forest loss, across four ecoregions of the Brazilian Atlantic Forest, affects functional diversity and specific traits of anuran communities, focusing on reproductive modes and body size. Specifically, we ask: (1) Does forest loss consistently reduce functional diversity of anurans across ecoregions? (2) Which

functional traits are filtered along the deforestation gradient, and is this filtering consistent among ecoregional species pools?

First, we hypothesize that functional dispersion (FDis) will be more consistently reduced by forest loss than functional richness (FRic). This prediction is grounded in the founds that even when species richness is maintained through the replacement of forest specialists by generalists, functional space is compressed towards traits associated with open habitats and increased functional redundancy (Matuoka et al. 2020, Weeks et al. 2025). Functional richness, being more directly dependent on species richness, may exhibit weaker or more heterogeneous responses, particularly where species replacement is sufficient to fill equivalent functional volume (Fetzer et al. 2015, Van Perre et al. 2020).

Second, we hypothesize that traits associated with specialized forest reproductive modes (e.g. direct development, oviposition and tadpoles in streams, oviposition and tadpoles in phytotelmata) will exhibit consistent negative responses to forest loss, whereas traits associated with generalized and open-habitat modes (e.g. oviposition and tadpoles in ponds, foam nests) will be neutral or positively associated with deforestation (Da Silva et al. 2012, Haddad & Prado 2005). This hypothesis is based on the role of humidity as a key environmental filter: species with specialized reproductive modes exhibit greater susceptibility to desiccation and depend on humid forest microhabitats that become scarce or ephemeral in degraded landscapes (Da Silva et al. 2012, Muller et al. 2013). Additionally, we expect body size (SVL) to respond positively to deforestation, consistent with the founds that larger body size reduces evaporative water loss in drier environments (Olalla-Tárraga et al. 2009, Urban et al. 2024).

Third, we hypothesize that the strength of functional filtering will vary among ecoregions as a function of the historical composition of regional species pools. In coastal ecoregions, characterized by high endemism and predominance of specialized forest lineages (Vasconcelos et al. 2014, da Silva et al. 2014), we predict more pronounced effects of forest loss on sensitive traits. In contrast, inland ecoregions, where regional pools are already composed predominantly of generalist species tolerant of lower humidity and greater seasonality (Benício et al. 2021, Gomes-Mello

et al. 2021), should exhibit attenuated or absent responses, reflecting historical filtering that has already excluded forest-dependent lineages (Garey et al. 2023).

Methods

Study area

The study was conducted using data from the Brazilian Atlantic Forest, a biodiversity hotspot that has undergone extensive anthropogenic transformation since colonization, resulting in a highly fragmented landscape dominated by small forest remnants, most of which lie outside protected areas (Vancine et al. 2024). We considered four ecoregions previously defined for anuran assemblages (Vasconcelos et al. 2014, Fig. 1), which broadly align with major vegetation types and biogeographic patterns shaped by topography, riverine barriers, and both historical and contemporary climatic regimes (Silva & Casteleti 2003, Brown et al. 2020).

The Southeast Inland ecoregion comprises seasonal semi-deciduous forests and transitional zones with the Cerrado below 700 m elevation, characterized by pronounced dry periods (2–6 months) (Oliveira-Filho & Fontes 2000, Colombo & Jol 2010). It experienced marked climatic instability during the Quaternary (Carnaval & Moritz 2008, Carnaval et al. 2014) and currently supports the lowest species richness and the smallest proportion of forest specialists (~ 33%, Polettini-Neto et al. in press). The Southern ecoregion, dominated by Araucaria forests above 500 m, has cooler and humid conditions without a marked dry season (Oliveira-Filho & Fontes 2000, Colombo & Joly 2010). Despite a similar history of climatic fluctuations, it supports relatively low richness and an intermediate proportion of forest specialists (~ 45%, Polettini-Neto et al. in press).

In contrast, the Southeast Coastal ecoregion is dominated by humid evergreen forests spanning a wide elevational gradient (50–2,200 m), with high and weakly seasonal precipitation (Oliveira-Filho & Fontes 2000, Colombo & Joly 2010). This region likely functioned as a climatic refugium during the Quaternary (Carnaval & Moritz, 2008, Carnaval et al. 2014) and it harbors the highest levels of anuran richness, endemism, and forest specialization (~ 64%, Polettini-Neto et al. in press). The Northeast Coastal

ecoregion includes semi-deciduous and evergreen forests along coastal mountain ranges (~1,000 m), under warmer and comparatively drier conditions (Vasconcelos et al. 2014, Vancine et al. 2018). It also contains refugial areas and supports the second highest species richness, with a similarly high proportion of forest specialists (~ 63%, Polettini-Neto et al. in press).

Database compilation and filtering

We compiled anuran community data primarily from the database of Vancine et al. (2018), supplemented with records from 2018–2024 obtained through systematic searches in Google Scholar, Scopus, and Web of Science using combinations of “amphibian*”, “anuran*”, “Atlantic Forest”, and “communit*”.

To ensure consistency with landscape-scale analyses (2.5 km radius), we applied strict inclusion criteria. We excluded studies with limited or biased sampling designs (e.g. pitfall-only surveys, taxonomically restricted sampling, single-habitat studies, exclusively diurnal sampling, or insufficient methodological detail). We also removed records with imprecise or incompatible spatial information (e.g. lacking coordinates, exceeding a 2.5 km spatial range, located outside the biome, or in coastal/island settings unsuitable for this buffer radius used). For studies with multiple nearby sampling points, a single central coordinate was used. To minimize temporal mismatches with landscape data, we excluded studies with sampling durations exceeding 60 months.This filtering resulted in 168 studies (with the total of 299 species), distributed across ecoregions: Southeast Inland (16), Southeast Coastal (85), Northeast Coastal (34), and Southern (33). Taxonomy was standardized following Frost (2024).

Forest cover and forest loss estimation

Forest cover was quantified using MapBiomas Collection 9.0 (Souza Jr. et al. 2020), derived from Landsat imagery (30 m resolution) spanning 1985–2023. Analyses were conducted in R (v4.4.2) using the *terra* and *raster* packages. Land cover classes were reclassified into forest and non-forest categories, with forest including all arboreal formations (e.g. dense forests, savanna woodlands, mangroves, and arboreal restinga), representing ~28% of the biome. We used the percentage of non-forest cover from the final year of each study included in the analysis.

We delineated 2.5 km buffers around each sampling site and calculated the proportion of forest within each buffer. Given the historically forested baseline of the biome, forest loss was defined as the percentage of non-forest cover within buffers, based on the final year of each study. To account for non-independence among sites within studies, values were averaged at the study level. Forest loss was standardized (centered and scaled) across all sites to enable comparisons among ecoregions.

Functional traits

Trait data were compiled for all species from literature, primarily from Haddad et al. (2013), Oliveira et al. (2017), and Vasconcelos et al. (2019). We characterized anuran species using functional traits related to reproductive mode and body size, which are expected to mediate species responses to forest loss through effects on microhabitat dependence, dispersal ability, and tolerance to altered microclimatic conditions. Functional traits were organized into a species-by-trait matrix including both continuous and binary traits.

Reproductive mode traits describe species reliance on specific microhabitats for reproduction and larval development, which are likely to be affected by deforestation. They were included as binary traits (presence/absence). These traits included oviposition site (pond, stream, arboreal vegetation, ground, leaf litter, terrestrial structure, rock, or on the adult's body), presence or absence of foam nests, tadpole habitat (pond, stream, arboreal phytotelmata, or burrows), type of development (direct or indirect), and tadpole nutritional mode (exotrophic or endotrophic).

Body size was represented by snout–vent length (SVL) and was included as a continuous trait. Body size is closely linked to metabolic capacity (Farrell & MacMahon, 1969, Gillooly et al. 2001), dispersal ability (Tejedo & Semlitsch 2000), and water balance (Urban et al. 2024), all of which are expected to influence species resilience to the warmer and drier microclimatic conditions associated with forest loss (Vasconcelos et al. 2010, Da Silva et al. 2012, Gómez-Mestre et al. 2012, Muller et al. 2013).

Functional diversity analyses

Functional diversity was quantified using two complementary indices that capture distinct components of functional trait space: functional richness (FRic) and functional dispersion (FDis). FRic represents the volume of multidimensional functional trait space occupied by the species in a community (Villéger et al. 2008), whereas FDis measures the mean distance of species to the centroid of trait space, reflecting trait dispersion and redundancy (Laliberté & Legendre, 2010).

Both indices were calculated using principal coordinate analysis (PCoA) on a Gower distance matrix to accommodate mixed trait types (Gower, 1971). When necessary, Cailliez correction was applied to ensure Euclidean properties of the functional space (Cailliez 1983). Functional diversity indices were computed using the dbFD function in the R package FD (Laliberté et al. 2014).

If species traits were assembled at random, regions with larger species pools would be expected to exhibit higher values of functional richness (FRic) and functional dispersion (FDis). To account for this influence of species pool size and random assembly processes, we therefore calculated standardized effect sizes (SES) for both FRic and FDis. Null communities were generated using the independent swap algorithm, which preserves species occurrence frequencies and site richness while randomizing species co-occurrence patterns (Gotelli & Entsminger 2003). Null models were implemented using the picante package (Kembel et al. 2010), with 999 permutations per site.

We tested the effects of forest loss on functional diversity using generalized linear models (GLM). The models were fitted for SES FDis and SES Fric as response variables. Each model included forest loss, ecoregion, sampling effort, and the interaction between forest loss and ecoregion as predictors. Sampling effort was summarized into a composite index combining sampling duration, number of sampling methods, and habitat types surveyed, and subsequently standardized. Model assumptions and fit were evaluated using simulation-based residual diagnostics implemented in the DHARMa package (Hartig 2022).

Standardized functional dispersion (SES FDis) and functional richness (SES FRic) were analysed using models fitted in the *glmmTMB* framework (Brooks et al. 2017). Heterogeneity in residual variance among ecoregions was accounted for by specifying

a dispersion model (*dispformula*) that allows variance to vary across groups. For SES FRic, we further adopted a Student's *t* error distribution (*t_family*), which is robust to non-normality and heavy-tailed residuals (Lange et al. 1989), thereby improving inference under heteroscedasticity.

Statistical significance was assessed using Type II ANOVA implemented in the car package (Fox & Weisberg, 2019). When significant differences in slopes among ecoregions were detected, we used estimated marginal trends to quantify and compare the effect of forest loss across ecoregions using the *emmeans* package (Lenth 2024), implemented via emtrends, followed by pairwise contrasts. All analyses were conducted in R (R Core Team 2025).

Trait-specific responses analyses

For each trait, we calculated the community-weighted mean (CWM) using the functcomp function in the FD package (Laliberté et al. 2014), considering only species that express each trait (i.e. with value = 1). For binary traits (reproductive modes traits), CWM values represent the proportion of species expressing each trait within a community, whereas for continuous traits (SVL) they represent the mean trait value of species present. All CWMs were standardized (z-scores) within each trait and ecoregion to allow comparison of effect sizes across traits while retaining regional variation.

We evaluated the effect of forest loss on each trait by fitting linear models with standardized CWM as the response variable, including forest loss, ecoregion, their interaction, and sampling effort as a covariate. This formulation allows estimation of both the overall (main effect) relationship between forest loss and trait composition and its variation among ecoregions. Trait responses were quantified using slope estimates, with effects classified based on 95% confidence intervals as negative (interval below zero), positive (interval above zero), or non-significant (interval overlapping zero).

Results

Functional diversity

Functional dispersion declined significantly with increasing forest loss ($\chi^2 = 7.39$, $p = 0.006$, Table 1, Figs. 1 and 2), indicating a progressive contraction of trait dissimilarity within communities. Functional dispersion differed among ecoregions ($\chi^2 = 41.94$, $p < 0.001$), and the interaction between forest loss and ecoregion was significant ($\chi^2 = 9.70$, $p = 0.021$), indicating that the relationship between forest loss and functional dispersion varied among ecoregions. Sampling effort had a small but significant effect ($\chi^2 = 4.68$, $p = 0.031$).

Across most ecoregions, functional dispersion tended to decline with increasing forest loss (Fig. 1). The strongest negative responses were observed in the Northeast and Southeast coastal ecoregions, whereas the Southeast inland ecoregion showed a weak positive trend, and in Southern ecoregion the effect was negative but not statistically significant. However, pairwise comparisons of slopes among ecoregions were not statistically significant, suggesting that differences in the strength of the forest loss effect among regions were moderate (Table S1 e S2).

In contrast, functional richness showed no significant relationship with forest loss ($\chi^2 = 0.0003$, $p = 0.985$, Table 2, Figs. 3 and 4), and the interaction between forest loss and ecoregion was not significant ($\chi^2 = 2.57$, $p = 0.464$). Sampling effort also had no detectable effect ($\chi^2 = 0.44$, $p = 0.505$). Differences among ecoregions were marginally significant ($\chi^2 = 7.70$, $p = 0.053$). Consistent with these results, estimated slopes of forest loss on functional richness were close to zero across all ecoregions, and pairwise comparisons indicated no significant differences among regions (Table S2 e S3).

Table 1. Results of Type II ANOVA testing the effects of forest loss, ecoregions, sampling effort, and their interaction on the standardized effect size of functional dispersion (SES FDis) in anuran assemblages.

	χ^2	df	P value
Forest loss	7.3921	1	**0.006**
Ecoregions	41.9448	3	**< 0.001**
Sampling effort	4.6766	1	**0.03**
Forest loss * Ecoregions	9.7027	3	**0.02**

Table 2. Results of Type II ANOVA testing the effects of forest loss, ecoregions, sampling effort, and their interaction on the standardized effect size of functional richness (SES FRic) in anuran assemblages.

	χ^2	df	P value
Forest loss	0.0003	1	0.98534
Ecoregions	7.6992	3	0.05265
Sampling effort	0.4437	1	0.50534
Forest loss * Ecoregions	2.5657	3	0.46353

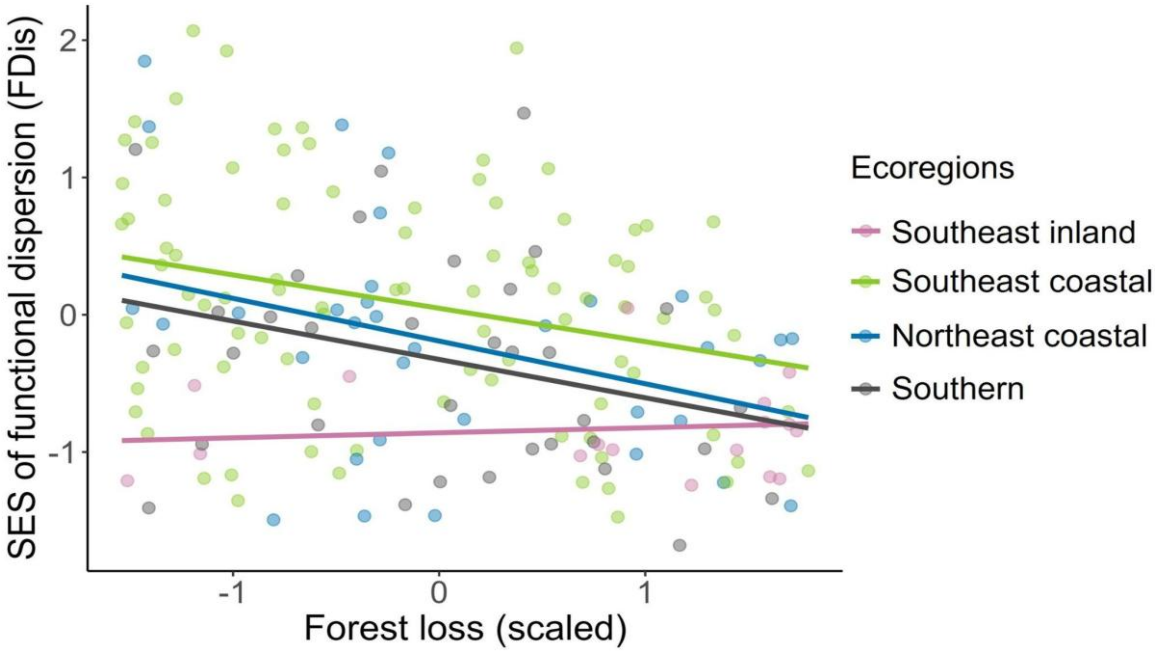

Figure 1. Relationship between forest loss (scaled) and the standardized effect size of functional dispersion (SES FDis) across ecoregions. Lines represent model-predicted values, and points show observed values. Different colors correspond to different ecoregions.

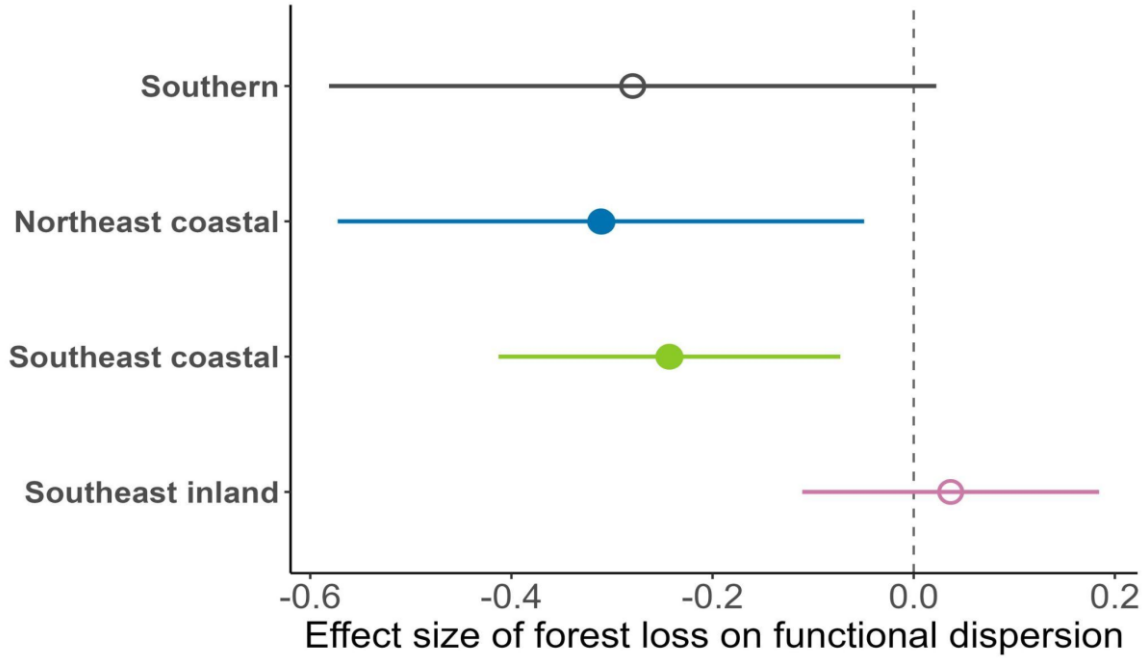

Figure 2. Estimated slopes (± 95% confidence intervals) of the effect of forest loss on the standardized effect size of functional dispersion (SES FDis) across ecoregions. Points represent slope estimates derived from generalized linear models, and horizontal bars indicate 95% confidence intervals. The dashed vertical line denotes a null effect (slope = 0). Filled symbols indicate slopes whose confidence intervals do not overlap zero (significant effect).

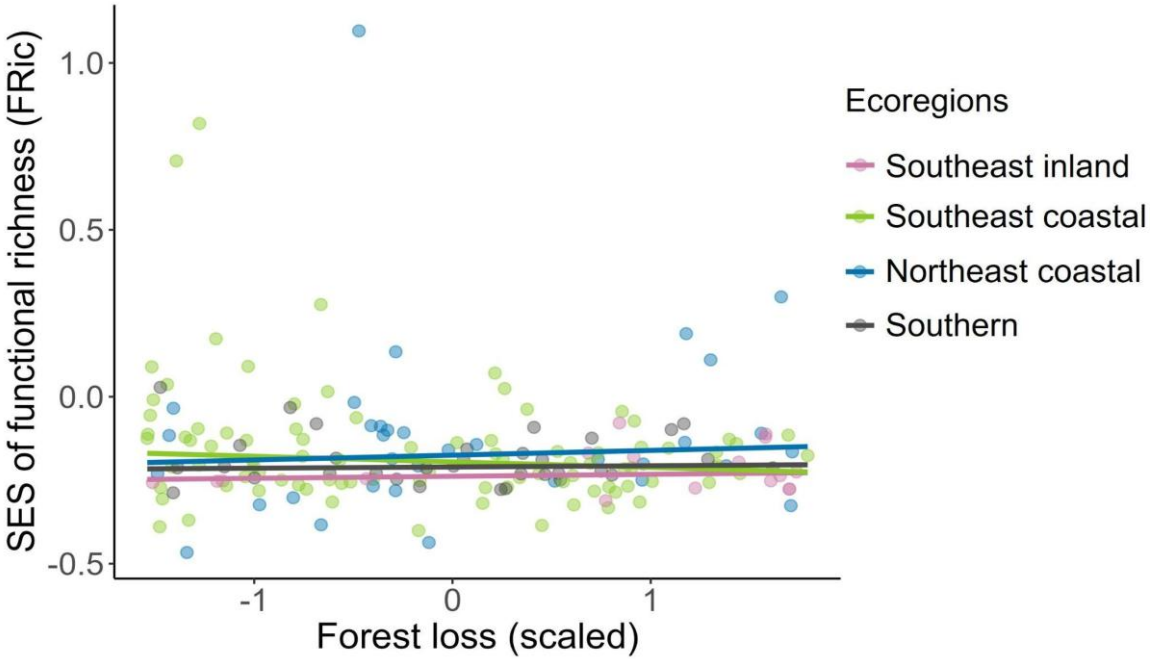

Figure 3. Relationship between forest loss (scaled) and the standardized effect size of functional richness (SES FRic) across ecoregions. Lines represent model-predicted values, and points show observed values. Different colors correspond to different ecoregions.

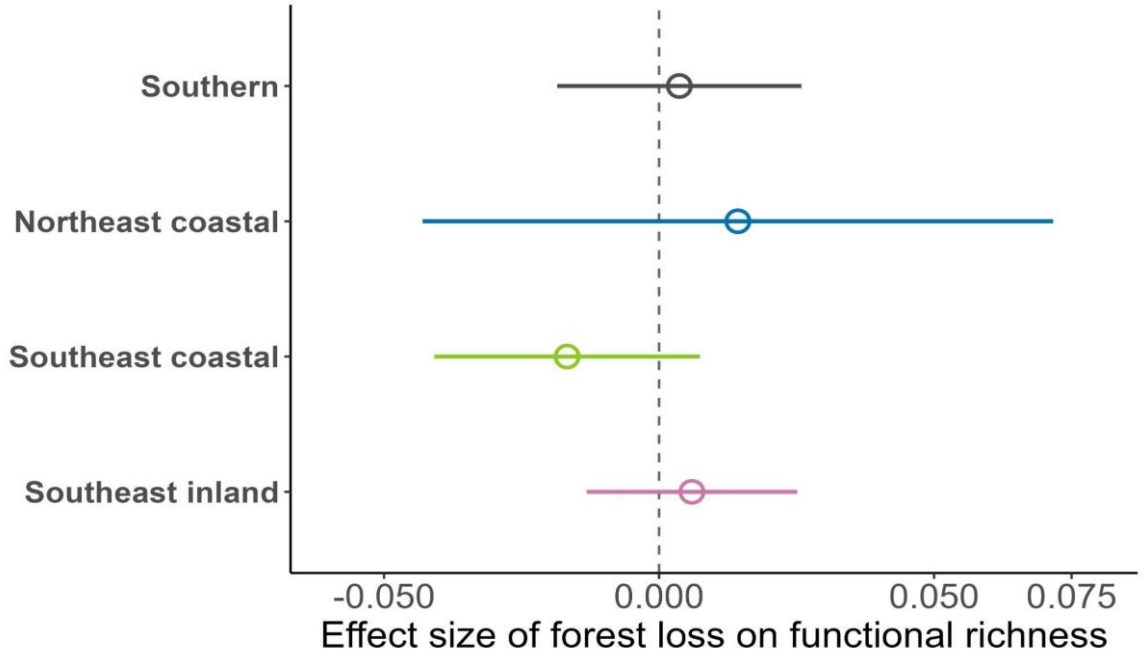

Figure 4. Estimated slopes (± 95% confidence intervals) of the effect of forest loss on the standardized effect size of functional richness (SES FRic) across ecoregions. Points represent slope estimates derived from a generalized linear model, and horizontal bars indicate 95% confidence intervals. The dashed vertical line denotes a null effect (slope = 0). Filled symbols indicate slopes whose confidence intervals do not overlap zero (significant effect).

Trait-specific responses

The effects of forest loss on community-weighted means (CWM) varied among ecoregions (Fig. 5 and 6). Traits such as oviposition and tadpoles in ponds, foam-nest construction, exotrophic tadpoles, and snout-vent length showed positive responses to forest loss, particularly in Southeastern and Northeastern coastal ecoregions ($\beta > 0$). In contrast, traits including tadpoles in streams or aerial plants, oviposition in leaf litter, endotrophic tadpoles, and direct development, exhibited negative responses to forest loss, with the strongest effects observed in Southeastern and Northeastern coastal ecoregions ($\beta < 0$). For several trait–ecoregion combinations, confidence intervals overlapped zero, indicating weak or no detectable effects, especially in Southeast inland and Southern ecoregion 4 (Fig. 5).

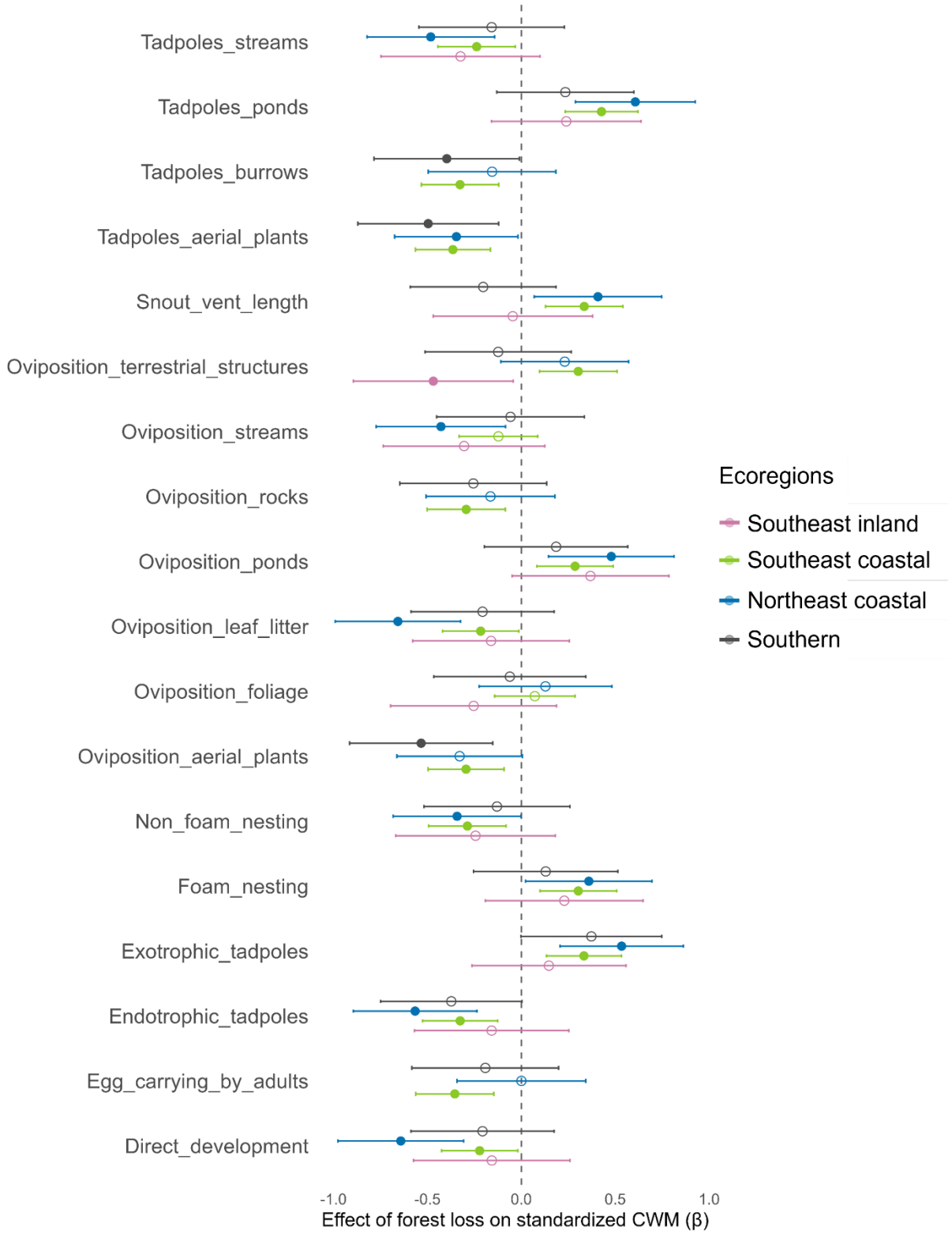

Figure 5. Trait-specific effects of forest loss on standardized community-weighted means (CWM) across four Atlantic Forest ecoregions (Southeast inland, Southeast coastal, Northeast coastal, and Southern). Points represent standardized regression coefficients (β) from linear models, and horizontal bars indicate 95% confidence intervals. Filled symbols denote statistically significant effects (confidence intervals not overlapping zero), whereas open symbols indicate non-significant effects. The vertical dashed line marks no effect (β = 0).

Discussion

Our study shows that forest loss drives a consistent decline in functional dispersion and promotes strong environmental filtering of key traits in anuran communities across the Atlantic Forest. These changes reflect a shift toward more functionally redundant assemblages dominated by generalist species adapted to reproduction in lentic water bodies and temporary ponds. Notably, this restructuring occurs even in the absence of substantial changes in functional richness, indicating that biodiversity loss may be masked by compensatory dynamics among species with similar ecological strategies. Importantly, these patterns vary across ecoregions, suggesting that regional context mediates the strength and direction of functional responses to forest loss.

The decline in functional dispersion indicates increased environmental filtering and trait convergence under forest loss. As environmental conditions become more homogeneous and restrictive, species with similar ecological strategies are favored, leading to communities dominated by a narrower set of trait combinations. This process reflects non-random species loss, in which functionally unique or specialized taxa are disproportionately filtered out, while generalist and disturbance-tolerant species persist or increase (Newbold et al. 2013, 2020, Clavel et al. 2011). Consequently, communities become more functionally redundant, reducing internal variability in trait composition.

In contrast, functional richness remained relatively stable despite these changes, suggesting that the overall volume of functional space is maintained. This apparent stability can be explained by compensatory dynamics, in which species losses are offset by the replacement of taxa with similar ecological roles (Mouillot et al. 2013, Matuoka et al. 2020, Pinho et al. 2025). As a result, although the range of trait values persists, the internal structure of the functional space becomes more clustered (Magnago et al. 2014, de Coster et al. 2015). This pattern indicates that functional richness alone may overestimate ecosystem resilience, as it fails to capture underlying shifts in trait composition and the erosion of functionally unique strategies.

The effects of forest loss on functional diversity were not uniform across ecoregions. Coastal regions showed more consistent responses, whereas effects were weaker or less clear in the southern ecoregion. In contrast, the inland southeastern ecoregion exhibited the most distinct patterns, highlighting the role of regional context in

mediating community responses. These differences likely reflect variation in the functional composition of regional species pools, which constrains how communities reorganize under environmental filtering (Heino et al. 2017, Leibold & Chase, 2018). In regions where species pools are more functionally diverse, environmental filtering may lead to stronger trait convergence, whereas in regions already dominated by similar strategies, additional filtering may produce weaker detectable changes.

Differences in community assembly processes further help explain these patterns. In the inland southeast ecoregion, amphibian assemblages are primarily structured by local environmental factors such as hydroperiod and habitat characteristics (Prado & Rossa-Feres, 2014), whereas in coastal regions, forest structure and microclimatic stability play a stronger role (Provete et al. 2014). Additionally, historical and biogeographical processes influence species pool composition across regions (Meynard et al. 2013, Vasconcelos et al. 2014, Heino et al. 2017). The inland Southeast includes species from both the Atlantic Forest and Cerrado biomes, many of which are adapted to drier and more seasonal conditions (da Silva et al. 2012, Vasconcelos et al. 2014), resulting in communities dominated by widespread and tolerant species (Melchior et al. 2017, Gomes-Melo et al. 2021). In contrast, coastal regions harbor a higher diversity of forest-dependent and micro-endemic species associated with humid and stable environments (Rossa-Feres et al. 2017, Vasconcelos et al. 2014).

Trait-specific responses reinforce these patterns. Forest loss was associated with declines in traits linked to humid and structurally complex environments, such as reproduction in leaf litter, streams, or bromeliads, and direct development. These strategies depend on stable microclimatic conditions and are particularly sensitive to reductions in humidity and increases in temperature and seasonality (Haddad & Prado 2005, da Silva et al. 2012). Conversely, traits associated with tolerance to drier and more variable conditions (such as pond breeding, foam-nest construction, exotrophic development, and larger body size) were positively associated with forest loss. The increase in body size is consistent with physiological constraints, as larger species experience lower rates of water loss (Olalla-Tárraga et al. 2009, da Silva et al. 2012), and may colonize new available environments, due to greater dispersal capacity.

Importantly, trait responses also varied across ecoregions, particularly between coastal and inland regions. In more humid and functionally diverse coastal systems, forest loss led to stronger shifts from specialized to generalist reproductive strategies, reflecting the loss of species dependent on stable microhabitats. In contrast, in inland regions already dominated by generalist and drought-tolerant species, trait responses were weaker, likely due to pre-existing environmental filtering and lower functional variability (Mayfield et al. 2010, Clavel et al. 2011).

Conclusion

Overall, our results show that forest loss consistently promotes environmental filtering in anuran communities, favoring species with similar ecological strategies and leading to more functionally redundant assemblages. This convergence suggests that habitat loss reduces environmental heterogeneity, constraining the range of viable trait compositions in the communities. Notably, these changes occur even in the absence of substantial shifts in functional richness, indicating that richness-based metrics may underestimate biodiversity change when functional redundancy masks underlying ecological simplification.

Importantly, responses to forest loss are both trait-dependent and ecoregion-specific. Variation in environmental gradients and the functional composition of regional species pools mediates how communities reorganize under disturbance. By integrating functional diversity patterns with trait-based responses, our results provide a more mechanistic understanding of how forest loss reshapes ecological communities.

These findings have direct implications for conservation. The loss of functionally distinct species may disproportionately affect ecosystem functioning, even when overall diversity appears relatively stable. Therefore, incorporating trait-based approaches into conservation planning is essential to better capture hidden dimensions of biodiversity loss and to maintain ecosystem integrity in human-modified landscapes.

More broadly, understanding how landscape-scale forest loss filters functional traits improves our ability to predict which species are likely to persist under ongoing environmental change. This, in turn, provides key insights into the long-term stability

of ecosystem functions and reinforces the importance of conserving not only species richness but also the diversity of ecological strategies across regions.

Data Availability Statement: All data supporting the findings of this study are openly available at Zenodo under DOI: 10.5281/zenodo.20547967

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Supplementary material

Table S1. Estimated slopes (± SE and 95% confidence intervals) of the relationship between forest loss and functional dispersion (SES FDis) for each ecoregion, obtained from a generalized linear model. Negative slopes indicate a decline in functional dispersion with increasing forest loss.

Ecoregion	Forest loss scaled trend	SE	df	lower.CL	upper.CL
Southeast inland	0.037	0.075	162	-0.111	0.184
Southeast coastal	-0.243	0.086	162	-0.413	-0.073
Northeast coastal	-0.311	0.133	162	-0.573	-0.049
Southern	-0.279	0.153	162	-0.581	0.022

Table S2. Pairwise comparisons of slopes describing the relationship between forest loss and functional dispersion (SES FDis) among ecoregions. Estimates represent differences between slopes, with associated standard errors, t-ratios, and Tukey-adjusted *p*-values.

Contrast	Estimate	SE	df	t.ratio	p.value
Southeast inland – Southeast coastal	0.280	0.113	162	2.474	0.068
Southeast inland – Northeast coastal	0.348	0.151	162	2.304	0.101
Southeast inland - Southern	0.316	0.170	162	1.857	0.251
Southeast coastal - Northeast coastal	0.068	0.158	162	0.432	0.973
Southeast coastal - Southern	0.036	0.175	162	0.208	0.997
Northeast coastal - Southern	-0.032	0.202	162	-0.156	0.999

Table S3. Estimated slopes (± SE and 95% confidence intervals) of the relationship between forest loss and functional richness (FRic) for each ecoregion, obtained from a generalized linear model. Positive or negative slopes indicate increases or decreases in functional richness with increasing forest loss.

Ecoregion	Forest loss scaled trend	SE	df	lower.CL	upper.CL
Southeast inland	0.006	0.010	Inf	-0.013	0.025
Southeast coastal	-0.017	0.012	Inf	-0.041	0.007
Northeast coastal	0.014	0.029	Inf	-0.043	0.072
Southern	0.004	0.011	Inf	-0.019	0.026

Table S4. Pairwise comparisons of slopes describing the relationship between forest loss and functional richness (FRic) among ecoregions. Estimates represent differences between slopes, with associated standard errors, t-ratios, and Tukey-adjusted *p*-values.

Contrast	Estimate	SE	df	t.ratio	p.value
Southeast inland – Southeast coastal	0.023	0.016	Inf	1.459	0.462
Southeast inland – Northeast coastal	-0.008	0.031	Inf	-0.273	0.993
Southeast inland - Southern	0.002	0.015	Inf	0.155	0.999
Southeast coastal - Northeast coastal	-0.031	0.032	Inf	-0.975	0.764
Southeast coastal - Southern	-0.020	0.017	Inf	-1.223	0.612
Northeast coastal - Southern	0.011	0.031	Inf	0.340	0.986

5 CONCLUSÃO GERAL

Esta tese demonstra que os efeitos da perda florestal sobre as comunidades de anuros da Mata Atlântica são complexos e dependem tanto da história biogeográfica das regiões quanto das características ecológicas das espécies. Nossos resultados revelam que a perda florestal não afeta a biodiversidade de maneira uniforme, produzindo respostas distintas entre ecorregiões e entre grupos de espécies com diferentes preferências de habitat e estratégias funcionais.

Quanto à riqueza taxonômica, verificamos que espécies especialistas de floresta são as mais negativamente afetadas pela redução da cobertura florestal, enquanto espécies associadas a áreas abertas tendem a ser favorecidas e espécies generalistas apresentam respostas mais neutras. Esses padrões indicam que a composição dos pools regionais de espécies e os diferentes históricas e características biogeográficas influenciam em como as comunidades respondem às mudanças contemporâneas da paisagem.

Quanto à diversidade funcional, observamos que a perda florestal promove filtragem ambiental, favorecendo espécies com estratégias ecológicas semelhantes e resultando em comunidades mais funcionalmente redundantes. Embora a riqueza funcional não apresente reduções expressivas, uma redução consistente da dispersão funcional indica uma simplificação ecológica das comunidades. Esses resultados sugerem que métricas baseadas exclusivamente em riqueza podem subestimar os impactos da perda de habitat ao não capturarem alterações mais sutis, porém ecologicamente relevantes, na organização funcional das assembleias.

Em conjunto, os resultados evidenciam que as respostas à perda florestal são dependentes dos atributos das espécies e do contexto biogeográfico em que as comunidades estão inseridas. Variações nos gradientes ambientais regionais e na composição funcional dos pools de espécies influenciam como as comunidades se reorganizam diante das perturbações, reforçando a necessidade de abordagens que integrem ecologia funcional, biogeografia e ecologia de paisagens para compreender os mecanismos que estruturam a biodiversidade.

Além de revelar os impactos da perda florestal sobre a diversidade taxonômica e funcional, nosso estudo contribui para o avanço do entendimento de como a perda de habitat atua na reconfiguração das comunidades de anuros e permite identificar quais grupos de espécies e quais atributos funcionais são mais vulneráveis às

mudanças ambientais. Ao demonstrar que espécies especialistas e determinadas estratégias funcionais são mais suscetíveis à perda florestal, fornecemos uma base mais robusta para compreender os mecanismos que promovem mudanças na biodiversidade em paisagens antropizadas.

A integração de informações biogeográficas e funcionais representa uma ferramenta valiosa para o planejamento da conservação, pois permite identificar regiões com maior potencial de perda de biodiversidade e priorizar essas áreas para ações de manejo e proteção. Essa abordagem é particularmente relevante em biomas altamente deflorstados, como a Mata Atlântica, onde os impactos da perda de habitat variam substancialmente entre regiões e grupos de espécies.

De forma mais ampla, nossa abordagem permitiu identificar tanto padrões gerais quanto respostas específicas das comunidades, contribuindo para previsões mais robustas sobre a persistência das espécies e a estabilidade dos ecossistemas diante das mudanças ambientais em curso. Assim, os resultados apresentados oferecem subsídios para o desenvolvimento de estratégias de conservação mais eficazes e espacialmente direcionadas, tanto para a Mata Atlântica quanto para outros ecossistemas sujeitos a intensas transformações antrópicas.