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Letízia Míriam Gomes de Jesus

Fatores que influenciam a Diversidade Beta de anfíbios da Mata Atlântica

Factors Influencing the Beta Diversity of Amphibians in the Atlantic Forest

Juiz de Fora
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Dissertação apresentada ao Programa de Pós Graduação em Biodiversidade e Conservação da Natureza da Universidade Federal de Juiz de Fora como requisito parcial à obtenção do título de Mestre em Biodiversidade e Conservação da Natureza. Área de concentração: Ecologia.

Orientador: Professor Doutor Henrique Caldeira Costa

Coorientador: Professor Doutor Mario Ribeiro Moura

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Aprovada em _____ de ______________ de _______

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> Isso partindo da ideia de que a vida é útil, mas a vida não tem utilidade nenhuma. A vida é tão maravilhosa que a nossa mente tenta dar uma utilidade a ela[.] A vida é fruição, é uma dança, só que é uma dança cósmica, e a gente quer reduzi-la a uma coreografia [utilitária]. (Krenak, 2020, p. 108).

RESUMO

A distribuição e abundância das espécies não são constantes ao longo das regiões e podem ser moldadas por gradientes ambientais. Assim, compreender como as alterações ambientais afetam a composição das assembleias é essencial para prever respostas da biodiversidade diante de mudanças climáticas. Esse desafio torna-se particularmente relevante na Mata Atlântica, uma das áreas mais biodiversas do planeta, que também abriga uma das faunas de anfíbios mais ameaçadas do mundo. Nesse contexto, este estudo investigou como a composição das espécies de anfíbios varia ao longo de gradientes ambientais nesse bioma, identificando os fatores contemporâneos mais influentes. Para isso, reunimos inventários de anfíbios disponíveis na literatura e os combinamos com variáveis bioclimáticas, edáficas e topográficas, utilizando análises de modelagem de dissimilaridade generalizada (GDM). Essa abordagem nos permitiu avaliarmos como o ambiente influencia a beta diversidade taxonômica, funcional e filogenética dos anfíbios da Mata Atlântica; identificar regiões mais suscetíveis a alterações na composição das espécies, nos atributos funcionais e nas linhagens filogenéticas dos anfíbios. Apesar da heterogeneidade da composição taxonômica dentre as assembleias, observamos que elas ocupam regiões similares no espaço funcional, indicando uma redundância ecológica entre as espécies. Essa impressão foi ainda reforçada pela forte correlação entre as diversidades funcional e filogenética, sugerindo que a história evolutiva dos anfíbios pode ter influenciado seus papéis ecológicos. Não surpreendentemente, grande parte das mudanças observadas na composição ocorre entre espécies proximamente relacionadas. Fatores ambientais como distância geográfica, isotermalidade e proporção de argila no solo emergiram como influentes nas três dimensões de beta diversidade, enquanto que outras variáveis, como proporção de silte no solo e precipitação no mês mais úmido, exerceram influências adicionais. Nossos resultados também revelaram um gradiente de diferenciação latitudinal, que indica que regiões do sul, da costa e do interior do nordeste da Mata Atlântica serão mais suscetíveis à mudanças expressivas em cenários climáticos futuros. Esses padrões reforçam o papel da estabilidade climática histórica e das características edáficas no delineamento da composição de espécies, das linhagens evolutivas e dos atributos funcionais. A redundância ecológica observada entre os anfíbios da Mata Atlântica pode representar um mecanismo de resiliência frente às mudanças climáticas, embora sua efetividade dependa de como esses padrões se distribuem regionalmente e de como cada espécie responde às alterações ambientais. Por fim, nossos resultados ressaltam a importância de abordagens macroecológicas no planejamento de estratégias de conservação. Nosso estudo ajuda a elucidar os processos ecológicos que moldaram e continuam a moldar a beta diversidade de anfíbios da Mata Atlântica, um bioma de alta prioridade para a conservação.

Palavras-chave: Anfíbios, Beta diversidade, Diversidade filogenética, Diversidade funcional, Diversidade taxonômica, GDM, Mata Atlântica.

ABSTRACT

The distribution and abundance of species vary across regions and can be shaped by environmental gradients. Thus, understanding how environmental changes affect assemblage composition is essential in predicting biodiversity responses under climate change. This challenge becomes particularly relevant in the Atlantic Forest, one of the most biodiverse regions on the planet and home to one of the most threatened amphibian faunas in the world. In this context, this study investigated how amphibian species composition varies along environmental gradients within this biome, identifying the most influential contemporary factors. To achieve this, we compiled amphibian inventories available in the literature and combined them with bioclimatic, edaphic, and topographic variables, using generalized dissimilarity modeling (GDM). This approach allowed us to evaluate how environmental factors influence the taxonomic, functional, and phylogenetic beta diversity of Atlantic Forest amphibians and to identify regions most susceptible to changes in species composition, functional traits, and phylogenetic lineages. Despite the heterogeneity in taxonomic composition among assemblages, we observed that they occupy similar regions in functional space, indicating ecological redundancy among species. This impression was further reinforced by the strong correlation between functional and phylogenetic diversity, suggesting that the evolutionary history of amphibians may have shaped their ecological roles. Predictably, most observed changes in composition occur among closely related species. Environmental factors such as geographic distance, isothermality, and clay content in soil emerged as major determinants across all three dimensions of beta diversity, while other predictors, including silt content in soil and precipitation of wettest month, showed additional effects. Our results also revealed a latitudinal differentiation gradient, indicating that regions in the south, as well as the northeastern coast and interior of the Atlantic Forest, will be more susceptible to substantial shifts under future climate scenarios. These patterns highlight the role of historical climate stability and edaphic characteristics in shaping species composition, evolutionary lineages, and functional traits. The ecological redundancy observed among Atlantic Forest amphibians may represent a mechanism of resilience in the face of climate change, although its effectiveness likely depends on how these patterns are distributed regionally and how individual species respond to environmental alterations. Finally, our findings highlight the importance of macroecological approaches in guiding conservation strategies. Our study contributes to clarifying the ecological processes that have shaped, and continue to shape, the amphibians beta diversity in the Atlantic Forest, a high conservation priority biome.

Keywords: Amphibia, Atlantic Forest, Beta diversity, GDM, Functional diversity, Phylogenetic diversity, Taxonomic diversity.

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LISTA DE ABREVIATURAS E SIGLAS

CBD	Compositional Beta-Diversity
FBD	Functional Beta-Diversity
PBD	Phylogenetic Beta-Diversity
PCoA	Principal Coordinates Analysis
PCA	Principal Component Analysis
GDM	Generalized Dissimilarity Modelling
VIF	Variance Inflation Factor
SSP / SSPs	Shared Socioeconomic Pathways
GCM / GCMs	General Circulation Models
MIROC6	Model for Interdisciplinary Research on Climate 6
HadGEM3-GC31-LL	Hadley Centre Global Environment Model (versão GC31-LL)
BCC-CSM2-MR	Beijing Climate Center Climate System Model 2-MR
BM	Brownian Motion
SVL	Snout-Vent Length
GHG	Greenhouse Gases

SUMÁRIO

1 INTRODUCTION

The distribution and abundance of species are not constant, with changes in biodiversity patterns often linked to environmental variations across space and time (Araújo et al., 2008; Kraft et al., 2011). Because species' response to the environment can vary, the composition of biological communities may change in asymmetrical ways, along environmental gradients (Whittaker, 1960, 1972; Anderson et al., 2011). This spatial variation in species composition, known as beta-diversity, can encompass not only the taxonomic compositional (CBD) dimension but also functional (FBD) and phylogenetic beta-diversity (PBD) (McGill et al., 2006). The FBD framework often quantifies dissimilarity in trait composition among communities, reflecting niche-based environmental filtering and biotic interactions (Swenson et al., 2012), while PBD measures the divergence in shared evolutionary history, offering insights into historical biogeographic and diversification processes (Cavender-Bares et al., 2009; Graham; Fine, 2008). All three beta-diversity dimensions (CBD, FBD, and PBD) can be influenced by environmental gradients, which act as selective pressures on trait evolution and phylogenetic assembly. Integrating these approaches allows for a more mechanistic understanding on how biodiversity will respond to environmental change (Bush et al., 2016; Socolar et al., 2016; Araújo et al., 2022), which is particularly relevant in regions undergoing rapid global change (Legendre, Borcard and Peres-Neto, 2005; Graham and Fine, 2008; Swenson, Anglada-Cordero and Barone, 2011).

Although unsustainable anthropogenic activities are widespread, their impact on beta-diversity dimensions can be particularly worrying in biodiversity hotspots, regions with exceptionally high endemism and extremely reduced natural cover (Habel et al., 2019; Trew; Maclean, 2021; Zachos; Habel, 2011). Among biodiversity hotspots, the Atlantic Forest in South America stands out as one of the most threatened tropical rainforests. This hotspot spans approximately 27 degrees of latitude, which impose a remarkable variation in its environmental conditions, particularly climate (Metzger, 2009). This biodiversity hotspot shows high endemicity across different taxonomic groups, including vascular plants (78% of species; Freitas *et al.*, 2016), birds (29% ; Vale *et al.*, 2018), mammals (31%; Souza *et al.*, 2019), reptiles (31%; Metzger, 2009), ants (50%; Silva *et al.*, 2024), and amphibians (78%; Rossa-Feres *et al.*, 2017). The overwhelmingly high endemism rate for Atlantic Forest amphibians can be linked to the combined influence of physiological constraints and low vagility of these organisms, which ultimately promote high rates of turnover across environmental gradients (Carnaval et al., 2014; Lourenço-de-Moraes et al., 2020; Marshall et al., 2018). Therefore, amphibians represent an ideal model group for disentangling the roles of ecological and evolutionary processes in shaping beta-diversity patterns, particularly in environmentally heterogeneous regions like the Atlantic Forest.

Amphibian biodiversity in the Atlantic Forest has been studied using various approaches, including: stacking of either coarsely drawn expert range maps and/or species occurrence records (Lourenço-de-Moraes et al., 2019, 2020), overlap of binary projections derived from species distribution modeling (Anunciação *et al.*, 2023), and compiling of inventory data with limited spatial coverage (Alves-Ferreira et al., 2022; Da

Silva; Almeida-Neto; Arena, 2014; Thome et al., 2020). While each approach has strengths and limitations, the extremely high endemism of Atlantic Forest amphibians suggests that methods accounting for rare species may yield less biased inferences about environmental change impacts (Villalobos et al., 2013). In this context, the 'assemble first, predict later' framework, where species are first sampled as biological assemblages before environmental modeling, offers distinct advantages for datasets containing numerous rarely observed species (Ferrier; Guisan, 2006). Herein we use an extensive database of Atlantic Forest amphibian inventories to investigate how compositional, functional, and phylogenetic beta-diversity respond to environmental variation.

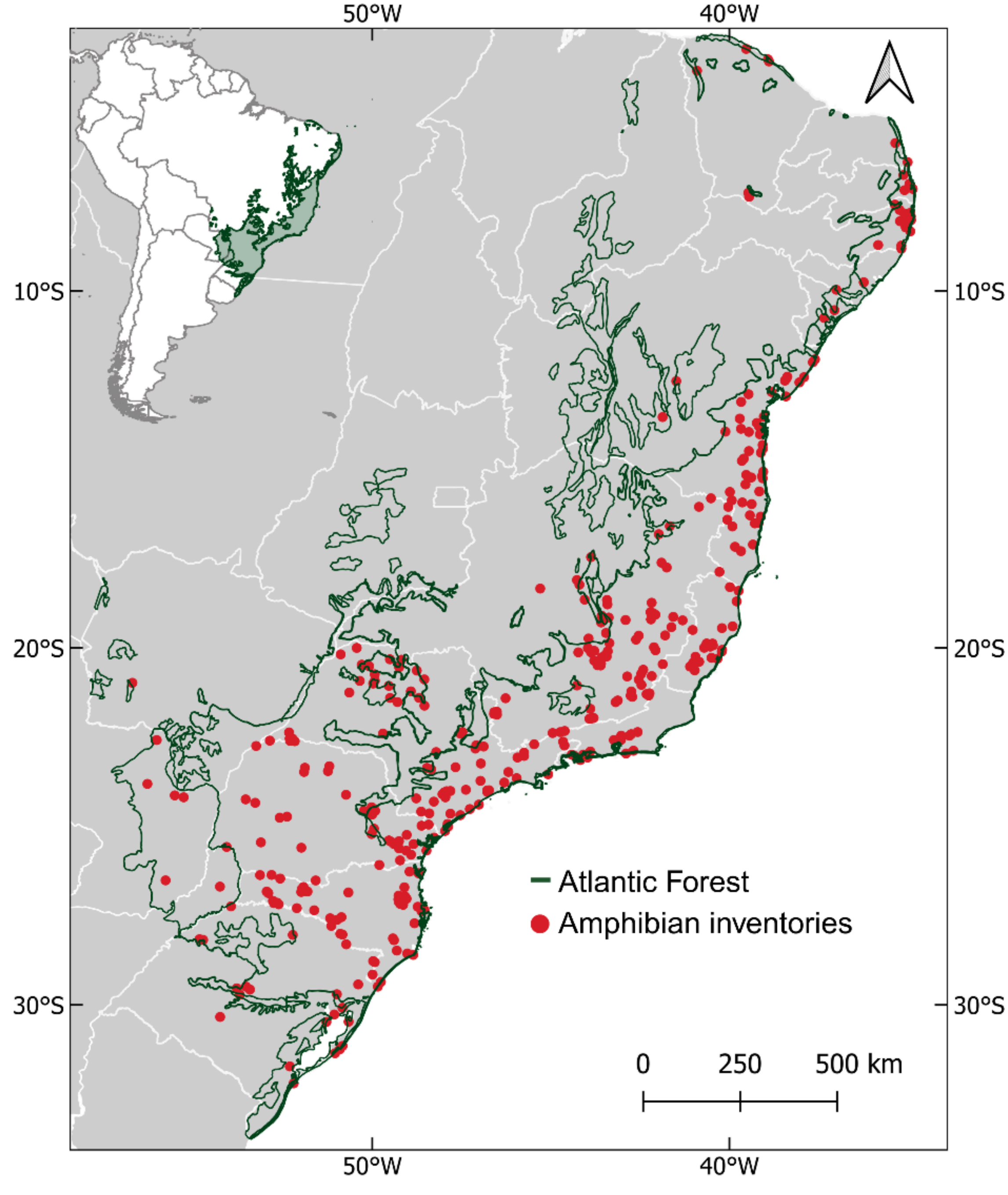
As ectothermic organisms with cutaneous respiration, amphibian metabolism and reproduction are highly sensitive to variations in temperature, humidity, and precipitation (Buckley; Jetz, 2007; Guedes; Feio; Moura, 2022; Hillman et al., 2008). Edaphic factors like soil texture and composition are further associated with skin health and burrowing habits in many amphibians (Nomura; Rossa-Feres; Langeani, 2009; Rossa-Feres et al., 2017a; Varela et al., 2018), besides potentially affecting vegetation structure and hydroperiod of amphibian habitats (Azevedo et al., 2021; Vitt; Caldwell, 2013). Given the Atlantic Forest's biodiversity importance and the particular vulnerability of amphibians to climate change as well as emerging diseases brought with it (Berger et al., 2016; Luedtke et al., 2023), this study aims to identify how climatic and edaphic factors influence compositional, functional, and phylogenetic beta-diversity of amphibians, and to assess the impact of projected climate change on amphibian beta-diversity, highlighting regions where substantial changes in species composition, functional traits and phylogenetic lineages are expected.

2 METHODS

2.1 INVENTORY DATA

We used amphibian inventories compiled from scientific papers, books, theses, dissertations, and management plans for protected areas in the Atlantic Forest (Moura et al., 2018). All inventories included at least 10 species, recorded using a minimum of two sampling methods in at least two sampling surveys — one during the dry season and another during the wet season, and were distant at least 5 km from each other (see Moura *et al.*, 2018 for further details on compilation of inventory data). In total, we used 354 inventories, covering 532 amphibian species **(Figure 1),** which currently represents nearly 90% of all species known to occur in the Atlantic Forest (Rossa-Feres et al., 2017b).

Figure 1 — Location of amphibian inventories in the Atlantic Forest, in South America.



Source: Elaborated by the author. (2025).

2.2 SPECIES PHYLOGENETIC DATA

To represent the evolutionary relationships among Atlantic Forest amphibians, we extracted a subset of species from a fully-sampled global amphibian phylogeny (Jetz; Pyron, 2018) that matched our regional dataset. We standardized taxonomic nomenclature to align species binomials with those in the phylogeny, retaining 90.2% (480 species) of the taxa reported in our inventory data. For the remaining 52 species absent from the phylogeny, we employed a conservative imputation approach by assigning each as a sister taxon to a congeneric species using the *add.tips* function in the *phangorn* R package (Jetz; Pyron, 2018; Schliep et al., 2017). Note that the Jetz and Pyron phylogeny already included phylogenetic imputed relationships for 211 of the 480 species originally included. To account for uncertainty in fully-sampled phylogenies, we repeated this procedure separately across a subset of 100 amphibian trees. The resulting set of phylogenetic trees was used for all subsequent analyses.

2.3 SPECIES TRAIT DATA

Many species attributes can be useful to inform biological characteristics inherent to a species that influence its evolutionary fitness (Cadotte; Carscadden; Mirotchnick, 2011; Luck et al., 2012). We assessed 7 continuous (morphometric) and 7 categorical (ecological) attributes that can be linked to habitat occupancy and trophic position in amphibians (Duellman; Trueb, 1994; Haddad; Prado, 2005; Wells, 2007) **(Table 1)**. The morphometric values were divided by the body length (snout-vent length, mm) to remove any dependence on body size. We log-10 transformed all morphometric traits to reduce data skewness.

2.4 PHYLOGENETIC SIGNAL IN TRAIT DATA AND IMPUTATION OF MISSING VALUES

Under phylogenetic autocorrelation, closely related taxa exhibit greater trait similarity than distant relatives due to shared evolutionary history (Freckleton, 2009). We quantified this signal in Atlantic Forest amphibians using Blomberg’s K-statistic (Blomberg; Garland Jr; Ives, 2003) for continuous morphometric traits and the D-statistic for binary traits (Fritz; Purvis, 2010). Blomberg’s K-statistic observed trait variation to Brownian-Motion (BM) expectations, where $K < 1$ indicates lack of phylogenetic signal, and $K > 1$ suggests more phylogenetic signal than expected under BM (conserved trait). The hypothesis testing assesses whether $K \neq 0$ (H_0, $K = 0$). For binary traits, the D-statistic evaluates phylogenetic clustering, where $D = 0$ matches BM expectations (strong conservatism), $D = 1$ indicates random distribution (labile trait, random phylogenetic structure). The hypothesis testing checks either if $D \neq 0$ (H_0, $D = 0$) or $D \neq 1$ (H_0, $D = 1$). For both metrics of phylogenetic signal (K and D), we assessed significance through 1000 permutational tests. To account for uncertainty in imputed evolutionary relationships, we computed the K and D for each phylogeny in the set of 100 amphibian trees. We then extracted the average K and its respective p-value across the 100 trees. Computations were performed using the R packages *phytools* (Revell, 2012) and *caper* (Orne et al., 2023).

To fill gaps in our trait data and improve the representation of functional trait space, we used the phylogeny-based imputation technique, *Rphylopars* (Goolsby; Bruggeman; Ané, 2017). This method uses the phylogenetic tree directly to impute missing values based on the phylogenetic covariances and correlated evolution between numeric attributes. For each one of the 100 amphibian trees derived from Jetz and Pyron (2018) fully-sampled phylogenies, we ran *Rphylopars* using the Brownian motion (BM) model of trait evolution. We then extracted the median value across the 100 trees for each imputed attribute per species. Because *Rphylopars* allows imputation only for continuous attributes (Goolsby; Bruggeman; Ané, 2017), the imputed values for binary variables can assume values different from 0–1. Thus, for each binary attribute, we made the imputed value binary using the 0.5 threshold. Computations were performed in R v. 4.2.3 using the packages *ape* (Paradis; Schliep, 2019) and *Rphylopars* (Goolsby; Bruggeman; Ané, 2017).

2.5 MEASURING BETA-DIVERSITY

Variation in species composition across different assemblages are typically measured using dissimilarity indices. Recent research has emphasized the importance of using dissimilarity measures that are independent of differences in species richness to accurately assess CBD patterns (Baselga; Leprieur, 2015). These measures are considered to reflect “true turnover” in species composition, as they are not influenced by gradients of richness differences among assemblages (Baselga, 2010). Thus, we quantified the compositional (CBD), phylogenetic (PBD), and functional beta-diversity (FBD) using the Simpson dissimilarity index, given its independence of richness differences (Koleff; Gaston; Lennon, 2003).

Compositional beta diversity (CBD) was computed using a presence-absence matrix derived from compiled inventory data. For phylogenetic beta-diversity (PBD), we calculated the phylogenetic Simpson dissimilarity index for each assemblage pair across all 100 amphibian trees. These pairwise dissimilarities were then averaged across trees to capture the overall pattern of shared evolutionary history among amphibian assemblages. Functional beta-diversity (FBD) was derived from the 14 species-level traits, first converted to pairwise distances between species using Gower's dissimilarity metric with equal weighting among traits. This approach prevented overrepresentation of multi-state categorical variables (e.g., microhabitat use, call site). The computation of FBD using a multidimensional framework requires assemblages to have at least 2^n species, where n is the number of traits (Villéger; Mason; Mouillot, 2008). Since our assemblages have a minimum of 10 species, we reduced trait dimensionality via Principal Coordinates Analysis (PCoA), retaining the three first axes. These synthetic traits showed strong concordance with the original Gower Distance matrix (Mantel Test $r = 0.86$, $p < 0.001$). FBD then quantified the shared portion of the synthetic trait space across amphibian assemblages. All computations were performed using the *betapart* R package (Baselga et al., 2023).

2.6 ENVIRONMENTAL CHARACTERIZATION

We used three broad sets of environmental layers to characterize the Atlantic Forest with respect to climate, soil, and topography. Climatic factors were represented by 19 bioclimatic variables downloaded from WorldClim (WorldClim, 2023). Edaphic variables were extracted from SoilGrids 2.0 for the depth of interval of 5-15 cm (Poggio et al., 2021), and included 10 variables representing physical (coarse fragments, bulk density, content of clay, sand and silt), chemical (cation exchange capacity, total nitrogen, soil organic carbon density, pH) and derived (organic carbon density) soil properties. Topographic layers were downloaded from EarthEnv (Amatulli *et al.*, 2018), and included elevation, roughness and slope.

Future climate projections depend on varying Shared Socioeconomic Pathways (SSPs), which describe distinct trajectories for greenhouse gas emissions and human population growth, developed in alignment with Generalized Circulation Models (GCMs) that simulate climate changes by accounting for diverse atmospheric processes (Masson-Delmotte et al., 2021). To minimize uncertainties about the choice of a particular GCM, we used projections of future climate according to three GCMs, namely: the Model for Interdisciplinary Research on Climate (MIROC6; Tatebe and Watanabe, 2018), the Hadley Centre Global Environment Model (HadGEM3-GC31-LL; Williams *et al.*, 2018), and the Beijing Climate Center Climate System Model (BCC-CSM2-MR; Wu *et al.*, 2019). We obtained future climate projections according to two SSPs: an optimistic (SSP-245) and pessimistic (SSP-585) scenario. Both SSPs projections considered the 2080-2100 time period. All environmental variables were obtained at the spatial resolution of 2.5 arc-min. We assumed that edaphic and topographic conditions would remain unchanged under future climate scenarios.

To reduce multicollinearity among the environmental variables, we used the variance inflation factor (VIF) to subsequently remove layers with the highest VIF until all remaining variables showed VIF < 5. This variable selection procedure resulted in the retention of six climatic variables (precipitation of wettest month, temperature seasonality, maximum temperature of warmest month, mean diurnal range, mean temperature of wettest quarter, and precipitation of coldest quarter); six edaphic variables (total nitrogen, cation exchange capacity, pH, content of silt, coarse fragments, and content of clay); and one topographic variables (slope).

2.7 DATA ANALYSIS

To verify how the contemporaneous environment explains compositional (CBD), phylogenetic (PBD), and functional beta-diversity (FBD) of Atlantic Forest amphibians, we used the Generalized Dissimilarity Modelling (GDM). This statistical approach is able to capture non-linear relationships between the spatial variation in biodiversity metrics (herein represented by CBD, PBD, and FBD matrices) and environmental gradients (Ferrier, 2002; Ferrier et al., 2004, 2007). Before computing the GDM, we squared-root our dissimilarity matrices to improve their Euclidean-properties (Legendre; De Cáceres, 2013).

To find the most parsimonious GDM, we performed a backward selection procedure through permutation tests. We used 100 iterations per variable, proceeding with removal of the least significant variable until the model had only significant ($p < 0.05$) variables. I-spline curves were then used to visualize the importance of the predictors. To obtain a spatially contiguous representation of CBD, PBD, and FBD, we used fitted functions from each respective GDM model to estimate beta-diversity across the environmental space represented by the selected predictors of each beta-diversity dimension (CBD, PBD, and FBD). We then reduced the number of dimensions of estimated dissimilarities through a principal component analysis (PCA), using the first three PCA-axes to build a RGB raster of CBD, PBD, and FBD through Atlantic Forest. Raster cells (estimated dissimilarity for amphibian assemblages) showing similar colors are projected to share comparable species composition. The analyses were carried out using the *gdm* package (Fitzpatrick et al., 2022), with all sites and site pairs (argument *sampleSites* = 1, *sampleSitePairs* = 1) with equal weights (*weightType* = "equal").

To identify regions subject to substantial turnover in species composition due to future climate change, we used the *predict.gdm* function of the *gdm* package to project the potential changes in amphibian beta-diversity between current and future climates. Our future projections consisted in a consensus raster represented as the average predictions across the three GCMs, for each future scenario (SSP245 and SSP585). Regions with higher values indicate areas where substantial changes in species composition are expected due to climate change.

3 RESULTS

The trait data for amphibians showed mixed patterns of phylogenetic structure. On one hand, highly conserved traits included body length (snout-vent length) and binary traits related to activity pattern, larval nutrition, life cycle, oviposition site, and microhabitat **(Table 1)**. On the other hand, all relative morphometric traits showed weak phylogenetic structure, along with traits representing macrohabitat and calling site preference for shrubs and refuges (e.g. bamboo, ground crevices). Therefore, of the 14 traits investigated, 50% were highly conserved across species of Atlantic Forest amphibians **(Table 1)**.

Table 1 — Species Amphibian traits, categories, justification and their respective phylogenetic signals. % Percentage of species in each category, Phylogenetic signal calculated through D-statistic for binary traits (D value(D=0 test result)/(D=1 rest result)), and Blomberg's K-statistic for continuous traits. * p value ≤ 0.05, ** p value ≤ 0.01, *ns* non significant.

Trait	**Categories**	**%**	**Functional justification**	**Phylogenetic Signal**
Ecological				
MacroHabitat	(a) Open Area, (b) Forest Area	35.16% 76.96%	Ecological traits that indicate reproductive success and habitat use for both adults and juveniles (Haddad et al.,	$0.36^{**/**}$ $0.55^{**/**}$
Microhabitat	(a) Aquatic, (b) Arboreous, (c) Cryptozoic,	3.25% 38.55% 30.72%		**-0,08**$^{ns/**}$ **-0,47**$^{ns/**}$ **-0,17**$^{ns/**}$

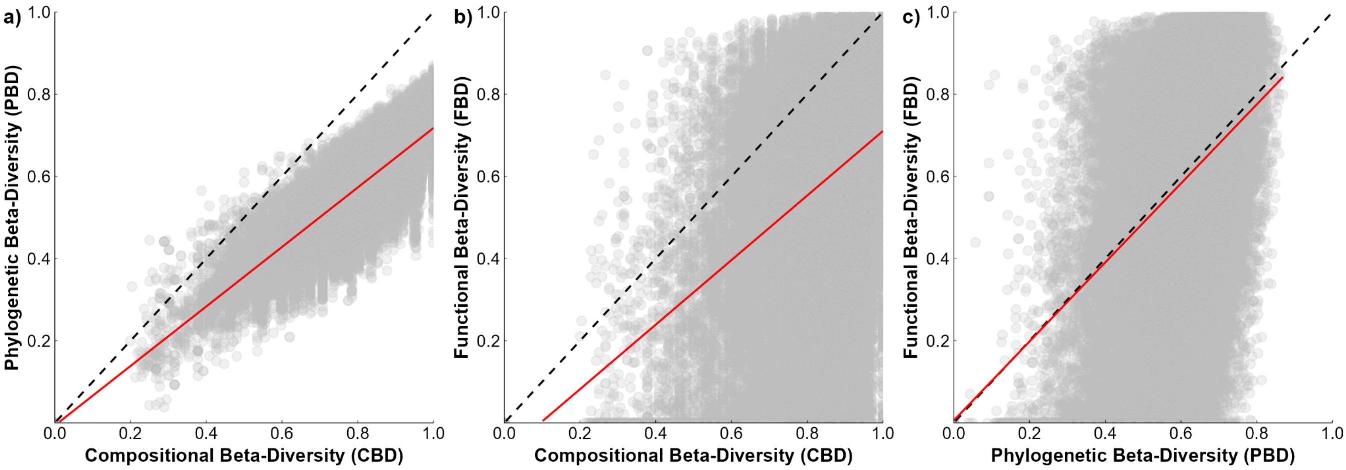
	(d) Phytotelmata, (e) Fossorial, (f) Rheophilic, (g) Terrestrial	2.95% 2.51% 10.64% 16.25%	2013; Nunes-de-Almeida; Haddad; Toledo, 2021).	$0,78^{*/ns}$ **-0,34**$^{ns/**}$ **-0,56**$^{ns/**}$ **-0,03**$^{ns/**}$
Call Site	(a) Swamp, (b) Slow stream, (c) Fast stream, (d) Bromeliad, (e) Forest floor, (f) Herbaceous, (g) Shrub, (h) Arboreous, (i) In refuge, (j) Rocky Outcrop	45.94% 9.75% 21.71% 7.83% 15.21% 62.19% 0.89% 1.92% 2.85% 1.48%		**-0,03**$^{ns/**}$ $0,32^{*/**}$ $0,19^{ns/**}$ $0,07^{ns/**}$ **-0,32**$^{ns/**}$ $0,73^{**/**}$ $0,89^{ns/ns}$ **-1,12**$^{ns/**}$ $0,73^{*/ns}$ **-0,59**$^{ns/**}$
Reproduction	(a) Life cycle biphasic,	84.34%		**-0,81**$^{ns/**}$
Oviposition	(a) Aquatic, (b) Non aquatic, (c) Animal	67.06% 31.76% 2.5%		**-0,34**$^{ns/**}$ **-0,25**$^{ns/**}$ **-1,19**$^{ns/**}$
Larval nutrition	(a) Endotrophic, (b) Exotrophic	11.08% 88.18%		**-0,24**$^{ns/**}$ **-0,21**$^{ns/**}$
Activity	(a) Diurnal, (b) Nocturnal	19.06% 84.78%		**-0,18**$^{ns/**}$ **-0,62**$^{ns/**}$
Morphometric				
Snout vent length			Mean male SVL (mm)	**0.00***
Head width (mm)			Indicate size of prey consumed (Alvarez-Grzybowska et al., 2020).	0.05
Eye diameter (mm)			Influence in detection of prey (Alvarez-Grzybowska et al., 2020).	0.02
Leg length (mm)			Locomotor modes can show microhabitat	0.03

Foot length (mm)	information (Buttimer; Stepanova; Womack, 2020; Stepanova; Womack, 2020).	0.02
Arm length (mm)		0.05
Hand length (mm)		0.03

Source: Elaborated by Mario R. Moura. (2025).

Amphibian assemblages in the Atlantic Forest had on average 24 species (min = 10, max = 71). Compositional beta-diversity (CBD) was high, with assemblages differing, on average, in 72.5% of their species (*βsim*=0.7250). Patterns of functional (FBD) and phylogenetic beta-diversity (PBD) were less pronounced: assemblages differed, on average, in 40.96% of functional trait space (*βsim*=0.4096%), and 31.32% of phylogenetic lineages (*βsim*=0.3132). When comparing pairwise dissimilarities, we observed that PBD averages out at lower numbers than CBD (Mantel Test r = 0.82, p < 0.001, **Figure 2a**), this pattern also happens when we compare FBD with CBD with the latter averaging out in higher numbers (Mantel Test r = 0.37, p < 0.001, **Figure 2b**). Lastly, as confirmed by the phylogenetic signal analysis, FBD shows a strong correlation with PBD (Mantel Test r = 0.40, p < 0.001) **(Figure 2c)**.

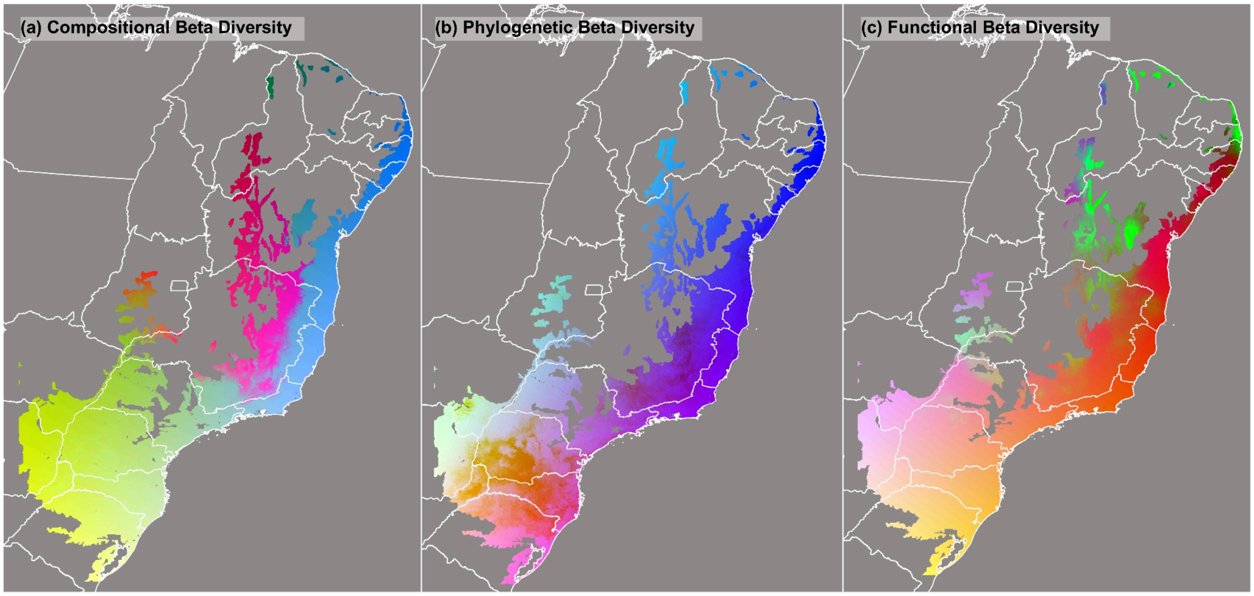
Figure 2 — Pairwise comparisons between three components of Beta-Diversity, Compositional (CBD), Phylogenetic (PBD), and Functional (FBD). The pairwise localities are represented in gray, and the red line represents the fitted trend.



Source: Elaborated by the author and Mario R. Moura. (2025).

CBD demonstrated a monotonic relationship with predicted ecological dissimilarity, with the most parsimonious model explaining 22% of the variation in species composition. In contrast, only 8.5% of the variation in PBD, and 1.6% in FBD were explained by each respective model. The first three axes from the principal component analysis using the estimated dissimilarities accounted for 99.9% of the variation, revealing a latitudinal distributional pattern **(Figure 3)**. The most important predictors returned in the backward selection for CBD were geographic distance (variable importance 33.89, $p < 0.05$), isothermality (variable importance 9.03, $p < 0.05$), and clay content in the soil (variable importance 4.57, $p < 0.05$). Considering the PBD, geographic distance (variable importance 19.24, $p < 0.05$), isothermality (variable importance 11.55, $p < 0.05$), clay (variable importance 9.58, $p < 0.05$), and silt content in the soil (variable importance 5.69, $p < 0.05$) emerged as the most influential predictors. As for the FBD, isothermality (variable importance 39.10, $p < 0.05$), precipitation of wettest month (variable importance 25.57, $p < 0.05$), and geographic distance (variable importance 4.06, $p < 0.05$) were the most influential predictors **(Figure 4).**

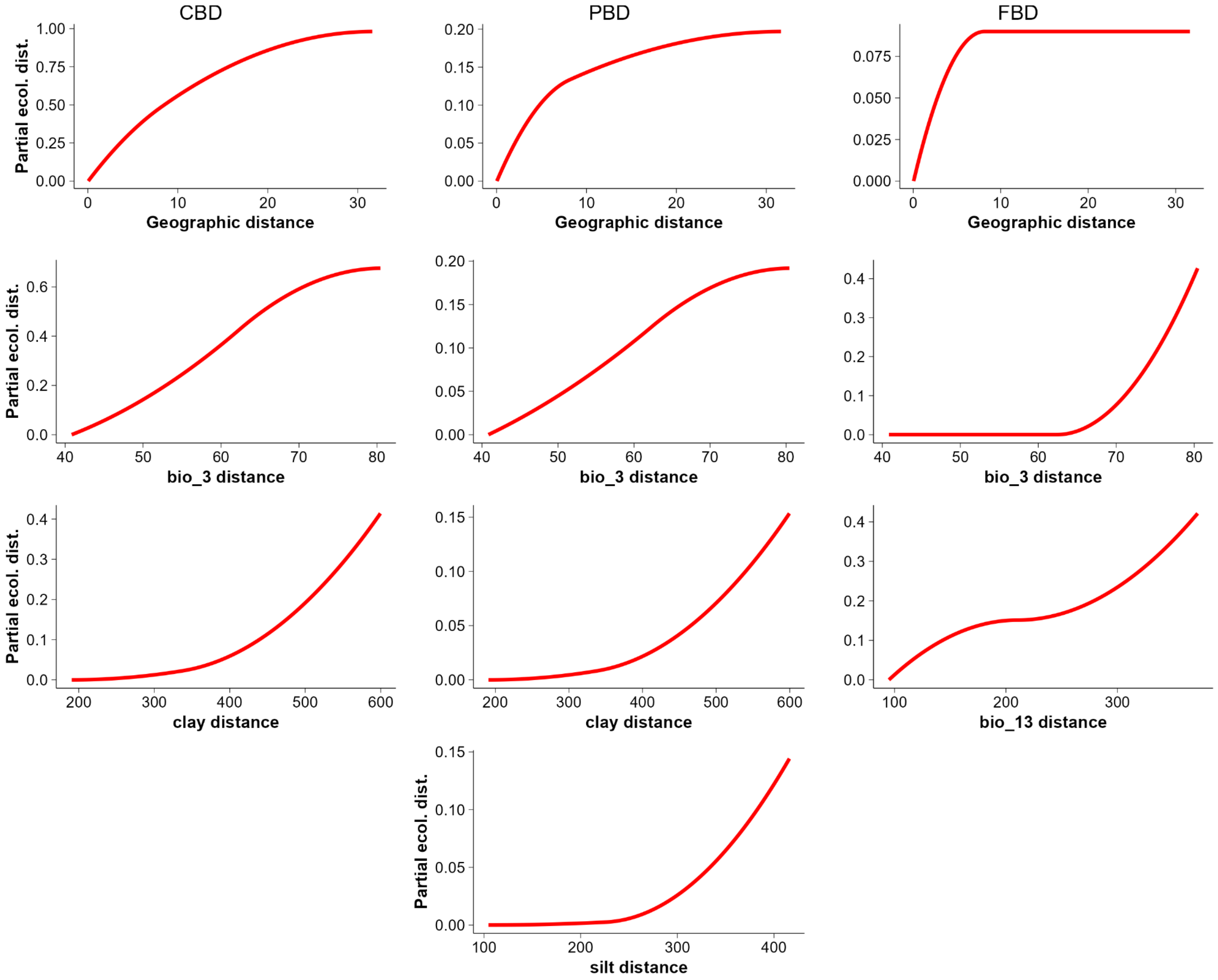
Figure 3 — Estimated dissimilarity across amphibian assemblages in the Atlantic Forest. RGB raster built with the first three PCA-axes representing the ecological dissimilarities for the (a) compositional (CBD), (b) phylogenetic (PBD), and (c) functional beta-diversity (FBD) of amphibians . Similar colours predict similar areas based on Simpson dissimilarity metric.The model result is presented as similarity or difference of colour between areas, but the specific colours do not translate to a linear progression of values.



Source: Elaborated by the author and Mario R. Moura. (2025).

Figure 4 — Relationships between ecological dissimilarity and environmental correlates of amphibian beta-diversity. Partial ecological distances were derived from the Generalized Dissimilarity Models (GDM) for compositional (CBD), phylogenetic

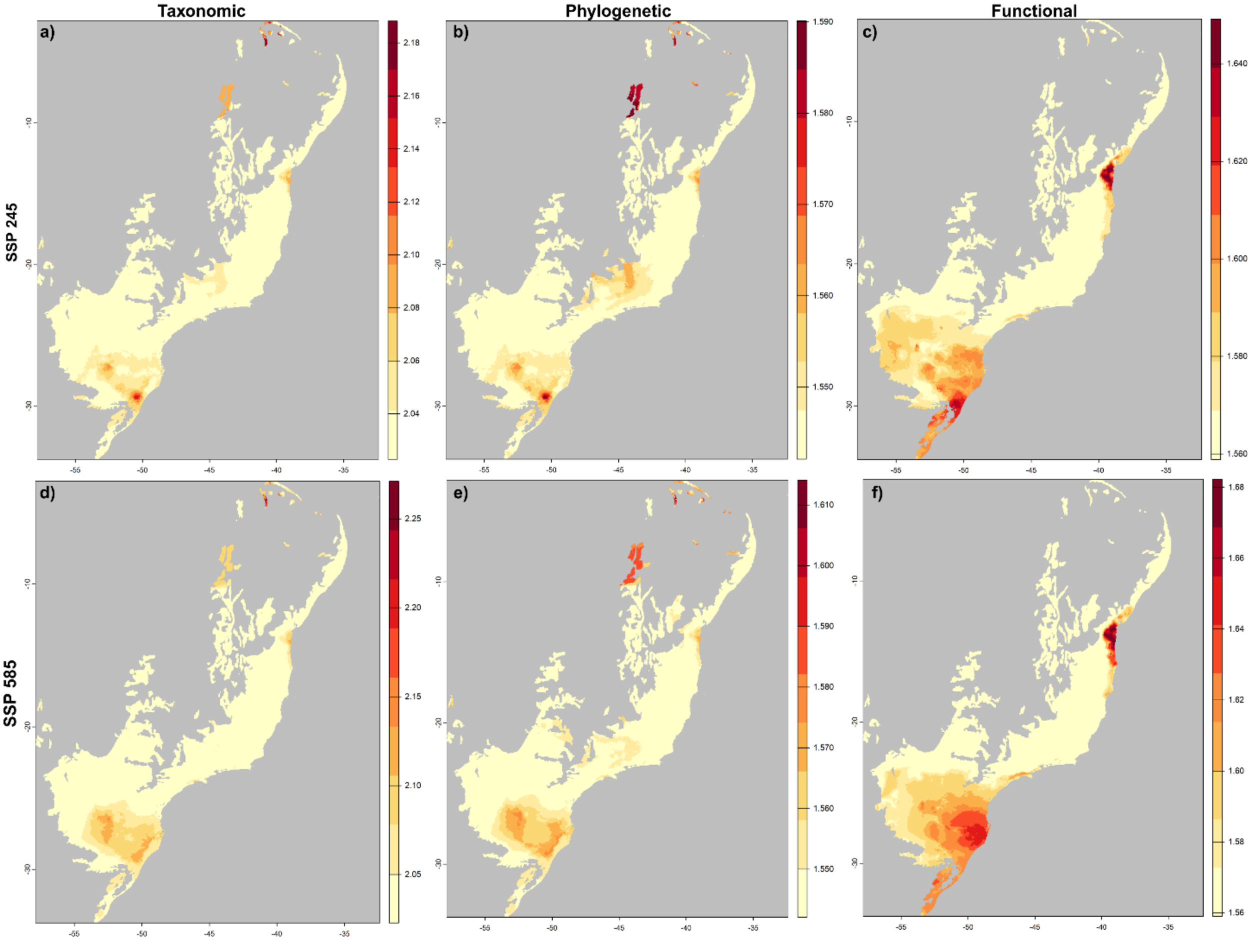
(PBD), and functional beta diversity (FBD). The fitted I-splines represent the partial ecological responses to variation in each predictor, while their maximum heights indicate the relative importance of each variable in explaining beta diversity patterns along corresponding environmental or geographic gradients. Environmental correlates returned as significant: Geographic distance, bio_3 (Isothermality), clay content in soil, bio_13 (precipitation of wettest month), and silt content in soil.



Source: Elaborated by the author and Mario R. Moura. (2025).

Projected climate change for the optimistic scenario (SSP245) is expected to affect CBD, PBD, and FBD mostly in the southern Atlantic Forest **(Figure 5a-c)**. Changes in amphibian beta-diversity are also projected for some interior forests in the northernmost region of this hotspot, particularly for the PBD. Lastly, for FBD, it will also impact the south, and northeastern of Atlantic Forest, but with much greater impact particularly in southern and coastal northeastern **(Figure 5c)**. While future patterns of CBD, PBD and FBD are qualitatively similar under the pessimistic scenario (SSP585), the magnitude of projected shifts is higher **(Figure 5d-f)**. The low standard deviation of the consensus raster of different GCMs indicated strong agreement among models.

Figure 5 — Temporal turnover in amphibian beta diversity across the Atlantic Forest. Consensus projections of expected changes in the composition (CBD), phylogenetic (PBD), and functional beta-diversity (FBD) across the three Generalized Circulation Models (GCMs) for the scenarios SSP-245 (a-c) and SSP-585 (d-f), considering the 2080-2100 time period.



Source: Elaborated by the author and Mario R. Moura. (2025).

4 DISCUSSION

We investigated how species composition (compositional beta-diversity - CBD), evolutionary relationships (phylogenetic beta-diversity - PBD), and ecological functions (functional beta-diversity - FBD) vary across the Atlantic Forest, aiming to uncover spatial patterns of biodiversity and the environmental factors that shape them. Although species composition varies across assemblages, these often occupy similar regions of functional trait space, indicating ecological redundancy. We also observed a strong correlation between functional (FBD) and phylogenetic (PBD) diversity, suggesting that evolutionary history influences ecological roles. Notably, most changes in species composition occur among closely related species. Environmental factors such as geographic distance, temperature variability (isothermality), and soil clay content significantly affect all three dimensions of beta diversity (taxonomic, phylogenetic, and functional). Additional influences include soil silt content, which affects PBD, and precipitation during the wettest month, which affects FBD. Our findings reveal a clear latitudinal gradient in assemblage differentiation and suggest that regions in the south, as well as the northeastern coast and interior, are likely to undergo substantial species turnover and community restructuring under future climate change scenarios.

Despite the pronounced latitudinal patterns observed in CBD and PBD, we found that environmental variables explained only a limited portion of the variation of the changes in species assemblages (biodiversity turnover), especially for FBD. One possible explanation is the relatively low variability in the functional traits included in our analysis. These traits encompassed a mix of continuous and categorical variables commonly used in ecological studies (Alves-Ferreira et al., 2022; Anunciação et al., 2023), covering morphological characteristics, reproductive strategies, and habitat preferences. Another contributing factor may be the high functional redundancy among amphibian species, meaning that even when species composition and evolutionary lineages change, the overall range of functional traits represented in assemblages remains largely consistent. As a result, subtle environmental changes may not lead to significant shifts in functional diversity, which remains consistently lower than taxonomic diversity (Gorczynski; Beaudrot, 2021; Strauß et al., 2010; Villalobos et al., 2013).

Historical climate changes, which caused habitat fragmentation, along with large rivers and mountain ranges, have shaped current amphibian lineages in the Atlantic Forest by limiting gene flow (Santos et al., 2020; Thomé et al., 2020). This suggests that the separation of functional lineages was mainly due to geographic isolation, rather than environmental filtering. Although the region is climatically diverse today, the Atlantic Forest has had a relatively stable climate over time (Carnaval and Moritz, 2008; Carnaval et al., 2009). We also found a weak correlation between FBD and PBD. In particular, traits related to macrohabitat use and body shape, especially limb measurements, did not show a strong phylogenetic signal. Since limb proportions are linked to locomotor strategies in amphibians, they can influence where species are found (Buttimer; Stepanova; Womack, 2020; Stepanova; Womack, 2020). The lack of phylogenetic signal in these traits suggests that different lineages evolved, independently, similar ways of moving, such as walking, hopping, jumping, or swimming, as they adapted to either forested or open environments. This points to functional convergence among lineages facing similar ecological conditions.

The influence of spatial factors over short distances may be linked to the limited dispersal capacity of amphibians. Due to their low vagility and high sensitivity to dehydration (Hopkins, 2007), amphibians face strong barriers when moving across the landscape (Buckley; Jetz, 2007; Duellman; Trueb, 1994; Early; Sax, 2011; Hillman et al., 2008). As ectothermic animals with semi permeable skin, their physiology and metabolism are closely tied to environmental conditions, especially humidity (Buckley; Jetz, 2007; Duellman; Trueb, 1994; Hillman et al., 2008). The variability in temperature and rainfall across the Atlantic Forest further limits their dispersal by restricting access to wet microhabitats, which are essential for their reproduction (Haddad; Prado, 2005).

We found that high isothermality values positively affect CBD, PBD, and especially FBD. Isothermality describes the ratio of daily to annual temperature variation; higher values indicating that day-to-night temperature fluctuations are greater than seasonal ones (O'Donnel; Ignizio, 2012; "WorldClim", 2024). Less pronounced seasonality (i.e., more uniform temperatures throughout the year), appears to influence beta diversity, particularly FBD. As ectotherms, amphibians depend on external temperature and moisture to regulate their activity and dispersal. Therefore, areas with stable temperature regimes throughout the year may offer more suitable and predictable habitats (Alves-Ferreira et al., 2022; Tytar et al., 2015). Moreover, regions with high isothermality and favorable precipitation patterns are considered more suitable for forest restoration, which supports the development of amphibian microhabitats (Maure et al., 2022; Santos; Silva; Higuchi, 2023). Thus, climatic stability emerges as a key factor in maintaining functional, taxonomic and phylogenetic diversity across amphibian assemblages in the Atlantic Forest.

To a lesser extent, physical soil (edaphic) properties influenced both taxonomic and phylogenetic beta diversity. Soil texture, defined by the relative proportions of silt, clay, and sand, controls water retention capacity (Geroy et al., 2011; "Specifications Tiered GlobalSoilMap products", 2015). Silt particles affect how clay particles are arranged, leading to larger pores that reduce water flow, whereas clay-rich soils tend to have smaller pores, which can increase both water flow and retention (Gao et al., 2020). Soils with great water retention capacity help reduce dehydration risks and may also support higher prey availability, both of which are crucial for maintaining amphibian populations, especially amid climatic fluctuations. Amphibians are physiologically and metabolically dependent on environmental moisture and temperature (Buckley; Jetz, 2007; Duellman; Trueb, 1994; Hillman et al., 2008). In the Atlantic Forest, rainfall variability restricts access to wet microhabitats that are essential for reproduction, thereby limiting dispersal (Haddad; Prado, 2005). Moreover, the fossorial behavior of some caecilians and anurans, combined with their reliance on soil-dwelling invertebrates as prey, suggests a further connection between amphibian assemblage structure and soil texture (Duellman; Trueb, 1994; Rossa-Feres et al., 2017a).

Our results indicate that climate change is expected to significantly affect amphibian beta diversity in the southern Atlantic Forest, the northeastern coastal region, and the interior forests outside the northernmost areas. These regions are projected to undergo substantial changes in taxonomic, phylogenetic and especially functional beta-diversity, with impacts being more severe under the pessimistic emissions scenario (SSP-585). As highlighted earlier, climatic stability emerged as the most explanatory bioclimatic factor. Rising greenhouse gas (GHG) emissions are increasing global temperatures and reducing atmospheric moisture, leading to more frequent and intense extreme climate events (Daryanto; Wang; Jacinthe, 2016; Ummenhofer; Meehl, 2017). FBD is projected to be particularly affected in the southern and northeastern coastal regions, likely due to its higher sensitivity to climatic variables, such as isothermality and precipitation, compared to edaphic conditions and geographic distance, which more strongly influence CBD and PBD. Moreover, traits related to locomotor mode and macrohabitat showed leak phylogenetic signal, suggesting that amphibians have independently evolved to occupy specific environmental conditions that are likely to change under future climate scenarios. Alterations in vegetation and climate regimes with ongoing pressures from agriculture, livestock production, and real estate development, could further exacerbate habitat fragmentation across the Atlantic Forest.

Using Generalized Dissimilarity Modeling (GDM), we improved the understanding of how amphibian diversity varies across space in the Atlantic Forest and how it may be affected by climate change. Our results show that environmental factors, especially climate stability and soil characteristics, are key drivers of differences in species composition, evolutionary lineages, and functional traits. We also found that many amphibian species share similar ecological roles, indicating high functional redundancy. This overlap may help ecosystems maintain their functions even if some species are lost (Walker, 1995; Rosenfeld, 2002). Because functional beta diversity (FBD) was the most sensitive to climate change in our study, this redundancy could help sustain amphibian communities under future environmental stress. However, we suggest that future studies examine how this redundancy is distributed across regions and whether functionally similar species respond differently to environmental change. Including biotic interactions like competition and predation could also improve predictions about species persistence. This is important, as different metrics of functional diversity may react differently to climate impacts (Gerisch, 2012). Lastly, we stress the importance of macroecological approaches that consider multiple aspects of biodiversity, not just species numbers, for more accurate conservation planning. Our findings underscore the ecological processes that shape amphibian beta diversity in the Atlantic Forest, a biome of high conservation priority.

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