

Opposite latitudinal gradients for species richness and phylogenetic diversity of endemic snakes in the Atlantic Forest

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Abstract

The decrease in species richness toward higher latitudes is an expected biogeographical pattern. This pattern could be related to particular environmental constraints and the evolutionary history of clades. However, species richness does not fully represent the evolutionary history of the clades behind their distributions. Phylogenetic diversity better clarifies the role of historical factors in biogeographical patterns. We analyzed environmental and historical drivers related to latitudinal variation in species richness and phylogenetic diversity of Atlantic Forest endemic snakes. We implemented species distribution models, from voucher-based locality points, to map the snake ranges and diversity. We used generalized additive mixed models to evaluate the relationships among the diversity metrics and area, topographical roughness, and past climate change velocity since the Last Maximum Glacial in the Atlantic Forest latitudinal gradient. Contrary to the expected general pattern, species richness was higher toward higher latitudes, being positively related to past climatic stability. Species richness also increased with total area and higher topographical roughness. Phylogenetic diversity, on the other hand, showed opposite relationships related to the same factors. Phylogenetic diversity increased with lower climatic stability in lower latitudes. Thus, dimensions of diversity were affected in different ways by historical and environmental constraints in this unique and threatened biodiversity hotspot.

Key words: biodiversity, latitudinal gradient, neotropical region, phylogenetic diversity, serpents, species richness.

One of the main challenges of ecology and biogeography is to understand the factors regulating species distributions across space and time (Stephens and Wiens 2003). The distribution of species richness across latitudes has been one of the most explored biological gradients in broad spatial scales (MacArthur 1972; Gaston 2000; Wiens and Donoghue 2004; Pylon and Burbrink 2009; Brown 2014; Kerkhoff et al. 2014). A prevalent pattern is an increased number of species toward the tropics, known as the latitudinal biodiversity gradient (LBG) (MacArthur 1972; Gaston 2000; Brown 2014; Kerkhoff et al. 2014). This pattern could be explained by the climatic stability variation across the latitudinal gradient, that is, higher historical climatic stability in lower latitudes (MacArthur 1972). However, species richness does not reflect the different dimensions of biological diversity (Magurran and McGill 2010). Additional components of diversity, such as phylogenetic diversity, highlight how phylogenetic relationships and evolutionary factors could affect biodiversity

across such gradients (Wiens and Donoghue 2004; Pylon and Burbrink 2009; Qian et al. 2015).

The species tolerances in relation to environmental factors—for example, variation in climate stability across habitats and regions—could lead to dispersal restrictions of lineages across latitudinal gradients (Wiens and Donoghue 2004; Pylon and Burbrink 2009; Chejanovski and Wiens 2014; Morinière et al. 2016). Environmental factors such as available area, climate, and topography have been considered as dispersal constraints and are important drivers of species richness and phylogenetic diversity variation across tropical biomes, such as the South American Atlantic Forest (Moura et al. 2017a, 2017b; Portillo et al. 2022). Guedes et al. (2018) suggest that species richness and phylogenetic diversity in the Neotropical region should respond similarly to historical and environmental factors. However, different clades might also respond in distinct ways to ecological factors, affecting the distribution of species across habitats (Currie 1991; Wiens

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and Donoghue 2004; Pyron and Burbrink 2009). Climatic zonation, for instance, can limit clade dispersal across latitudinal ranges, shaping their biogeographical patterns (Harrison and Grace 2007). Furthermore, the geographical constraints of lineages to latitudinal belts where their ancestral emerged should be associated with adaptive traits related to specific climatic conditions (Wiens and Donoghue 2004; Pyron and Burbrink 2009). The geographical origins of different clades have been suggested to influence diversity patterns in the Neotropical region, with remarkable patterns for snakes (Cadle and Greene 1993). Thus, the evolutionary history of clades and the historical biogeography might be considered when we seek to understand the drivers regulating the distribution of the highly diversified faunas throughout biodiversity hotspots.

The geographical distribution of the Atlantic Forest endemic fauna has been associated with past forested refugia of the Late Quaternary (Carnaval et al. 2014). A noteworthy congruence of such areas has been observed for vertebrates (see Figueiredo et al. 2021). Climate stability over time is important to understand historical components predicting diversity dimensions in complex biomes such as the Atlantic Forest (Paz et al. 2021). Glaciations and forest stability have been pointed out as relevant factors to understanding the contemporary diversity and endemism of this biodiversity hotspot (see Sandel et al. 2011; Carnaval et al. 2014; Moura et al. 2017a). In this way, the last glaciation period should be crucial to understand the historical biogeography of the Atlantic Forest (Moura et al. 2017a). Past climate fluctuations are important constraints for lineages' distribution along the Atlantic Forest latitudinal gradient (Carnaval et al. 2014; Moura et al. 2017a). Species richness and phylogenetic diversity data from multi-taxon analyses in this geographical domain demonstrate that distinct plant and animal clades are differently influenced by distinct environmental and evolutionary drivers (Brown et al. 2020). For snakes, different co-distributed species have been identified across the Atlantic Forest, which has been interpreted as the outcome of historical drivers and environmental constraints for species dispersal (Barbo et al. 2021). However, patterns of richness and phylogenetic diversity of snakes along the latitudinal gradient in this complex and rich biodiversity hotspot are not yet clearly explored.

The species-area relationships should be also considered as habitat suitability and can regulate biological diversity (MacArthur 1972; Wiens and Donoghue 2004; Mittelbach et al. 2007; Pyron and Burbrink 2009; Portillo et al. 2019). The extent of available suitable habitats can influence the diversity of species and lineages along biodiversity hotspots (Brown et al. 2020). On the other hand, besides the geographical extent, habitat heterogeneity may promote highly diversified faunas in determined habitats (Pyron et al. 2015), as demonstrated in the Atlantic Forest mountain ranges of southeastern Brazil (Vasconcelos et al. 2014; Barbo et al. 2021). In this way, species richness and phylogenetic diversity of snakes should be positively related to available area and topographical heterogeneity in the Atlantic Forest (Moura et al. 2017a, 2017b; Portillo et al. 2019; Barbo et al. 2021).

The high number of endemic species and its extensive latitudinal range define the South American Atlantic Forest as an excellent model to understand the influences of area, climate, and topography on its biological diversity (see Myers et al. 2000). This region encompasses almost the entirety of

the vast coastal region of Brazil, also crossing limited areas in Paraguay and northeastern Argentina (Myers et al. 2000; Olson et al. 2001; Ribeiro et al. 2009, 2011). The Atlantic Forest is one of the most distinctive and complex biogeographical regions in the globe (Guedes et al. 2018; Azevedo et al. 2020; Barbo et al. 2021), and is a threatened global biodiversity hotspot, including around 2.1% of the total endemic vertebrates worldwide (Myers et al. 2000). It is also one of the richest areas in the Neotropical region (Myers et al. 2000; Guedes et al. 2018; Nogueira et al. 2019), harboring more than half snake species occurring in all Brazilian territory (Nogueira et al. 2019; Barbo et al. 2021).

We addressed here the latitudinal variation of species richness and phylogenetic diversity of the endemic snakes from the Atlantic Forest. We analyzed the influence of climatic stability, regarding past climate change velocity since the Last Maximum Glacial on species richness and phylogenetic diversity along the latitudinal variation. We also assessed the effects of the area—geographical extent—and topographical complexity—roughness—across the gradient. We then explored the following questions: 1) do species richness and phylogenetic diversity present the general pattern of the LBG, with the highest values in lower latitudes? and 2) different dimensions of diversity are influenced by the available area, climatic stability, or topographical complexity? Our major aim is to better understand the latitudinal variation of those different components of diversity in the Atlantic Forest and to provide clues on the evolution of such highly diversified taxon in this biodiversity hotspot.

Materials and Methods

Dataset

We used the most detailed voucher-based dataset of locality records for snakes in Brazil (Nogueira et al. 2019) to map the distribution of species. The latitudinal gradient analyzed extends from 5° to 34° south. Among the 412 species of snakes recorded in all Brazilian territory (Nogueira et al. 2019), we identified 78 endemic snakes with restricted locality points to Atlantic Forest ecoregions *sensu* Olson et al. (2001). We thinned the presence records for each endemic species to one record per 35 km² radius, using the “spThin” R package (Aiello-Lammens et al. 2015) to reduce the influence of collection biases (see Guedes et al. 2018) on modeling techniques (see below). The complete list of species and sample sizes is available in [Supplementary Appendix S1](#) ([Supplementary Table S1](#)).

We mapped the distribution of endemic snakes with only 1 or 2 locality records for the Atlantic Forest using a buffer of 50 km surrounding the occurrence points (13 species). We selected this buffer size to not overinflate the effect of occurrence points out of the east and north limits of the Atlantic Forest and to include island species without a huge effect in the southeastern latitudinal degrees. For species with 3–5 records (9 species), we produced convex hulls (Hijmans and Elith 2015; Zizka et al. 2020) due to the inability to correctly evaluate species distribution models in such cases. For the remaining small-ranged species (13 species), we implemented univariate and bivariate ensemble small models (ESMs, i.e., using 1 environmental variable or pairs of variables each time—Breiner et al. 2015). Finally, we used an ensemble of models including all variables for species with sufficient sample sizes (43 species), keeping the balance of at least 5 records

per variable to train the models, avoiding overfitting problems as explained below and in [Supplementary Appendix S1](#). All maps are available in the [Supplementary material](#).

Species distribution models were trained and projected in a geographical background corresponding to a 3° buffer (~300 km) around the Atlantic Forest ([Figure 1](#)). In this way, we standardized a unique background for all species distribution modeling. The environmental variables for modeling were downloaded from the CHELSA V.2.1 database (www.chelsa-climate.org), a high-resolution climatological model ([Karger et al. 2017](#)), and aggregated to a 10-min resolution (~20 km × 20 km). We implemented a principal component analysis on the 19 bioclimatic variables to decrease collinearity while capturing most of the climatic variation ([Dormann et al. 2012](#); [Zizka et al. 2020](#)). We selected the 3 first principal components as predictor variables in models ([Zizka et al. 2020](#)), corresponding to 97% of the total variation among all variables. We kept a balance of at least 5 unique presence records per predictor (see [Passos et al. 2019](#)), using cross-validation (kfold = 5) and 10 replications per species to validate the models and to avoid overfitting ([Merow et al. 2014](#)). For this reason, we implemented the ESMs for species with fewer records ($N = 6-16$), fitting the models using only 1 or 2 predictors each time with the 3 possible combinations (PC1 + PC2, PC1 + PC3, and PC2 + PC3), and ensembled the predictions based on modeling performances ([Breiner et al. 2015](#)). For the remaining species, we used the 3 first principal components for standard ensemble modeling, that is, the combination of the predictions of different modeling algorithms (see [Zizka et al. 2020](#)). From the resulting ensemble predictions, in cells more than 100 km away from the known species records, we weighted the suitability values by the inverse of the distance from point records ([Rosauer et al. 2015](#); i.e., regions far away from the species records will receive increasingly smaller values of occurrence probability).

We previously tested the model performance of distinct modeling algorithms and kept a balance between simple and more complex ones to minimize the effect of different sample sizes and to maximize the importance of inter-model variability ([Merow et al. 2014](#)). We then selected 4 different modeling algorithms for our ensembling approach. The bioclim model was selected because of its low complexity and to include a presence-only algorithm (see [Merow et al. 2014](#)). The GLM model was included as it is less influenced by the number of pseudo-absences ([Barbet-Massin et al. 2012](#)). We also used the statistical model SVM of artificial intelligence for pairwise support between environmental variables ([Guo et al. 2005](#); [Pouteau et al. 2012](#); [Cornuault et al. 2013](#)). This approach has also increased performance for rare species ([Pouteau et al. 2012](#)). Lastly, Maxent was included due to its great predictive power and better performance for ensemble approaches ([Elith et al. 2006](#); [Grimmett et al. 2020](#)).

We measured model performance with the area under the curve (AUC) of the receiver operation characteristic and the true skill statistics (TSS). We ensembled the models weighting the predictions of each algorithm with the TSS metric ([Guisan et al. 2017](#); [Zizka et al. 2020](#)). We also performed sensitivity tests with different numbers of pseudo-absences (equal to the number of presences, twice and 10 times the number of presences) and 3 different threshold metrics (sensitivity equal specificity, kappa, and sensitivity plus specificity). We found that using the same number of pseudo-absences as the number of presences was better evaluated for the standard ensemble models with all variables included, and ESMs were better evaluated using twice the number of presences. We then used these values of pseudo-absences for each modeling strategy (see more details in [Supplementary Appendix S1](#)). The different thresholds for producing binary maps of presence-absence presented similar performances and yielded almost identical

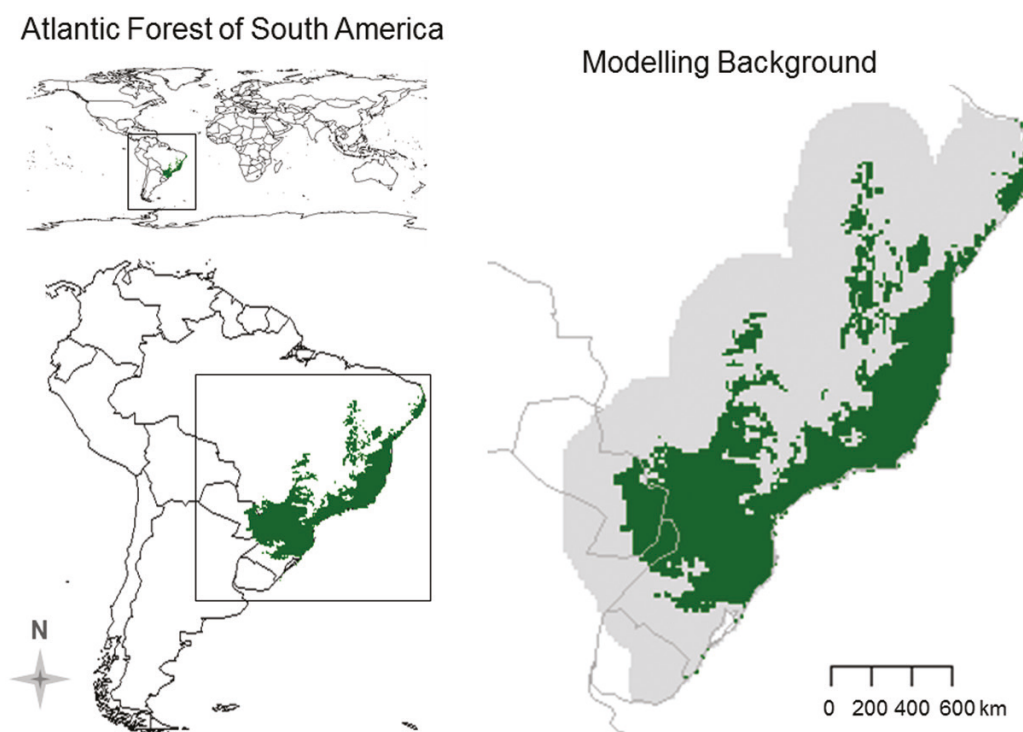


Figure 1 The South America Atlantic Forest according to [Olson et al. \(2001\)](#) highlighted in green. The 3° buffer (~300 km) around the Atlantic Forest in gray shade on the right map corresponded to the species modeling background (see details in Materials and Methods).

results when mapping the diversity patterns in the region (see [Supplementary Appendix S1—Supplementary Figure S1](#)). Therefore, we used the sum of sensitivity and specificity ($sp + se$) as the threshold for producing binary maps of predicted presence, an approach that maximizes the TSS (max-TSS) ([Guisan et al. 2017](#)). All modeling procedures were implemented in the “sdm” R package ([Naimi and Araujo 2020](#)).

Species richness and phylogenetic diversity

Species richness was calculated by overlapping all binary maps. We obtained the evolutionary relationships among species from fully sampled phylogenies for Squamate reptiles available in [Tonini et al. \(2016\)](#) from which we calculated mean values for each grid cell (see the consensus phylogeny derived from [Tonini et al. 2016](#), [Figure 2](#)). Species missing in phylogenies (*Bothrops sazimai*, *Liodyphlops sousai*, and *Thamnodynastes nattereri*) were not included in the analyses. The phylogenetic diversity index (PDI *sensu* [Tsirogiannis and Sandel 2016](#)) was calculated with the “PhyloMeasures” R package ([Tsirogiannis and Sandel 2015, 2016](#)) as the difference between the local phylogenetic diversity and the mean phylogenetic diversity across all area divided by the standard deviation. That is the standardized effect size of phylogenetic diversity *sensu* [Faith \(1992\)](#), which is independent of species richness ([Tsirogiannis and Sandel 2016](#)). Higher values of PDI indicate the prevalence

of relative phylogenetically distant clades. The negative values indicate that assemblages were phylogenetically clustered, with an increase in the presence of phylogenetically related species. The phylogenetic analyses were based on distributional data and a sample of 100 trees, from which we calculated the mean values of PDI for each grid cell.

Environmental and historical constraints

All predictor variables were concatenated to the same spatial resolution as the diversity metrics explained above (see [Figure 3](#)). The past climatic change velocity since the Last Glacial Maximum period during the Late Quaternary (downloaded from [Sandel et al. 2011](#)) was used to represent the past climatic stability across the gradient. The geographical extent of the Atlantic Forest was determined by the sum of raster cells’ area in each latitudinal degree (*sensu* [Olson et al. 2001](#)). We then calculated the topographical roughness from the altitudinal raster of the Bioclim database ([Fick and Hijmans 2017](#)) as the difference between the altitude of a focal cell and a mean value of its 8 surrounding cells ([Hijmans et al. 2021](#)).

Data analysis

We evaluated the collinearity among the 3 predictors with variance inflation factor (VIF) analyses ([Zuur et al. 2010](#)) in the “usdm” R package ([Naimi 2017](#)). The VIF values were

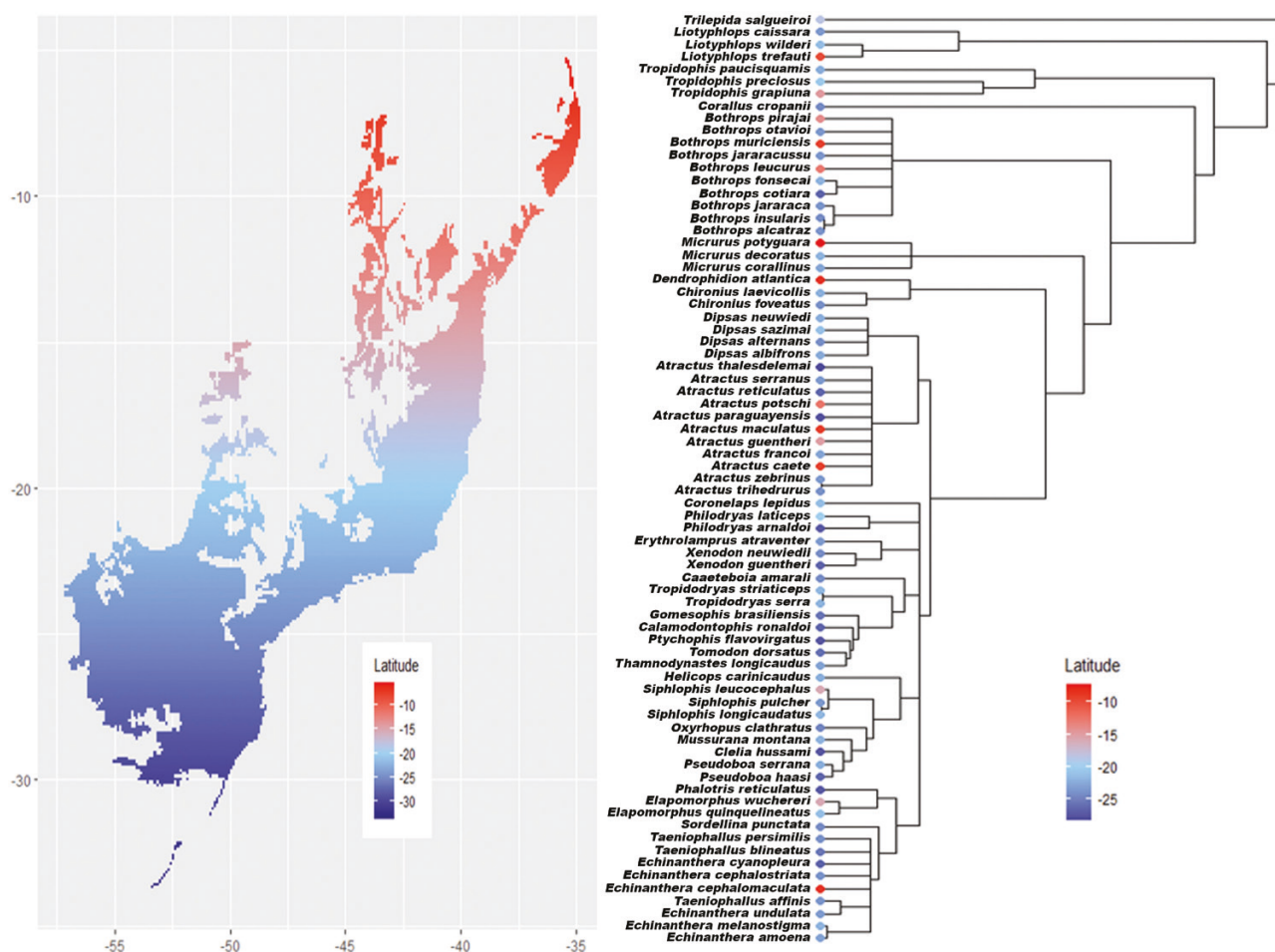


Figure 2 Phylogenetic tree of Atlantic Forest endemic snakes pruned from the consensus phylogeny of [Tonini et al. \(2016\)](#). Reddish to bluish colors represent lower to higher values of latitude. Bluish shades on the tips of the tree represent the centroid of species ranges toward higher latitudes, and the reddish shades toward the lower latitudes in the Atlantic Forest geographic domain.

lower than 1.5, indicating no collinearity problems among the selected environmental predictors. To make the degree of variation among variable values and model coefficients comparable, we standardized all variables by scaling them to have the same range of variation, that is, mean values centered in $zero \pm$ the standard deviation (Hijmans et al. 2021). We then analyzed the relationships between the diversity metrics and predictors using generalized additive mixed models (GAMMs) (Wood 2006, 2021) in the “mgcv” R package (Wood 2021). Beyond the possibility of controlling for spatial autocorrelation, GAMM is also useful for investigating and inferring complex or non-linear relationships among variables. The models were then implemented controlling spatial autocorrelation on predictors, using the latitude and longitude of grid cells as covariates with Gaussian correlation. We used the smooth functions (smooths) and splines to show the relationship

between response and predictor variables. All analyses were performed in the R software (R Core Team 2020).

Results

We identified 78 endemic snakes belonging to 8 families in the Atlantic Forest, 31.3% out of 249 species recorded in this domain (see Nogueira et al. 2019). All models were reasonably well evaluated and used for mapping species richness and phylogenetic diversity. Values of AUC from ESMs varied from 0.97 to 1, and TSS from 0.86 to 1. Values of AUC from ensemble models with all variables included varied from 0.88 to 1, and TSS from 0.68 to 1 (Supplementary Appendix S1—Supplementary Tables S2–S4).

Species richness was lower in northern areas and close to the borders and higher in the southeastern region of the Atlantic

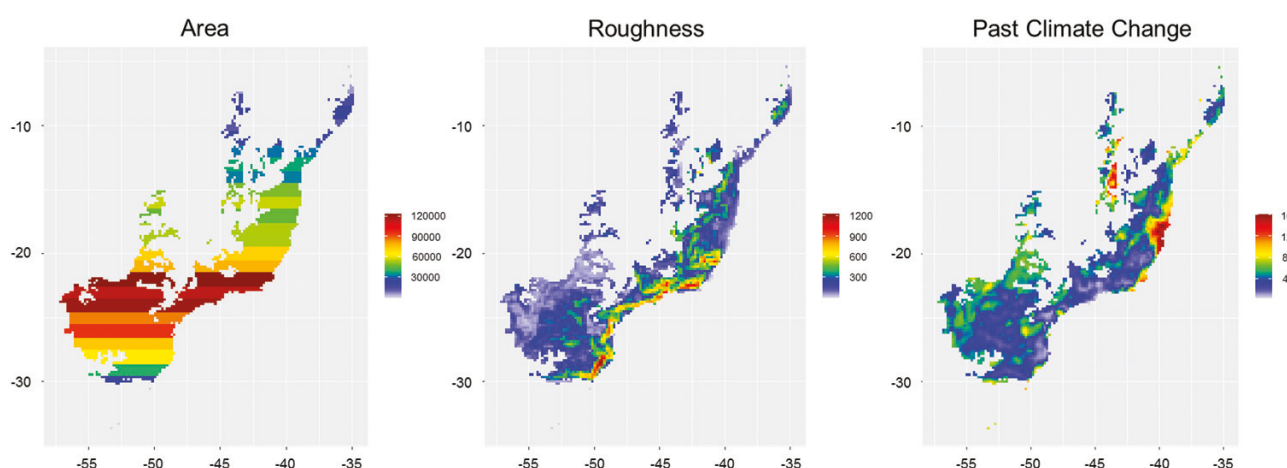


Figure 3 Environmental variables used as predictors of species richness and phylogenetic diversity: area in square kilometers per latitudinal degree (area), topographical roughness (roughness), and past climate change velocity since the Last Maximum Glacial period (past climate change).

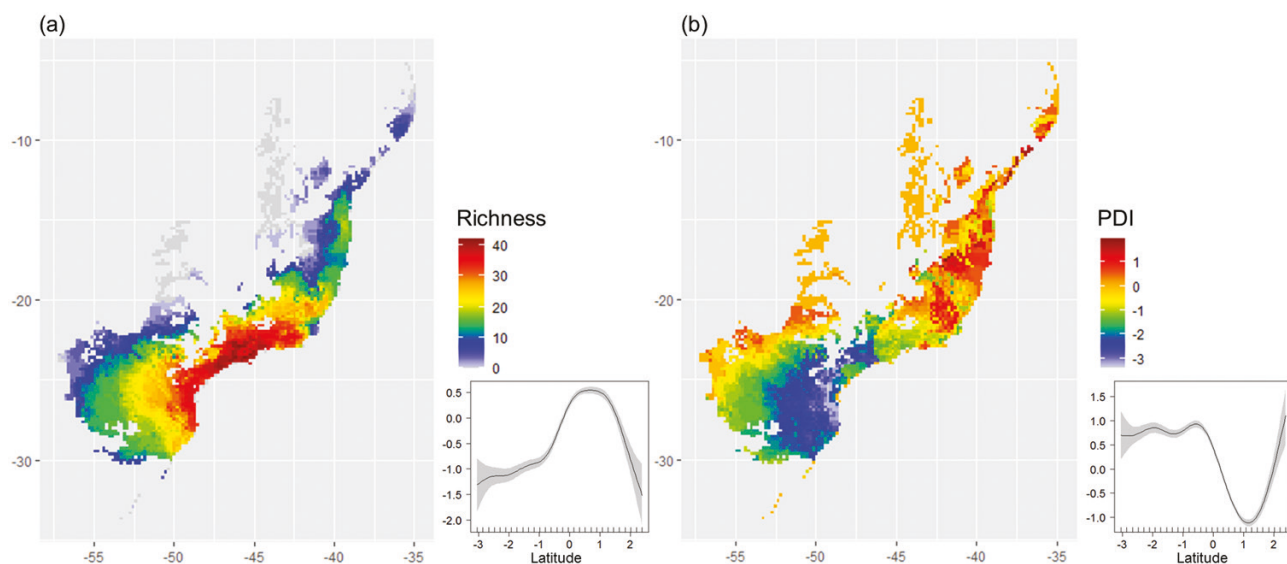


Figure 4 Geographical distribution and latitudinal gradients of species richness (A, $miN = 0$ and $max = 42$) and phylogenetic diversity (B, $miN = -3.42$ and $max = 1.98$) of endemic snakes at 20 km^2 resolution in the South American Atlantic Forest. The graphics on the bottom right of the maps are the splines generated by generalized additive mixed models (GAMMs) for species richness and phylogenetic diversity against latitude (values were standardized to have the same range of variation—mean zero $\pm$ standard deviation). In the latitude axis on such graphs, -3 corresponds to 5° south, -2 corresponds to 20° south, and 2 corresponds to 30° south. Values of phylogenetic diversity (PDI) are independent of species richness (see Materials and Methods).

Forest, decreasing again in the southern portion (Figure 4A). The highest values of species richness were observed between 20° and 28° south, with 36–52 endemic species per latitudinal belt (latitudes –22, –23, and –24 south with 48, 52, and 47 species, respectively—results not shown), while the maximum values by pixel were 42 species (Figure 4A). On the other hand, northern, northeastern, and western areas presented the highest values of phylogenetic diversity (PDI), decreasing toward higher latitudes (Figure 4B). The negative values of PDI also indicate that assemblages were phylogenetically clustered, in general, corresponding to areas with the highest values of species richness. All predictors had a significant relationship with species richness ($R^2 = 0.52$, $P < 0.001$; Table 1) and phylogenetic diversity ($R^2 = 0.32$, $P < 0.001$ for area and past climate and $P = 0.01$ for roughness; Table 1).

Our results indicated a high positive species-area relationship ($F = 130.81$, $P < 0.001$; Table 1—Figure 5). On the other hand, the largest and richest areas showed slightly lower phylogenetic diversity, inversely related to area ($F = 51.34$, $P < 0.001$; Table 1—Figure 5). Species richness presented a monotonic increase with increasing topographical roughness ($F = 27.93$, $P < 0.001$; Table 1—Figure 5). However, roughness had low explanation power to explain a slight negative relationship with phylogenetic diversity ($F = 2.74$, $P = 0.01$; Table 1—Figure 5). Phylogenetic diversity was positively related to climatic change velocity ($F = 15.93$, $P < 0.001$; Table 1—Figures 3–5). Then, phylogenetic diversity was predominantly higher in regions with lower topographical complexity, and lower climatic stability. The opposite pattern was observed for species richness, with the largest values in the southeastern mountain ranges of the Atlantic Forest, presenting higher topographical complexity and climatic stability.

Discussion

The latitudinal gradient of species richness for endemic snakes of the Atlantic Forest is distinct from the expected general pattern of LBG (MacArthur 1972; Gaston 2000; Brown 2014; Kerkhoff

et al. 2014). While species richness increases toward higher latitudes and then decreases, the opposite occurs with phylogenetic diversity. These results reinforced the proposed general division between northern and southern regions of the Atlantic Forest, a result of a high species turnover of terrestrial endemic vertebrates (Carnaval et al. 2014), as well as already observed for the phylogenetic beta-diversity among snake assemblages (Moura et al. 2017b). All tested environmental predictors were significantly related to both species richness and phylogenetic diversity of Atlantic Forest endemic snakes.

The species richness was generally higher toward higher latitudes, demonstrating a positive relationship between taxonomic diversity and geographical extent. The species-area relationships have been considered as an important factor related to higher snake richness, as already shown in the southeastern coastal islands of the Atlantic Forest (Portillo et al. 2019). However, our results demonstrate that a high number of endemic species is concentrated in coastal regions which are not interconnected toward the east-west in the greatest latitudinal ranges, thus minimizing the area effect. Contact areas of Cerrado such as the Serra do Espinhaço and Canastra plateau could correspond to dispersal barriers for the Atlantic Forest fauna across such latitudinal belts (see Azevedo et al. 2016). In this way, the area of continuous patches of ombrophilous dense forested habitats should be considered an important factor for the high number of endemic species in the southeastern coastal strip (Brown et al. 2020).

The monotonic relationship of topographical roughness and species richness should be related to the higher complexity of southeastern mountainous ranges as shown in Figures 4A and 5. Another important gradient should be the altitudinal variation on mountain ranges, which should be analyzed in finer scales and higher resolution datasets. Moreover, almost all species-rich coastal environments in the southeastern region present higher topographical roughness (see also Figure 3), which is in line with the general trend of increasing richness in more topographically complex areas (see Azevedo et al. 2016; Pan et al. 2019), even with lower phylogenetic diversities observed. Thus, we highlight the topographical

Table 1 Results from generalized additive mixed models (GAMMs) of species richness (SR), phylogenetic diversity index (PDI), and environmental predictors. The smooth functions are indicated by s() for geographical extent s(area), topographical complexity s(roughness), and the past climatic change velocity during the maximum glacial period from the Late Quaternary s(past climate). Degrees of freedom (*df*), Akaike information criterion (*AIC*), log likelihood (*logLik*), adjusted R^2 , and deviance explained are presented. The estimated degrees of freedom (*df*), *F* values (*F*), and the associated probability (*P* value) for each variable are also shown

Model	<i>df</i>	<i>AIC</i>	<i>logLik</i>	R^2 (adj)	Deviance (%)
SR ~ s(Area) + s(Roughness) + s(Past climate)	19.96	2403.94	–1192.97	0.52	52.29
	<i>df</i>	<i>F</i>	<i>P</i>		
Area	6.55	130.81	< 0.001		
Roughness	6.72	27.93	< 0.001		
Past climate	5.67	24.62	< 0.001		
	<i>df</i>	<i>AIC</i>	<i>logLik</i>	R^2 (adj)	Deviance (%)
PDI ~ s(Area) + s(Roughness) + s(Past climate)	18.89	4701.98	–2341.99	0.32	32.17
	<i>df</i>	<i>F</i>	<i>P</i>		
Area	8.60	51.34	< 0.001		
Roughness	5.44	2.74	0.01		
Past climate	3.84	15.93	< 0.001		

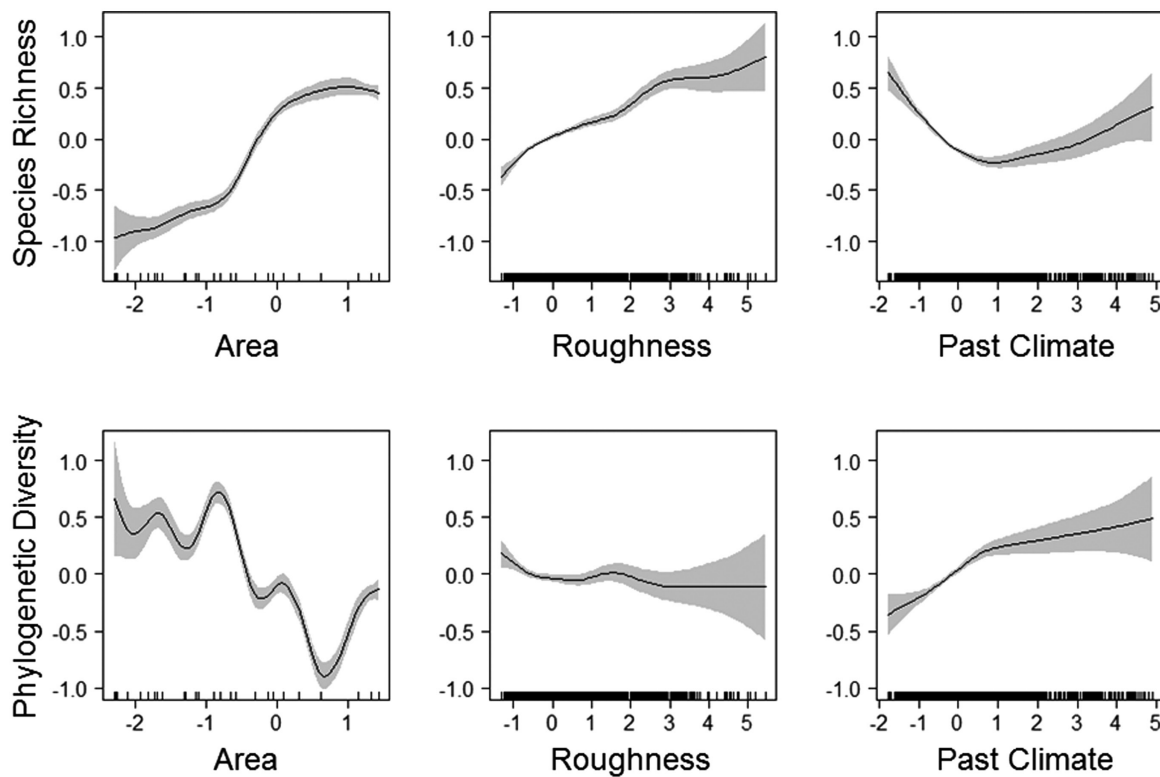


Figure 5 Relationships between species richness, phylogenetic diversity index, and the predictors provided by the generalized additive mixed models (GAMMs). The values of all variables (predictors and response) were standardized to mean zero $\pm$ the standard deviation. The gray area corresponds to the 95% confidence interval. The rugs on the x axis indicate the distribution of values of the environmental variables.

roughness from the ecoregion of the Serra do Mar Coastal Forests (*sensu* Olson et al. 2001) in the southeastern Atlantic Forest presenting the highest number of endemic snakes in this geographical domain. Furthermore, topographical complexity and vegetation structure might be also associated with climatic heterogeneity across the Atlantic Forest territory (Carnaval et al. 2014; Moura et al. 2017a). We then propose that ecological niches and environmental heterogeneity might lead to different diversification rates along the Atlantic Forest latitudinal gradient and to the contrasting values of species richness and phylogenetic diversity in such highly complex areas. Moreover, additional approaches regarding the reconstruction of the ancestral distribution of lineages and measures of diversification rates should complement this view.

The negative values of phylogenetic diversity in the richest southeastern regions might indicate that environmental filtering could structure the lineage composition of snakes, as well as the ecological requirements among clades should be evolutionarily conserved (Moura et al. 2017b). Azevedo et al. (2020) argued that the high diversity of snakes from the Neotropical region is related to the complex history of clades, their origin, colonization processes, and diversification into distinct regions (see also Cadle and Greene 1993). Climatic stability should be an important predictor of phylogenetic diversity, while topography variables could be more related to phylogenetic endemism (Paz et al. 2021). Climatic stability should influence the diversification processes across environmental gradients regarding clade-specific climatic tolerances and historical processes (Colwell et al. 2016). Regions with historical instability should maintain lower speciation rates than regions with stable climates, as demonstrated by African mammals (Kamilar et al. 2015) and angiosperm trees (Qian et al. 2015). The climatic stability also influences species

turnover and speciation rates along latitudinal gradients of salamanders (Kozak and Wiens 2007, 2010), as in our results of historical climatic stability related to higher species richness in Atlantic Forest snakes. The phylogenetic conservatism of precipitation niche breadths among younger clades should be also related to the high species richness toward higher latitudes (see Portillo et al. 2022), even with the lower phylogenetic diversity observed. Furthermore, plants also demonstrated more recent diversifications in higher latitudes (Giehl and Jarenkow 2012), which could explain the opposite values of species richness and phylogenetic diversity of Atlantic Forest snakes. Thus, areas with higher species richness tend to be composed of phylogenetically closer clades (Moura et al. 2017b), which consequently decreases the phylogenetic diversity index in the region.

The clade composition in northern areas could be also influenced by higher species turnover in Atlantic Dry Forests (*sensu* Olson et al. 2001), riverine barriers restricting clade dispersal to southern regions, and/or higher phylogenetic uniqueness from northeastern endemism areas (see Barbo et al. 2021). However, the higher historical climatic stability is evidenced as an important factor shaping species turnover and lineage composition for Atlantic Forest endemic vertebrates, including snakes (Carnaval et al. 2014; Moura et al. 2017b). The distinctiveness between species richness and phylogenetic diversity should be related to the historical climate, with northern dryer and warmer environments and southern cooler and wetter in the Atlantic Forest (see Carnaval et al. 2014). Furthermore, our results also reinforce the importance of past forested refugia during the Late Quaternary (see Carnaval et al. 2014; Moura et al. 2017b; Costa et al. 2018), maintaining highly diversified endemic faunas in regions with higher historical climatic stability.

Our results indicate that different dimensions of biodiversity can be affected in different ways by environmental and historical factors. Historical climatic stability was related to increased species richness, however, not phylogenetic diversity. Such findings are in line with phylogenetic niche conservatism predictions (see also Moura et al. 2017b), probably regarding niche evolution and higher diversification rates related to physical and environmental heterogeneity (e.g., the Atlantic Forest mountainous ranges), even among more recent clades (see Pyron et al. 2015). Thus, we point out that a complete view of the biodiversity distribution can be better understood by considering the complex interactions between ecological and evolutionary drivers, as well as different dimensions of biodiversity, as observed in the patterns of endemic snakes along the latitudinal gradient of the Atlantic Forest biodiversity hotspot.

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Author contributions

J.T.M.P. and R.J.S. planned the study. F.E.B. prepared and revised the dataset. J.T.M.P. and J.A.R.A. implemented the methods. All authors discussed and wrote the manuscript together.

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Conflict of Interest

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

References

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP, 2015. spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38:541–545.

Azevedo JA, Guedes TB, Nogueira CC, Passos P, Sawaya RJ et al., 2020. Museums and cradles of diversity are geographically coincident for narrowly distributed neotropical snakes. *Ecography* 43:328–339.

Azevedo JA, Valdujo PH, Nogueira CC, 2016. Biogeography of anurans and squamates in the Cerrado hotspot: Coincident endemism patterns in the richest and most impacted savanna on the globe. *J Biogeogr* 43:2454–2464.

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W, 2012. Selecting pseudo-absences for species distribution models: How, where and how many? *Methods Ecol Evol* 3:327–338.

Barbo FE, Nogueira CC, Sawaya RJ, 2021. Variance and regionalization patterns in snakes of the South American Atlantic Forest megadiverse hotspot. *J Biogeogr* 48:823–832.

Breiner FT, Guisan A, Bergamini A, Nobis MP, 2015. Overcoming limitations of modelling rare species by using ensembles of small models. *Methods Ecol Evol* 6:1210–1218.

Brown JH, 2014. Why are there so many species in the tropics? *J Biogeogr* 41:8–22.

Brown JL, Paz A, Reginato M, Renata CA, Assis C et al., 2020. Seeing the forest through many trees: Multi-taxon patterns of phylogenetic diversity in the Atlantic Forest hotspot. *Divers Distrib* 26:1160–1176.

Cadle JE, Greene HW, 1993. Phylogenetic patterns, biogeography, and the ecological structure of neotropical snake assemblages. In: Ricklefs RE, Schluter D, editors. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. Chicago: University of Chicago Press, 281–293.

Carnaval AC, Waltari E, Rodrigues MT, Rosauer D, VanDerWal J et al., 2014. Prediction of phylogeographic endemism in an environmentally complex biome. *Proc Biol Sci* 281:20141461.

Chejanovski ZA, Wiens JJ, 2014. Climatic niche breadth and species richness in temperate treefrogs. *J Biogeogr* 41:1936–1946.

Colwell RK, Gotelli NJ, Ashton LA, Beck J, Brehm G et al., 2016. Midpoint attractors and species richness: Modelling the interaction between environmental drivers and geometric constraints. *Ecology Lett* 19:1009–1022.

Cornuault J, Khimoun A, Harrigan RJ, Bourgeois YX, Milá B et al., 2013. The role of ecology in the geographical separation of blood parasites infecting an insular bird. *J Biogeogr* 40:1313–1323.

Costa GC, Hampe A, Ledru MP, Martinez PA, Mazzochini GG et al., 2018. Biome stability in South America over the last 30 kyr: Inferences from long-term vegetation dynamics and habitat modelling. *Glob Ecol Biogeogr* 27:285–297.

Currie DJ, 1991. Energy and large-scale patterns of animal- and plant-species richness. *Am Naturalist* 137:27–49.

Dormann CF, Schymanski SJ, Cabral J, Chuine I, Graham C et al., 2012. Correlation and process in species distribution models: Bridging a dichotomy. *J Biogeogr* 39:2119–2131.

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S et al., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.

Faith DP, 1992. Conservation evaluation and phylogenetic diversity. *Biol Conserv* 61:1–10.

Fick SE, Hijmans RJ, 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37:4302–4315.

Figueiredo MSL, Weber MM, Brasileiro CA, Cerqueira R, Grelle CEV et al., 2021. Tetrapod diversity in the Atlantic Forest: Maps and gaps. In: Marques MCM, Grelle CEV, editors. *The Atlantic Forest: History, Biodiversity, Threats and Opportunities of the Megadiverse Forest*. Switzerland: Springer, 185–204.

Gaston KJ, 2000. Global patterns in biodiversity. *Nature* 405:220–227.

Giehl ELH, Jarenkow JA, 2012. Niche conservatism and the differences in species richness at the transition of tropical and subtropical climates in South America. *Ecography* 35:933–943.

Grimmett L, Whitsed R, Horta A, 2020. Presence-only species distribution models are sensitive to sample prevalence: Evaluating models using spatial prediction stability and accuracy metrics. *Ecol Model* 431:109194.

Guedes TB, Sawaya RJ, Zizka A, Laffan S, Faurby S et al., 2018. Patterns, biases and prospects in the distribution and diversity of Neotropical snakes. *Glob Ecol Biogeogr* 27:14–21.

Guisan A, Thuiller W, Zimmermann NE, 2017. *Habitat Suitability and Distribution Models: With Applications in R*. Cambridge: Cambridge University Press.

- Guo Q, Kelly M, Graham CH, 2005. Support vector machines for predicting distribution of Sudden Oak Death in California. *Ecol Model* 182:75–90.
- Harrison S, Grace JB, 2007. Biogeographic affinity helps explain productivity-richness relationships at regional and local scales. *Am Naturalist* 170:S5–S15.
- Hijmans RJ, Elith J, 2015. Species distribution modeling with R. *R Cran*:1–78. <http://cran.nexr.com/web/packages/dismo/vignettes/sdm.pdf>
- Hijmans RJ, Etten JV, Summer M, Cheng J, Baston D et al., 2021. Package “raster.” *R Cran*:1–249. <https://cran.r-project.org/web/packages/raster/raster.pdf>
- Kamilar JM, Beaudrot L, Reed KE, 2015. Climate and species richness predict the phylogenetic structure of African mammal communities. *PLoS ONE* 10:e0121808.
- Karger DN, Conrad O, Böhrer J, Kawohl T, Kreft H et al., 2017. Climatologies at high resolution for the earth's land surface areas. *Sci Data* 4:1–20.
- Kerkhoff AJ, Moriarty PE, Weiser MD, 2014. The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. *Proc Natl Acad Sci U S A* 111:8125–8130.
- Kozak K, Wiens JJ, 2010. Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Lett* 13:1378–1389.
- Kozak KH, Wiens JJ, 2007. Climatic zonation drives latitudinal variation in speciation mechanisms. *Proc Biol Sci* 274:2995–3003.
- MacArthur RH, 1972. *Geographical Ecology: Patterns in the Distribution of Species*. New Jersey: Princeton University Press.
- Magurran AE, McGill BJ, 2010. *Biological Diversity: Frontiers in Measurement and Assessment*. New York: Oxford University Press.
- Merow C, Smith MJ, Edwards TC Jr, Guisan A, McMahon SM et al., 2014. What do we gain from simplicity versus complexity in species distribution models? *Ecography* 37:1267–1281.
- Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM et al., 2007. Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecol Lett* 10:315–331.
- Morinière J, Van Dam MH, Hawlitschek O, Bergsten J, Michat MC et al., 2016. Phylogenetic niche conservatism explains an inverse latitudinal diversity gradient in freshwater arthropods. *Sci Rep* 6:1–12.
- Moura MR, Argôlo AJ, Costa HC, 2017a. Historical and contemporary correlates of snake biogeographical subregions in the Atlantic Forest hotspot. *J Biogeogr* 44:640–650.
- Moura MR, Costa HC, Argôlo AJ, Jetz W, 2017b. Environmental constraints on the compositional and phylogenetic beta-diversity of tropical forest snake assemblages. *J Anim Ecol* 86:1192–1204.
- Myers M, Mittermeier RA, Mittermeier CG, Fonseca G, Kent J, 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- Naimi B, 2017. Package “usdm.” *R Cran*:1–18. <https://cran.r-project.org/web/packages/usdm/usdm.pdf>
- Naimi B, Araujo MB, 2020. Package “sdm”: Species distribution modelling. *R Cran*:1–47. <https://cran.r-project.org/web/packages/sdm/sdm.pdf>
- Nogueira CC, Argôlo AJ, Arzamendia V, Azevedo JA, Barbo FE et al., 2019. Atlas of Brazilian snakes: Verified point-locality maps to mitigate the Wallacean shortfall in a megadiverse snake fauna. *South Am J Herpetol* 14:1–274.
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GV et al., 2001. Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience* 51:933–938.
- Pan X, Liang D, Zeng W, Hu Y, Liang J et al., 2019. Climate, human disturbance and geometric constraints drive the elevational richness pattern of birds in a biodiversity hotspot in southwest China. *Global Ecol Conserv* 18:e00630.
- Passos P, Azevedo JA, Nogueira CC, Fernandes R, Sawaya RJ, 2019. An integrated approach to delimit species in the puzzling *Atractus emmeli* complex (Serpentes: Dipsadidae). *Herpetol Monogr* 33:1–25.
- Paz A, Brown JL, Cordeiro CLO, Aguirre-Santoro J, Assis C et al., 2021. Environmental correlates of taxonomic and phylogenetic diversity in the Atlantic Forest. *J Biogeogr* 48:1377–1391.
- Portillo JTM, Barbo FE, Sawaya RJ, 2022. Climatic niche breadths of the Atlantic Forest snakes do not increase with increasing latitude. *Curr Zool* 68:535–540.
- Portillo JTM, Ouchi-Melo LS, Crivellari LB, Oliveira TAL, Sawaya RJ et al., 2019. Area and distance from mainland affect in different ways richness and phylogenetic diversity of snakes in Atlantic Forest coastal islands. *Ecol Evol* 9:3909–3917.
- Pouteau R, Meyer JY, Taputuarai R, Stoll B, 2012. Support vector machines to map rare and endangered native plants in Pacific islands forests. *Ecol Inf* 9:37–46.
- Pyron RA, Burbrink FT, 2009. Can the tropical conservatism hypothesis explain temperate species richness patterns? An inverse latitudinal biodiversity gradient in the New World snake tribe Lamprodelphini. *Glob Ecol Biogeogr* 18:406–415.
- Pyron RA, Costa GC, Patten MA, Burbrink FT, 2015. Phylogenetic niche conservatism and the evolutionary basis of ecological speciation. *Biol Rev* 90:1248–1262.
- Qian H, Wiens JJ, Zhang J, Zhang Y, 2015. Evolutionary and ecological causes of species richness patterns in North American angiosperm trees. *Ecography* 38:241–250.
- R Core Team, 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R foundation for statistical computing. Available at <https://www.R-project.org>.
- Ribeiro MC, Martensen AC, Metzger JP, Tabarelli M, Scarano F et al., 2011. The Brazilian Atlantic Forest: A shrinking biodiversity hotspot. In: Zachos FE, Habel JC, editors. *Biodiversity Hotspots*. Berlin: Springer, 405–434.
- Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM, 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biol Conserv* 142:1141–1153.
- Rosauer DF, Catullo RA, VanDerWal J, Moussalli A, Moritz C, 2015. Lineage range estimation method reveals fine-scale endemism linked to Pleistocene stability in Australian rainforest herpetofauna. *PLoS ONE* 10:e0126274.
- Sandel B, Arge L, Dalsgaard B, Davies RG, Gaston KJ et al., 2011. The influence of Late Quaternary climate-change velocity on species endemism. *Science* 334:660–664.
- Stephens PR, Wiens JJ, 2003. Explaining species richness from continents to communities: The time-for-speciation effect in emydid turtles. *Am Naturalist* 161:112–128.
- Tonini JFR, Beard KH, Ferreira RB, Jetz W, Pyron RA, 2016. Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biol Conserv* 204:23–31.
- Tsirogiannis C, Sandel B, 2015. Package “PhyloMeasures.” *R Cran*:1–32. <http://cran.nexr.com/web/packages/PhyloMeasures/PhyloMeasures.pdf>
- Tsirogiannis C, Sandel B, 2016. PhyloMeasures: A package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography* 39:709–714.
- Vasconcelos TS, Prado VH, Silva FR, Haddad CF, 2014. Biogeographic distribution patterns and their correlates in the diverse frog fauna of the Atlantic Forest hotspot. *PLoS ONE* 9:e104130.
- Wiens JJ, Donoghue MJ, 2004. Historical biogeography, ecology and species richness. *Trends Ecol Evol* 19:639–644.
- Wood SN, 2006. Low-rank scale-invariant tensor product smooths for generalized additive mixed models. *Biometrics* 62:1025–1036.
- Wood SN, 2021. Package “mgcv.” *R Cran*:1–323. <https://cran.r-project.org/web/packages/mgcv/mgcv.pdf>
- Zizka A, Azevedo J, Leme E, Neves B, Costa AF et al., 2020. Biogeography and conservation status of the pineapple family (Bromeliaceae). *Divers Distrib* 26:183–195.
- Zuur AF, Ieno EN, Elphick CS, 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1:3–14.