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ECOSYSTEMS

Biogeographic history and environmental gradients modulate non-stationary patterns of tropical tree diversity

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Abstract: Here we studied the entire Atlantic Forest hotspot to investigate whether the effect of different environmental predictors depends on the phylogenetic extension and the biogeographical history of different Atlantic Forest sectors. We used occurrence data of 3,183 plant species with arboreal or arborescent habits. We reconstructed climatic stability across 120,000 years using the Random Forest method. Then, we compared the effect of biogeographical history, topographic, and climatic variables on species richness and phylogenetic diversity using Geographically Weighted Regression (GWR) models. Niche conservatism drives the strength and direction of environmental correlates with tree diversity, interacting with the biogeographical and phylogenetic extension considered. Low current climate seasonalities were the main drivers of species richness and phylogenetic diversity variation across the Atlantic Forest. Whereas in higher phylogenetic extension, topographic heterogeneity increased the number of tree species independent of the sector, deep-past climate stability favored phylogenetic diversity by increasing relict lineages of distant clades in all forests, but with anomalies in the southern sector. This investigation yields substantial evidence that the response of the northern and southern sectors of the Atlantic Forest to identical environmental conditions diverges significantly, providing compelling support for the imprint of phylogenetic heritage in generating non-linear diversity patterns.

Key words: Atlantic Forest, Climatic stability, Hotspot, Phylogenetic diversity, Topographic heterogeneity, Woody plants.

INTRODUCTION

Biogeographical history drives regional species pools mediated by habitat area and geological age (Zobel 2016). Moreover, climate, dispersal ability, and species interactions boost speciation rates, which determines biodiversity patterns across scales (Schluter & Pennell 2017, Nogués-Bravo et al. 2018). Therefore, the larger the past opportunity for speciation, the higher the number of species in a particular habitat, which also determines the phylogenetic structure of the regional communities (Gerhold et al. 2018, Lososová et al. 2015). Consequently, by considering the influence of environmental gradients on species pools from regions with different biogeographic and evolutionary histories, it is possible to untangle the scale dependence of processes driving biodiversity patterns (e.g., Lessard et al. 2012). The imprint of distinct biogeographical and evolutionary histories arises by comparing different ecosystems with similar climatic conditions, where interesting diversity anomalies are observed. The temperate flora of Asia is twice as rich in species than in North America (Qian & Rickefs 2000). This anomaly also occurs in tropical forests of South America and Africa, where, even with a representation of similar botanical families, South America is three times richer (Silva de Miranda et al. 2022). These patterns seem to originate from the interaction between historical climate stability and the process of niche conservatism, which restricts species from leaving and thriving outside their ancestral climate regimes (see Wiens & Donoghue 2004). Therefore, explicitly comparing regions with distinct biogeographical histories allows the identification of processes that can be generalized from those that are contingent on driving biodiversity changes (Qian & Ricklefs 2000).

The Atlantic Forest is considered a hotspot of tropical diversity (Mittermeier et al. 2004), which provides valuable clues to fill the gaps in general macroecological patterns (McGill 2019), setting species and phylogenetic diversity because of three potential mechanisms. First, the Atlantic Forest carries a mixed heritage of a mixture of temperate floristic elements derived from the separation of Gondwana (e.g., Araucariaceae, Canellaceae, and Cunoniaceae), especially in the southern sector, and tropical elements resulting from Laurasia migrations (e.g., Annonaceae, Araceae, and Burseraceae) both in the southern and northern sectors (Eisenlohr & de Oliveira-Filho 2015, Fiaschi & Pirani 2009, Fiaschi et al. 2016). Second, it has undergone different climatic stability dynamics during glacial period oscillations (Carnaval et al. 2014). Third, this Domain has substantial climatic and topographic heterogeneity associated with extensive latitudinal (8 – 28° S), longitudinal (32 – 58° W), and altitudinal gradients (0-3000 m above sea level) (Muylaert et al. 2018). In its entirety, the Atlantic Forest presents a remarkable variety of physiognomies, the delimitation and sectorization of which have been the subject of intense debates. The commonly adopted types of vegetation are correlated with variations in temperature and precipitation patterns, including the Dense Broadleaf Forest (evergreen), the Seasonal Semideciduous Forest, the Seasonal Deciduous Forest, the Mixed Broadleaf Forest (Araucaria forest), the Steppe, the Savanna, the Open Broadleaf Forest, the Pioner Formations and the Ecological Refuges (IBGE 2008, Marques et al. 2021).

Biogeographical studies suggest that the Atlantic Forest might divide around the Rio Doce (situated between latitudes -18°S and -21°S) into two large sectors: north and south (Fiaschi & Pirani 2009). Additionally, more recent studies, based on composition (taxonomic or phylogenetic), indicate a much higher number of separations into distinct blocks, between 7 and 21 (Cantidio & Souza 2019, Rezende et al. 2021). However, these smaller blocks cluster together and form two large blocks that support the existence of large north and south sectors (Cantidio & Souza 2019). There is no consensus on whether this river is ecologically effective for all the taxonomic groups. Several studies have argued that this river is not a barrier. Instead, it matches other ecological barriers that favor species turnover between the northern and southern sectors (Saiter et al. 2016). More specifically, (i) there is a historically stable area at the southern border of Bahia state (Carnaval & Moritz 2008, Carnaval et al. 2014), (ii) limiting factors to plants regarding precipitation in the equatorial and tropical sectors (northern sector) (Neves et al. 2017, Saiter et al. 2016), and (iii) temperature and energy seasonality in the southern sector (Neves et al. 2017, Saiter et al. 2016). Furthermore, it is essential to investigate whether plant communities in the northern and southern sectors respond differently to environmental factors. Once this trend is confirmed, evidence has emerged that the split between Gondwanan (historically older) and Laurasian blocks (historically more recent) imprinted in the phylogeny of Atlantic Forest plants can be an additional factor driving species turnover.

Topographic heterogeneity is one of the various non-exclusive explanations for the megadiversity of the Atlantic Forest (Massante & Gastauer 2023). Empirical evidence demonstrates that environmental heterogeneity is a driver of species richness, regardless of the studied system (Stein et al. 2014). The suggested underlying mechanisms for this relationship are the multiplication of available niche spaces, the formation of shelters against climate fluctuation, and the promotion of specialization cradles (Stein et al. 2014, Allouche et al. 2012, Fjeldså et al. 2012). Despite the ubiquity of this relationship, it is necessary to conduct studies that test the non-linear relationships between heterogeneity and other facets of diversity (Stein et al. 2014), especially in tropical and environmentally complex hotspots, such as the Atlantic Forest.

Additionally, the theory predicts that the direction and strength of the environmental-diversity relationship are context-specific. For instance, the effect of environmental variables on species diversity varies over space (Gouveia et al. 2013), which means that local scale processes constitute a spatial disaggregation of global scale processes (Fotheringham et al. 2002). For example, the current instability in precipitation in the northern sector might negatively impact plant diversity (Neves et al. 2017, Oliveira-Filho et al. 2014, Saiter et al. 2016), while topographic heterogeneity could have a strong positive effect in regions with large climate seasonality owing to the buffering effect (Fjeldså et al. 2012, Stein et al. 2014). Deep climate stability has positive effects on the diversity of regions that maintain species pools constantly through time and space (Gerhold et al. 2018), as in the southern sector. Another factor that generates context-specific responses is the phylogenetic extension. For example, the evolutionary history of ancestral plant clades, such as pteridophytes and gymnosperms, is much older than that of angiosperms. Therefore, the response of these organisms to climate varies from the responses of recent clades, given their preference for more shade, mild, and moist climates, given niche conservatism restrictions (Kooyman et al. 2014).

In this study, we divided the Atlantic Forest into sectors to account for niche conservatism, reflecting various biogeographical dynamics in the formation of patterns of plant diversity. Specifically, we investigated how average climate conditions and stability (from the deep past into current patterns) and topography heterogeneity affect tree species richness and phylogenetic diversity in the Atlantic Forest. We used one of the most extensive plant databases for macroecological studies available for Atlantic Forest, with more than 3,000 species from almost 1,700 localities (Oliveira-Filho 2017). We set forward three predictions regarding the causes of variation in these diversity patterns, none of which are necessarily linear or self-excluding: (i) climatic seasonality and severity reduce taxonomic and phylogenetic diversity. The more species-diverse regions of the Atlantic Forest have milder temperatures and less seasonal precipitation (Neves et al. 2017), reflecting their tendency to conserve tropical climate niches (Segovia et al. 2020). (ii) As topographic heterogeneity increases, so do species richness and phylogenetic diversity. Topographic heterogeneity increases the number of species found in the species pool once it provides suitable conditions for species persistence with different environmental requirements (Allouche et al. 2012), and (iii) climatic stability over the past 120 ka increases species richness and phylogenetic diversity. Climatically stable environments (museums) promote relict-lineage persistence (Gerhold et al. 2018).

MATERIALS AND METHODS

Database

The occurrence data of the arboreal or arborescent plants of the Atlantic Forest (hereafter, called 'trees') derive from the NeoTropTree database (NTT, Oliveira-Filho 2017). This database was built on extensive surveying of tree species lists checked by specialist taxonomists. The researchers constructed plants' geographical occurrence based on a standardized cutoff method of trees with a height of at least 3m (Oliveira-Filho 2017). The database initially contained 4,431 species distributed in 1,755 sampled locations.

We checked each species' taxonomic status using the most updated classification system, based on the Brazilian Flora 2020 (Carvalho 2017). Occurrence data were combined into 713 grids of 0.5° x 0.5° of latitude and longitude (~ 50 km at the equator). We chose to aggregate data into grids in order to limit the impact of poorly sampled taxa in local species lists and to allow comparisons with macroecological studies that utilized a similar strategy (e.g., Menini Neto et al. 2016, Loyola et al. 2014). The Integrator Limit by Muylaert et al. (2018) (Figure S1a) is the broadest delimitation available in the Atlantic Forest *lato sensu*, which is the predominant circumscription in this system (Neves et al. 2017). Therefore, we have chosen to maintain only the grids within the outer edges. Rare species (less than three occurrences) and those not recognized in any taxonomic indexation tools were excluded to avoid misassignment errors.

After these procedures, 451 grids remained with 3,183 species used in the subsequent analyses (Figure S1b, c).

We assigned the higher taxonomy hierarchies using the 'flora' package (Carvalho 2017) from the R 3.5.1 program (R Development Core Team 2019).

Delimitation of the climate spaces within the Atlantic Forest

To separate the biogeographical pools of the Atlantic Forest, we decided to use the classical delimitation into two groups: North, and South. Several studies corroborate this division, but the precise separation of the northern and southern sectors remains controversial (Carnaval et al. 2014, Fiaschi & Pirani 2009, Saiter et al. 2016, Rezende et al. 2021). We decided to replicate the method of separating the two pools used by Carnaval et al. (2014) for replicability and compatibility for comparison. We performed the Principal Component Analysis (PCA) using the variables temperature, precipitation, and temperature seasonality extracted from WorldClim version 2.0 (Fick & Hijmans 2017). Afterward, we submitted the first PCA axis (79.04% of explicability) to a cluster analysis algorithm (selecting groups using *k-means*) to separate the two unique climate spaces that characterize the Atlantic Forest (Carnaval et al. 2014). The two groups identified by the cluster analysis were separated around the latitude -20°S, which agrees closely with the turnover position of the floristic composition indicated in the literature (e.g., Fiaschi & Pirani 2009, Saiter et al. 2016). After defining grid position and splitting the regions as northern and south, the northern portion of the Atlantic Forest was represented by 156 grids and the southern portion by 295 grids. We used this separation of sectors later in modeling climate stability over the past 120 ka while maintaining their climate envelopes.

We performed PCA analyses and *k-means* using the 'base' package and conducted the extraction of climatic variables with the 'raster' package (Hijmans et al. 2016) (R Development Core Team 2019).

Phylogenetic trees

We created four phylogenetic trees to investigate the variation of phylogenetic diversity across biogeographic regions. Two phylogenies contain only angiosperms (considered here as low phylogenetic extension) from the northern and southern sectors, and the other two contain pteridophytes, gymnosperms and angiosperms (higher phylogenetic extension; Figure S2).

We created the phylogenetic hypothesis for angiosperms using sections of the ALLMB megatree (356,305 species), which describes the Spermatophyta groups (Smith & Brown 2018). We also included taxa available in the *GenBank* and *Tree of Life* version 9.1. We used a backbone produced by Magallón et al. (2015) using three protein-coding plastid genes (*atpB*, *rbcL*, and *matK*) and two nuclear markers (18S and 26S). As ALLMB does not contain pteridophytes and gymnosperms, we merged the evolutionary hypotheses of angiosperms with a phylogenetic tree that contained these groups. Pteridophyte and gymnosperm phylogenies were sectioned from the *PhytoPhylo* tree (31,383 taxa) using scenario 3 (which generates scenarios homologous to those of the BLADJ algorithm) (Qian & Jin 2016). This megatree of vascular plants has taxa from *The Plant List* version 1.1 (TPL, www.theplantlist.org), with the dating of genetic zones available at *GenBank* (18S, 26S, ITS, *matK*, *rbcL*, *atpB* and *trnL-F*) and 39 fossil calibrations (Zanne et al. 2014). Of the 3,183 species, 297 were not found in the megatrees and were inserted as polytomies at the base of the genus or family (when they *were singletons)*, observing the relatedness suggested by Angiosperm Phylogeny Website Version 14 (Stevens 2001). The two northern phylogenetic trees have approximately 18.5% polytomies (258 for angiosperms and 260 for all woody plants), while the two southern trees have approximately 19% polytomies (238 for angiosperms and 240 for all woody plants). We believe that our results are not strongly affected by polytomies, as we used the NRI, which is less sensitive to this phylogenetic uncertainty (Molina-Venegas & Roquet 2014).

Climatic and topographic variables

We used eight climatic variables to represent the current climate (extracted from 1970 to 2000) and one topographic heterogeneity variable. The climatic variables that were extracted from WorldClim were: mean annual temperature, temperature seasonality, mean temperature in the hottest quarter, mean temperature in the coldest quarter, mean annual precipitation, precipitation seasonality, mean precipitation in the wettest quarters, and mean temperature in the driest quarters (Fick & Hijmans 2017). Terrain roughness index - *tri* (Wilson et al. 2007) was used as a proxy for topographic heterogeneity and was extracted from ENVIREM (Title & Bemmels 2018). The *tri* is based on digital elevation models (DEM) and is calculated by comparing a central cel with its eigth cells surrounding it, using the sum change in elevation (Riley et al. 1999). By doing this type of comparison, *tri* is able to express the amount of elevation difference between adjacent cells, being a good proxy for topography heterogeneity. The tri index, based on the proposition by Riley et al. (1999), is divided into seven classes of unequal range, but an equal area with increasing values of topographic heterogeneity: level = 0-80 m; nearly level = 81-116 m; slightly rugged = 117 -161 m; intermediately rugged = 162-239 m; moderately rugged = 240-497m; highly rugged = 498-958 m, and; extremely rugged = 959-4367 m. Spatial environmental heterogeneity is deemed responsible for promoting higher diversity due to factors such as increased environmental gradients, increased number of habitats, and buffering of adverse conditions (Stein et al. 2014).

Before performing statistical analyses, we analyzed the correlation between predictor variables (northern and southern sectors individually) and removed those variables with a correlation higher than ρ > 0.7 (Pearson). We imposed two conditions: (i) terrain roughness (tri) and climatic stability had priority to be maintained whether they are correlated with current climatic variables; (ii) when the climatic variables were correlated, we consulted the literature to choose the most important in determining the diversity of each sector (Figure S3).

Climate modeling

We used bioclimatic descriptors for the current climate and deep-past climatic reconstructions derived from Hadley Centre for Climate Change (Fuchs et al. 2013) to quantify climatic stability over the past 120 ka (Late Quaternary) in the northern and southern areas of the Atlantic Forest separately.

We performed a distribution modeling of the northern and southern portions of the Atlantic Forest using a Random Forest classification algorithm (Breiman 2001). Random Forest is a machine-learning algorithm that performs successive and independent classifications based on classification trees generated by random data samplings (Breiman 2001). This approach is robust to performing climatic modeling due to its ability to calculate the relative importance of each variable regarding the influence on the model's total accuracy (Cutler et al. 2007). We used each grid's centroid to extract the variables and run the model (156 grids in the northern and 295 in the southern). We assume that the distance between centroids in the 0.5° grids is sufficiently large to tackle sampling biases and reduce spatial autocorrelation (see, e.g., Barratt et al. 2017). We trained our model using 451 random absence points spread throughout South America, except for the Atlantic Forest, to ensure that the model effectively discriminated the bioclimatic characteristics of the focal system. We generated 500 classification trees to discriminate the northern and southern portions climatically. We used the square root of the number of variables as the parameter for selecting candidate variables for each of the classification tree's splitting nodes. In summary, after extracting the variables from Hadley Centre, the following procedure was employed: the distribution points of the trees in the present were obtained and inserted into a model using Random Forest. In this model, current climatic variables were used to predict the potential distribution of the trees throughout the study area. The best Random Forest model was selected and applied to the past to predict the potential distribution of the trees during each time period. Thus, the Random Forest generated a distribution model for each period, and the resulting layers were combined to identify the areas of stability where the trees were present.

To define climatic stability areas over the past 120 ka in the northern and southern areas of the Atlantic Forest, we hindcast the current distribution model of climatic variables to 31 time periods (in intervals of 4 ka) for both regions separately. We used six environmental variables to characterize the current climate in the Atlantic Forest sectors: average annual temperature, the average temperature in the warmest quarters, the average temperature in the coldest quarters, average annual rainfall, precipitation in the wettest quarters, and precipitation in the driest quarters (Table SI). The values obtained with the 31 distribution models per sector range from the deep past (120,000 years) up to the present. We overlapped the 31 distribution models to create a continuous layer that represents climatic stability. The stability values range from 0 (maximum instability) to 32 (maximum stability). Random Forest models' results demonstrate that the northern and southern sectors have undergone quite different biogeographical dynamics over the past 120 ka. northern has shown few and disjoint stability areas, whereas southern presents a wide, stable corridor in almost all its extension (Figure S4).

Taxonomic and phylogenetic composition and diversity indices

To test the premise of distinct regional pools between the two sectors of the Atlantic Forest, we performed a Principal Coordinate Analysis (PCoA) using a Jaccard dissimilarity method to compare tree species composition turnover. Likewise, we compared the phylogenetic composition between the sectors using Principal Coordinates of Phylogenetic Structure axes (PCPS, Duarte et al. 2016). The PCPS is an index of pairwise phylogenetic divergences between sites, whose first eigenvalues represent differences in the phylogeny's deep nodes (Duarte et al. 2016). We used the packages "ape" (Paradis & Schliep 2019) and "PCPS" (Debastiani 2016) in R software (R Development Core Team 2019) to implement the PCoA and PCPS analysis. We used species richness and phylogenetic diversity (Net Relatedness Index: NRI) as dependent variables. The NRI was computed using "taxa labels" null model (shuffling 1000 times distance matrix labels). NRI is primarily a divergence index (Tucker et al. 2017) and represents deep phylogenetic relationships. NRI values vary from -∞ to + ∞, which represent dispersed and clustered communities, respectively. Therefore, a grid with a clustered phylogenetic structure presents a subset of the regional pool that is closely related. Conversely, a grid with a dispersed community phylogenetic structure has a subset of distantly related species. NRI values were calculated using the 'picante' package (Kembel et al. 2018).

Statistical analyses

Are taxonomic and phylogenetic composition of the sectors different?

We used a Permutational Multivariate Analysis of Variance (PERMANOVA) test to test the taxonomic and phylogenetic composition differences between northern and southern species pools. This PERMANOVA model includes the PCoA and PCPS analysis scores, representing more than 80% of cumulative eigenvalues in all PERMANOVA analyses. We ran all these statistical analyses using the 'vegan' package (Oksanen et al. 2019) in R software (R Development Core Team 2019). Besides, we used the BETADISPER function to identify whether potential significant differences in taxonomic or phylogenetic composition were determined by location or dispersion effects (Anderson & Walsh 2013).

How do the environmental gradients, topographic heterogeneity and climatic stability affect the taxonomic and phylogenetic diversity of trees?

We used a Geographically Weighted Regression (GWR) to test how current climate, topographic heterogeneity, and climatic stability determine species richness and phylogenetic diversity. GWR is a model to deal with spatial non-stationarity between environmental gradient and species diversity (Gouveia et al. 2013), allowing us to disentangle the spatial variation in the local importance of distinct predictor variables (Fotheringham et al. 2002). GWR is based on the traditional regression method but estimates local rather than global regression parameters, which allows the detection of non-stationary patterns. GWR compares the effect of predictor variables on the dependent variables (species richness or phylogenetic diversity), weighting each data point (grid cell) by its spatial proximity. Therefore, grid cells close to a focal grid cell are weighted heavier than distant ones (Fotheringham et al. 2002). We defined spatial proximity based on an optimal kernel bandwidth selected with a cross-validation method (Páez et al. 2011). Thus, we were able to obtain regression slopes and coefficients of determination (R2 values) for each grid cell (Fotheringham et al. 2002). Moreover, because it is an extended regression model, we can also obtain the main predictor variables affecting the spatial variation of plant richness or phylogenetic diversity.

We also tested our predictions using conditional autoregressive models (CAR), which incorporate the global tests of spatial autocorrelation potentially present in the response variables. In all models, we consider the diversity of the pools in the northern and southern sectors separately. Since results using GWR and CAR were similar, we decided to show GWR statistics in the main text because it allows appropriate interpretations about the scale-dependency of climate-diversity relationships. One can find the results of CAR models in the supplementary material (Figure S5, S6, S7; Table SII). Moreover, we used Moran's *I* correlation coefficient to investigate the spatial structure of the GWR residuals. We did not find evidence of spatial autocorrelation in residuals that could affect the model fit.

RESULTS

Macroecological patterns of taxonomic and phylogenetic diversities of trees from the Atlantic Forest

The 3,183 tree species are distributed unevenly throughout the Atlantic Forest, with a marked increase in species richness eastwards (Figure S4b). There is also a concentration of species richness in the contact region between the northern and southern sectors (around latitude -20º). The northern sector encompasses 2,860 species, although its area is approximately half of the southern sector, which has 2,502 species. Species richness in the northern sector is higher even when the number of grids was controlled (i.e., rarefied richness, Figure S8 a, b).

Regarding phylogenetic diversity considering all woody trees, we found that large eastern areas in the central portion of the Atlantic Forest have lower NRI values (between latitudes -22º S and -23º S), which means they are phylogenetically dispersed. This concentration of phylogenetic diversity is close to the contact region between the northern and southern sectors. Additionally, grids that exhibit higher phylogenetic dispersion, are predominantly concentrated in the southern sector (Figure S4c).

Are there differences in the taxonomic and phylogenetic composition between sectors?

We observed that the phylogenetic composition was different between the northern and southern sectors of the Atlantic Forest sectors, considering both all groups of trees ($R^2 = 0.11$, $p < 0.001$) or angiosperms only ($R^2 = 0.07$, $p < 0.001$). Indeed, the most important difference comes when we consider the higher phylogenetic extension (Figure 1a, b). We also found a distinct regional species pool when comparing species composition between the northern and southern sectors (all tree groups: $R^2 = 0.11$, $p < 0.001$; angiosperms: $R^2 = 0.11$, $p < 0.001$; Figure 1c, d).

How do current and deep-past climate, and topographic heterogeneity influence the taxonomic and phylogenetic diversity of plants?

Our results show that low climatic seasonality has a consistent and generally positive effect

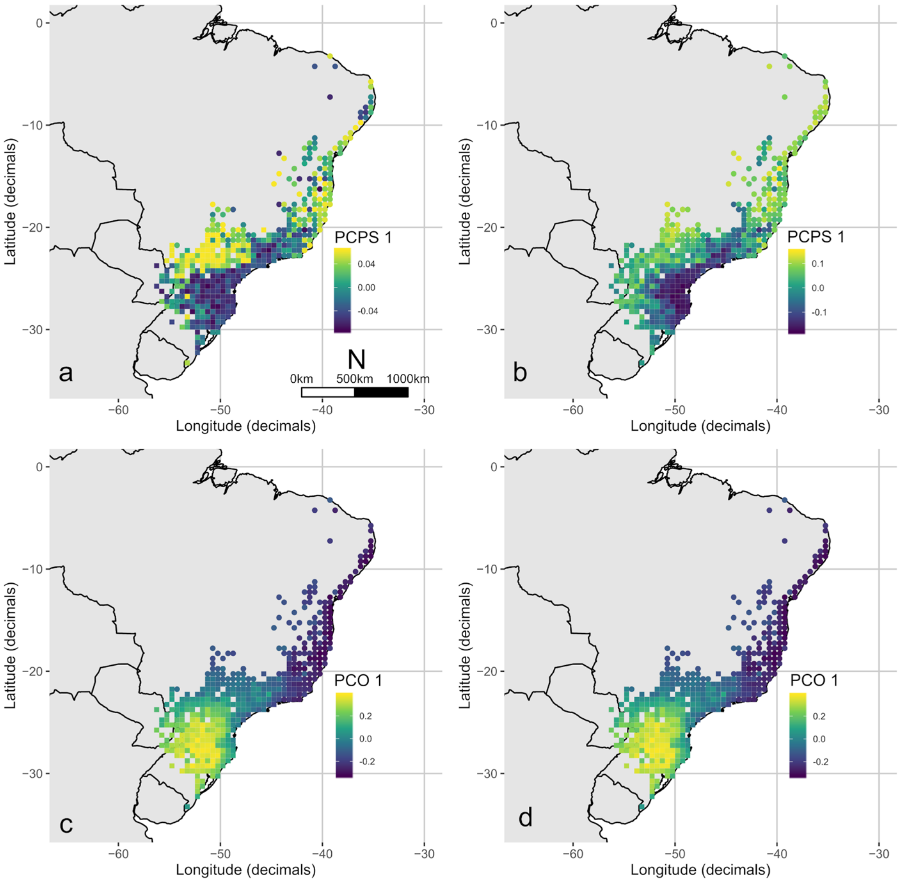

Figure 1. Changes in the phylogenetic and taxonomic composition of trees across the Atlantic Forest sectors. a = changes in phylogenetic composition considering all tree species; b = changes in phylogenetic composition considering only angiosperms; c = changes in taxonomic composition considering all tree species; d = changes in taxonomic composition considering only angiosperms. Northern sector grids are circular and southern sector grids are square.

on species richness and phylogenetic diversity. Specifically, we found that precipitation and temperature seasonality, average precipitation, precipitation in the wettest quarter, and topographic heterogeneity (tri) affected the number of species at the higher phylogenetic extension (R^2 = 57%). Whereas precipitation and temperature seasonality had a negative effect on the species richness of all trees in the northern sector, this effect was negative, absent, or even positive in the southern sector (Figure 2a-f, Table I). When we considered only angiosperms, the number of species was affected by precipitation and temperature averages and seasonality and precipitation in the wettest quarter (*R*2 = 73%) At this phylogenetic extension, precipitation and temperature seasonality had a negative effect on species richness in the northern sector, while this effect was negative, absent, or positive in the southern sector (Figure 3a-f, Table I). These results suggest that both biogeographical history and phylogenetic extension generate distinct environment-diversity relationships.

Likewise, the GWR models have good predictive power when fitting phylogenetic structure (NRI) against environmental variables. First, at the higher phylogenetic extension (all woody trees), temperature and precipitation averages and seasonality, precipitation in the wettest quarter, and long-term stability affected the phylogenetic structure (R2 =49%, Table I). Temperature and precipitation seasonality favored phylogenetic clustering in the northern sector, mainly in regions close to the Rio Doce River (between latitudes -18°S and -21°S). In addition, increased climate seasonality had a positive or weak effect on phylogenetic diversity in some regions in the southern sector (Figure

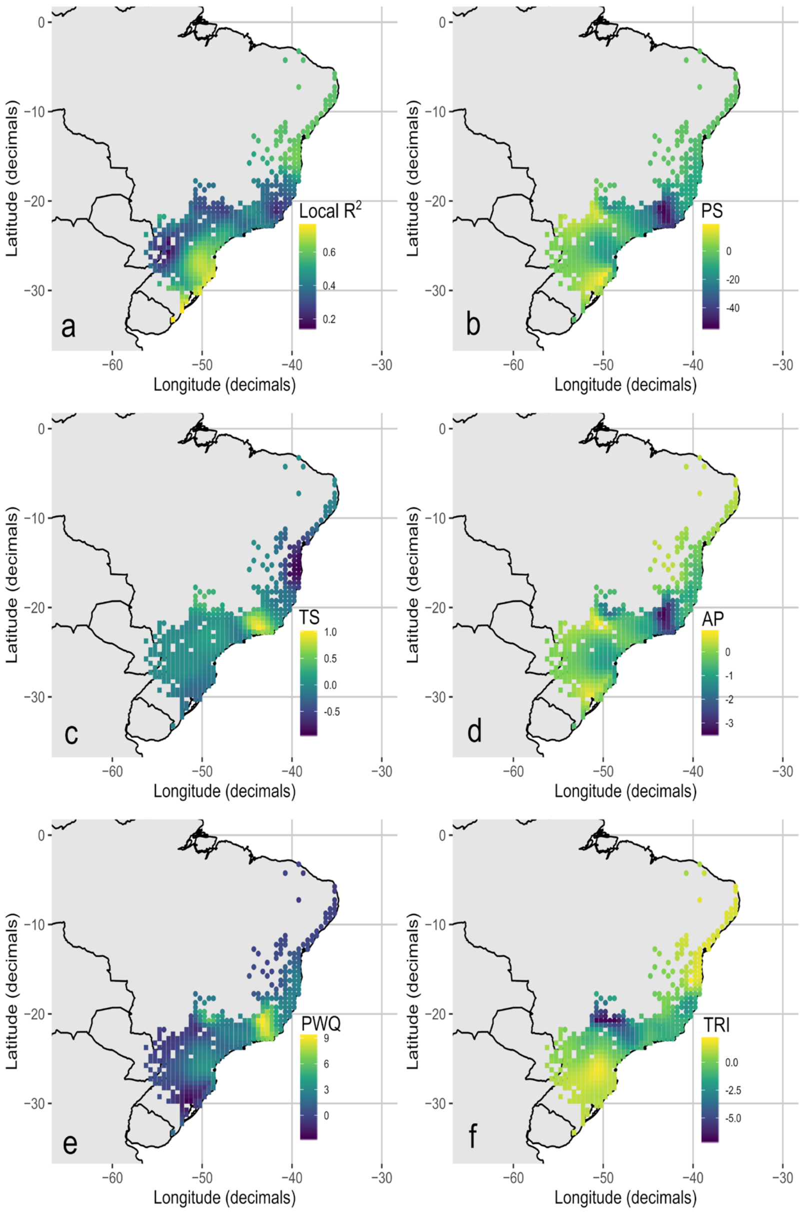

Figure 2. Drivers of species richness of all trees of Atlantic Forest. a = predictive ability of the model for species richness; b = model coefficients for precipitation seasonality; c = model coefficients for temperature seasonality; d = model coefficients for mean annual precipitation; e = model coefficients for mean precipitation in the wettest quarter; f = model coefficients for terrain roughness index. northern sector grids are circular and southern sector grids are square.

4a-e, Table I). In this comparison, significant NRI values (compared to random communities) represented 62 of all Atlantic Forest cells (13.7%). Among these, in the northern sector, 25 exhibited phylogenetic clustering, and 9 displayed phylogenetic dispersion; whereas in the southern sector, there were 22 with phylogenetic clustering and 6 with phylogenetic dispersion (Figure S9a).

The deep-past climatic stability affected the phylogenetic structure only when considering the higher phylogenetic extension, suggesting that the oldest clades of plants (e.g., arborescent ferns and pines) were the most responsive to historical imprints of climate throughout the time. Current stability had a strong and positive effect on the phylogenetic structure across the whole latitudinal gradient in the Atlantic Forest, except for the semideciduous dry forest in the Southwestern portion of this ecosystem (Figure 4f, Table I). When we considered only the phylogenetic structure of angiosperms, average

Table I. **Geographically Weighted Regression models (GWR) showing the effects of environmental, topographic, and historical variables on taxonomic and phylogenetic diversity at different phylogenetic extensions (angiosperms and all trees) in the Atlantic Forest.**

Diversity facet (Model adjusted R^2)	***Variables***	***Minimun***	***Maximun***	***Median***	***F-statistic***	***p-value***
Angiosperm richness (R^2 = 0.73)	Intercept	-583.35	3165.09	682.68	1.55	<0.001
	PS	-45.42	18.48	-3.70	2.42	<0.001
	TS	-1.05	0.42	0.012	5.81	<0.001
	AP	-3.25	1.79	-0.27	2.08	<0.001
	AT	-4.94	2.67	-1.13	1.37	<0.01
	PWQ	-3.86	8.98	0.83	2.12	<0.001
All trees richness (R^2 = 0.57)	Intercept	-1938.7	2168.1	483.26	1.06	<0.001
	PS	-54.97	18.48	-3.60	2.24	<0.001
	TS	-0.96	1.01	-0.003	4.81	<0.001
	AP	-3.52	0.88	-0.304	1.67	<0.001
	PWQ	-2.82	9.32	1.41	1.86	<0.001
	TRI	-7.18	2.18	0.39	2.35	<0.001
Angiosperm NRI (R^2 = 0.62)	Intercept	-16.43	7.21	-5.23	1.45	<0.01
	TS	-0.003	0.003	0.000	1.70	<0.001
	AP	-0.014	0.011	0.001	1.45	<0.01
	AT	-0.002	0.067	0.032	1.40	<0.01
All trees NRI (R^2 = 0.49)	Intercept	-14.09	20.07	-5.31	2.56	<0.001
	PS	-0.29	0.21	0.006	2.73	<0.001
	TS	-0.004	0.003	0.001	2.57	<0.001
	AP	-0.018	0.020	0.001	2.88	<0.001
	AT	-0.002	0.067	0.028	2.38	<0.001
	PWQ	-0.044	0.032	-0.004	1.813	<0.001
	Stability	-0.091	0.15	-0.018	1.447	<0.05

NRI = Net Relatedness Index; PS = precipitation seasonality; TS = temperature seasonality; AP = annual average precipitation; AT = annual average temperature; PWQ = Precipitation in the wettest quarter; TRI = terrain roughness index

annual temperature, temperature seasonality, and average precipitation played a role in the NRI values (R2 = 62%). Specifically, whereas temperature seasonality favored phylogenetic clustering in the northern sector, it increased phylogenetic dispersion or had a weak effect on the southern (Figure 5a-d, Table I). For angiosperms, significant NRI values represented 132 of all Atlantic Forest (29.3%). Among these, in the northern sector, 13 exhibited phylogenetic clustering, and 15 displayed phylogenetic dispersion; whereas in the southern sector, there were 3 with phylogenetic clustering and 101 with phylogenetic dispersion (Figure S9b).

Interestingly, in both GWR models using species richness or phylogenetic diversity as

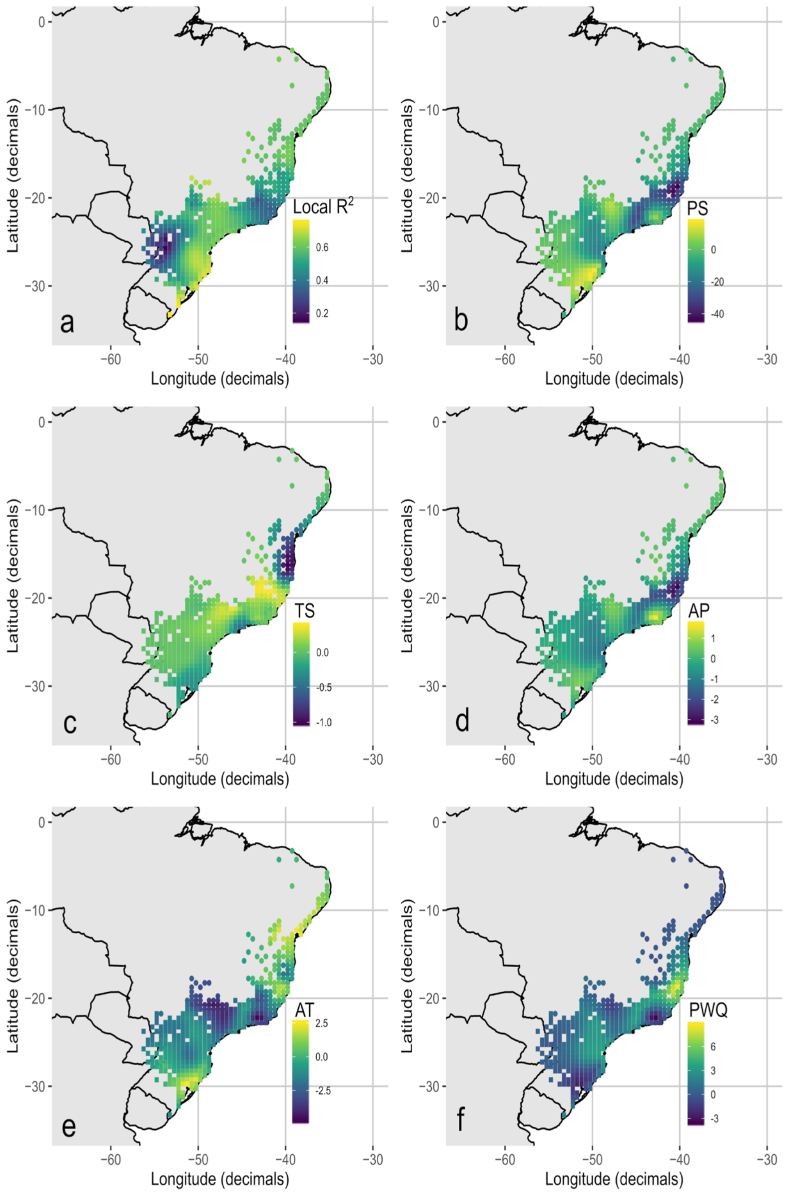

Figure 3. Drivers of species richness of angiosperm trees of Atlantic Forest. a = predictive ability of the model for species richness; b = model coefficients for precipitation seasonality; c = model coefficients for temperature seasonality; d = model coefficients for mean annual precipitation; e = model coefficients for mean annual temperature; f = model coefficients for mean precipitation in the wettest quarter. northern sector grids are circular and southern sector grids are square.

dependent variables, the models at the lower phylogenetic extension (only angiosperms) explained almost~15% more variation than in the higher phylogenetic extension (all woody trees).

DISCUSSION

Our findings showed that macroecological processes and plant distribution patterns in the Atlantic Forest are context dependent. When dividing the Atlantic Forest into northern and southern sectors, the tree communities are taxonomically and phylogenetically distinct. These findings are consistent with previous research, which has identified the Atlantic Forest as a composite biogeographical domain with no sister groups (Fiaschi & Pirani 2009). Low interannual seasonality consistently affected species richness and phylogenetic diversity along the Atlantic Forest (supporting Prediction 1), but the strength and direction of these

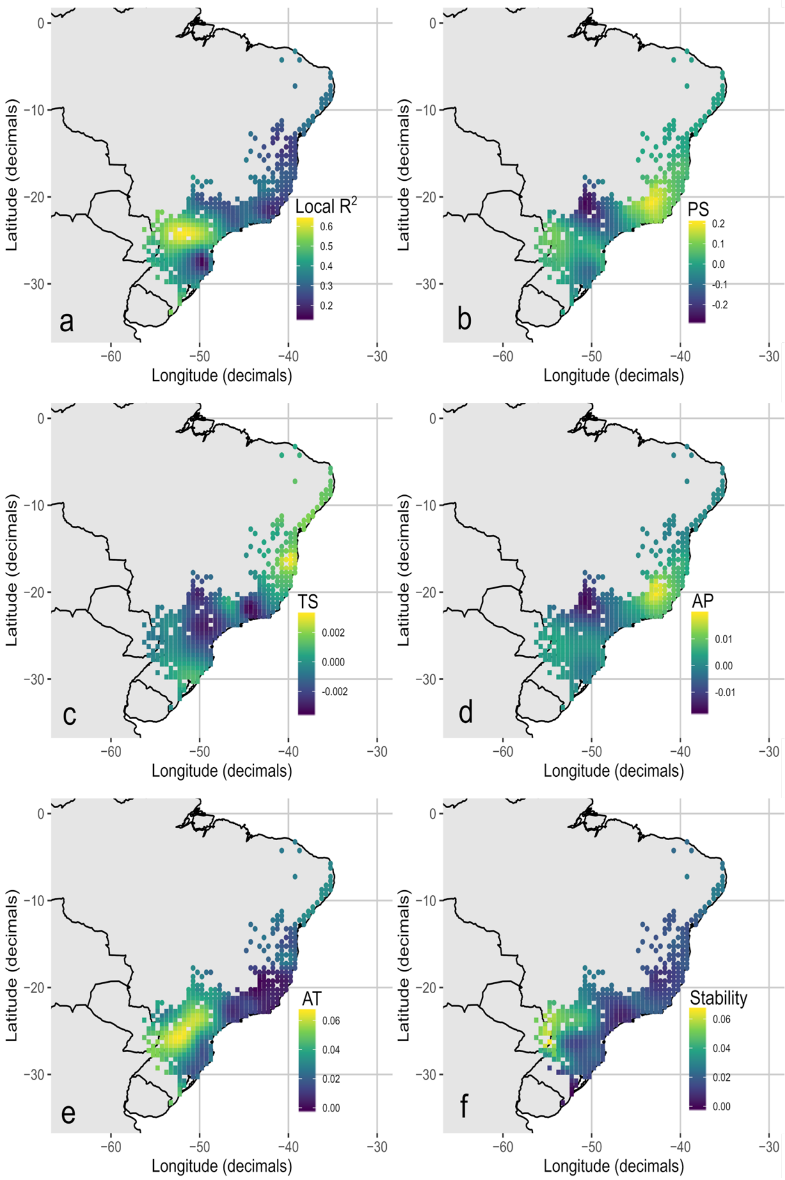

Figure 4. Drivers of phylogenetic diversity of all trees of Atlantic Forest. a = predictive ability of the model for phylogenetic diversity; b = model coefficients for precipitation seasonality; c = model coefficients for temperature seasonality; d = model coefficients for mean annual precipitation; e = model coefficients for mean annual temperature; f = model coefficients for climate stability over the last 120,000 years according to the Random Forest. We omitted precipitation in the wettest quarter from the figure due to space limitations and low explanatory power. Northern sector grids are circular and southern sector grids are square.

relationships are dependent on the peculiarities of sectors with different biogeographic histories. We found partial support for predictions 2 and 3, as the effects of topographic heterogeneity (Prediction 2) and deep-past climatic stability (Prediction 3) were dependent on whether species richness or phylogenetic diversity was used as the dependent variable. Thus, while topographic heterogeneity promotes the accumulation of various species, deep-past climate stability benefits relict lineages from older clades across the Atlantic Forest.

Low interannual seasonality and high climate averages caused most of the variation in patterns of species richness and phylogenetic diversity across the Atlantic Forest, which supports our predictions and reinforce previous findings linking climate and macroecological patterns in this hotspot (e.g., Eisenlohr & de Oliveira-Filho 2015, Neves et al. 2017, Oliveira-Filho et al. 2014). Thus, it is well established

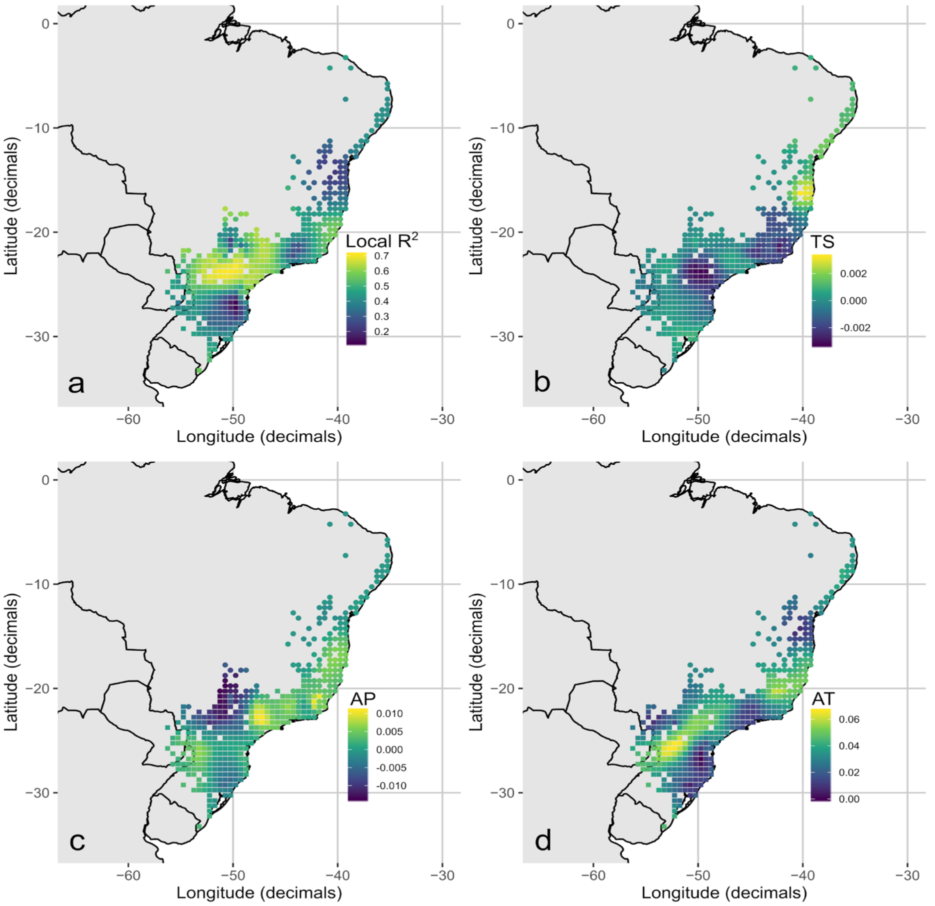

Figure 5. **Drivers of phylogenetic diversity of angiosperm trees of Atlantic Forest. a = predictive ability of the model for phylogenetic diversity; b = model coefficients for temperature seasonality; c = model coefficients for mean annual precipitation; d = model coefficients for mean annual temperature. Northern sector grids are circular and southern sector grids are square.**

that precipitation and temperature are the main environmental factors driving the climatic envelope split in the North and South portions of the Atlantic Forest, respectively (Eisenlohr & de Oliveira-Filho 2015, Oliveira-Filho et al. 2014). Climatic niche conservatism is likely the main factor underlying these patterns (Rezende et al. 2021).

However, we go a step further in untangling those well-known large-scale climate-diversity patterns, by identifying that the relative importance of diversity drivers shifts spatially in response to sectors, that have different biogeographic dynamics in the Atlantic Forest. Some patterns dissected by our models add an explicit spatial interpretation that differs from those advocated in some previous studies (e.g., Neves et al. 2017). For instance, the effects of current precipitation and temperature stability were more consistent in the northern sector, where increasing instability decreased species richness and increased phylogenetic clustering. Conversely, in the southern sector, the patterns related to the current climate were more complex. Specifically, abrupt changes in the relationship between climatic gradients and diversity were found in regions where the transition from flat relief to higher elevations occurs, such as the limits of *Serra do Mar*, *Serra da Mantiqueira* and *Planalto das Araucárias*.

The results, which deviate from commonly encountered standards (anomalies), in the patterns of taxonomic richness and phylogenetic diversity found mainly in the southern sector, are consistent with niche conservation leading to different responses of its species pool to environmental factors. The southern sector of the Atlantic Forest is marked by an enormous diversity of climatic and topographic gradients, in addition to its mixed biogeographical heritage (Oliveira-Filho & Fontes 2000, Neves et al. 2017, Rezende et al. 2021). Probably the discrepancies in diversity patterns found in the southern sector are the results of niche conservatism interacting with the various physiognomies that form this sector. For example, the contact between mixed, evergreen, semideciduous and cloud forests in the great mountain ranges has distinct, non-exclusive effects on diversity patterns. The semideciduous forest of the Atlantic Forest shares a considerable number of species with the evergreen physiognomies (Neves et al. 2017), while also having considerable levels of endemism (Rezende et al. 2021). This mixture, makes us find communities with high phylogenetic dispersion, given the mix of phylogenetically old floristic elements with relatively recent ones. Additionally, the locations that remained more stable during climate oscillations in the deep past may have been so since more remote times, allowing the slow formation of new species from ancient phylogenetic groups. Massante & Gastauer (2023) found a tendency in mountainous regions of the southwest Atlantic Forest (cloud forests) to present an expressive species richness associated with a tendency towards deep phylogenetic agglomeration (positive NRI values).

We also demonstrated that topographic heterogeneity has a significant and consistent positive effect on the species richness of woody trees in the Atlantic Forest regardless of the biogeographical scale. A previous meta-analysis has shown a positive relationship between complex environments and higher taxonomic diversity in different taxonomic groups and ecosystems (Stein et al. 2014). Thus, three general mechanisms might play a role in explaining why environmental heterogeneity increases diversity. First, heterogeneity creates environmental gradients that enable coexistence. Second, heterogeneity has a deep past historical effect benefitting the creation of habitat refugees in extreme conditions. Third, isolation and adaptation in those refugees would lead to speciation creating hotspots of diversity (Stein et al. 2014, Svenning et al. 2009). Our results also reveal a connection between topographic heterogeneity and climatic seasonality contingent on certain biogeographical regions. Specifically, in the northern sector, heterogeneity had a more positive effect on species richness in sites where temperature and precipitation were markedly unstable. Thus, although precipitation seasonality might decrease species richness, environments containing higher topographic heterogeneity might overcome this negative effect, enhancing opportunities for the occurrence of a larger number of species (Table I, Figure 5b). In Atlantic Forest, a more constant water availability provided by air humidity input in mountainous sites under water restriction reduces the probability and intensity of dry periods in these areas that have a substantial topological difference when compared to flatlands in the northern (Fjeldså et al. 2012, Thomas & Barbosa 2008). This pattern would be associated with a larger presence of refuges in sites with higher heterogeneity which, in turn, leads to greater diversity.

We also demonstrated that the southern portion of the Atlantic Forest was climatically more stable than the northern one using a 120 ka interval. This result disagrees with some classical studies, which suggested large areas of climate stability for the Atlantic Forest's northern sector (Carnaval & Moritz 2008). Historically, ancient groups (like pteridophytes, gymnosperms, and some basal angiosperms) have a Gondwanan origin dependent on stable climatic areas due to their climatic niche conservatism (Kooyman et al. 2014). In this way, the existence of large and continuous climatic stable areas has enabled them to be present in the southern sector by pursuing the mesic climatic zones they are "captive" through the time (Kooyman et al. 2014). We have shown that historical climatic stability maintains tree phylogenetic diversity (when including pteridophytes and gymnosperms) even in those few stable areas in the northern sector, which is the opposite of our prediction. In general, climatic stability favors the coexistence of less phylogenetically related species in most of the Atlantic Forest. However, the unique stable areas favoring closely related lineages were those located in the Interior seasonal forest of the southwestern portion (Brazil-Paraguay's contact zone). The physiognomy in this region is probably composed of phylogenetically close plant communities, that are captive to a climate envelope recently evolved that has been conserved in this region while preventing the establishment of more "tropical" groups of other nearby forest types (see Neves et al. 2020). This pattern needs future investigation using a fine-scale approach.

We investigated the phylogenetic structure of all arboreous plants (~3,100 species) across the Atlantic Forest Domain, using the most comprehensive and complete dataset of this biodiversity hotspot. Besides, we advance previous analysis in this ecosystem by considering different biogeographical and phylogenetic extensions, which have improved our understanding of tree biogeography in tropical forests. Our results emphasize that tree communities respond differently to climatic, topographic, and historical variables, depending on contingencies that arise at different biogeographical or phylogenetic extensions. Our results indicate that low climate seasonality is the primary cause of trees' high diversity in the Atlantic Forest. Also, there are interactions between climate and topography that buffer the negative effects of climatically unstable regions in species diversity. We argue that the varying biogeographical history of Atlantic Forest sectors induces distinct evolutionary pathways of tree communities, which, by its turn, will mediate how climate and topographic variables will determine the maintenance of particular lineages in different regions. Moreover, dissecting the non-stationarity between environmental and diversity gradients with appropriate statistical models may reveal processes affecting biodiversity patterns that could be hidden in a particular unstudied scale. Overall, our findings reinforce the need for integrative approaches separating the scale dependency of environmental variables and macroecological patterns.

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SUPPLEMENTARY MATERIAL

Figure S1-S9.
Table SI-SII.

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PSMF, TGS and MJNR conceived the ideas and analyzed the data; LSOM created models of past climates; ATOF collected the data. All authors contributed by commenting and writing the paper.