

## Research paper

# Assembly structures of coastal woody species of eastern South America: Patterns and drivers

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## ABSTRACT

Tropical regions have provided new insights into how ecological communities are assembled. In dry coastal communities, water stress has been hypothesized to determine plant assembly structure by favoring preadapted lineages from neighboring ecosystems, consistent with functional clustering. However, it is unclear whether this hypothesis is sufficient to explain how coastal communities in tropical ecosystems are assembled. Here, we test whether water stress or other factors drive community assembly in woody plant communities across the coastal zone of Brazil, a tropical ecosystem. We characterized functional and phylogenetic structures of these communities and determined the underlying environmental factors (e.g., water stress, historical climate stability, edaphic constraints, and habitat heterogeneity) that drive their community assembly. Assemblages of coastal woody species show geographically varied patterns, including stochastic arrangements, clustering, and overdispersion of species relative to their traits and phylogenetic relatedness. Topographic complexity, water vapor pressure, and soil nutrient availability best explained the gradient in the functional structure. Water deficit, water vapor pressure, and soil organic carbon were the best predictors of variation in phylogenetic structure. Our results support the water-stress conservatism hypothesis on functional and phylogenetic structure, as well as the effect of habitat heterogeneity on functional structure and edaphic constraints on functional and phylogenetic structure. These effects are associated with increased phenotypic and phylogenetic divergence of woody plant assemblages, which is likely mediated by abiotic filtering and niche opportunities, suggesting a complex pattern of ecological assembly.

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## 1. Introduction

The processes that drive species composition in ecological communities have long eluded ecologists (Clements, 1905; Gleason, 1939; MacArthur and Levins, 1967; Diamond, 1975; Pavoine and Bonsall, 2011). Nevertheless, some general principles – or assembly rules – have been established to explain how and why only a subset of species available in the regional pool occurs in a local community (Belyea and Lancaster, 1999; Götzenberger et al., 2012;

Mittelbach and McGill, 2019). Specifically, species sorting in a locality depends on the interaction of three processes over temporal and spatial scales: (i) dispersal, (ii) abiotic filtering (i.e., conditions), and (iii) biotic filtering (e.g., resource use and partitioning). In other words, communities comprise species from the regional pool that can reach the site and possess features that enable them to cope with conditions and assimilate resources despite the presence of other species (HilleRisLambers et al., 2012; Mittelbach and McGill, 2019).

The detection of assembly rules in community ecology often involves measures of similarity among the observed species regarding their ‘functional traits’ through measures of assemblages’ functional structure (Webb et al., 2002; Petchey and Gaston, 2006; Emerson and Gillespie, 2008). As evolutionarily related species tend to share similar traits (Wiens and Graham, 2005), metrics

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based on phylogenetic distance can reflect, to some degree, the patterns of trait similarity of the assemblages (Webb et al., 2002; Cavender-Bares et al., 2009). However, it is now clear that the functional structure may differ from the phylogenetic structure because of the evolutionary patterns of phenotypic divergence or convergence between species. Therefore, investigating both patterns can shed light on the evolutionary and ecological factors that affect assemblage formation (Cadotte et al., 2013; Gerhold et al., 2015; Davies, 2021).

Recent theoretical advances have clarified the interplay between environmental factors and patterns in assemblages' functional and phylogenetic structures. Assemblages under more pronounced abiotic constraints may have more similar species; that is, they are functionally clustered (Pavoine et al., 2011). However, these species can be phylogenetically overdispersed when their trait similarity results from evolutionary convergence (Davies, 2021). Conversely, competition between species with similar niches can lead to overdispersed functional structures, but exhibit phylogenetic clustering depending on the evolutionary modes of the traits involved. However, competition can also lead to functional and phylogenetic clustering if species differ in their competitive ability (Mayfield and Levine, 2010; Liu et al., 2018). Therefore, understanding the patterns of both the functional and phylogenetic structures of assemblages in different environmental contexts is essential to clarifying how different evolutionary and ecological contexts conflate to form existing compositions of ecological communities.

For angiosperms in dry regions, the prevailing explanation posits that water shortage favors drought-tolerant species, resulting in functionally clustered plant assemblages (Cornwell and Ackerly, 2009; Qian and Sandel, 2017; Kubota et al., 2018; Qian et al., 2019). Qian et al. (2016) articulated this explanation with the phylogenetic conservatism of functional traits and proposed that water-depleted sites select for adapted and more closely related species, referring to this explanation as the 'water-stress conservatism hypothesis'. This hypothesis is supported by plant assemblages from multiple habitats, including coastal regions, where species sorting appears to be determined by tolerance to abiotic conditions (Cornwell and Ackerly, 2009; Brunbjerg et al., 2012; Jiménez-Alfaro et al., 2015; Sperandii et al., 2019).

However, this hypothesis has been rarely explored in tropical coastal ecosystems, which have high levels of lineage diversity and different abiotic and biotic processes (Swenson et al., 2012; Yang et al., 2014). For instance, in these ecosystems, functional and phylogenetic structures are driven by factors such as habitat heterogeneity, soil properties, climate stability, and human activity. Habitat heterogeneity can enhance niche partitioning and the coexistence of distinct lineages and functional types, leading to overdispersion (Cramer and Willig, 2005; Liu et al., 2014; Báez et al., 2022). Depleted soils can favor species with superior competitive abilities, resulting in functionally and phylogenetically more clustered assemblages (Coyle et al., 2014; Lourenço et al., 2021). More stable climates may have lower extinction rates, which can favor the accumulation of different lineages and traits at lower richness levels, resulting in overdispersal or increasing species similarity as more species of the same lineages are added as species richness accumulates, increasing clustering (Fine, 2015; Feng et al., 2017; Bose et al., 2018). Human disturbance can also favor conflicting scenarios, including species that are more tolerant to disturbance from either a few or multiple lineages, leading to clustering or overdispersion, respectively (Ding et al., 2012; Satdichanh et al., 2015).

On the eastern coast of South America, sandy coastal plains harbor a dry vegetation formation known as the Restingas, which is influenced by the physical features of coastal environments, such as

geologically recent sandy substrate, maritime wind blow, and high insolation (Villwock et al., 2005; DaSilva and Pinto-da-Rocha, 2011). Evidence suggests that the Restingas flora has a complex origin, including adjacent ecosystems from the phytogeographic domains of the Atlantic rainforest, Caatinga seasonally dry forests, and Amazon rainforest (Rizzini, 1997; Scarano, 2002; Fernandes and Queiroz, 2015). Previous studies have shown that water constraints reduce the variability of lineages and phenotypes within Restinga assemblages (Vitória et al., 2019; Massante and Gerhold, 2020; Lourenço et al., 2021). Based on these findings, the water-stress conservatism hypothesis suggests that these assemblages comprise phenotypically and functionally clustered species (Qian et al., 2016). Therefore, it remains unclear whether water stress or other mechanisms are involved in structuring plant assemblages in tropical coastal ecosystems.

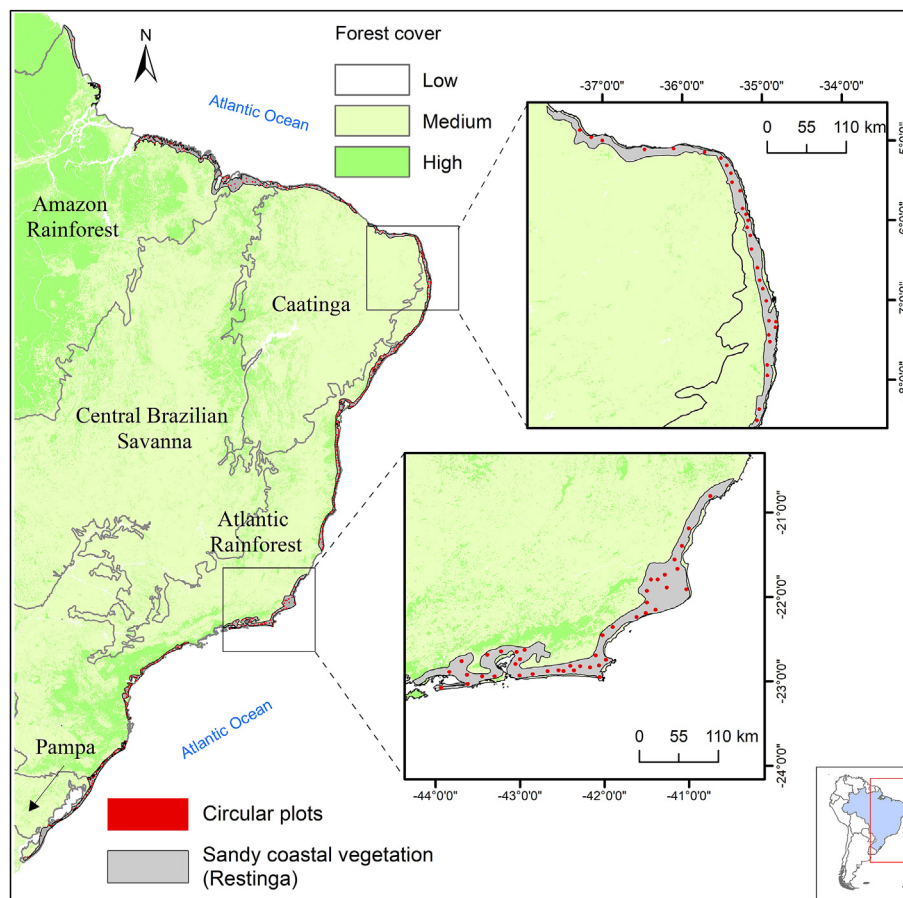
Here, we test whether water stress or other factors drive woody plant assemblages in the Restingas of Brazil, a tropical coastal ecosystem. For this purpose, we characterized these communities' functional and phylogenetic structures and determined what factors (e.g., climate, habitat, soil, and human activity) underlie these structures.

## 2. Material and methods

### 2.1. Study design and data handling

We defined the study area by creating a polygon from the overlapping contours of the coastal plains and plant formations associated with the Brazilian Coastal Zone (Fig. 1 and Table S1). In Restingas, occurrence points are concentrated within distinct segments along the Brazilian Coastal Zone, interspersed by areas where no sampling efforts have been made. These regions with a high density of occurrence points serve as precise indicators of the Restinga sites. An approach that considers areas where occurrence points are densely concentrated will likely result in many records per sampling unit, thereby enhancing inventory completeness (see section 'Definition of well-surveyed plots' below). Thus, we used circular plots to select the sampling units (Fig. 1; R codes in Appendix A). In the initial step, we employed a hierarchical approach to cluster the occurrence points based on a distance matrix. Subsequently, we established the membership for each point within a group at a distance of 15 km. Specifically, the points located within this radius were categorized into the same group. Then, circular plots with a diameter of 2.5 km were created, centered within each group of points. Owing to the distribution pattern of occurrence records, the selection of a distance value for point group classification greater than or less than 15 km resulted in either a reduced number of records per plot or plot overlap. Conversely, opting for circular plots with a diameter exceeding 2.5 km leads to an excessive number of plots extending beyond the coastline (see Fig. S1). Our decision regarding distance and plot diameter was influenced by these trade-offs. Throughout these procedures, we used QGIS software (QGIS Development Team, 2020) and the R packages (R Development Core Team, 2018) *geosphere* (Hijmans et al., 2023a), *vegan* (Oksanen et al., 2018), and *dismo* (Hijmans et al., 2023b).

Plant occurrence records of angiosperms in the study area were extracted from the Botanical Information and Ecology Network (BIEN) database (Enquist et al., 2016, accessed July 19, 2023). We included unique records of native species with valid names. We selected trees and shrubs only, following the species classification of BFG life forms (2018). We also removed the woody plants of the Brazilian Mangroves (Kjerfve and Lacerda, 1993) to obtain a species typical of Restingas vegetation. We used the *BIEN* and *Flora* packages in R software (Maitner et al., 2017; R Development Core Team,



**Fig. 1.** Delimitation of sandy coastal vegetation (Restingas) in eastern South America with adjacent biomes. The circular plots had a diameter of 2.5 km.

2018; Carvalho, 2020). We retained 50,237 records of trees and shrubs for analyses.

## 2.2. Environmental data

We selected environmental predictors that were potentially related to water deficit, climatic stability, environmental heterogeneity, edaphic factors, and human activities. The water-stress conservatism effect was represented by water vapor pressure, precipitation seasonality, solar radiation (retrieved from the WorldClim 2.1 database; Fick and Hijmans, 2017), and water deficit. Water vapor pressure was included because of its potential to increase plant evapotranspiration and soil water evaporation rates (Massmann et al., 2019; Grossiord et al., 2020). We included solar radiation because of its critical role in moisture removal from soil and plants through solar irradiance (Heck et al., 2020), although we acknowledge that this predictor has other direct effects on vegetation (Moeslund et al., 2013). Water deficit was determined as the difference between potential evapotranspiration (PET) and actual evapotranspiration (AET) obtained from the CGIAR-CSI database (Trabucco and Zomer, 2019). When PET is higher than AET, the water deficit is positive, indicating that the vegetation is constrained by water (Littell and Gwozdz, 2011).

The climatic stability effect was described by the average historical variability of temperature and precipitation. We obtained maps of annual mean temperature and annual precipitation of the present and the last glacial maximum (CCSM4) from the WorldClim 1.4 database (Hijmans et al., 2005) and calculated the difference between the current mean annual temperature and that of the last

glacial maximum, and the difference of the annual precipitation between these periods. The effect of habitat heterogeneity was described using the coefficient of variation of altitude (retrieved from the EarthExplorer data portal; US Geological Survey, 2019) and terrain slope (Fischer et al., 2008). To account for the edaphic effect, we combined pH, organic carbon density, and total nitrogen from the SoilGrids database (ISRIC, 2020) with nutrient availability and soil water capacity obtained from the Harmonized World Soil Database (Fischer et al., 2008). Specifically, nutrient availability considers soil fertility based on texture, organic carbon, and total exchangeable bases (Fischer et al., 2008). Finally, we considered the effects of human activities using population density and urban infrastructure (Venter et al., 2016). We considered collinearity when Pearson's  $r \geq 0.7$  among variables. After that, we retained a set of independent variables, first removing those that i) exhibit a higher correlation with a larger number of other variables and ii) possess a weaker correlation with the metrics of functional and phylogenetic structure. This process eliminated solar radiation, soil water capacity, total nitrogen, and urban infrastructure (Table S2).

## 2.3. Definition of well-surveyed plots

From the occurrence records, we calculated the inventory completeness (given as a percentage) for each circular plot, which was defined as the ratio between the observed and predicted numbers of species (Lobo et al., 2018). We calculated this ratio using the Rational curve for species saturation (Ratkowski, 1990), using cells with more than 100 records (i.e., approximately the mean of the number of records among all cells) and completeness higher



than 50% as well-surveyed cells. This criterion is similar to that adopted by other authors (cf. Sousa-Baena et al., 2014; Stropp et al., 2016; Oliveira et al., 2021). Our selection procedure for sampling units resulted in 329 circular plots entirely contained within the Restingas contour polygon (Fig. 1). Inventory completeness varied between 2% and 82%, with only 55 (17% of the total) well-sampled circular plots (hereafter referred to as assemblages) retained for analysis (Figs. S2–S4). The procedures were performed using the *Raster* (Hijmans et al., 2019) and *KnowBr* (Lobo et al., 2018) packages in the R environment (R Development Core Team, 2018).

#### 2.4. Functional traits and phylogenetic tree

To measure functional structure, we selected three plant functional traits: leaf area (mm<sup>2</sup>), whole plant height (m), and dispersal syndrome (biotic and abiotic). We selected these traits considering their consistency in expressing plant responses to abiotic (i.e., environmental factors) and biotic filters (i.e., competitive interactions). For instance, height and leaf area are related to plant responses to climate, soil resources (e.g., water and nutrient availability), and competitive interactions, whereas dispersal syndromes are related to plant colonization potential and disturbances (Lavorel and Garnier, 2002; Cornelissen et al., 2003). We also selected these attributes based on their availability to species from the study region. For each species, we obtained values for these attributes using the following databases and research sources: BIEN (Enquist et al., 2016), TRY – ‘Plant Trait Database’ (only dispersal syndrome, Kattge et al., 2020), ‘Global Spectrum of Plant Form and Function Dataset’ (leaf area and whole plant height, Díaz et al., 2022), and unpublished/published scientific data (Appendix A). The *BIEN* package (Maitner et al., 2017) in R (R Development Core Team, 2018) was used in this step.

We addressed the data gaps in functional traits for some species using an imputation approach. We used the Random Forest method, based on machine learning algorithms, which adds missing values of categorical or continuous traits using other known variables (Pantanowitz and Marwala, 2009). The procedure can fill in any missing trait value for any species in the dataset based on the associations among other traits. Good accuracy of the procedure depends on at least 70% data availability (Penone et al., 2014). We assessed the accuracy of the imputation method using two error measures: the Normalized Root Mean Squared Error (NRMSE) for continuous traits and the Proportion of Falsely Classified (PFC) for categorical traits. In both cases, the error ranged from zero (i.e., accurate) to unity (i.e., estimate not different from random) (Li et al., 2015a; Lenz et al., 2020). We performed the imputation procedure with 79% of the known traits, thus achieving high reliability (Table S3). The error measures indicated low inaccuracy of trait estimation (NRMSE = 0.32; PFC = 0.27) and were thus assumed to be acceptable for our purposes. For this procedure, we used the *missForest* (Stekhoven and Bühlmann, 2012) package in R (R Development Core Team, 2018). Finally, we obtained a matrix consisting of both the original and imputed attribute values, which was subsequently employed for functional structure analyses.

To investigate the phylogenetic structure, we used the dated phylogeny of spermatophytes (ALLOTB; Smith and Brown, 2018). This phylogeny was generated from molecular data (GenBank) within the Open Tree of Life Project (Smith and Brown, 2018), being the most complete for this group of plants and with the highest proportion of well-resolved species present in Restingas thus far (cf. Zanne et al., 2014; Gastauer and Meira-Neto, 2017; Jin and Qian, 2022, 2023). Species missing from the phylogeny (208 species, ~11%) were randomly inserted into the most derived clades, usually genera or families (Table S9) (e.g., Ma et al., 2016; Qian et al., 2016). As this procedure adds uncertainty to the analyses, we ran the

analyses for 100 possible phylogenies generated by Scenario 3 of the *V.PhyloMaker2* package. All steps described were performed in R (R Development Core Team, 2018) using the *ape* (Paradis et al., 2004) and *V.PhyloMaker2* (Jin and Qian, 2022) packages.

#### 2.5. Functional and phylogenetic structure

We used the net relatedness index (NRI) and nearest taxon index (NTI) (Webb, 2000; Webb et al., 2002) to describe both functional (NRI-F and NTI-F, respectively) and phylogenetic (NRI and NTI, respectively) structures. The NRI is based on the mean phylogenetic distance (MPD), a metric that estimates the mean phylogenetic distance between all possible combinations of species pairs in a sample. The NTI is based on the nearest taxon distance (MNTD), which estimates the mean phylogenetic distance between each species and its nearest relative in the sample (Webb, 2000; Webb et al., 2002). While NRI represents the overall phylogenetic structure of the community, NTI captures terminal phylogenetic clustering (Webb, 2000; Swenson, 2014). Thus, structuring mechanisms can be assessed across both older lineages and close relatives in the Restinga assemblages (Massante and Gerhold, 2020).

NRI and NTI were estimated by comparing the MPD and MNTD observed to the expected values resulting from random community assembly dynamics. These are standardized measures for assessing community assembly processes (Webb et al., 2002; Pausas and Verdú, 2010). Thus, we compared the observed MPD and MNTD values for each community against a null model with 999 randomizations. We used the “independent swap” randomization algorithm, which changes the composition of the assemblages (i.e., co-occurrence of species) while maintaining the frequency of occurrence of the species and the richness of the assemblages (Gotelli and Entsminger, 2003; Kembel, 2009). The independent swap generates more restricted null models, improving the statistical performance over other algorithms (Hardy, 2008; Miller et al., 2017). These null models identify the effects of stochastic or deterministic processes (i.e., environmental filtering or limiting similarity) on assemblage structuring (Kembel, 2009; Miller et al., 2017). For the phylogenetic structure, we also compared the observed MPD and MNTD values for each community with the expected values from the DAMOCLES model (Pigot and Etienne, 2015). This dynamic null model of community assembly quantifies the phylogenetic structure of co-occurrence between species, incorporating the historical effects of colonization, local extinction, and speciation (Pigot and Etienne, 2015).

We computed the average NRI and NTI values for each plot using estimates derived from all 100 phylogenetic hypotheses. NRI-F and NTI-F were generated using a square matrix that expresses functional distances based on the Gower index (Gower, 1971). Functional and phylogenetic clustering are significant when the metric values (i.e., NRI-F, NRI, NTI-F, and NTI) exceed 1.96, whereas overdispersion is considered significant when these values are below –1.96 (Webb et al., 2002; Vamosi et al., 2009). These steps were performed using the *vegan* (Oksanen et al., 2018), *FD* (Laliberté et al., 2015), *picante* (Kembel et al., 2010), and *DAMOCLES* (Pigot and Etienne, 2015) packages in R (R Development Core Team, 2018).

The functional structure can be coupled to the phylogenetic structure because of the phylogenetic conservatism of traits. To check for this effect, we performed a linear regression analysis between phylogenetic and functional metrics (Nascimento et al., 2018). We also tested the phylogenetic signal of traits using Pagel’s lambda ( $\lambda$ ) coefficient (Pagel, 1999) for the continuous characters and the D statistic (Fritz and Purvis, 2010) for the categorical character transformed into a binary discrete variable. These

analyses were conducted using 'phytools' and 'caper' (Revell, 2012; Orme et al., 2023) in the R package, respectively. As only NRI-F exhibited a relationship with NRI ( $R^2 = 0.14$ ;  $p < 0.01$ ), in accordance with the phylogenetic signal of leaf area ( $\lambda = 0.40$ ;  $p < 0.01$ ) and plant height ( $\lambda = 0.74$ ;  $p < 0.01$ ), we used the obtained values of the residuals of the relationship to correct for the phylogenetic effect (see Nascimento et al., 2018). The residuals and original NRI-F values were used in the model selection process (see below).

### 2.6. Drivers of functional and phylogenetic structure

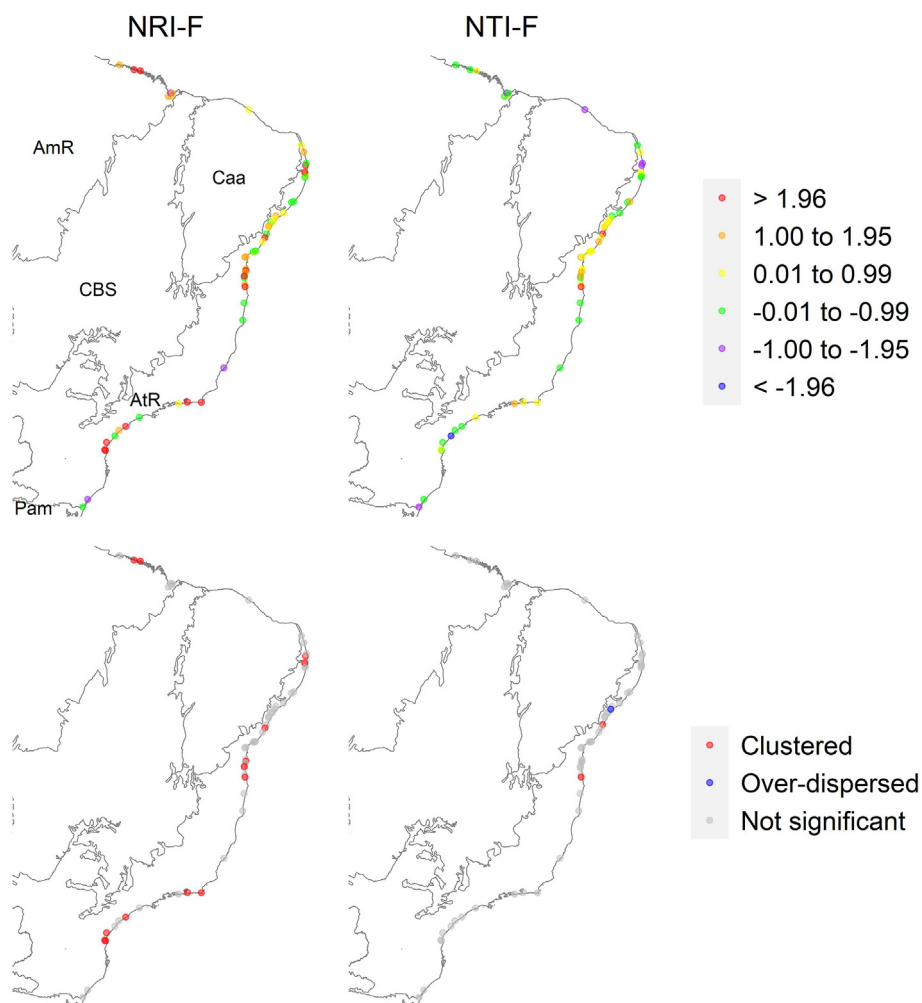
We used a model selection approach to test hypotheses for patterns of functional and phylogenetic structures. During this procedure, multiple competing predictors are compared to identify the model that best explains the data (Johnson and Omland, 2004). We used linear regression models to evaluate the individual contribution of each variable present in the best models to the variation in functional and phylogenetic structures (Legendre and Legendre, 2012). We adopted Akaike's Information Criterion corrected for small sample sizes (AICc) to identify the most parsimonious model from a forward-backward search (Burnham and Anderson, 2004). This method removes the variables and adds new ones at each step to identify the model with the lowest AICc. We also checked the residuals of linear regressions for spatial

autocorrelation using spatial correlograms generated by Moran's I index (Legendre and Legendre, 2012). Given the absence of spatial autocorrelation (Moran's I  $< 0.15$ ), we did not use spatial regression analysis. For these procedures, we used the R packages (R Development Core Team, 2018), *spdep* (Bivand et al., 2023), *MASS* (Ripley et al., 2023), and *QuantPsys* (Fletcher, 2022).

### 3. Results

More than half of the NRI-F and NTI-F values were positive (38 and 30 assemblages for NRI-F and NTI-F, respectively), indicating a tendency toward functional similarity among species (Fig. 2). We found 14 assemblages (~25%) with NRI-F values that were significantly higher than those expected by chance, that is, clustered (Fig. 2). No assemblage exhibited NRI-F values significantly lower than those expected by chance, that is, overdispersed (Fig. 2). For NTI-F, we found two assemblages (~5%) with values significantly higher than those expected by chance and one assemblage (~2%) with values significantly lower than those expected by chance (Fig. 2). However, in most cases, the assemblages exhibited a tendency toward a stochastic pattern.

Regarding phylogenetic structure, we found phylogenetically clustered assemblages, with the majority of the NRI and NTI values being positive (40 and 45, respectively). We found an average of 12



**Fig. 2.** Maps of functional structure of assemblages of woody plants in the Brazilian Restingas, eastern coast of South America. Values of functional structure that differ from a null model are shown in the maps below. Abbreviations: Pam = Pampa, AtR = Atlantic Rainforest, Caa = Caatinga, CBS = Central Brazilian Savanna, AmR = Amazon Rainforest.

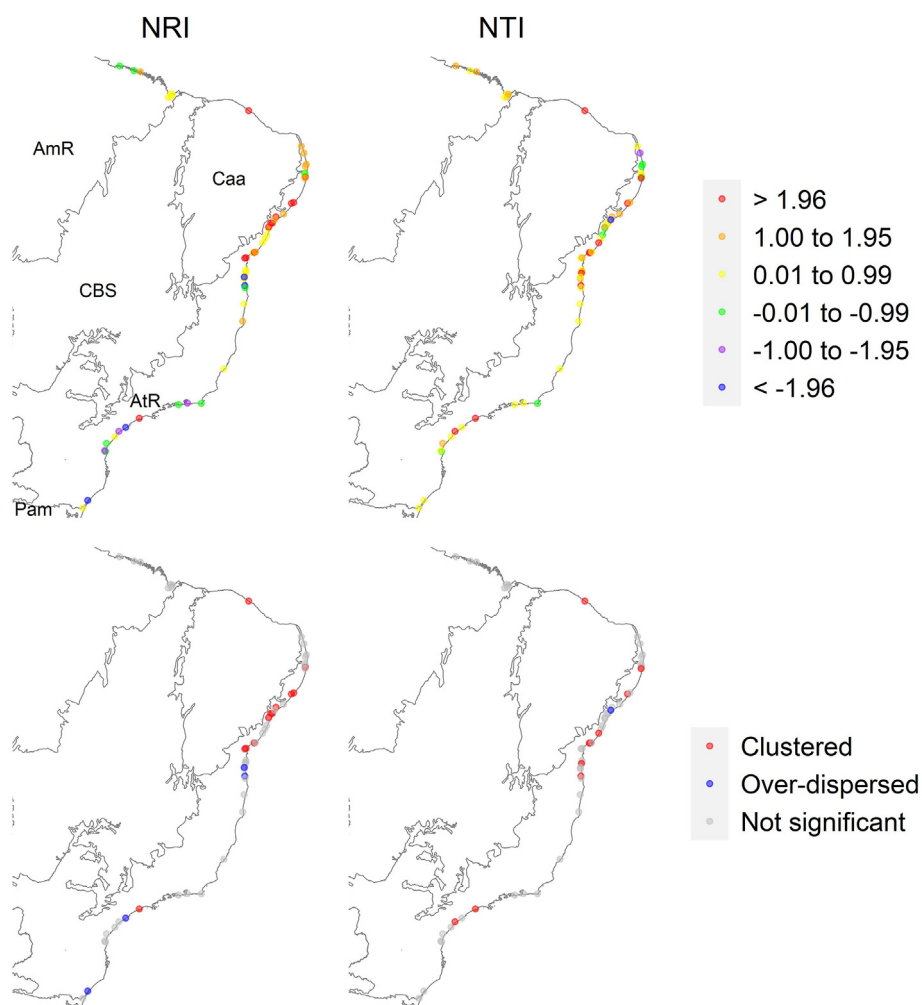
assemblages (~22%) with a significantly higher NRI than expected by chance. In contrast, on average, four assemblages (~7%) had NRI values that were significantly lower than expected by chance (Fig. 3). For NTI, we found 10 assemblages (~18%) with values significantly higher than those expected by chance, and only one assemblage (~2%) with values significantly lower than those expected by chance (Fig. 3). When historical processes were incorporated through the DAMOCLES model, we observed 43 assemblages (~78%) with NRI values significantly higher than those expected by chance. Regarding NTI, we identified 28 assemblages (~51%) with values significantly exceeding chance expectations, whereas only two assemblages (~3%) demonstrated values significantly lower than those expected by chance (Fig. S5). Therefore, the DAMOCLES null model results agreed with the general tendency for phylogenetic clustering among the assemblages.

From the model selection approach using the Akaike Information Criterion (AICc), the altitude variation coefficient (negative effect) exhibited significant effects in the best model for NRI-F and phylogenetically unconstrained NRI-F. Conversely, the best model for NTI-F revealed a significant positive effect of water vapor pressure and soil nutrient availability while also accounting for a negative effect of terrain slope (Tables 1, S4–S6 and Fig. S6). Regarding phylogenetic structure, the best model for the spatial pattern of the NRI included only water deficit with a significant

effect. For NTI, both water vapor pressure and organic carbon emerged as significant factors in the model. NRI was positively related to water deficit, as was NTI with water vapor pressure and organic carbon (Tables 1, S7–S8 and Fig. S6).

#### 4. Discussion

We found varying patterns of functional and phylogenetic structure in the Restingas of Brazil, with a predominance of stochastic arrangements, followed by clustering and fewer cases of overdispersion. Random patterns can result from neutral dynamics, such as stochastic colonization (Hardy and Senterre, 2007). However, they can also arise from conflicting deterministic processes canceling each other out, especially depending on the degree of phylogenetic conservatism of traits (see Cavender-Bares et al., 2004; Kraft et al., 2007; Zhou et al., 2021). When phylogenetic conservatism is low, as for the traits analyzed in the species from the Restinga, the emerging pattern of functional and phylogenetic structures can offer clues to the conflicting processes involved. For example, low conservatism with competitive interactions may lead to functional overdispersion and random phylogenetic structures (Cavender-Bares et al., 2004; Kraft et al., 2007). Together with high phylogenetic and functional diversity in heterogeneous habitats, low phylogenetic conservatism can result in random functional



**Fig. 3.** Maps of phylogenetic structure of assemblages of woody plants in the Brazilian Restingas, eastern coast of South America. The phylogenetic structure was obtained by averaging the 100 randomizations using different phylogenies. Values of phylogenetic structure that differ from a null model are shown in the maps below. Abbreviations: Pam = Pampa, AtR = Atlantic Rainforest, Caa = Caatinga, CBS = Central Brazilian Savanna, AmR = Amazon Rainforest.

**Table 1**

The best models of environmental predictors for the patterns of the functional and phylogenetic structure of plants according to the Akaike Information Criterion corrected for sample size (AICc). ALT: altitude variation coefficient; C: soil carbon density; DEN: human population density; NUT: soil nutrient availability; PRE-VAR: historical precipitation change; SLO: terrain slope; TEMP-VAR: historical temperature change; VAP: water vapor pressure; WD: Water deficit. Note: values of the regression coefficients and  $R^2$  are standardized.

Metric	Predictor	VIF	Slope ( $\beta$ )	$R^2$	AICc
NRI-F	ALT	1.0	-0.431***	0.277***	33.11
	DEN	1.2	0.212		
	WD	1.2	-0.182		
NRI-F phylogenetically unconstrained	ALT	1.0	-0.428**	0.180***	31.33
	PRE-VAR	1.0	-0.179		
NTI-F	VAP	1.5	0.333*	0.296**	0.01
	NUT	1.0	0.295*		
	SLO	1.0	-0.280*		
	WD	1.3	0.233		
NRI	WD	2.9	0.699***	0.360***	33.11
	C	3.7	0.374		
	VAP	2.2	0.309		
	TEMP-VAR	1.4	0.191		
	ALT	1.0	0.170		
	VAP	1.7	0.456*		
NTI	C	1.7	0.407*	0.131*	5.72

\*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; \* $p < 0.05$ .

structures with overdispersed or random phylogenetic structures (Weiher and Keddy, 1995; Sobral and Cianciaruso, 2016). Alternatively, low phylogenetic conservatism together with abiotic filtering and great dispersal can yield phenotypic convergence and random phylogenetic structures (Cavender-Bares et al., 2004; Martiny et al., 2013), which seems to fit our case better.

The above conclusion stems from the finding that assemblages from the Restingas of Brazil that departed from stochasticity were mostly clustered. In other words, these assemblages harbor species with more similar traits and belong to fewer lineages (Pausas and Verdú, 2010). This pattern of functional and phylogenetic clustering is consistent with the role of environmental filtering (Massante and Gastauer, 2023), as found in other regions with pronounced environmental constraints (Gong et al., 2019). In fact, the ten more speciose families (8% of all families) of the Restingas comprised approximately 60% of all species, similar to the order level, in which three of the 34 orders (Myrtales, Malpighiales, and Fabales) comprised half of all species (Scarano, 2002; Massante and Gerhold, 2020). Overall, these findings support the prevailing view of environmental filtering in assemblages subjected to harsh environmental conditions (Kubota et al., 2018; Gong et al., 2019).

The few isolated cases of functional and phylogenetic overdispersion can hardly be attributed to the pervasive effect of within-clade competition and phenotypic divergence, as theory claims (Gerhold et al., 2015; Davies, 2021). They are more likely to have resulted from alternative processes, such as dispersal and colonization by distantly related and functionally divergent species (Li et al., 2015b). This scenario also supports the above reasoning that the clustering tendency is counterbalanced by high dispersal (Cavender-Bares et al., 2004; Martiny et al., 2013). Alternatively, they may also be due to incomplete sampling of local assemblages, which is an issue in our dataset. As sampling effort and thus species richness increase, the chance of both phylogenetic and functional clustering also increases because of the filling of regional lineages and their trait space (Ordóñez and Svenning, 2018). Note that this effect can also lead to an underestimation of clustering relative to stochastic assemblages. If this is the case, it reinforces our conclusion and other existing evidence of a greater role of environmental filtering in this type of ecosystem.

The above reasoning also seems to be supported by the existence of a few divergent assemblages that exhibited phylogenetic

overdispersion and functional clustering. This relationship is not uncommon (e.g., Swenson and Enquist, 2009; Zhao et al., 2022; Mastrogianni et al., 2023). It can be influenced by various factors and may be independent across gradients (Xu et al., 2019; Zhou et al., 2021). This indicates that species with similar functional traits belong to distantly related lineages (Emerson and Gillespie, 2008; Yang et al., 2014), thus emphasizing our claim of a greater role for environmental filtering in driving trait convergence and dispersal of distantly related species from other regions, resulting in assemblage structures that are more prone to clustering (Cavender-Bares et al., 2004; Liu et al., 2018).

Our conclusion of a tendency to environmental filtering is again supported by the effect of environmental factors, especially water constraints and soil properties on the patterns of both functional and phylogenetic structures. We found lower phylogenetic variability in warmer and drier regions associated with reduced functional variability (e.g., Vitória et al., 2019; Gong et al., 2019; Aguirre-Gutiérrez et al., 2020). This effect is consistent with the water-stress conservatism hypothesis (Qian et al., 2016), whereby warmer and drier regions of the Restingas filter species from the regional pool that are better equipped to establish in its water-constrained conditions (Weiher and Keddy, 1995; Amorim and Melo-Jr, 2017; Melo-Jr and Boeger, 2017; Silva and Souza, 2018).

The positive effects of soil carbon and nutrients on functional and phylogenetic structures add an interesting role to resource availability. Richer soils allow for more similar species as also do the climatic constraints. This indicates an association between resource availability and trait disparity, as expected from the effect of competition, which is often treated as opposed to environmental filtering (Webb et al., 2002). However, these effects are not necessarily mutually exclusive and can act together along the gradient between clustering and overdispersal (Cavender-Bares et al., 2004; Nascimento et al., 2018). In the Restingas, this appears to be the case, where resource availability reinforces clustering at the upper end of trait similarity, at which environmental filters predominate. In its turn, habitat heterogeneity negatively affects functional and phylogenetic structures. This suggests that a greater variety of habitats allow the establishment of more distinct species, lowering the clustering through allowing for higher variability in lineages and traits (Moeslund et al., 2013; Oliveira et al., 2021). Altogether, these conflicting effects account for the predominance of random



assemblages regarding functional and phylogenetic structures, depicting a complex set of ecological processes acting together at the Restingas.

## 5. Conclusions

Our study has shown that the Restingas plant assemblages exhibit diverse patterns of functional and phylogenetic structures and a combination of ecological processes that drive these patterns, despite persistent knowledge gaps. The patterns include a predominance of stochastic arrangements, but with a tendency towards functional and phylogenetic clustering, pointing to a prevailing role of habitat filtering as the leading mechanism. Factors linked to water limitation, soil properties, and habitat heterogeneity were the main drivers of assemblage structure, with varying degrees of accordance between functional and phylogenetic assembly patterns. Taken together, these findings suggest a complex set of interactions between abiotic filtering and resource availability, in which closely related and pre-adapted lineages are generally favored. Overall, the combination of high tropical diversity with strong abiotic constraints and niche opportunities of the Restingas seems to add further complexity to the understanding of the interplay between patterns and processes in ecological assemblages at the macroscale. At the same time, they remain plagued with knowledge gaps that, if surmounted, could accelerate progress on this matter.

## CRediT authorship contribution statement

**Eduardo Vinícius da Silva Oliveira:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Myrna Friederichs Landim:** Writing – review & editing, Supervision, Conceptualization. **Sidney F. Gouveia:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pld.2024.04.006>.

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