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Soil-associated drivers of plant traits and functional composition in Atlantic Forest coastal tree communities

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Abstract. The severe deforestation of Brazil's Atlantic Forest and the increasing effects of climate change underscore the need to understand how tree species respond to climate and edaphic factors. To identify the most important environmental drivers of coastal Atlantic Forest diversity and functional composition, we studied 42 plots of coastal Atlantic Forest (restinga), which has a high diversity of plant communities and spans strong environmental gradients. We examined how forest physiognomy and functional composition respond to changes in the environment, hydraulic, and soil properties. We tested different hypotheses relating the roles of nutrients and soil water availability in driving shifts in tropical forest diversity and functioning. We collected wood samples and leaves from ~85% of the plant species identified in the forest inventory and estimated the community-weighted tree height, aboveground biomass, basal area of individual plants, specific leaf area, wood density, and the total tree biomass per community by the sum of all trees' aboveground biomass per plot. We measured water table depth and 24 physicochemical soil parameters. Hypotheses relating to these factors were formalized via both generalized additive models and piecewise structural equation models and null models of community assembly. Increasing drought, as reflected by increasing water table depth, coarse sand, and soil concentration of aluminum (>6 cmol/kg), was found to be a primary driver of shifts in all measured functional traits. Water table depth was found to be the main environmental driver of restinga species diversity, but shifts in species richness were largely decoupled from functional richness and functional dispersion. Our results suggest that decreases in soil water availability are a central driver of local phenotype–environment matching and that increasing water limitation increases the role of environmental filtering on multiple traits. Our results show that drought leads to a strong convergence (standardized effect size < -1.95) in forest function and leads to shifts to smaller statured forest in particular. These findings reveal important differences in the drivers of forest structure and functioning, suggesting that changes in local spatial variation in soil and moisture variables will be a central issue in restinga management and conservation.

Key words: aboveground biomass; aluminum; Atlantic Forest; Brazil; biodiversity; functional traits; physiognomy; restinga; salinity; soil gradients; water availability; water table depth.

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INTRODUCTION

Tropical tree species' distributions are influenced by variation in soil nutrient availability, highlighting the role of soils in functional assembly and biogeography (Webb and Peart 2000, Russo et al. 2005, John et al. 2007, Chadwick and Asner 2018), and the importance of resource competition as a mechanism structuring tropical plant communities (John et al. 2007). Soil plays a fundamental role in the diversity and functioning of tropical forests, and underlies a complex interacting system of forest taxonomic composition and soil formation, driving patterns of niche differentiation at the global scale (Fujii et al. 2018). A combination of soil attributes including nutrient availability, soil structure, and water availability together determines variation in tropical forest diversity and function at broad scales (Cole 1960, Phillips 2009), and often drives differences between biomes (such as forest and savanna). Few studies have looked at how these same properties affect local-scale heterogeneity in vegetation physiognomy of environmentally diverse systems of restinga (de Assis et al. 2011, Magnago et al. 2013).

Despite research efforts to date (e.g., De Oliveira-Filho et al. 1989, Oliveira-Filho and Ratter 1995, Neves 2017, Bueno et al. 2018, Silva de Miranda et al. 2018), it remains an open question as to how changes in soil nutrients, texture, soil water availability, and chemistry affect local forest biodiversity, structure, and physiognomy. Physiognomy is defined as "the form and function of vegetation; the appearance of vegetation that results from the life-forms of the predominant plants" (Shimwell 1984) (attributed to Cain and de Oliviera Castro 1959). Studies that focus on strong environmental gradients can help guide our understanding of determinants of ecosystem structural composition and, eventually, ecological responses to environmental changes (Cornwell and Ackerly 2009, Violle et al. 2011, Guittar et al. 2016).

Restinga is a distinct type of coastal tropical and subtropical moist broadleaf forest, found in eastern Brazil (Scarano 2009). Restinga is characterized by high variation in soil properties and water availability over short geographic distances. In Brazil's Atlantic Forest, the dramatic shift in restinga physiognomy has been attributed to several environmental variables (Marques et al. 2015), among which are soil fertility (Lourenço Junior and Cuzzuol 2009), salinity (Lourenço et al. 2013), organic matter, aluminum saturation (Rodrigues et al. 2013), soil texture, and water table depth (Cooper et al. 2017). It has been suggested that water table depth and microtopography (fine-scale variation in soil relief, creating valley regions with wet soils and higher sites with dry soils) may be the most important variable driving restinga forest structure and plant functional traits (here defined as "any trait which impacts fitness indirectly via its effects on growth, reproduction and survival"; Violle et al. 2007).

The steep environmental gradients that characterize the restinga offer a unique opportunity to assess several hypotheses for how shifts in water availability and soil attributes effect changes in the diversity of tropical forest form and function. Strong abiotic gradients are expected to result in shifts or gradients in forest function due to phenotype–environment matching. Specifically, the "adaptive trait hypothesis" states that shifts in trait composition across environmental gradients reflect selection for optimal matching of phenotypes with local abiotic conditions (Levins 1968, Carnicer et al. 2013). In addition, steep gradients in soil characteristics associated with increasing stress and resource limitation over short geographic distances are expected to reduce functional diversity and thus exert strong "environmental filtering" (Fisher 1960, Swenson et al. 2012). According to the "favorability hypothesis," environmental filtering would be reflected in the loss of rare phenotypes at the edges of trait space (a reduction in the variance of traits) being selected against in harsher environments.

The sharp abiotic soil gradients in the restinga enable one to assess the role of increased drought and nutrient limitation and the strength of environmental filtering as dispersal limitation is minimized in this system as geographic distances are short (often less than several kilometers). Over such short distances, environmental filtering should be more apparent and would result in differential selection of a limited subset of individuals with traits that are best adapted to persist and grow in soils poor in nutrients and that have high aluminum tolerances (de Britez et al. 2002*a*,*b*). Specifically, physicochemical soil properties, such as increasingly limiting nutrient concentrations, base saturation, acidity, cation exchange capacity, organic matter, and aluminum saturation (de Almeida et al. 2011), have been noted to constrain restinga plant growth (Marques et al. 2015). Furthermore, the porous restinga soils result in low soil fertility and low water retention capacity (Cooper et al. 2017), which may impose constraints on plant biomass productivity (Lambers et al. 2008, Santiago-García et al. 2019). In water-limited conditions, plants exhibit more conservative strategies, such as small body size and low specific leaf area (Cornwell and Ackerly 2009, Katabuchi et al. 2012), and the production of thick and scleromorphic leaves with increased longevity (Wright et al. 2004, Lambers et al. 2008), as are typically found in restinga plant species (Mantuano et al. 2006, De Aguiar-Dias et al. 2012, Melo Júnior and Torres Boeger 2015, Pinedo et al. 2016).

Here, we use the unique strong environmental gradients of the restinga to test the assumptions and predictions of the "adaptive trait hypothesis" and the "favorability hypothesis." In doing so, we also address the following questions: (1) how do environmental variables interact with each other to influence water and nutrient availability at a fine spatial scale?; (2) what are the main environmental drivers of forest biomass, functional composition, and diversity in restinga forests?; (3) are strong gradients of stress associated with water and nutrient availability also reflected in patterns of functional composition consistent with a role of environmental filtering?; and (4) do these drivers influence restinga forest physiognomy, functional composition, and diversity? Through the measurement of a suite of plant traits and 25 environmental variables in 42 restinga plant communities, we develop a mechanistic understanding of the system functioning and the interaction between environmental variables and its effects on forest biodiversity, physiognomy, and trait composition. Moreover, we argue that assessing such drivers underlying restinga forest structure sheds light on broader questions regarding the factors controlling tropical forest diversity and functioning.

Materials and Methods

Study area and aboveground surveys

The restinga forest is one of the most environmentally diverse habitats of Atlantic Forest (Thomas and Garrison 1998, Scarano 2009, Neves et al. 2017), comprising a high diversity of plant assemblages (Pereira 1990). The environmental diversity is attributed to the conspicuous soil mosaic and topographic variation arising from the recent transgressive and regressive events from the quaternary (Suguio and Martin 1990), forming a steep gradient of soil water and soil texture. The topography affects the water flow, which tends to accumulate in lower sites that are characterized by shallow water table depth and organic soils (floodable or permanently flooded forests), while upper sites (non-floodable areas, 4–6 m higher in elevation than the floodable sites) are comprised of well-drained and sandy soils, creating continuous soil gradients of water, soil texture, and nutrient availability.

Data collection for this study took place in Paulo Cezar Vinha State Park, which is located in Guarapari municipality of Espirito Santo State, Brazil (Fig. 1a), and is a restinga protected area, with several discrete plant communities that are found side by side. Pereira (1990) reported 11 well-defined plant communities in this park, ranging from small shrubs to tree communities, which show increasing structural complexity from the shore toward the inland areas (Pereira 1990, Assis et al. 2004). The study area (Fig. 1b) covers a short flooding gradient transition, where we previously set up 42 plots (measuring 5 m × 25 m) across three forest types: floodable, intermediate, and dry forests (Fig. 1c) (Lourenço et al. 2020). All trees with a diameter at the breast height (dbh) $\geq$5 cm were tagged and identified to species, and height and dbh were measured. The small spatial scale throughout the plant communities occurs allowed us to precisely track the strong continuous flooding gradient, from the wetter end to drier end of the gradient (207.4 ± 60.7 m), increasing the sampling accuracy in detecting the effect of soil gradients in wood and leaf traits, and overall forest composition.

Maps were drawn using the "maptools" (Bivand and Lewin-Koh 2017) and "raster" packages (Hijmans 2017) in the R Statistical Environment (R Core Team 2018).

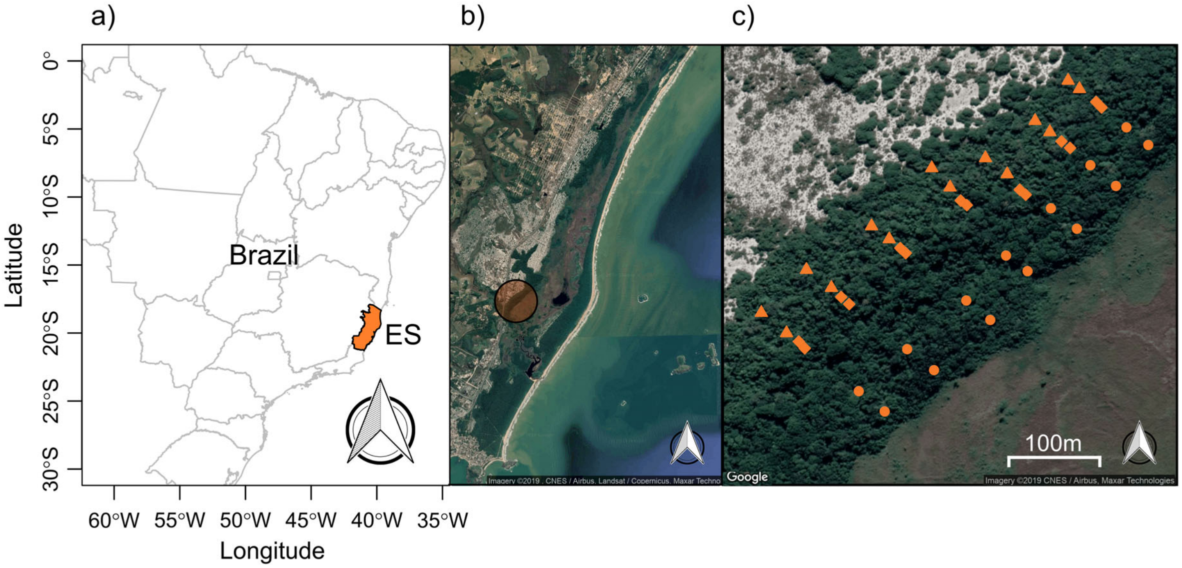

Fig. 1. (a) Map of Brazil, highlighting the location of the state of Espírito Santo (orange); (b) Paulo Cesar Vinha State Park and study area location (orange dot); and (c) a detailed map of the study area, showing the 42 plots (or local communities) distributed across floodable (circles), intermediate (squares), and dry (triangles) sites. The maps were drawn using the "maptools" (Bivand and Lewin-Koh 2017) and "raster" packages (Hijmans 2017) in the R Statistical Environment (R Core Team 2018).

Measuring and estimating plant traits

We estimated the total aboveground biomass of each tree (dbh ≥ 5 cm) to calculate the total aboveground biomass per community (TAGB, the sum of the biomass of all individual trees in one community) and to calculate the community-weighted mean (CWM) and variance (CWV) of aboveground biomass (AGB) (see Supporting Information for details). For the AGB estimation of each tree, we utilized Chave's pantropical models via computeAGB function provided by the "BIOMASS" R package (Chave et al. 2014), which requires tree height, diameter at the breast height (dbh), and wood density (WD) data.

We collected wood samples from branches of five individuals per species and per site (floodable, intermediate and dry) to accurately determine the wood density of each species in each specific environment. The sampling of the branch segment for the analysis was standardized for its position along the tree (first basal branch), its position along the branch (~2 m from the branch tip), its diameter (1.10 ± 0.37 cm, without the bark), and its maturity. We sampled the largest number of tree species possible (~85% of the species in the cumulative relative abundance), following the handbook for standardized measurements in plant functional traits (Pérez-Harguindeguy et al. 2013). The number of species sampled to achieve 85% of the plant communities was determined according to the previous forest inventory (Lourenço et al. 2020). The samples were then hydrated for 12 h, and the wood volume was calculated according to the water displacement method (Chave 2005), with the support of a high precision balance. We then dried the samples in an oven at 60°C and weighed them. WD (in g/cm^3) was determined by dividing the wood dry mass by its volume. The WD of the 15% less abundant and unsampled plant species was estimated from the "getWoodDensity" function from R "BIOMASS" package (Chave et al. 2014), using "SouthAmericaTrop" as the "region" argument.

We measured leaf area, wet weight, and dry weight of the leaf to calculate the specific leaf area (SLA) of each species. We collected three leaves per individual and five individuals per species. The SLA mean values of each species were used to calculate the community-level weighted means (CWMs) of SLA for each of the 42 plots in this study, using the function provided in the Supporting Information. The weighted procedure is a well-established approach in trait-based ecology (Grime 1998, Lavorel et al. 2011, Ricotta and Moretti 2011, Sides et al. 2014, Enquist et al. 2015) to estimate the contribution of each species to the total functional trait composition of a given ecological community, especially when the trait values of every single individual in the community are not available. Thus, the CWM calculations were made by the species mean trait values weighted by the species abundance already available in the previous forest inventory (Lourenço et al. 2020). The basal area of each tree was calculated based on the dbh values, previously measured in the forest inventory (Lourenço et al. 2020). For simplicity, each plot was defined as a local plant community.

Soil sampling and analysis

Nutritional and physicochemical soil composition was measured in each plot via soil sampling. Five soil samples were collected per plot at a depth of 15 cm and were then homogenized in the field to produce one compound soil sample per plot. Several parameters were determined by the soil analysis, including coarseness (proportion of fine and coarse sand, silt, and clay); nutrients (P, K, Na, Ca, Mg, Al, H+Al [potential acidity], Zn, Mn, Cu, and B); organic matter (OM); pH; and sodium saturation index (SSI), aluminum saturation index (ASI), base saturation (BS), base saturation index (BSI), effective cation exchange capacity (CEC), and cation exchange capacity in a pH of 7 (CEC7), following the Brazilian Agricultural Research Corporation protocol (Donagema et al. 1997) (Table 1).

Table 1. Environmental variables measured and included in the forward selection analysis.

Variable measured	Abbreviation	Measurement units
Nutrient		
Phosphorus	P	(mg/kg)
Potassium	K	(mg/kg)
Sodium	Na	(mg/kg)
Calcium	Ca	Calcium ion [Ca^{2+}], (cmolc/kg)
Magnesium	Mg	Magnesium ion [Mg^{2+}], (cmolc/kg)
Aluminum	Al	Aluminum ion [Al^{3+}], (cmolc/kg)
Zinc	Zn	(mg/kg)
Manganese	Mn	(mg/kg)
Copper	Cu	(mg/kg)
Boron	B	(mg/kg)
Texture		
Coarse sand	Coarse	(%)
Fine sand	Fine	(%)
Silt	Silt	(%)
Clay	Clay	(%)
Physicochemical		
Cation exchange capacity	CEC	(cmolc/kg)
Cation exchange capacity (pH 7)	CEC7	CEC in a pH of 7 (cmolc/kg)
Base saturation index	BSI	(%)
Base saturation	BS	(cmolc/kg)
Sodium saturation index	SSI	(%)
Aluminum saturation index	ASI	(%)
Potential hydrogen	pH	pH in water, KCl, and $CaCl_2$ (1:2.5)
Potential acidity	H + Al	Sum of H and Al ions (cmolc/kg)
Others		
Water table depth	WT	Distance from the soil surface (meters)
Soil water retention	SWR	Soil water retention capacity (%)
Soil organic matter	SOM	(%)

We also measured the soil water retention capacity or soil water retention (SWR) for each plot. This was achieved by collecting two soil samples (15 cm depth) per plot using flexible pipes to remove the soil layer in such a way as to preserve the integrity of their original structure. We added water to both samples until the wetted soil samples exceeded their maximum water retention capacity. When the water stopped draining from samples, they were weighed in a balance, dried in an oven at 60°C, and daily weighed until they reached a constant weight. The SWR was determined by the following equation: SWR = mass of ([wet soil − dry soil]/wet soil), following procedures detailed in Donagema et al. (1997).

Water table (WT) depth was directly measured in the floodable areas by digging shallow holes in the soil, when necessary. The WT depths of the intermediate and dry plots were estimated by measuring the slope variation from the nearby floodable area. Thus, the WT depth of the upper regions was calculated by the height variance along the soil slope. The chemical and texture soil analyses were performed at the INCAPER (Instituto Capixaba de Pesquisa, Assistência Técnica e Extensão Rural) Research Institute.

Variable selection

Overall, we measured 25 soil and moisture variables as environmental predictors of plant functional traits, total aboveground biomass per community (TAGB was calculated by the sum of every single tree into the community), and forest functional and taxonomic diversity. Of the plant traits measured, we chose to investigate tree height, basal area, aboveground biomass (AGB), specific leaf area (SLA), and wood density (WD). We calculated the community-weighted mean and variance of these individual-level measured plant traits, according to the equation and R code provided in the Supporting Information.

The sum of all tree biomass per community or total aboveground biomass (TAGB) was the final response variable used in model 1 (Fig. 2a) to test the direct and indirect effects of the soil parameters and plant traits on forest biomass, whereas the community-weighted AGB was used to assess the shifting of AGB mean and its variance across plant communities and the continuum water table depth gradient.

The functional diversity indices were calculated by the "dbFD" function from the "FD" R package, version 1.0-12 (Laliberté and Legendre 2010), and are shortly described in Table 2. The null model was made for each community-weighted trait (AGB, basal area, SLA, WD, and tree height) and also considering them jointly to the calculation of the standardized effect size (SES) based on the functional richness (FRic). For single traits, FRic is calculated by the range of trait variation, whereas the convex hull volume (Cornwell et al. 2006) is used for multiple traits (Laliberté and Legendre 2010). To determine main community assembly patterns, the trait similarity of coexisting species is compared with theoretical random communities created by appropriated null models, which were calculated keeping the species richness of each community constant during the randomization, following procedures of Mudrák et al. (2016). If FRic of the observed trait values is lower or higher than expected by chance, we assume trait convergence or divergence, respectively, which are interpreted in terms of abiotic or biotic mechanisms (Mason et al. 2013). Based on Mudrák et al. (2016), we established that trait dissimilarity is significantly lower or upper than expected by chance for SES values equal to -1.96 and 1.96, respectively.

The selection of the environmental variables here used as forest structure was based on the literature and statistical procedures of variable selection (Table 3) via generalized additive models (GAM) and generalized linear models (GLMs), following the framework of Paquette and Messier (2011) and analysis scripts in Neves et al. (2017) (see the Supporting Information for details). This technique uses (1) a forward selection method of the environmental variable for redundancy analysis (RDA); and (2) additional and progressive elimination of collinear variables based on their variance inflation factor (VIF) and ecological relevance, maintaining only those with VIF < 4 (Quinn et al. 2002). VIF was calculated using the R^2 value of the regression of one variable against all other explanatory variables. The GAM and GLM analyses were conducted in the R statistical environment (R Core Team 2018), using the package "vegan" (Oksanen et al. 2018).

Structural equation modeling

Multiple analytical methods were used in conjunction with one another to allow us to assess the effects of the most important environmental drivers on forest trait composition (Fig. 2a) and diversity (Fig. 2b). Statistically significant environmental variables were forward-selected in GAM analysis for each response variable (AGB, SLA, BA and height). Following the framework of Paquette and Messier (2011), variable selection through forward selection analysis (Blanchet et al. 2008) and the background from the scientific literature (see Supporting Information), we constructed piecewise structural equation models (SEMs) (Lefcheck 2016) and carried out independent-effects analysis (Grace et al. 2012). SEMs allow hypothesis testing about the network of causal relationships between observables in a system and their relative strengths, without knowing ahead of time which variables will have positive, negative, direct, or indirect effects on those observables.

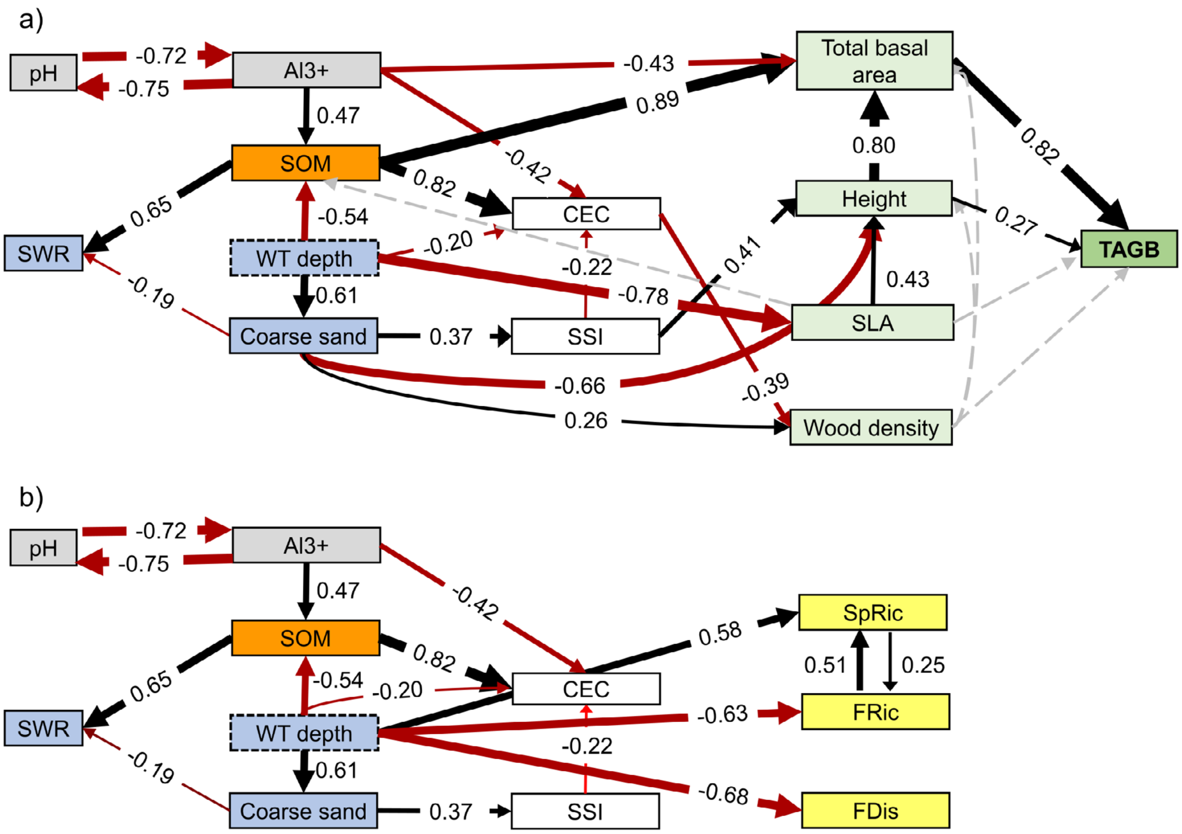

Fig. 2. Simplified models, obtained by piecewise structural equation modeling, using the environmental variables of ecological relevance to explaining forest trait composition, according to the scientific literature and the forward selection analysis applied to all measured environmental variables. Shown are models for the environmental drivers of: (a) forest trait composition—total aboveground biomass (TAGB), tree height, total basal area, wood density, and specific leaf area (SLA); and (b) diversity indices—species richness (SpRic), functional richness (FRich), and functional dispersion (FDis)—from 42 restinga plant communities. Positive numbers (black arrows) represent positive effects of one variable on another, and negative numbers (red arrows) represent negative effects. The statistically insignificant effects on predictor–response relationships (gray arrows) are shown, as well (*P*-value <0.05). Larger magnitudes indicate larger effect sizes. TAGB was indirectly affected by the environmental variables via their effects on plant height, SLA, and total basal area. The flooding reduced the species richness but had a positive effect on functional richness, likely by increasing the variability in plant height and basal area. The soil variables here used are aluminum (Al3+), soil organic matter (SOM), water table depth (WT), soil water retention capacity (SWR), the proportion of coarse sand in the soil, index of soil acidity (pH), soil fertility given by cation exchange capacity (CEC), and soil salinity by sodium saturation index (SSI) that is the proportion of sodium considering other cations in the soil.

Piecewise SEMs were used to reveal relationships between predictor variables (soil properties) and response variables (plant traits and forest diversity) (Michaletz et al. 2018). The piecewise SEM analysis is performed with AIC model selection (Shipley 2013) and is better than traditional SEM analysis for small data sets (Michaletz et al. 2018). We used "piecewiseSEM" (Lefcheck 2016) and "hier.part" (Walsh and Nally 2013) packages for R software environment (R Core Team 2018) to carry out the construction and analysis of the piecewise structural equation model. Detailed information about the model construction, including the selection

Table 2. Summary description of the response variables defined as total community values, community-weighed mean, and diversity indices.

Total community values	Unit	Description/ecological importance	Reference
Total aboveground biomass (TAGB)	kg m^{-2}	Sum of all tree aboveground biomass per unit of area. Biomass accumulation resulted from community productivity.	
Total basal area	cm^{-2}	Sum of all tree basal area in a community. Total area occupied by tree trunks. Proxy for competition intensity.	Paquette and Messier (2011)
Community-weighted mean (CWM)			
Aboveground biomass	kg	Mean value of species biomass in a community. Mean biomass accumulation considering the dominant species in a community, resulting from species mean productivity.	
Plant height	m	Mean value of species height in a community. Multiple functions, including competitive vigor and resource use strategies (e.g., light)	Pérez-Harguindeguy et al. (2013)
Basal area	cm^{-2}	Mean value of species basal area in a community. Proxy for competition intensity.	Paquette and Messier (2011)
Specific leaf area (SLA)	cm^{-2} g^{-1}	Mean value of the amount of leaf area per unit of dry mass allocated to the leaf. Proxy for resource use strategies via photosynthesis.	Wright et al. (2004), Pérez-Harguindeguy (2013)
Wood density (WD)	g cm^{-3}	Mean value of the amount of dry mass allocated per volume of wood. Associate with tree structural support, water use and growth strategies, and biomass allocation.	Chave et al. (2009), Pérez-Harguindeguy (2013)
Diversity metrics			
Species richness	Unitless	Number of species in a community.	
Functional richness	Unitless	Amount of functional trait space filled by species in a community.	Villéger et al. (2008)
Functional dispersion	Unitless	Mean distance of individual species to the centroid of all species in a community.	Laliberté and Legendre (2010)

criteria for the choice of the exogenous and endogenous variables, their ecological relevance, and the concept underlying the SEM equation designs can be found in the Supporting Information in the online version of this article.

RESULTS

Interactions between soil variables and effects on water and nutrient availability

Water table (WT) depth, given the variation in the soil microtopography, has a fundamental role in the soils of restinga forest, causing direct and indirect effects on most of its physicochemical properties. The increasing of WT toward drier sites has a positive influence on coarse sand (0.61) and negatively affects soil organic matter (SOM, −0.54) (Fig. 2a), ultimately producing negative indirect effects on soil water retention (SWR, −0.46) and cation exchange capacity (CEC, −0.44) (Table 4). Moreover, WT depth exerts a stronger influence on SOM in comparison with aluminum (Fig. 3).

The soil pH and soluble aluminum (Al^{3+}) mutually interact in a synergy that increases both soil acidity and aluminum concentration (Fig. 2a). The direct effect of Al on CEC is negative (−0.42); however, its positive indirect effect on CEC via SOM (0.38) virtually neutralizes such negative effect (Table 3). Moreover, SOM exerts larger independent effects on CEC compared with Al (Fig. 3), and it has important implications for soil humidity, with positive and predominant effects on SWR in comparison with coarse sand (Figs. 3 and 4).

Effects of soil parameters on forest trait composition and aboveground biomass

Overall, GAM analysis (Table 3) selected soil parameters related to water availability (WT depth, coarse sand, and SWR) as the main predictors of forest trait composition and total aboveground biomass (TAGB), whereas Al, Na, soil fertility (CEC), and soil acidity seem to have a lower or secondary effect on the response variables. However, SEM analysis shown in the

Table 3. Selection of environmental variables related to total aboveground biomass (TAGB), total basal area, and community-weighed mean tree height, specific leaf area (SLA), and wood density (WD).

Variable	Adj. R^2 cum.	ΔAIC	F	Pr(>F)
AGB				
Coarse sand	0.182	216.99	10.13	0.002**
Sodium saturation index (SSI)	0.238	214.92	3.96	0.044*
<All variables>	0.509			
Height				
Coarse sand	0.268	34.476	16.008	0.002**
Sodium saturation index (SSI)	0.410	26.332	10.665	0.004**
<All variables>	0.596			
SLA				
Water table depth (WT)	0.640	321.84	73.999	0.002**
<All variables>	0.681			
Total basal area				
Coarse sand	0.249	679.83	14.644	0.004**
H + Al	0.364	673.80	8.225	0.006**
Al3+	0.431	670.03	5.589	0.04*
<All variables>	0.672			
Wood density				
Soil water retention (SWR)	0.616	−245.09	66.875	0.002**
Fine sand	0.725	−258.23	16.922	0.006**
Cation exchange capacity (CEC)	0.755	−262.15	5.752	0.022*
<All variables>	0.797			

Notes: Goodness of fit of predictor variables was assessed through adjusted coefficients of determination, the Akaike information criterion (AIC), F-test values, and significance tests ($P < 0.01$ in all cases). Adj. R^2 cum. = cumulative adjusted coefficient of correlation represents total variance explained by each model. Asterisks * and ** indicate the significance of the P-value (F statistic) at < 0.05 and < 0.01, respectively.

models' diagram (Fig. 2a) and the decomposition of the standardized effect size (Table 4) reveals that these parameters predominantly exert important indirect effects on forest traits. In this sense, TAGB is mainly indirectly affected by Al (−0.41) and SOM (0.73) via their effect on plant height and basal area, respectively.

Increasing WT depth has a negative and direct influence on specific leaf area (SLA; −0.78) and indirect effects on tree height (−0.33) and basal area (−0.48), and it is correlated with the changes in wood density (WD) and aboveground biomass (AGB) (Figs. 2a and 3). Similarly, coarse sand affects plant height (−0.66) (Fig. 2a) and represents major independent effects on WD (Fig. 4), likely as a result of the soil dryness. Soil dryness and low soil fertility (low CEC) seem to favor higher WD (Fig. 2a), whereas salinity via sodium saturation index (SSI) is positively associated with tree height (0.41) and basal area (0.31) (Fig. 2a and Table 4).

Water table depth effects on restinga forest diversity

The species and functional diversity of the restinga forest are driven by WT depth (Fig. 2b and Fig. 3). Toward drier environments, there is an increase in species richness (SpRic), whereas functional richness (FRic) and functional dispersion (FDis) decrease (Fig. 2b). The drier conditions reduced the forest trait variability, as shown in the community-weighted variance of tree height and basal area (Fig. 4), which is an indirect measurement of the interspecific variation of these traits in each forest plot. The null models show negative trends of standardized effect size (SES) values toward drier communities, exhibiting more negative values for basal area and tree height (Fig. 5), whose functional diversity is more affected by drought.

These results show that SpRic and FRic follow opposite trends across the WT depth gradient, reflecting in a low influence of SpRic on FRic (0.25) in drier plant communities, whereas in the inverse direction, FRic exerts a higher direct effect on SpRic (0.51) of wetter plant communities where plant species are more functionally distinct, despite in lower number (Fig. 2b and Fig. 5).

DISCUSSION

Microtopographic variability in water table depth drives changes in soil nutrient and water availability by its effect on soil texture and organic matter

We found a few general trends defining strong edaphic gradients in restinga soils, and variability in WT depth due to microtopography seems to play a key role in soil properties. Toward the dry environments (greater WT depth), soils become sandier and more well drained (Appendix S1. Fig. S1), and poorer in soil organic matter (SOM) and nutrients (Appendix S1. Fig. S2). Nutritional impoverishment toward the drier communities has been related to increased leaching of nutrients in well-drained soils of restinga plant communities in upper, non-floodable sites (Lourenço Junior and Cuzzuol 2009, Magnago et al. 2010), as textural characteristics are highly associated with the retention of nutrients in restinga soils (Cooper et al. 2017). Overall, we measured base saturation (BS) lower than 10 (Appendix S1. Fig. S2), indicating low nutritional soil reserves, which may be even more impoverished in restinga soils than in similar tropical soils because of high rainfall and the sandy soil texture (Rodrigues et al. 2013).

In contrast, we found larger amounts of SOM in lower sites likely due to the reduction of its biological decomposition in anoxic floodable soils (Meirelles et al. 2012), and SOM has a prevailing effect on soil fertility via cation exchange capacity (CEC). These findings are in agreement with the literature, as SOM exerts an important control on nutrient availability in tropical forests (Tiessen et al. 1994), where CEC is highly dependent on SOM, particularly in restinga soils (Coelho et al. 2010). Moreover, the major influence of SOM on SWR highlights that the organic matter in the soil is not just important for soil fertility in tropical forests, but also important for keeping the soil humidity (Hudson 1994, Huntington 2006), which may have important implications in forests functioning during periods of reduced rainfall, for instance.

We found that all soils were strongly acidic (pH < 5) and with a high concentration of alu-

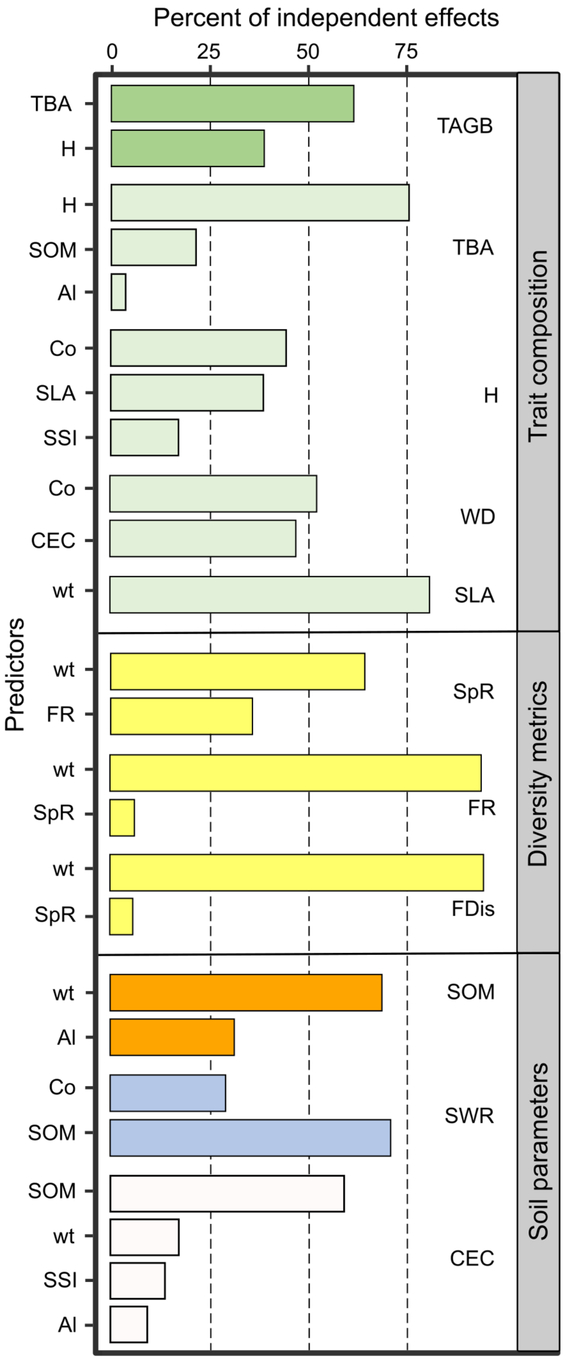

Fig. 3. The separate independent effect of soil drivers on forest trait composition (aboveground biomass [AGB], basal area [BA], plant height, and wood density [WD]); diversity (species richness [SpR], functional richness [FR], and functional dispersion [FDis]); and soil parameters (soil organic matter [SOM], soil water retention [SWR], and cation exchange capacity [CEC])

(Fig. 3. *Continued*)

in 42 restinga plant communities. The separate independent effect is calculated by piecewise structural equation model selection via d-separation and Akaike's information criterion (Shipley 2013, Lefcheck 2016). Total basal area (TBA), tree height (H), soil organic matter (SOM), aluminum (Al), coarse sand (Co), specific leaf area (SLA), sodium saturation index (SSI), cation exchange capacity (CEC), water table depth (WT), functional richness (FR), and species richness (SpR) are the predictors, whose independent effects on forest biotic and abiotic parameters are investigated.

minum (Al) (>6 cmol/kg) (Appendix S1. Fig. S2). The mutual effect between Al and soil pH suggests synergic effects keeping high acidity and Al concentration in restinga soils, whose origin relies on its mineralogical background (Gomes et al. 2007). Al exerts a central role in the restinga soil formation in a process called podzolization, consisting of the translocation of Al and organic materials from the surface to the soil subsurface, to form the spodic horizon (Gomes et al. 2007, Coelho et al. 2010). The deposition and release of Al promoted by the high soil acidity should maintain a high concentration of Al in the soil, producing profound effects on nutrient availability of restinga soils (Marques et al. 2015).

Soil aluminum concentration appears to have a more complex relationship with restinga soil fertility. Despite its lower independent effects on soil parameters, Al has a positive effect on SOM (Fig. 2). Despite a few studies reporting similar findings, this result suggests that the elevated concentration of Al in the soil stimulates the accumulation of SOM by the reduction of its biological decomposition (Mulder et al. 2001). It is worth noting that we did not find significant relationships in the opposite direction (SOM to Al), which could support the hypothesis of SOM controls on aluminum solubility (Berggren and Mulder 1995).

Acidity is also a key factor to understand balances in soil fertility, as it is known that below a pH of 5, the availability of essential nutrients in the soil, including N, P, K, Ca, and Mg, can be severely depleted (Lambers et al. 2008). In contrast, a higher concentration of hydrogen cations in the soil may increase the nutrient inputs by increasing the weathering rates of soil organic matter (Lambers et al. 2008). Thus, floodable plant communities may take advantage of the higher acidity of organic soils and specifically the

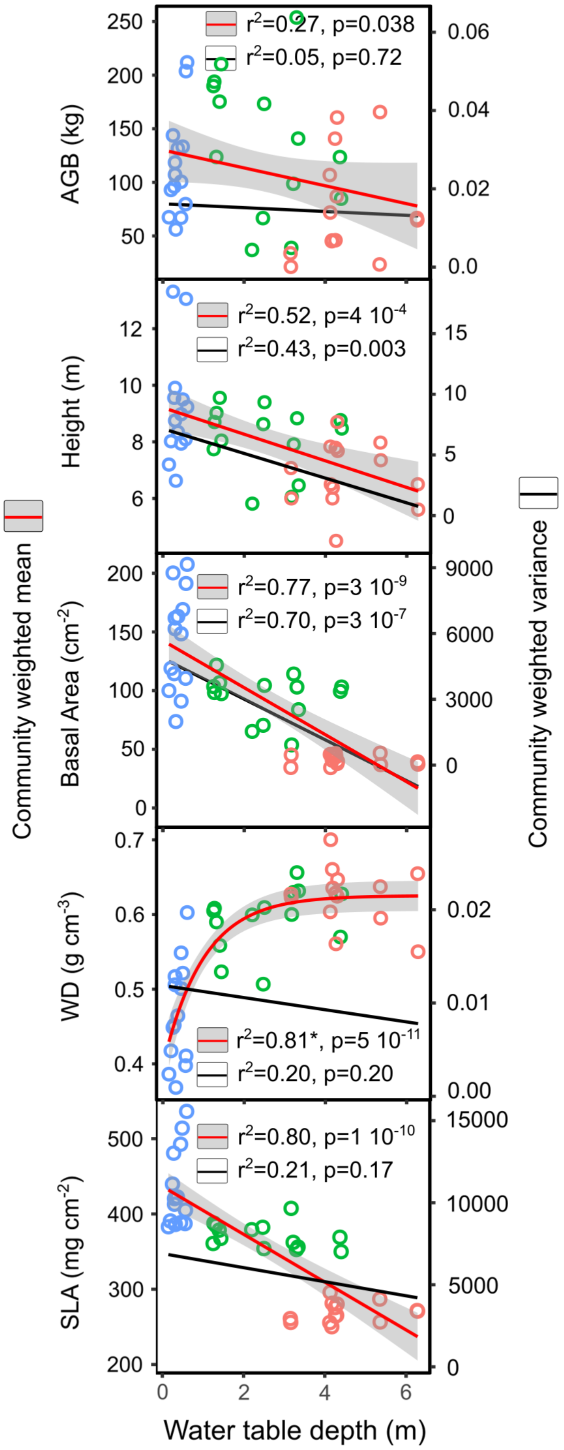

Fig. 4. Effect of water table depth on community-weighed mean and variance of aboveground biomass (AGB), plant height, basal area (BA), wood density (WD), and specific leaf area (SLA) in 42 restinga local

(Fig. 4. *Continued*)

plant communities. The WT-SLA r^2 calculation was based on log-transformed data, creating a linear relationship for the calculation. Plots from floodable (blue circles), intermediate (green circles), and dry (red circles) sites.

Table 4. Piecewise structural equation models exploring drivers of forest biomass, functional traits composition, and diversity.

	Response variable									
	(a) Plant traits and soil properties							(b) Diversity indices		
Parameter	TAGB	TBA	H	SLA	WD	SOM	CEC	SpRic	FRic	FDis
TBA	**0.82**, 0.82, NA	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
H	**0.92**, 0.27, 0.65	**0.80**, 0.80, NA	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
SLA	**0.10**, 0.004, 0.09	**0.14,** −0.15, 0.29	**0.43**, 0.43, NA	. . .	. . .	**−0.31**, −0.31, NA	. . .	. . .	. . .	. . .
WTD	**−0.15**, −0.08, −0.07	**−0.49**, −0.01, −0.48	**−0.19**, 0.14, −0.33	**−0.62**, −0.78, 0.16	**0.37**, 0.21, 0.16	**−0.63**, −0.54, −0.09	**−0.64**, −0.20, −0.44	**0.26**, 0.58, −0.32	**−0.49**, −0.63, 0.14	**−0.66**, −0.68, 0.02
Coarse sand	**−0.07**, 0.10, −0.17	**−0.68**, −0.16, −0.52	**−0.51**, −0.65, 0.14	**−0.03**, −0.04, 0.01	**0.27**, 0.26, 0.01	**−0.25**, −0.26, 0.01	**0.04**, −0.04, 0.08	**0.20**, 0.21, −0.01	**−0.23**, −0.24, 0.01	**0.04**, 0.04, NA
Al	**−0.48**, −0.07, −0.41	**−0.01**, −0.43, 0.42	**0.38**, 0.28, 0.10	**0.13**, 0.29, −0.16	**0.12**, NA, 0.12	**0.52**, 0.47, 0.05	**−0.04**, −0.42, 0.38	**−0.29**, −0.24, −0.05	**0.25**, 0.24, 0.01	**−0.08**, −0.08, NA
SOM	**0.70**, −0.03, 0.73	**0.56**, 0.89, −0.33	**0.23**, 0.11, 0.12	**−0.33**, −0.34, 0.01	**−0.17**, 0.15, −0.32	. . .	**0.85**, 0.82, 0.03	. . .	. . .	. . .
NaSat	**0.05**, −0.05, 0.10	**0.22**, −0.09, 0.31	**0.41**, 0.41, NA	**−0.01**, −0.02, 0.01	. . .	. . .	**−0.22**, −0.22, NA	**0.07**, 0.04, 0.03	**0.17**, 0.14, 0.03	**0.07**, 0.07, NA
SpRic	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	**0.25**, 0.25, NA	. . .
FRic	. . .	. . .	. . .	. . .	. . .	. . .	. . .	**0.51,** 0.51, NA	. . .	. . .
FDis	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	**−0.01**, −0.01, NA	. . .

Values are expressed as standardized effect sizes: total effect (in boldface) followed by direct effect and indirect effect values. These parameters were directly assessed via forest total aboveground biomass (TAGB), total basal area (TBA); the community-weighted means of tree height (H), specific leaf area (SLA), and wood density (WD); and the diversity indices of species richness [SpRic], functional richness [FRich], and functional dispersion [FDis] for 42 woody plant communities of restinga habitats of Atlantic Forest. AIC_c is Akaike's information criterion estimated from Shipley's *d*-separation test (Shipley 2013). *C*, df, *P*, and AIC_c values for variables in (a): 3, 12, 1, and −140. *C*, df, *P*, and AIC_c values for variables in (b): 11, 20, 0.95, and −140. An ellipsis ("...") or "NA," indicates no effect between predictor and response variable.

release of nitrogen compounds from the SOM, explaining the strong positive effect of SOM on the total basal area.

Sodium positively influences tree height, and aluminum has a complex relationship with tree basal area

The positive effect of sodium on tree height opens an interesting discussion about the role of sodium in coastal ecosystems, which has been predominantly placed under the perspective of environmental stress and limiting factors to the forest structure and diversity (Pereira 1990, Scarano 2002, Pimentel et al. 2007). It has been hypothesized that the increasing soil salt (NaCl) concentration toward the coast and the influence of the saline spray by the proximity to the ocean (Griffiths 2006) may act as a filter on the functional and taxonomic composition of coastal plant communities, selecting species with salt-tolerant traits, such as high leaf mass per area, thicker leaves, and the capacity of salt exclusion

(Poorter et al. 2009). However, the presence of salt may also accelerate the biological decomposition of the litter in tropical forests by increasing the abundance and activity of decomposers (Kaspari et al. 2009), suggesting an indirect and positive effect of sodium on the increase in soil nutrients (e.g., nitrogen compounds), which may benefit the growth of plant species adapted to sodic soils.

Additionally, sodium may have a direct positive effect on plant growth (Subbarao et al. 2003). In a discussion about essential nutrients, Subbarao et al. (2003) present several arguments to include Na within the definition of functional nutrient, which is “an element that is essential for maximal biomass production or can reduce the critical level of an essential element by partially replacing it in an essential metabolic process.” In conditions of soil nutrient shortage, Na can replace K in sodic soils, given their chemical similarity. Both elements compete for the same absorption sites in the plant root system, and Na can assume some K-related metabolic functions, such as osmoticium for cell enlargement and accompanying cation for long-distance transport (Subbarao et al. 2003).

The soil saturation index (SSI) or the Na proportion concerning the other cations in the soil is below 5% in our study site (Appendix S1. Fig. S2), which is lower than that found in sites nearer to the shoreline (10% to 21.7%) (Lourenço

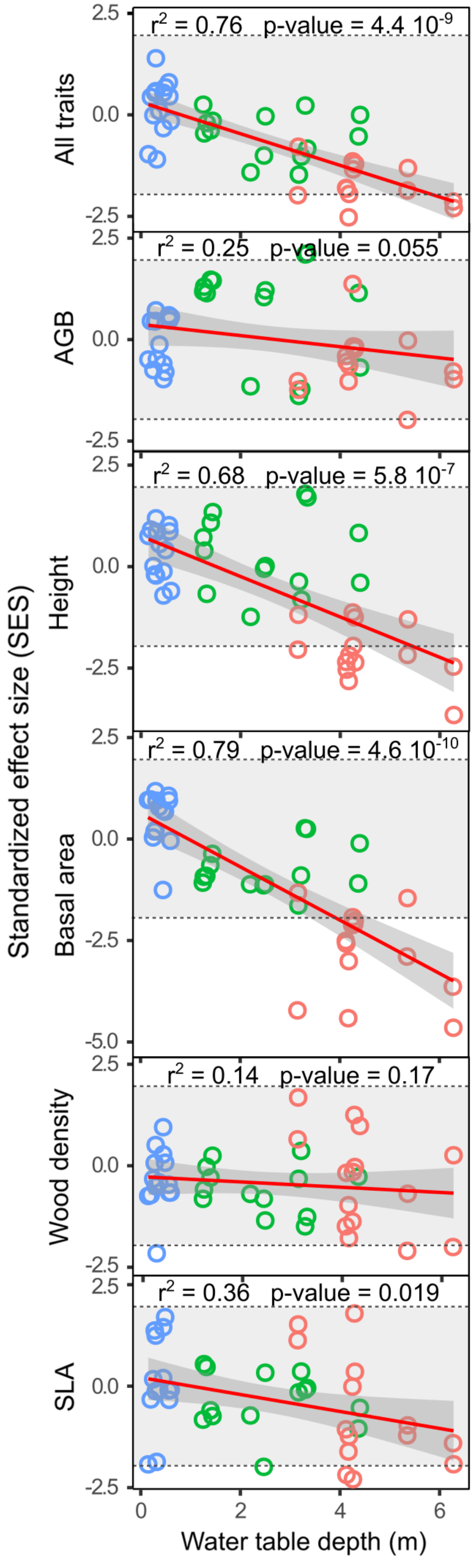

Fig. 5. Correlation between standardized effect size

(Fig. 5. *Continued*)

(SES) and water table depth gradient in 42 plots across floodable (blue circles), intermediate (green circles), and drier (red circles) plant communities of restinga. SES values higher than 1.96 (above the gray area) or lower than −1.96 (bellow the gray area) mean that the functional richness (FRic) is significantly different than expected by chance, representing trait divergence or convergence, respectively (Mudrák et al. 2016). The SES is based on the FRic of all traits and for traits separately, that is, community-weighted aboveground biomass (AGB), tree height, basal area, wood density, and specific leaf area (SLA). The FRic (for all traits) was calculated as the convex hull volume, but for single traits or dimensions, FRic was measured as the range of trait values.

Junior and Cuzzuol 2009) and other coastal forest systems (Tran et al. 2015). Thus, considering that SSI > 15% is the reference value for sodic soils (Shainberg and Levy 2005, Prezotti 2013), the soil sodicity in our study area is low. However, as salinity depends on the interaction of several soil parameters (e.g., electrolyte concentration, soil texture, and aluminum concentration), even SSI values lower than 5% could cause sodic behavior in soils (Halliwell et al. 2001) and negative effects on plant growth (Shainberg and Levy 2005).

In this context, the positive effect of SSI on tree height challenges the idea of sodium as a limiting factor of coastal plant communities and suggests that Na may be exerting an important role in restinga plant nutrition, possibly supplementing the nutritional lack of K soil content (Appendix S1. Fig. S2). Moreover, as salinity was recently reported to distinguish restinga forests from other environmentally marginal habitats of the Atlantic Forest (Neves 2017), we argue that Na should be important to the system functioning, as has been observed in other tropical forests (Kaspari et al. 2009).

Aluminum concentration, in turn, is typically high in restinga soils and is considered a limiting factor for plant growth (Bojórquez-Quintal et al. 2017). We found a higher concentration of aluminum in our study site (>6 cmol/kg, Appendix S1. Fig. S2) than that reported in earlier studies of restinga plant communities (Magnago et al. 2013, Rodrigues et al. 2013, Melo Júnior and Torres Boeger 2015). Al solubility and availability are known to be related to the increase in soil acidity (Lambers et al. 2008); we found that Al availability was higher toward the wet end of the flooding gradient, where soils also showed strong acidity (pH = 3.6). The combination of high Al and acidity (pH < 5.5) in the soil is known for resulting in toxic conditions for many plant tissues, constraining growth and the uptake of several essential nutrients (Richards 1952, US EPA 2003, Bojórquez-Quintal et al. 2017). Thus, Al may also play a primary role in determining local physiognomic characteristics, including plant height, aboveground biomass, and other aspects of vegetation form (Neri et al. 2013).

Nevertheless, our findings contrast with the hypothesis of Al as a simple limiting factor of forest structure and physiognomy. We show that Al has a complex relationship with the tree basal area, mediated by SOM, which seems to minimize its potential negative effects on tree basal area, whereas it causes a slightly positive effect on tree height. It has been demonstrated that the application of Al can stimulate the uptake of N, P, and K in acidic soils (Osaki et al. 1997), enhancing the growth of some native plant species that have adapted to acidic conditions through exclusion or accumulation of Al (Watanabe and Osaki 2006), which was reported for some species found in restinga forests, including *Tapirira guianensis* (de Britez et al. 2002*a*) and *Faramea marginata* (de Britez et al. 2002*b*). Other benefits of Al in Al-adapted plants include increased defense against pathogens, alleviation of abiotic stress, and increased metabolism and antioxidant activity (Bojórquez-Quintal et al. 2017).

The accumulation of aluminum in leaves and seeds and the positive effect of the soil-available aluminum in plant survival have been reported in some native plants of the Brazilian *Cerrado* ecosystem (Haridasan 2008), which shares several plant species with restinga forests, such as those we found in our study area: *Tapirira guianensis*, *Calophyllum brasiliense*, *Protium heptaphyllum*, *Myrcia rostrata*, *Xylopia sericeae*, *Alchornea triplinervia*, *Pseudobombax grandiflora*, *Emmotum nitens*, *Pera glabrata*, *Amaioua guianensis*, and *Cecropia pachystachya* (Lourenço et al. 2020). The similarity of both systems regarding the high aluminum soil content and the co-occurrence of several plant species reinforces our findings of the importance of aluminum in the functioning of restinga forests.

Aboveground biomass in restinga is driven by a small number of dominant, tall tree species

When placing the selected predictors and the response variables in a multivariate context, we notice that the total aboveground biomass (TAGB) is indirectly influenced by the soil variables via their effects on plant height and basal area. Similar findings have been reported in other coastal wetland plant communities (Yi et al. 2020) and tropical forests (Finegan et al. 2015), including Amazon lowland habitat types with contrasting edaphic environments (Baraloto et al. 2011), where forest biomass seems to be mostly driven by well-coordinated changes in tree height and basal area across gradients of soil water availability (Hernández-Calderón et al. 2014). Although wood density (WD) has been claimed as an important parameter for the accurate estimation of forest biomass (Mitchard et al. 2014), WD has an insignificant effect on TAGB, although plant communities strongly differ in WD values. Similarly, it has been proposed the variation in AGB is related to a gradient of WD in the Amazon forest (Baker et al. 2004); however, no consistent relationship has been found corroborating this hypothesis (Stegen et al. 2009).

The larger leaf area per mass, tree body size, and biomass show that tree species at wetter communities tend to be more resource-acquisitive (Wright 2004, Paquette and Messier 2011, Díaz et al. 2016), while the shortage of water in nutrients imposes more conservative strategies of resource use in drier communities, which tends to be composed of small trees with little and thick leaves (Cornwell and Ackerly 2009, Katabuchi et al. 2012), and denser wood that is associated with the accumulation of carbon compounds (e.g., lignin) (Chave et al. 2009) and anatomical modifications (e.g., higher fiber fraction and small vessels; *manuscript in preparation*) to reinforce the wood structure against the strong negative water potentials in drier environments (Swenson and Zambrano 2017). Importantly, this shifting in forest trait composition has been demonstrated to be linked to changes in species distribution along the environmental gradients in our study site (Lourenço et al. 2020) and other restinga plant communities (Magnago et al. 2013), which corroborate the adaptive trait hypothesis; that is, the strong abiotic gradients are selecting for optimal phenotypes, strongly influencing the forest trait composition that shifts in a gradient function.

In summary, considering that the most resource-acquisitive plant communities in wetter regions are those with a lower number of species, we argue that productivity (e.g., AGB accumulation) in restinga is mostly driven by the presence of dominant species that are essential to the ecosystem functions (Grime 1998, Cardinale et al. 2007). Hence, the restinga forest functioning and maintenance of important ecosystem services (e.g., carbon storage) rely on a few dominant species with more resource-acquisitive traits and larger body size, whose loss may have major consequences to the ecosystem stability (Díaz and Cabido 2001).

Small spatial scale heterogeneity matters for restinga forest ecology and management

The results suggest a filtering effect on the functional richness of drier communities, driven by the reduction in the tree height and basal area variability, decreasing the functional dispersion of these plant traits at a fine spatial scale. The null models corroborate the environmental filtering hypothesis, as we found consistent trends of decline in SES values, with a larger number of communities exhibiting significant and negative SES values (< -1.96) for tree height and basal area; that is, the dissimilarity is significantly lower than expected by chance for these traits (Mason and Bello 2013, Carboni et al. 2014), which are converging (Carboni et al. 2014) toward drier communities, where trees have smaller body sizes. Such trait convergence in unproductive conditions could be caused by higher fitness of stress-tolerant species, more abundant in the species pool of these drier sites (Mudrák et al. 2016). This is reflected in the loss of rare phenotypes (e.g., trees with large body size) in harsher environments, as predicted by the favorability hypothesis.

Thus, if in one direction drought is selecting a larger number of functionally redundant species with drought-tolerant and conservative traits, in the opposite direction flooding is causing a filtering effect on the taxonomic composition of the plant communities, selecting those species that are capable of tolerating seasonal flooding and taking advantage of more fertile sites. These results show functional trait composition and ecological process driving taxonomic and functional diversity in restinga, and highlight important ecological differences at a small spatial scales. This large heterogeneity at small spatial scales will be central to the management and conservation of these threatened coastal habitats of Atlantic Forest.

CONCLUSIONS

The soils of restinga habitats exhibit steep gradients of nutrients and water availability on a small spatial scale that was predominantly driven by the variability in water table depth along with microtopography. This soil-associated driver explained the shift in forest trait composition and physiognomy, where tree height and basal area, but not wood density, of the dominant species were the biological drivers of forest biomass (AGB). Similar findings are reported in Amazon lowland habitats (Baraloto et al. 2011) and other tropical forests (Slik et al. 2010), reflecting important implications to forest biomass estimations (Mitchard et al. 2014). Interestingly, the lack of strong negative effects jointly with slightly positive effects of sodium and aluminum on forest traits suggests complex soil–plant interactions possibly influencing community dynamics (Fukami and Nakajima 2013), which may point to the adaptation of restinga tree species to tolerate and likely use aluminum (de Britez et al., 2002*a*,*b*) and sodium (Subbarao et al. 2003) to favor plant growth.

Our analyses show that several soil parameters, especially those related to water availability, drive important ecological processes in the restinga. Such local-scale edaphic heterogeneity and the associated species replacement across the soil gradients (Lourenço et al. 2020) are documented at a larger spatial scale in the Amazon forest, where soil texture leads to plant specialization and therefore contributes to the diversity of the flora (Fine et al. 2005). The diversity shifts in restinga plant communities captured by our analysis support the favorability hypothesis. The environmental filtering caused by soil dryness in the upper regions limits functional diversity (standardized effect size < -1.96), thereby forcing trees to strongly converge to small body size, ultimately resulting in the loss of rare phenotypes (i.e., tall trees). Contrastingly, the excess of water in the floodable, lower region limits species diversity while body size variability of trees increases, suggesting that plants adapted to flooding can take advantage of more fertile sites to grow taller, favoring forest functional diversity and the occurrence of rare phenotypes.

Soil gradients of water and nutrients are hypothesized to deeply affect tropical forest trait composition, as plant species tend to possess traits adapted to better perform according to the availability of environmental resources, such as larger leaves and body sizes in more productive environments (Westoby 1998). Although such trait variability is expected to occur at wider spatial scales in tropical forests (Messier et al. 2017), our results show an important role of local scale shaping restinga forest functional trait composition. The differences in plant community structure found in restinga along microtopographic gradients reflect deep local-scale differences in these communities with regard to resource acquisition strategies, shifting from conservative (drier forest) to acquisitive (wetter forest) set of traits (Wright et al. 2004, Chave et al. 2009), which have important implications for the forest conservation and management.

Given the high species richness, extremely high level of endemism, and the small fraction of the original forest cover remaining, there has been an increasing need for preservation of Atlantic Forest habitats (Scarano 2009, Joly et al. 2014), which are ranked among the top five hotspots of biodiversity in the world (Myers et al. 2000). Here, we highlight the importance of the local-scale investigations to a deeper understanding of the factors controlling tropical plant communities' function and diversity, ultimately providing valuable information for the management and conservation of similar systems as these threatened habitats of the Atlantic Forest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3629/full

Appendix S1: Additional analyses of soil properties, plant functional traits and detailed descriptions of the variable selection criteria and structural equation models designs.

Metadata S1: A brief description of the R code files used for the analysis.

Data S1: R code used in the variable selection procedure, SEM analysis and for the community weighted mean and variance calculations.