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RESEARCH ARTICLE

FUNCTIONAL TRAITS OF DOMINANT PLANT SPECIES OF THE BRAZILIAN SANDY COASTAL PLAIN

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ABSTRACT

Variation in the functional traits of plants stem from evolutionary and environmental drivers that operate on different scales. Such traits are linked to growth, survival, and reproduction of organisms and tend to vary less in harsh environments. This study evaluated the variation in leaf and wood traits of dominant plant species of different types of restinga vegetation to answer (i) which traits respond most to edaphic conditions and (ii) in which vegetation type are species more functionally redundant. The functional attributes considered were height of individuals, leaf inclination angle, leaf area, leaf dry matter content, specific leaf area, wood density, tangential vessel diameter, vessel frequency, conductivity index, and vulnerability index. The analyses of functional attributes, diversity, and functional redundancy in association with the edaphic parameters of organic matter content, cation exchange capacity, and gravimetric moisture used SYNCSA software. The relationship between edaphic and functional attributes was determined by linear regression. ANOVA revealed variations in the morphological and anatomical attributes of the species. The optimal subset of leaf attributes that maximize species convergence include leaf inclination angle and specific leaf area. Convergence was expressed by all of the attributes of wood measured. Strong correlations appeared between optimal attributes and soil variables. Functional diversity progressively increased towards the forest formation, while functional redundancy was higher in herbaceous formations. There is evidence of a directional environmental filter that acts with a greater selective force on the herbaceous formations, since species growing in resource-limited environments tend to develop more convergent morpho-anatomical adjustments.

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INTRODUCTION

Functional diversity has recently been used to better understand ecological and evolutionary patterns and processes of communities and ecosystems (Pérez-Harguindeguy *et al.*, 2013). It measures the value and range of functional traits among organisms (Tilman, 2001), which represent the diversity of species niches and functions (Villeger *et al.*, 2008). The functional traits of an organism are relevant when they improve environmental limits in dealing with habitat requirements, and be they morphological, physical, biochemical, behavioral or phenological, they influence the contribution of the species to ecosystem functioning (Cadotte *et al.*, 2001).

Species interactions and habitat filtering have a strong influence upon functional diversity, and can act at different spatial and temporal scales (Grime, 2006). The diversity of functional traits present in a given ecosystem determines the fluxes of matter and energy and, in the long term, the properties and stability of the ecosystem (de Bello *et al.*, 2009; Pérez-Harguindeguy *et al.*, 2013). Organisms, such as plants, with similar responses to the environment and similar effects on ecosystem functioning, can be grouped into functional response types and functional effect types. The former generally groups species that respond similarly to biotic and abiotic conditions. The species that form a given functional group may result from the selection of species from a regional species pool that share ecological tolerances (de Bello, 2009). Studies that link functional traits, use of resources, and community dynamics are relatively new in the literature (Chave *et al.*, 2009). Some works have shown that functional traits play an important role in species success in many

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stressful environments (Cornwell and Ackerly, 2010), such as restingas. *Restingas* are vegetation types that have developed on sand cords of the coastal plain formed by quaternary sea-level changes. The first studies on Brazilian *restingas* were developed in the state of Rio de Janeiro (Franco *et al*., 1996; Scarano *et al*., 2001; Rosado and de Mattos, 2010; Rosado *et al*., 2013b). The main functional attributes identified in tree species in response to environmental heterogeneity were morphological (ex. specific leaf mass), physiological (ex. leaf water potential), and phenological (ex. longevity and leaf mortality). In environments where resources are scarce (ex. *restingas*), plants develop conservative strategies for their use, which are mainly traits related to survival (Donovan *et al*., 2011). The existence of structural patterns (Pimentel *et al*., 2007) and specific functional attributes in different floristic communities (Boeger and Gluzezak, 2006; Rosado and de Mattos, 2010; Bonilha *et al*., 2013) clearly show that the spatial and temporal features of *restinga* influence the development of vegetation and the inherent characteristics of species. Variation in the community structure of *restinga,* and the functional attributes of species present in this ecosystem, have been found to be strongly related to soil nutrient and water availability and to high soil salinity (Bonilha *et al*., 2013; Santos-Filho *et al*., 2013). *Restingas* are characterized by a gradient from more open vegetation and harsher conditions close to the sea to denser vegetation and less stressful conditions inland (Scarano *et al*., 2001; Silva and Britez, 2005). Thus, *restingas* represent a model for studying how functional attributes vary among vegetation types by comparing the dominant species This study evaluated the contribution of the functional attributes of the leaves and wood of dominant species in different *restinga* vegetation types in order to answer the following questions: (i) Which functional attributes of leaves respond most to edaphic conditions? put any expectations here (ii) Which functional attributes of wood respond most to water availability along the *restinga* gradient? put any expectations here (iii) In which vegetation type (herbaceous sandbank, shrub restinga, shrub-tree restinga and transition forest) are species more functionally redundant?

MATERIALS AND METHODS

Study area

The study was conducted in *restinga* vegetation within the 6,667 ha Acaraí State Park in the municipality of São Francisco do Sul on the northeastern coast of the state of Santa Catarina, Brazil (26º 17 'S and 48º 33' W, Figure 1). Strongly influenced by maritime moisture, the climate is mesothermal with hot summers and no defined dry season. Average annual rainfall is 2,372 mm, and average annual temperature is 21.3°C (EPAGRI, 2014). This area is covered by herbaceous *restinga* (RH) in quartzipsamments soil, shrub *restinga* (RS) and shrub-tree *restinga* (RST) on ferrihumiluvic spodosol soil and transition forest (FT) on hydromorphic ferrihumiluvic spodosol + haplic organosol soils (EPAGRI, 2002). The edaphic gradient is characterized by low organic matter and low water retention near the sea, which increase inland towards the forest environment (Melo Jr. and Boeger, 2015).

Data collection

Data were collected in three transects perpendicular to the shoreline and 1.5 km equidistant from each other. For 22 dominant species (Table 2), we collected twenty fully expanded and uninjured leaves from 15 individuals for each species along transects. The canopy height of each individual was measured with a telemetric rule. Ten leaves between 3o. to 6o. node from the apex were selected to measure leaf insertion angle (Moreira, 2005). For compound leaves, each leaflet was interpreted as a single leaf (Bongers and Popma, 1990). Leaves were soaked in water for 12 hours to obtain their fresh weight (g) and then dried in an oven for 48 hours at 60 ºC to obtain their dry mass (g). The content of leaf dry mass was calculated by the ratio of fresh to dry leaf mass (CMSF, g; Garnier *et al*., 2001). Leaf area (cm^2) of 10 leaves for each individual was assessed from images created with a flatbed scanner calibrated with Sigma Scan PRO software (version 5.0, SPSS Inc., Chicago, IL, USA). Specific leaf area was defined by the ratio between leaf area and leaf dry mass (cm^{2}g^{-1}).

Wood samples were collected from the main branch of shrubs and individual trees at 1.3 m above the ground (Barros *et al*., 2001), while in small shrubs they were collected from the base of the stem. Wood density (gcm-^{3}) was given as the ratio between dry weight and sample volume, following protocol 11941 of the NBR (ABNT, 2003) and specific gravity. Wood anatomy was assessed by histological slides that were prepared according to standard protocols for studying wood anatomy (Johansen, 1940). Wood sections were stained with Astra blue and safranin (Bukatsch, 1972) and mounted in synthetic resin (Paiva *et al*., 2006). Vessel tangential diameter (VD, µm) and frequency (VF, nºmm^{-2}) (IAWA, 1989) were estimated from pictures of cross sections taken by a camera coupled to an Olympus microscope with Dino Eye software. The conductivity index, defined as the ratio of vessel radius to the fourth power to vessel frequency (Zimmermann, 1983 modified by Fahn *et al*., 1986), and the vulnerability index, defined as the ratio between vessel diameter and vessel frequency (Carlquist, 1977), were calculated to verify the influence of the environmental gradient on the efficiency of water transport and susceptibility to cavitation. Leaf and wood traits were then linked to the edaphic factors that vary most along the *restinga* gradient, such as organic matter content (gdm^{-3}), cation exchange capacity (mmol$_c$dm^{-3}), and gravimetric moisture (%), (Table 1) (Melo Jr. and Boeger, 2015).

Table 1. Environmental variables for each studied vegetation type along the edaphic gradient in the Acaraí State Park. Legend: organic matter (OM, g.dm^{-3}), cation exchange capacity (CEC, mmolc.dm^{-3}) and gravimetric moisture (GM, %)

Variable	Vegetation type			
	Herbaceous restinga	Shrub restinga	Shrub and tree restinga	Transition forest
OM	7.3 ± 0,4	14.0 ± 1,6	14.67 ± 1,9	82.7 ± 2,0
CEC	23.1 ± 3,6	30.10 ± 1,8	30.47 ± 3,8	305.5 ± 15,4
GM	4.9 ± 0,4	8.8 ± 0,6	14.1 ± 1,1	102.4 ± 8,0

Data analysis

After testing the normality of residuals, mean values were compared by ANOVA and Tukey *post hoc* test, $p < 0.05$ (Borcard *et al*., 2011) in R software (Crawley, 2007).

Data were organized into three different matrices for functional analysis: (i) B = matrix of the species described by the selected functional traits; (ii) W = matrix containing the relative frequencies (RF, %) of each species per transect

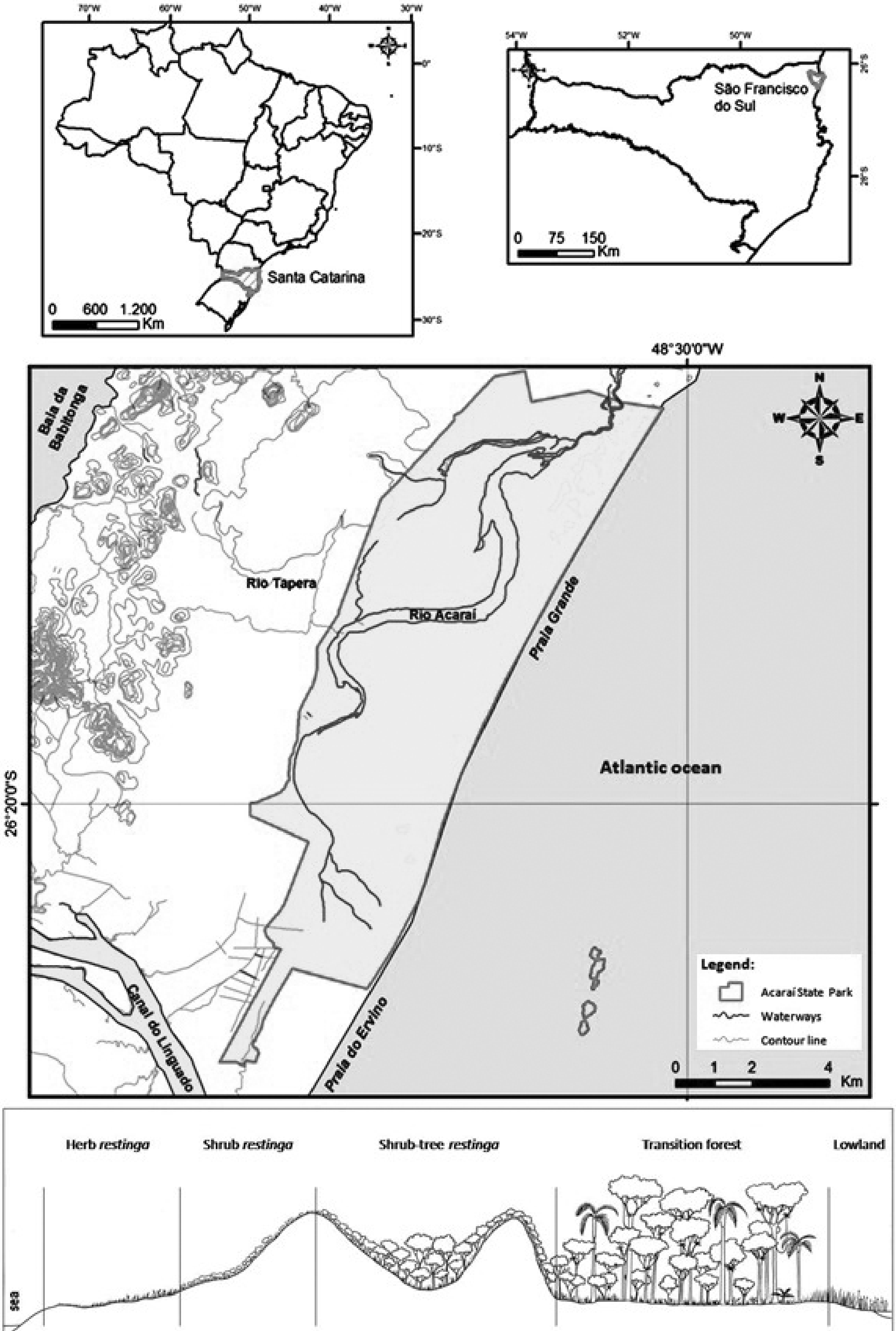

Figure 1. Location of the study area and profile of formations of *restinga* at the Acarai State Park, São Francisco do Sul, Santa Catarina State, Brazil

along the gradient for a total of 12 communities; and (iii) E = matrix of the environmental variables (organic matter, cation exchange capacity and gravimetric moisture) to which communities are subjected (Pillar, 1999). The functional traits that maximize convergence between the studied species (trait convergence assembly patterns - TCAP) (Pillar *et al*., 2009), the Gini-Simpson diversity index (SD), and the functional diversity index (FD) versus environmental gradient, measured by Rao's quadratic entropy (Rao, 1982), were evaluated using SYNCSA software (Pillar and Orlóci, 2004). Rao's FD indicates the expected dissimilarity of a trait between two individuals chosen randomly from a community (Ricotta, 2005). It ranges from 0 (complete overlap) to 1 (no overlap) and is, therefore, the sum of dissimilar traits of all possible pairs of species weighted by their abundance in the community (de Bello *et al*., 2009).

Considering matrix T (T = B'W) provided by TCAP, the functional pattern of communities, which expresses the average traits in communities weighted by the number of individuals, was used to evaluate the relationship between the optimal subsets of traits and soil variables (organic matter, cation exchange capacity) by linear regression (Legendre and Legendre, 1998). Functional redundancy (FR), defined here as the number of species with similar characteristics in a community, was calculated within each *restinga* vegetation type by the equation FR = SD - FD, where: SD = Gini-Simpson index and FD = functional diversity index. If SD is equal to FD, redundancy is zero and all species are functionally different. If FD is zero, all species are functionally identical and redundancy is maximum (Bello *et al*., 2007).

RESULTS

Leaf and wood traits varied widely among species and plant formations (Table 2), with individual height, leaf area, wood density, vessel frequency, and vulnerability index varying the most. The optimal subset of leaf attributes that maximizes the convergence of species along the soil gradient associated with organic matter and cation exchange capacity, comprise specific leaf area and leaf insertion angle. The TCAP level found for these attributes was highly significant for organic matter (ρ (TE) = 0.928, p = 0.001) and CEC (ρ(TE) = 0.892, p = 0.001). Strong relationships were found between foliar attributes and edaphic traits, indicating varying strategies of species along the soil gradient. Organic matter was inversely related to leaf insertion angle ($r^2 = 0.83$, p = 0.001) and positively related to specific leaf area ($r^2 = 0.73$, p = 0.001). The relationship between cation exchange capacity and these leaf attributes showed a similar tendency ($r^2 = 0.78$, p = 0.001 and $r^2 = 0.76$, p = 0.001) (Figure 2). Besides the differences shown by ANOVA, all wood traits highlight the convergence of species along the soil gradient, when associated with gravimetric moisture. TCAP level, expressed by wood density, vessel density, vessel frequency, conductivity index, and vulnerability index was highly significant (ρ (TE) = 0.930, p = 0.001). Strong correlations were found among vessel diameter, conductivity index, and vulnerability index, and weaker correlations were obtained for wood density and vessel frequency, indicating adjustments to enhance hydraulic conductivity or an absence of a pattern for the species along the gradient. Gravimetric moisture was positively correlated to vessel diameter ($r^2 = 0.86$, p = 0.001), IC ($r^2 = 0.91$, p = 0.001), and vulnerability index ($r^2 = 0.95$, p = 0.001). Weak and negative correlations were obtained between gravimetric moisture and wood density ($r^2 = - 0.30$, p = 0.05) and VF ($r^2 = - 0.19$, p = 0.05) (Figure 2). Functional diversity (FD Rao), based on leaf and wood traits that maximize the convergence among the 22 studied species showed increasing values along the gradient, indicating a progressive increase of dissimilarity among species towards FT (Table 3). An inverse relation was observed for functional redundancy among the species of each sandbank formation associated with the studied soil variables, with increasing values towards the herbaceous formation (Table 3).

DISCUSSION

The observed variation among functional traits of leaves and wood of *restinga* species indicates selective and contrasting forces along the gradient. These forces impose some restrictions to, and conditions for, the ecological strategies directly linked to the survival of these species. The environmental conditions and scarcity of resources in soils closer to the sea act as environmental filters that can negatively influence the establishment and permanence of individuals in such places (Weiher and Keddy, 1999). Thus, the dominant species of each vegetation type are more able to colonize these sites and use the available resources (Felfili and Rezende, 2003). The higher functional redundancy observed among vegetation types close to sea (FR = 0.61) when compared to those more distant (FR = 0.47) associated with organic matter shows that RH species tend to be more similar in their ecological requirements, although this similarity accentuates intraspecific competition (Pillar *et al*., 2009). At the other extreme, higher dissimilarity among species and lower functional redundancy in RST (Table 3) indicate that an increase of functional diversity expands the coexistence of species and reduces species competition for the same resources (de Bello *et al*., 2009). Our results point out a directional action of the environmental filter. The mean values of specific leaf area, vessel diameter, conductivity index and vulnerability index increase towards the forest transition, which means that the increase in nutrient and water availability causes a greater investment by plants in assimilation tissues and xylem conductivity. The mean values of leaf insertion angle, which is inversely proportional to other traits, is additional evidence this same action by the environmental filter. Lower water availability and high light intensity entail morphological adjustments, such as leaf verticalization and a consequent reduction of leaf transpiration (Wang *et al*., 2007).

In this study, leaf insertion angle and specific leaf area were the attributes that best explained species convergence. The leaves of RH species possess the largest insertion angles. Vertically orientated leaves, as is the case with the vegetation types growing closer to the sea, are common in environments with high light and water stress (Boeger and Gluzezak, 2006). Higher mean values for specific leaf area in transition forest indicate that species invest more in photosynthetic structures, because more resources (nutrients and water) are available to them (Vendramini *et al*., 2002). On the other hand, species with limited nutritional and water resources had lower values of specific leaf area. This xeromorphic characteristic (low specific leaf area) is a response to a high C:N ratio, where the excess of C is invested in mechanical tissue (Sobrado, 2009) as observed in non-succulent plants of sand seed banks (Li *et al*., 2005; Boeger and Gluzezak, 2006). Plants that grow in sandy soils with low fertility and water content usually have xeromorphic leaves, even in tropical rain forests (Cao, 2000).

Table 2. Mean values and respective standard deviations of functional attributes of leaves and wood of studied species from Acaraí State Park. Abbreviations: species importance value (SIV) relative frequency (RF), Height (H,m), leaf inclination angle (LIA,^{0}), leaf area (LA, cm^2), leaf dry matter content (CMSF,g), specific leaf area (SLA, cm^2g^{-1}), wood density (WD, gcm^{-3}), vase diameter (VD, µm), vase frequency (VF, n^0mm^2), conductivity index (CI) vulnerability index (VI). Different letters in columns indicate significant differences among species within a vegetation type (ANOVA, *post hoc* Tukey, $p < 0.05$)

Vegetation type/Species	SIV	RF	H	LIA	LA	CMSF	SLA	WD	VD	VF	CI	VI
Herbaceous restinga												
Blutaparon portulacoides	14.63	7.6	0.13 ± 0.02 b	67.71 ± 2.80 b	1.31 ± 0.31 e	0.05 ± 0.01 e	60.94 ± 24.11 c	-	-	-	-	-
Canavalia rosea	15.30	6.8	0.10 ± 0.01 c	76.33 ± 6.04 a	22.63 ± 1.49 a	0.14 ± 0.01 c	94.39 ± 8.55 a	-	-	-	-	-
Ipomoea imperati	13.59	10.6	0.09 ± 0.01 d	68.83 ± 3.09 b	10.88 ± 0.56 c	0.10 ± 0.02 d	83.85 ± 14.49 b	-	-	-	-	-
Remirea maritima	12.76	9.8	0.08 ± 0.01 e	68.00 ± 3.57 b	0.69 ± 0.05 f	0.26 ± 0.04 b	60.13 ± 10.96 c	-	-	-	-	-
Scaevola plumieri	16.17	6.1	0.33 ± 0.02 a	67.50 ± 3.37 b	12.44 ± 0.87 b	0.09 ± 0.02 d	50.67 ± 15.66 cd	-	-	-	-	-
Smilax campestres	18.44	10.6	0.05 ± 0.004 f	67.67 ± 2.82 b	3.31 ± 0.58 d	0.34 ± 0.05 a	59.62 ± 9.04 c	-	-	-	-	-
Stylosanthes viscosa	14.84	5.3	0.04 ± 0.01 g	68.50 ± 3.51 b	0.23 ± 0.03 g	0.29 ± 0.06 b	75.14 ± 17.74 b	-	-	-	-	-
Shrub restinga												
Clusia criuva	22.01	10.8	1.45 ± 0.13 a	58.67 ± 3.41 b	32.82 ± 1.07 a	0.23 ± 0.02 b	52.00 ± 8.17 c	0.68 ± 0.02 b	70.83 ± 8.27 b	12.42 ± 1.67 c	123047.80	5.66
Guapira opposita	78.33	10.8	0.97 ± 0.14 d	62.00 ± 4.01 a	4.89 ± 0.62 b	0.15 ± 0.03 c	81.97 ± 12.28 a	0.50 ± 0.05 c	27.62 ± 7.97 d	17.65 ± 3.61 b	2060.77	1.56
Myrcia pulchra	35.53	10.0	1.15 ± 0.09 c	60.83 ± 4.31 a	4.77 ± 0.50 b	0.36 ± 0.02 a	56.15 ± 0.56 c	0.89 ± 0.04 a	40.38 ± 5.09 c	70.32 ± 10.22 a	2363.01	0.57
Norantea brasiliensis	28.01	6.9	1.29 ± 0.08 b	60.17 ± 5.42 a	34.67 ± 0.90 a	0.25 ± 0.02 b	68.65 ± 6.19 b	0.50 ± 0.02 c	78.44 ± 11.85 a	17.35 ± 3.96 b	136373.78	4.52
Shrub and tree restinga												
Ilex theezans	28.94	7.0	3.53 ± 0.59 c	53.33 ± 4.90 a	14.04 ± 1.09 b	0.28 ± 0.06 c	53.48 ± 9.88 c	0.66 ± 0.02 c	55.07 ± 6.36 c	56.68 ± 8.37 b	10134.33	0.97
Myrsine venosa	29.54	6.5	4.80 ± 0.51 b	52.50 ± 5.14 a	17.13 ± 1.25 a	0.33 ± 0.03 b	35.10 ± 2.57 d	0.84 ± 0.02 a	63.12 ± 5.95 b	39.45 ± 6.85 c	25147.86	1.60
Ocotea pulchella	40.71	7.0	6.35 ± 0.84 a	49.33 ± 3.10 b	6.02 ± 0.70 e	0.57 ± 0.07 a	65.68 ± 10.90 b	0.66 ± 0.01 c	105.53 ± 9.10 a	23.99 ± 2.21 d	323234.81	4.40
Pera glabrata	39.90	7.5	4.57 ± 1.05 b	50.20 ± 4.33 b	10.29 ± 0.83 c	0.19 ± 0.03 e	70.73 ± 8.54 a	0.74 ± 0.02 b	104.87 ± 19.49 a	14.41 ± 2.61 e	524791.45	7.28
Ternstroemia brasiliensis	36.12	7.0	4.63 ± 0.59 b	52.40 ± 4.44 a	9.73 ± 0.91 d	0.20 ± 0.03 d	64.10 ± 6.29 b	0.63 ± 0.04 c	53.62 ± 8.77 c	97.67 ± 6.70 a	5289.64	0.55
Transition forest												
Alchornea triplinervia	25.37	5.4	8.43 ± 0.80 a	31.83 ± 5.10 c	14.07 ± 1.42 c	0.58 ± 0.04 a	78.97 ± 15.17 d	0.44 ± 0.02 d	128.44 ± 19.15 c	7.59 ± 1.33 d	2240987.47	16.92
Andira fraxinifolia	20.85	5.4	6.37 ± 1.01 c	34.00 ± 5.99 bc	10.72 ± 1.66 d	0.42 ± 0.08 b	99.15 ± 16.05 c	0.64 ± 0.05 b	171.05 ± 26.89 a	3.51 ± 1.32 e	15246381.11	48.74
Calophyllum brasiliense	47.74	8.4	7.93 ± 0.97 b	36.50 ± 4.70 b	37.64 ± 2.21 a	0.33 ± 0.06 c	82.38 ± 5.99 d	0.78 ± 0.01 a	163.86 ± 20.86 b	10.76 ± 2.00 c	4187545.59	15.23
Dalbergia frutescens	19.86	5.4	6.07 ± 0.71 c	38.67 ± 3.41 a	2.71 ± 0.81 e	0.21 ± 0.07 e	137.09 ± 18.63 a	0.65 ± 0.02 b	45.26 ± 2.82 e	101.87 ± 12.55 a	2574.49	0.44
Nectandra oppositifolia	24.55	6.0	8.87 ± 0.89 a	33.33 ± 5.07 c	33.08 ± 2.10 b	0.44 ± 0.05 b	56.81 ± 4.42 e	0.54 ± 0.02 c	126.36 ± 17.30 c	10.08 ± 1.87 c	1580730.94	12.54
Schinus terebinthifolius	22.56	6.0	7.63 ± 0.65 b	28.83 ± 3.09 d	3.83 ± 0.55 e	0.28 ± 0.08 d	119.88 ± 18.48 b	0.55 ± 0.02 c	70.48 ± 10.25 d	72.07 ± 10.37 b	21398.78	0.98

Thus, specific leaf area can be used as an indicator of ecological strategies related to productivity in environments with water stress (Niklas and Christianson, 2011) and low soil fertility (Hodgson *et al*., 2011). This last indicator can be interpreted as an important environmental driver that controls the functions of terrestrial ecosystems (Shipley *et al*., 2006). The occurrence of patterns of convergence in plant communities is widely acknowledged. However, there is no consensus on which environmental contexts favor more convergences (Wilson, 2007). Some studies on the *restingas* of the state of Rio de Janeiro, Brazil, show that hydric availability is a determining factor in the success of plant species that colonize the sand coast, where traits such as specific leaf mass, succulence, leaf thickness, and leaf density are convergent. These ecophysiological traits can be interpreted as important connections between plant attributes and the ommunitystructure of *restingas* (Rosado and de Mattos, 2010). Other traits, such as height, leaf area and fresh/dry leaf mass ratio, which were interpreted in other studies as indicators of strategies of resource use and conservation (Vaieretti *et al*., 2007; Pérez-Harguindeguy *et al*., 2013), were not significant in the present study. These traits are probably related to a different environmental scale or are secondarily functional for the environmental resources tested (Petchey and Gaston, 2006).

The most significant wood traits associated with gravimetric moisture, such as vessel diameter, conductivity index, and vulnerability index, showed a strong positive relationship with hydric variation along the edaphic gradient and the maximization of species convergence. Although wood density and vessel frequency presented a weak relationship with gravimetric moisture, they do collaborate in hydraulic conductivity in the *restinga*, being related to the security and efficiency of water transport (Westoby & Wright, 2006). The relationship between water transport security and efficiency is well-known (Bhaskar *et al*., 2007). It is a trade-off triangle in xylem evolution, where conductive efficiency is inversely proportional to both mechanical support and resistance to dysfunction via embolism (Baas *et al*., 2004). Embolism may reduce water transport and lead to lower stomatal conductance (Pratt *et al*., 2005), lower photosynthetic rates (Brodribb and Feild, 2000), and branch death (Davis *et al*., 2002). Larger vessel diameters and lower vessel frequencies in wood species of transition forest seem to be a response to higher water availability in soil (gravimetric moisture), entailing higher efficiency and lower security of water transport. However, in species with larger vessel diameters under strong hydric stress (i.e., in RS and RST), wood may have a higher density to reduce the risk of vessel rupture.

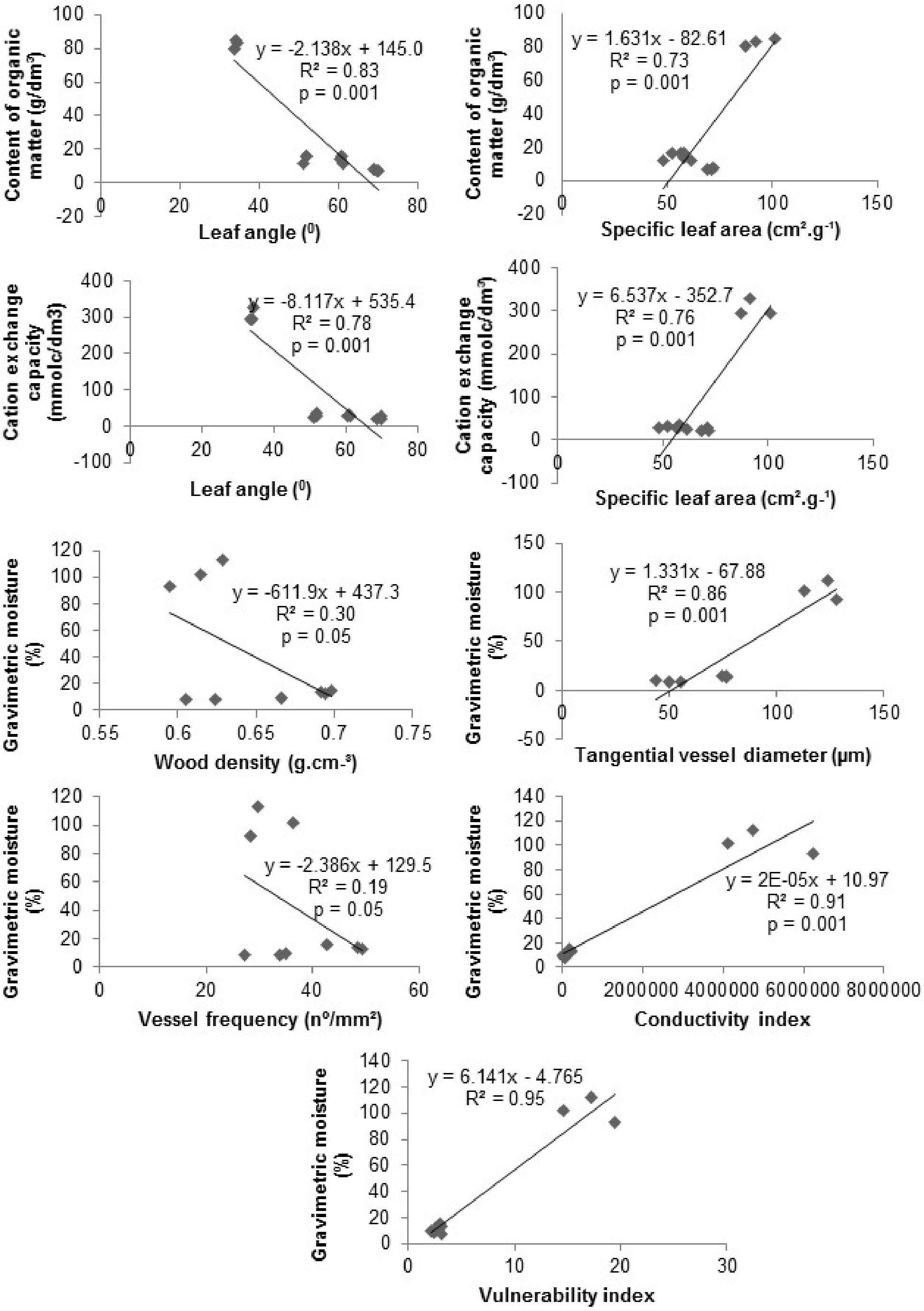

Figure 2. Linear regressions between soil attributes and traits of leaves and wood that maximized the convergence among species in distinct vegetation types of *restinga*

Table 3. Gini-Simpson index (SD), functional diversity index (FD) and functional redundancy (FR) of vegetation types of *restinga* related to soil traits along the edaphic gradient in Acaraí State Park. Abbreviations: herbaceous *restinga* (RH), shrub *restinga* (RS), shrub and tree *restinga* (RST), transition forest (FT), organic matter (OM, gdm^{-3}), cation exchange capacity (CEC, mmol$_c$dm^{-3}) and gravimetric moisture (GM, %)

Edaphic trait	Index	Vegetation types			
		RH	RS	RST	FT
	SD	0.82	0.71	0.79	0.82
OM	FD	0.21	0.22	0.31	0.35
	FR	0.61	0.49	0.48	0.47
	SD	0.82	0.71	0.79	0.82
CEC	FD	0.21	0.21	0.30	0.36
	FR	0.61	0.50	0.49	0.46
	SD	-	0.71	0.79	0.82
GM	FD	-	0.22	0.32	0.47
	FR	-	0.49	0.47	0.35

This trade-off between transport efficiency and security has been reported in most species, based on larger vessels and lower frequency per area unit, and is usually observed in tropical woody species (Barros *et al*., 2006). In species that grow in more restrictive soil conditions (ex. *Myrcia pulchra*), more frequent vessels with smaller diameters represent a strategy to reduce the risks of embolism in stressful conditions, because water adheres more to vessel walls, thus preventing bubble formation (Castro *et al*., 2009). However, recent studies indicate that wood anatomical traits contributing to higher water transport efficiency may be dissociated from the attributes that increase resistance to embolism, since these processes have evolved independently (Bhaskar *et al*., 2007). Wood density can be a good predictor of plant response to water availability (Rosado *et al*., 2013a) and resistance to embolism in dry environments (Sperry, 2003), because it can maintain water conductivity by lowering the water potential of xylem (Westoby and Wright, 2006). Our results show a strong connection between some traits and resource availability along the edaphic gradient of the *restinga*. Vegetation types under water and nutrient restrictions include more competitive species, with more redundant traits, independently of their phylogenetic relatedness. The structural variation in leaf and wood traits of these species reflect a higher pressure of the environmental filter closer to the sea. The vegetation types growing where more nutrients and water are available exhibit a higher dissimilarity among dominant species, attenuating their ecological requirements and interspecific competition. The similarity of attributes maximizing convergence among species indicates that organic matter, cation exchange capacity, and gravimetric moisture are features that greatly influence the occupation and survival of vegetation on the sand plain coast of southern Brazil.

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