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FUNCTIONAL DIVERSITY OF *RESTINGA* SHRUB SPECIES ON THE COASTAL PLAIN OF SOUTHERN BRAZIL

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ABSTRACT

The present study aimed to evaluate the influence of the limiting environmental factors of *restinga* onmorphoanatomical functional attributes related to the growth and development of shrub species. The study was carried out in 100m² sampling units of *resting* shrub communities on the coastal plain of southern Brazil. Environmental variables and 27 morphoanatomical attributes of leaves and stems were evaluated. The diversity and functional redundancy of attributes, considering environmental data matrices, functional attributes and the abundance of species, were measured using the software SYNCSA. The functional attributes that maximized convergence among the studied species were, for the leaf: simple leaf blades, alternate phyllotaxis, leaf area, leaf inclination, thickness of palisade parenchyma, thickness of spongy parenchyma, dorsiventral mesophyll and stomatal density. For the stem, the significant attributes were: plant height, wood density, vesselelement length, fiber wall thickness and vessel frequency. The results showed that in spite of the high species diversity, environmental filters imposeoverlap of the shrub species of the *restinga* communities through convergence of attributes that optimize the use and conservation of resources.

INTRODUCTION

Functional attributes can be any morphological, physiological or phenological characteristic at the cellular, histological or organismal level. They can also be strategies for with use that can affect the fitness of a plant and determine how it interacts in the environment, thereby influencing other trophic levels (Poffand Zimmerman, 2010; Pérez-Harguindeguy *et al*., 2013). These attributes may reflect strategies of interspecific competition and coexistence among species (Callaway *et al*., 2003), influence ecosystem functions (Hooper *et al*., 2005; McGill *et al*., 2006; Violle*et al*., 2007) and elucidate mechanisms of colonization and nutritional dynamics (Madritchand Hunter, 2003;Gamfeldt and Kallstrom, 2007).

It is presumedthat species have different adaptive strategies, which allow them to survive environmental variation through plastic responses (Pugnaire and Valladares, 1999). Thus, traditional floristic-structural studies that are based on taxonomic identity and measurements of height, diameter, cover and abundance of species are insufficient for explaining patterns of community organization and ecosystem functioning because they do no consider the range of ecological responses and functional differences among species (Cianciaruso *et al*., 2009; Mouchet, *et al*., 2010). Among the topics of greatest interest in ecology is variation in ecological responses of plant formations that settle along environmental gradients, because these situations facilitate a better understanding of the function and structure of ecosystems (Mouchet*et al*., 2010; Cianciaruso *et al*., 2012; 2013). This variation is influenced by biotic and/or abiotic environmental factors and is recognized as important in the biology and evolutionary ecology of plant groups (Bradshaw, 2006). The processes that organize communities among environmental gradients can be understood by examining functional diversity, since different arrangements of functional characteristics canimply different mechanisms of coexistence (Petchey*et al*., 2007), extensions of geographic distribution (Valladares *et al*., 2007) and complementary relationships or overlapping niches between speciesof plants(Villéger*et al*., 2010;Baraloto, 2012). Studies of functional ecology in *restinga* environments can reveal patterns that favor the understanding of the functionalityof species, since these ecosystems are governed by environmental factors with marked variation on a short spatio-temporal scale, and often limit the establishment and development of

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salinity and nutrient deficiency (Scarano*et al*., 2001; Scarano, 2002). In this way, it can be said that the plant communities that characterize *restinga*s are directly influenced by environmental filters that model the functional responses of their species (Melo Júniorand Boeger, 2016; Melo Júnior and Boeger, 2017). In recent years, functional diversity has been a prominent theme in ecological studies of *restinga*s of the South and Southeast regions of Brazil, revealing patterns of functional convergence of attributes in face of environmental conditions. These studies have demonstrated that, in addition to the existence of the modularization of functional responses given by plants, in certain physico-chemical conditions convergent functional attributes converge in ecophysiological responses such as the water content of the apoplast, carbon and nitrogen isotopes and CAM metabolic route (Gessler, 2008; Rosado and Mattos, 2010;Rosado *et al*., 2013a; Rosado *et al*., 2013b); in phonological responses such as leaf longevity and leaf death rate (Rosado and Mattos, 2010); and in morphoanatomical responses, such as leaf inclination angle, plant height, leaf area, specific leaf area, mesophyll thickening, epidermal thickening, dry mass, presence of crystals in the mesophyll, hypostomaticleaves and diameter, frequency and length of vessel elements (Mantuano *et al*., 2006;Boeger and Gluzezak, 2006; Melo Júnior and Boeger, 2016; Liberatoand Melo Júnior, 2016; Silva and Melo Júnior, 2016; Melo Júnior and Boeger, 2017; Melo Júnior and Boeger, 2017; Amorim and Melo Júnior, *in press*). In order to increase the understanding of functional patterns aong plant species of *restingas*, the present study aimed to describe the functional diversity of woody species of a *restinga* shrub community. The hypotheses addressed by the study are: i) the limiting conditions of the *restinga* environment act as environmental filters that accentuate the functional convergence of attributes related to the growth and development of the plant species of the shrub formation of *restinga*, thereby reducing the phylogenetic distance among them; and ii) among the limiting conditions, edaphic nutrition exerts the greatest influence on the morphological and anatomical functional attributes of *restinga*shrub species.

MATERIAL AND METHODS

Study area

The study area comprises a *restinga* remnant of about 6,667 ha belonging to the Parque Estadual Acaraí (PEA), a conservation unit located on the coastal plain of São Francisco do Sul, state of Santa Catarina, South Brazil (S 26°14'38", W 48°38'18"; Figure 1) (Melo Júnior and Boeger, 2015). The climate of the region is characterized as humid mesothermic with hot summers (Cfa of Köppen). Rainfall is well distributed throughout the year and reaches an annual average of 1,830 mm (Climate-data, 2016). The vegetation of PEA is compartmentalized in different communities along a soil gradient, and is characterized by formations of herbaceous *restinga*, shrub *restinga*, shrub-tree *restinga* and transitional forest (Melo Júniorand Boeger, 2015), as well as other less representative formations such as submontane dense ombrophylous forest, floodplains and mangroves (FATMA, 2008).

Sample design

Five sample units belonging to shrub *restinga* were demarcated in the field by allocating 10m x 10m (100m^2) plots parallel to the coastline and separated by a kilometer to guarantee their independence. Each sampling unit was considered as a distinct community. As an inclusion criterion, we considered all woody or sub-woody species of shrub habit present in each of the communities. Taxonomic identification of the selected species was based on the list of flora produced for PEA (Melo Júniorand Boeger, 2015). In the five communities, 13 shrub species were collected with a total abundance of 373 individuals. In each community a single individual of each species was randomly selected for measurement of height and stem-base diameter. A total of 30 fully expanded sun leaves were collected from between the 3rd to the 5th nodes from the apex of the branches and fixed, and wood was obtained from the base of the largest diameter tiller of each individual sampled. The morphological functional attributes of leaves were based on n = 25, while the anatomical functional attributes of both leaf and stem were based on n = 30. Morphological attributes considered were: plant height (PH, m), measured in the field with the aid of a telemetric ruler; stem diameter (STD, cm) measured in the field using a measuring tape; type of leaf blade [simple (SL) orcomposite (CL)], phyllotaxis, [alternate (AP) oropposite (OP)], leaf dry mass (LDM, g),obtained with an analytic balance; leaf inclination angle (LIA, °), measured in the field with the use of a protractor; leaf area (LA, cm²), obtained by means of image capture using a desk scanner and measuring with Sigma Scan Pro 5.0 software; specific leaf area (SLA, cm^2.g^{-1}), obtained by means of the ration between leaf area and dry mass (Witkowski and Lamont, 1991); and presence or absence of trichomes(TR) and leaf glands (LG), determined with the aid of a stereomicroscope. Leaf anatomical attributes were evaluated by means of the preparation of permanent histological slides from cross sections of the middle-third of the leaves made using a rotating microtome (Leica RM2265) for histobiometry of thickness of: adaxial face of the epidermis + cuticle (EAD, µm), palisade parenchyma (PP, µm), spongy parenchyma (SP, µm) and the abaxial face of the epidermis + cuticle (EAB, µm). The presence or absence of hypodermis (HP) and the type of mesophyll [dorsiventral (DMor isobilateral (IM)] were also observed. Stomatal density (SDE, n°.mm^{-2}) was determined by counting 301mm² fields of the abaxial surface of the leaf obtained by enamel molding (Segatto*et al*., 2004), with the aid of a clear camera associated with optical microscopy.

The attributes of wood considered were the physical property of basic density, and anatomical characters related directly to conductivity and hydraulic safety. For determining the basic density of wood (WD, g.cm^{-3}), the hydrostatic balance method was adopted (ABNT, 2003). The anatomical attributes were observed and measured using Dino Eye 2.0 software coupled to an Olympus CX31 photomicroscope from permanent histological slides. For the production of histological slides, specimens were softened by cooking in glycerinated water and sectioned in transverse, longitudinal tangential and radial longitudinal planes using a sliding microtome (Kraus and Arduim, 1997). The histological sections were cleared in sodium hypochlorite, stained in 1% safranine alcohol solution, dehydrated in an increasing alcohol series (Kraus and Arduim, 1997) and mounted with stained-glass varnish-type synthetic resin (Paiva *et al*., 2006). Dissociated material was obtained by a modification of the Franklin method (Kraus and Arduim, 1997). The anatomical attributes of the wood considered were: porosity (POR), vessel length (VL, µm), vessel frequency (VF, n°.mm^{-2}), tangential vessel diameter (VD, µm), fiber length

(FL, µm) and fiber wall thickness (FWT, µm). Measurement of wood attributes followed the recommendations of IAWA (1989).

Determination of environmental variables

The environmental conditions of each community were characterized by litter thickness, edaphic nutrition, salinity (sodium content) water availability and photosynthetically active radiation (PAR) incident on the sampled individuals. Litter thickness was taken at the vertices and at the center of each sampling plot (community) using a centimeter ruler.

Table 1. Characterization of soil nutrients and salinity of five *restinga* shrub communities of ParqueEstadualAcaraí, São Francisco do Sul, Santa Catarina, Brazil, and the correlation between soil variables represented by components 1 and 2 of the principal component analysis (PCA)

Variable	Communities					PCA	
	1	2	3	4	5	Comp1	Comp2
pH	5.20	5.40	5.20	5.40	5.70	-0.067	0.400
Ca (cmol.dm^{-3})	0.80	0.50	0.30	0.70	1.00	0.389	-0.008
Mg (cmol.dm^{-3})	0.40	0.20	0.30	0.30	0.50	0.393	0.109
Al (cmol.dm^{-3})	0.20	0.10	0.10	0.10	0.00	0.176	-0.290
H+Al (cmol.dm^{-3})	2.20	1.60	1.60	1.20	1.60	0.048	0.441
CTC (cmol.dm^{-3})	1.50	0.80	0.70	1.20	1.50	0.366	0.174
SB (%)	36.30	31.00	26.90	49.50	49.70	0.327	0.043
MO (%)	1.20	0.50	0.70	0.70	0.80	0.233	0.366
S (mg.dm^{-3})	19.90	9.60	9.70	10.10	9.80	0.265	-0.004
K (mg.dm^{-3})	28.00	16.00	16.00	24.00	24.00	0.215	-0.319
Cu (mg.dm^{-3})	0.219	0.183	0.282	0.536	0.343	0.145	0.438
Zn (mg.dm^{-3})	0.997	0.793	0.925	1.279	1.184	0.352	-0.221
Na (mg.dm^{-3})	20.00	20.00	16.00	20.00	20.00	0.316	-0.200
Variance explained by components						0.469	0.341
Percentage of total variance explained (%)						46.9	34.1

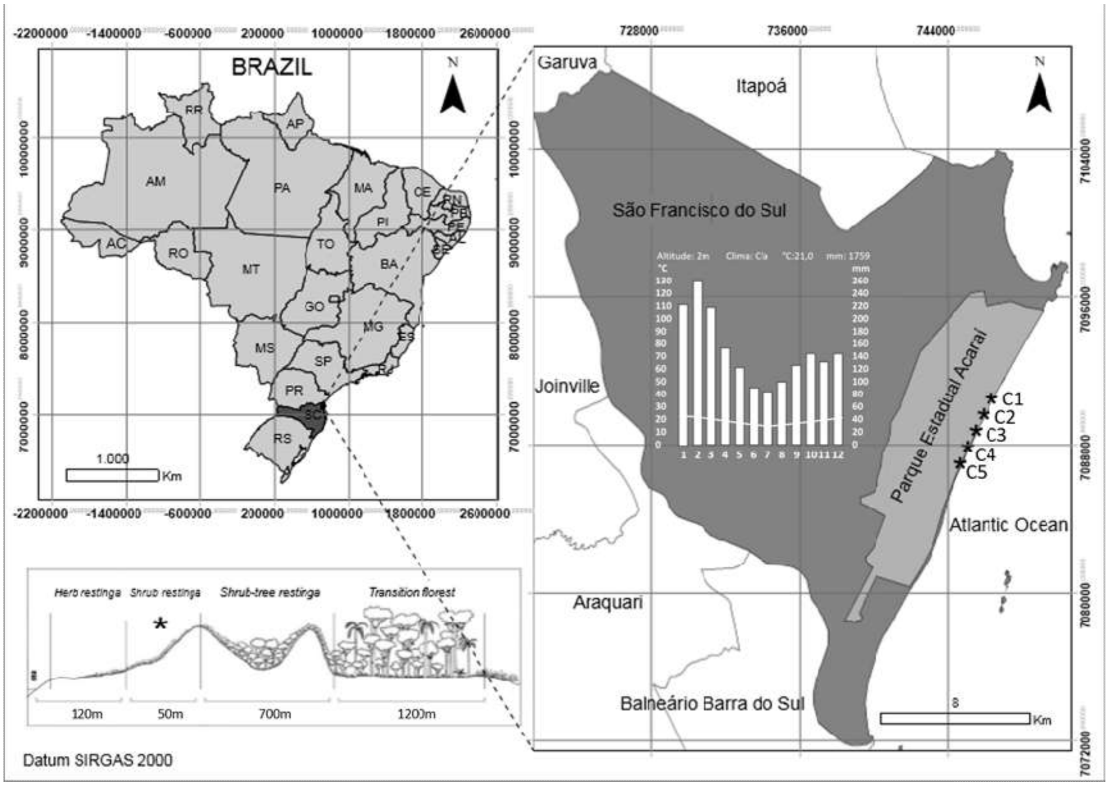

Figure 1. Location of the study area and respective climatic and spatial characteristics of the *restinga* of ParqueEstadualAcaraí, São Francisco do Sul, Santa Catarina, Brazil. Legend: *C1 – *C5: *restinga* shrub communities studied

Soil collection for nutritional and salinity analysis was done by opening five pits for the removal of 15 cm of soil, which, after

community (Embrapa, 2011). Soil water availability was determined from five soil samples per community using the gravimetric moisture method (Embrapa, 2013). The photosynthetically active radiation (PAR) incident on the sampled individuals was measured in the field with the aid of a digital luxmeter (Instrutherm, THAL-300).

Statistical and functional analysis of communities

Means and standard deviations were calculated for all thefunctional attributes evaluated. After testing for normality, the mean values of attributes were compared by ANOVA and the post-hoc Tukey test with p <0.05 (Borcard *et al*., 2011). To determine the edaphic variables that best explained the

Table 2. Functional attributes of leaves of the woody species of *restinga* shrub communities of ParqueEstadualAcaraí, São Francisco do Sul, Santa Catarina, Braszl. Legend: leaf dry mass (LDM, g), leaf area (LA, cm²), leaf specific area (SLA, cm2.g-1), leaf inclination angle (LIA, º), adaxial epidermis (EAD, µm), palisade parenchyma (PP, µm), spongy parenchyma (SP, µm), abaxial epidermis (EAB, µm) and stomatal density (SDE, n.mm-1). Values represent means ± standard deviation. Different letters in columns indicate significant differences among species by formation (ANOVA, p < 0.0001)

Community	Species	LDM (F=2248)	LA (F=1858)	SLA (F=831.1)	LIA (F=44.33)	EAD (F=348.6)	PP (F=685.3)	SP (F=2488)	EAB (F=177.3)	SDE (F=261.2)
1	*Guapira opposita*	0.07 ± 0.01 ^{b}	5.55 ± 0.49 ^{b}	79.08 ± 9.07 ^{de}	65.17 ± 6.36 ^{de}	34.81 ± 4.10 ^{c}	173.53 ± 7.62 ^{f}	289.73 ± 8.89 ^{c}	23.89 ± 2.44 ^{bc}	145.46 ± 76.10 ^{a}
	Myrsineparvifolia	0.14 ± 0.01 ^{d}	7.42 ± 0.81 ^{b}	52.77 ± 5.90 ^{ac}	59.33 ± 5.83 ^{bc}	30.88 ± 0.83 ^{b}	142.91 ± 6.60 ^{d}	314.50 ± 26.41 ^{d}	30.03 ± 1.07 ^{d}	99.53 ± 45.63 ^{a}
	Myrsineguianensis	0.10 ± 0.01 ^{c}	50.51 ± 6.15 ^{e}	120.39 ± 8.19 ^{f}	64.67 ± 5.24 ^{de}	60.62 ± 7.52 ^{e}	62.80 ± 11.19 ^{a}	303.31 ± 20.97 ^{cd}	45.07 ± 7.62 ^{f}	242.44 ± 60.60 ^{b}
	Myrcia pulchra	0.17 ± 0.01 ^{e}	6.97 ± 0.42 ^{b}	41.77 ± 4.30 ^{ab}	67.67 ± 5.04 ^{e}	31.67 ± 0.66 ^{bc}	149.80 ± 9.39 ^{e}	481.16 ± 27.43 ^{f}	25.35 ± 1.56 ^{c}	862.58 ± 139.20 ^{d}
	Senna bicapsularis	0.03 ± 0.01 ^{a}	3.13 ± 0.36 ^{a}	97.35 ± 24.58 ^{e}	66.50 ± 4.76 ^{de}	42.21 ± 5.64 ^{d}	83.53 ± 9.34 ^{b}	91.24 ± 1.96 ^{b}	26.19 ± 4.79 ^{c}	288.38 ± 77.04 ^{b}
	Schinus terebinthifolius	0.65 ± 0.04 ^{g}	43.92 ± 2.90 ^{d}	67.65 ± 6.23 ^{cd}	63.17 ± 4.25 ^{cd}	62.18 ± 7.42 ^{e}	127.22 ± 10.55 ^{c}	387.25 ± 23.57 ^{e}	33.55 ± 4.92 ^{e}	262.86 ± 59.25 ^{b}
	Swartzialangsdorffii	0.05 ± 0.01 ^{a}	3.04 ± 0.26 ^{a}	65.89 ± 13.82 ^{bcd}	56.50 ± 3.97 ^{b}	15.39 ± 1.98 ^{a}	79.83 ± 4.14 ^{b}	56.07 ± 1.69 ^{a}	13.24 ± 1.03 ^{a}	145.47 ± 70.66 ^{a}
	Ternstroemia brasiliensis	0.35 ± 0.05 ^{f}	10.43 ± 0.59 ^{c}	30.19 ± 5.07 ^{a}	48.83 ± 5.68 ^{a}	41.33 ± 1.68 ^{d}	137.44 ± 3.49 ^{d}	580.37 ± 22.72 ^{g}	21.40 ± 1.57 ^{b}	408.32 ± 99.18 ^{c}
Community	Species	LDM (F=1535)	LA (F=5819)	SLA (F=89)	LIA (F=97.93)	EAD (F=331)	PP (F=226.6)	SP (F=3544)	EAB (F=350.2)	SDE (F=310.1)
2	*Baccharisdracunculifolia*	0.04 ± 0.01 ^{a}	3.11 ± 0.47 ^{b}	79.85 ± 13.49 ^{c}	62.17 ± 3.64 ^{c}	29.04 ± 1.11 ^{c}	172.09 ± 3.73 ^{e}	174.43 ± 8.96 ^{b}	23.95 ± 1.43 ^{d}	127.60 ± 50.60 ^{a}
	Clusia criuva	0.72 ± 0.09 ^{d}	33.36 ± 1.72 ^{d}	46.85 ± 6.01 ^{a}	65.33 ± 4.14 ^{cd}	18.67 ± 1.57 ^{b}	151.70 ± 12.97 ^{c}	425.20 ± 16.77 ^{e}	17.77 ± 1.32 ^{c}	165.88 ± 75.45 ^{a}
	Guapira opposita	0.11 ± 0.01 ^{b}	6.21 ± 0.55 ^{c}	58.72 ± 5.36 ^{b}	67.50 ± 5.21 ^{d}	35.93 ± 4.40 ^{f}	177.41 ± 10.99 ^{e}	349.36 ± 8.01 ^{d}	28.40 ± 3.61 ^{e}	168.43 ± 58.27 ^{a}
	Myrsineparvifolia	0.14 ± 0.01 ^{c}	6.59 ± 0.60 ^{c}	46.32 ± 6.33 ^{a}	47.00 ± 5.35 ^{a}	31.62 ± 2.95 ^{d}	114.72 ± 8.11 ^{a}	350.80 ± 18.43 ^{d}	29.16 ± 2.40 ^{e}	196.50 ± 84.55 ^{a}
	Myrcia pulchra	0.12 ± 0.02 ^{bc}	6.05 ± 0.72 ^{c}	51.46 ± 11.17 ^{ab}	67.67 ± 5.04 ^{d}	33.99 ± 1.89 ^{e}	159.99 ± 8.17 ^{d}	284.30 ± 6.06 ^{c}	15.21 ± 0.99 ^{b}	1000.38 ± 206.94 ^{c}
	Schinus terebinthifolius	0.02 ± 0.01 ^{a}	1.36 ± 0.16 ^{a}	87.23 ± 14.70 ^{c}	52.50 ± 5.04 ^{b}	15.88 ± 1.49 ^{a}	134.60 ± 3.23 ^{b}	86.80 ± 2.07 ^{a}	13.05 ± 0.90 ^{a}	293.48 ± 60.60 ^{b}
Community	Species	LDM (F=353.3)	LA (F=345.1)	SLA (F=65.56)	LIA (F=88.08)	EAD (F=672.4)	PP (F=833.6)	SP (F=3059)	EAB (F=451.9)	SDE (F=114.1)
3	*Baccharisdracunculifolia*	0.05 ± 0.01 ^{a}	5.47 ± 0.64 ^{b}	111.18 ± 23.53 ^{d}	65.33 ± 3.20 ^{c}	25.72 ± 4.12 ^{b}	94.47 ± 3.98 ^{a}	233.75 ± 6.35 ^{d}	25.10 ± 2.30 ^{c}	125.06 ± 91.96 ^{a}
	Guapira opposita	0.08 ± 0.01 ^{b}	5.43 ± 0.88 ^{b}	74.74 ± 18.37 ^{bc}	66.00 ± 3.32 ^{c}	77.96 ± 4.65 ^{d}	126.86 ± 10.20 ^{b}	246.56 ± 7.97 ^{e}	35.17 ± 3.07 ^{d}	148.02 ± 60.09 ^{a}
	Myrcia pulchra	0.18 ± 0.03 ^{d}	8.10 ± 0.93 ^{c}	47.17 ± 9.90 ^{a}	65.17 ± 3.59 ^{c}	22.34 ± 1.14 ^{b}	171.82 ± 5.46 ^{c}	262.81 ± 6.24 ^{f}	17.91 ± 1.05 ^{b}	581.86 ± 103.70 ^{d}
	Solanumpseudoquina	0.10 ± 0.02 ^{c}	12.97 ± 1.80 ^{d}	127.81 ± 21.85 ^{e}	57.83 ± 4.68 ^{b}	104.65 ± 12.77 ^{e}	89.73 ± 6.09 ^{a}	117.92 ± 9.50 ^{b}	82.29 ± 13.07 ^{f}	331.76 ± 119.51 ^{b}
	Schinus terebinthifolius	0.04 ± 0.01 ^{a}	3.29 ± 0.80 ^{a}	83.26 ± 25.59 ^{c}	60.50 ± 4.61 ^{b}	15.54 ± 1.18 ^{a}	210.17 ± 2.60 ^{d}	163.30 ± 0.97 ^{c}	12.61 ± 0.97 ^{a}	364.94 ± 120.10 ^{b}
	Ternstroemiabrasiliensis	0.09 ± 0.01 ^{b}	5.50 ± 0.67 ^{b}	64.24 ± 10.81 ^{b}	63.83 ± 3.64 ^{c}	36.89 ± 1.53 ^{c}	122.86 ± 13.99 ^{b}	338.45 ± 8.82 ^{g}	39.48 ± 6.00 ^{d}	188.85 ± 87.02 ^{a}
	Varroniacurassavica	0.19 ± 0.02 ^{d}	14.77 ± 2.23 ^{e}	79.44 ± 13.06 ^{c}	47.67 ± 3.41 ^{a}	83.72 ± 13.70 ^{d}	123.98 ± 8.59 ^{b}	96.83 ± 14.11 ^{a}	48.05 ± 5.54 ^{e}	487.43 ± 42.57 ^{c}
Community	Species	LDM (F=826.6)	LA (F=1503)	SLA (F=5731)	LIA (F=81.97)	EAD (F=741.3)	PP (F=1165)	SP (F=9241)	EAB (F=760)	SDE (F=284.2)
4	*Baccharisdracunculifolia*	0.05 ± 0.01 ^{a}	4.29 ± 0.48 ^{a}	90.69 ± 15.99 ^{b}	61.33 ± 4.72 ^{c}	20.61 ± 2.61 ^{bc}	84.18 ± 8.27 ^{a}	250.39 ± 11.75 ^{d}	16.56 ± 1.87 ^{c}	122.50 ± 51.65 ^{a}
	Clusia criuva	1.22 ± 0.16 ^{d}	63.99 ± 8.00 ^{e}	53.60 ± 9.78 ^{a}	54.17 ± 4.93 ^{b}	20.58 ± 2.02 ^{bc}	91.61 ± 8.21 ^{b}	476.40 ± 14.04 ^{h}	20.98 ± 2.54 ^{d}	176.09 ± 72.91 ^{ab}
	Guapira opposita	0.06 ± 0.01 ^{a}	3.82 ± 0.48 ^{a}	64.24 ± 9.17 ^{ab}	63.87 ± 4.58 ^{cd}	31.61 ± 2.56 ^{d}	148.99 ± 13.30 ^{cd}	201.74 ± 5.45 ^{c}	30.48 ± 2.54 ^{e}	155.67 ± 73.83 ^{a}
	Myrsineguianensis	0.53 ± 0.14 ^{c}	34.67 ± 3.18 ^{d}	61.45 ± 7.08 ^{ab}	70.33 ± 2.92 ^{e}	55.20 ± 5.58 ^{f}	95.43 ± 7.83 ^{b}	285.55 ± 9.53 ^{e}	51.31 ± 4.85 ^{f}	112.29 ± 52.17 ^{a}
	Myrcia pulchra	0.16 ± 0.01 ^{b}	7.01 ± 0.74 ^{b}	45.10 ± 5.09 ^{a}	65.50 ± 2.74 ^{d}	19.07 ± 1.18 ^{b}	152.41 ± 3.22 ^{d}	342.89 ± 5.21 ^{f}	14.07 ± 1.10 ^{b}	882.99 ± 129.89 ^{e}
	Schinus terebinthifolius	0.04 ± 0.01 ^{a}	3.47 ± 0.22 ^{a}	92.99 ± 16.37 ^{b}	63.67 ± 4.54 ^{cd}	14.02 ± 1.00 ^{a}	79.40 ± 2.64 ^{a}	59.43 ± 2.54 ^{a}	11.84 ± 0.58 ^{a}	357.28 ± 78.73 ^{c}
	Ternstroemiabrasiliensis	0.08 ± 0.01 ^{a}	4.27 ± 0.43 ^{a}	50.42 ± 7.35 ^{a}	63.67 ± 3.46 ^{cd}	44.39 ± 1.23 ^{e}	223.17 ± 7.46 ^{eh}	414.28 ± 6.59 ^{g}	31.63 ± 4.15 ^{e}	242.44 ± 75.45 ^{b}
	Varroniacurassavica	0.16 ± 0.01 ^{b}	11.27 ± 0.80 ^{c}	68.78 ± 5.98 ^{ab}	48.5 ± 4.76 ^{a}	22.11 ± 3.75 ^{c}	142.88 ± 7.25 ^{c}	78.61 ± 6.42 ^{b}	10.39 ± 1.31 ^{a}	706.90 ± 165.41 ^{d}
Community	Species	LDM (F=1203)	LA (F=2411)	SLA (F=222.5)	LIA (F=57.16)	EAD (F=397.9)	PP (F=912.1)	SP (F=1867)	EAB (F=588.5)	SDE (F=179.3)
5	*Guapira opposita*	0.08 ± 0.01 ^{bc}	5.67 ± 0.70 ^{b}	70.22 ± 9.48 ^{c}	70.33 ± 5.40 ^{e}	37.32 ± 3.05 ^{e}	168.12 ± 12.74 ^{e}	188.55 ± 13.46 ^{c}	25.53 ± 4.04 ^{d}	145.46 ± 54.51 ^{a}
	Myrsineguianensis	0.95 ± 0.13 ^{f}	51.62 ± 4.63 ^{e}	55.34 ± 8.84 ^{b}	61.17 ± 5.52 ^{c}	65.75 ± 8.73 ^{g}	110.24 ± 9.07 ^{a}	286.44 ± 16.82 ^{e}	52.69 ± 6.37 ^{e}	160.78 ± 54.51 ^{a}
	Myrcia pulchra	0.13 ± 0.01 ^{d}	7.17 ± 0.82 ^{c}	56.89 ± 6.63 ^{b}	67.17 ± 4.49 ^{de}	22.53 ± 1.47 ^{b}	140.83 ± 4.65 ^{d}	271.00 ± 9.53 ^{d}	12.52 ± 0.90 ^{ab}	757.94 ± 117.84 ^{c}
	Schinus terebinthifolius	0.29 ± 0.03 ^{e}	11.81 ± 1.05 ^{d}	40.83 ± 4.34 ^{a}	65.17 ± 3.82 ^{d}	26.48 ± 4.44 ^{c}	231.22 ± 9.48 ^{f}	345.40 ± 11.51 ^{f}	14.95 ± 1.22 ^{b}	370.04 ± 112.09 ^{b}
	Senna bicapsularis	0.03 ± 0.01 ^{a}	4.16 ± 0.37 ^{a}	141.86 ± 21.44 ^{f}	65.00 ± 3.47 ^{cd}	33.38 ± 2.44 ^{d}	120.60 ± 4.00 ^{bc}	154.72 ± 15.61 ^{b}	21.68 ± 2.95 ^{c}	311.34 ± 48.97 ^{b}
	Solanumpseudoquina	0.09 ± 0.01 ^{cd}	10.38 ± 1.11 ^{d}	112.06 ± 20.72 ^{e}	50.17 ± 6.63 ^{a}	44.08 ± 5.05 ^{f}	125.73 ± 5.65 ^{c}	156.56 ± 6.85 ^{b}	21.09 ± 1.91 ^{c}	339.42 ± 74.37 ^{b}
	Psidiumcattleianum	0.05 ± 0.01 ^{ab}	3.89 ± 0.56 ^{a}	83.58 ± 9.04 ^{d}	56.33 ± 5.07 ^{b}	17.20 ± 0.50 ^{a}	117.56 ± 2.23 ^{b}	75.96 ± 0.98 ^{a}	11.20 ± 0.42 ^{a}	359.83 ± 87.98 ^{b}

Table 3. Functional attributes of wood of woody species of *restinga* shrub communitiesofParqueEstadualAcaraí, São Francisco do Sul, Santa Catarina, Brazil. Legend: plant height (PH, m), stem diameter (STD, cm), wood density (WD, g.cm-^{3}), tangential diameter of vessel elements (VD, µm), vessel frequency (VF, µm), vessel element length (VL, µm), fiber length (FL, µm) and fiber wall thickness (FWT, µm). The values represent means ± standard deviation. Different letters in columns indicate significant differences among species by formation (ANOVA, $p < 0.0001$)

Community	Species	PH (F=6.152)	STD (F=2.068)	WD (F=4.6)	VD (F=155.9)	VF (F=391.3)	VL (F=783.6)	FL (F=482.7)	FWT (F=140.4)
1	*Guapira opposita*	1.8 ± 0 ^{d}	4.0 ± 0 ^{b}	0.49 ± 0 ^{a}	53.58 ± 9.51 ^{a}	19.83 ± 3.53 ^{a}	192.49 ± 19.23 ^{a}	431.19 ± 44.41 ^{a}	4.94 ± 0.33 ^{c}
	Myrsineparvifolia	2.0 ± 0 ^{f}	13.0 ± 0 ^{g}	0.65 ± 0 ^{d}	51.77 ± 6.31 ^{a}	50.13 ± 12.62 ^{c}	327.46 ± 38.67 ^{c}	501.63 ± 43.04 ^{b}	5.46 ± 0.69 ^{d}
	Myrsineguianensis	1.6 ± 0 ^{c}	9.0 ± 0 ^{f}	0.70 ± 0 ^{f}	71.39 ± 9.24 ^{b}	30.67 ± 5.53 ^{b}	516.53 ± 53.65 ^{e}	1179.23 ± 109.33 ^{e}	5.63 ± 0.38 ^{d}
	Myrcia pulchra	0.9 ± 0 ^{a}	4.5 ± 0 ^{c}	0.89 ± 0 ^{g}	50.59 ± 6.56 ^{a}	62.23 ± 5.03 ^{d}	278.40 ± 28.31 ^{b}	796.91 ± 43.27 ^{d}	4.05 ± 0.51 ^{b}
	Senna bicapsularis	1.4 ± 0 ^{b}	2.5 ± 0 ^{a}	0.69 ± 0 ^{e}	82.81 ± 9.26 ^{c}	21.20 ± 3.10 ^{a}	598.11 ± 38.69 ^{f}	1202.48 ± 115.32 ^{e}	3.13 ± 0.51 ^{a}
	Schinus terebinthifolius	1.6 ± 0 ^{c}	7.0 ± 0 ^{e}	0.49 ± 0 ^{a}	56.72 ± 8.60 ^{a}	28.33 ± 4.94 ^{b}	340.50 ± 28.29 ^{cd}	595.90 ± 46.91 ^{c}	3.14 ± 0.49 ^{a}
	Swartzialangsdorffii	1.9 ± 0 ^{e}	6.0 ± 0 ^{d}	0.51 ± 0 ^{b}	104.60 ± 12.61 ^{d}	82.10 ± 6.66 ^{f}	818.98 ± 58.09 ^{g}	1174.37 ± 132.93 ^{e}	5.68 ± 0.53 ^{d}
	Ternstroemiabrasiliensis	1.8 ± 0 ^{d}	6.0 ± 0 ^{d}	0.52 ± 0 ^{c}	50.40 ± 4.57 ^{a}	70.87 ± 7.07 ^{e}	361.56 ± 38.16 ^{d}	602.61 ± 50.07 ^{c}	5.56 ± 0.55 ^{d}
Community	Species	PH (F=1.482)	STD (F=9.943)	WD (F=2.201)	VD (F=202.9)	VF (F=1521)	VL (F=820.2)	FL (F=505.7)	FWT (F=275.3)
2	*Baccharisdracunculifolia*	0.9 ± 0 ^{a}	6.0 ± 0 ^{b}	0.67 ± 0 ^{c}	47.92 ± 5.31 ^{a}	148.70 ± 10.47 ^{e}	294.82 ± 28.94 ^{c}	371.62 ± 29.19 ^{a}	3.51 ± 0.38 ^{b}
	Clusia criuva	1.9 ± 0 ^{f}	6.0 ± 0 ^{b}	0.71 ± 0 ^{e}	101.34 ± 11.06 ^{d}	20.10 ± 5.11 ^{b}	623.64 ± 36.29 ^{d}	1350.46 ± 182.92 ^{d}	6.02 ± 0.46 ^{e}
	Guapira opposita	1.3 ± 0 ^{d}	4.5 ± 0 ^{a}	0.60 ± 0 ^{b}	71.13 ± 9.66 ^{c}	13.27 ± 3.83 ^{a}	202.28 ± 25.91 ^{a}	616.40 ± 69.71 ^{c}	3.80 ± 0.45 ^{bc}
	Myrsineparvifolia	1.0 ± 0 ^{b}	6.5 ± 0 ^{c}	0.68 ± 0 ^{d}	54.86 ± 3.61 ^{b}	70.30 ± 5.69 ^{d}	298.85 ± 25.83 ^{c}	467.09 ± 48.30 ^{b}	4.00 ± 0.40 ^{c}
	Myrcia pulchra	1.6 ± 0 ^{e}	8.5 ± 0 ^{d}	0.91 ± 0 ^{f}	46.38 ± 4.31 ^{a}	64.73 ± 7.14 ^{c}	287.45 ± 31.82 ^{bc}	445.24 ± 37.48 ^{b}	4.84 ± 0.39 ^{d}
	Schinus terebinthifolius	1.1 ± 0 ^{c}	6.0 ± 0 ^{b}	0.51 ± 0 ^{a}	76.82 ± 10.94 ^{c}	71.73 ± 6.69 ^{d}	272.69 ± 17.75 ^{b}	631.71 ± 54.80 ^{c}	2.53 ± 0.24 ^{a}
Community	Species	PH (F=4.141)	STD (F=2.75)	WD (F=3.987)	VD (F=185.6)	VF (F=940.1)	VL (F=255.7)	FL (F=370.6)	FWT (F=434.3)
3	*Baccharisdracunculifolia*	1.1 ± 0 ^{b}	6.0 ± 0 ^{d}	0.73 ± 0 ^{f}	55.35 ± 6.39 ^{d}	134.3 ± 11.67 ^{e}	267.82 ± 23.52 ^{b}	439.00 ± 42.70 ^{b}	2.49 ± 0.26 ^{a}
	Guapira opposita	1.4 ± 0 ^{d}	8.0 ± 0 ^{e}	0.58 ± 0 ^{c}	48.50 ± 7.04 ^{bc}	15.13 ± 3.80 ^{a}	345.68 ± 48.39 ^{d}	629.70 ± 42.62 ^{d}	6.25 ± 0.42 ^{d}
	Myrcia pulchra	1.5 ± 0 ^{e}	4.5 ± 0 ^{b}	0.92 ± 0 ^{g}	29.61 ± 2.74 ^{a}	60.17 ± 9.00 ^{b}	360.38 ± 16.05 ^{de}	912.58 ± 45.17 ^{f}	3.71 ± 0.35 ^{b}
	Solanumpseudoquina	1.0 ± 0 ^{a}	4.0 ± 0 ^{a}	0.55 ± 0 ^{a}	73.29 ± 10.92 ^{e}	62.30 ± 6.55 ^{bc}	308.35 ± 14.36 ^{c}	637.61 ± 22.93 ^{d}	3.49 ± 0.37 ^{b}
	Schinus terebinthifolius	1.0 ± 0 ^{a}	4.0 ± 0 ^{a}	0.55 ± 0 ^{b}	42.96 ± 8.49 ^{b}	81.70 ± 5.81 ^{d}	185.54 ± 12.52 ^{a}	388.07 ± 61.85 ^{a}	2.56 ± 0.31 ^{a}
	Ternstroemiabrasiliensis	1.4 ± 0 ^{d}	5.5 ± 0 ^{c}	0.66 ± 0 ^{e}	51.77 ± 6.04 ^{cd}	67.73 ± 5.46 ^{c}	380.81 ± 35.03 ^{e}	580.40 ± 47.44 ^{c}	5.33 ± 0.49 ^{c}
	Varroniacurassavica	1.2 ± 0 ^{c}	4.0 ± 0 ^{a}	0.60 ± 0 ^{d}	87.82 ± 9.95 ^{f}	19.67 ± 4.52 ^{a}	181.65 ± 26.52 ^{a}	773.84 ± 79.95 ^{e}	3.45 ± 0.32 ^{b}
Community	Species	PH (F=2.443)	STD (F=1.775)	WD (F=8.538)	VD (F=355.8)	VF (F=1016)	VL (F=342.7)	FL (F=560.8)	FWT (F=601.3)
4	*Baccharisdracunculifolia*	1.3 ± 0 ^{b}	7.0 ± 0 ^{d}	0.72 ± 0 ^{g}	34.50 ± 4.16 ^{a}	145.60 ± 15.12 ^{e}	229.40 ± 41.24 ^{ab}	545.44 ± 41.26 ^{b}	5.53 ± 0.38 ^{c}
	Clusia criuva	1.6 ± 0 ^{d}	5.0 ± 0 ^{a}	0.69 ± 0 ^{f}	84.31 ± 13.07 ^{d}	17.50 ± 2.36 ^{a}	252.79 ± 35.13 ^{b}	1165.16 ± 111.01 ^{e}	7.70 ± 0.59 ^{d}
	Guapira opposita	1.5 ± 0 ^{c}	6.0 ± 0 ^{b}	0.46 ± 0 ^{a}	68.54 ± 10.45 ^{c}	15.30 ± 4.45 ^{a}	230.32 ± 21.20 ^{ab}	439.78 ± 26.25 ^{a}	2.54 ± 0.24 ^{a}
	Myrsineguianensis	2.1 ± 0 ^{g}	8.0 ± 0 ^{f}	0.58 ± 0 ^{c}	173.36 ± 26.29 ^{f}	13.86 ± 3.97 ^{a}	679.09 ± 31.56 ^{e}	1294.45 ± 140.90 ^{f}	5.81 ± 0.39 ^{c}
	Myrcia pulchra	1.7 ± 0 ^{e}	9.0 ± 0 ^{g}	0.86 ± 0 ^{h}	31.44 ± 3.82 ^{a}	51.93 ± 6.50 ^{c}	303.41 ± 34.18 ^{c}	784.90 ± 39.61 ^{cd}	3.38 ± 0.32 ^{b}
	Schinus terebinthifolius	1.5 ± 0 ^{c}	7.5 ± 0 ^{e}	0.56 ± 0 ^{b}	75.45 ± 12.36 ^{cd}	67.30 ± 7.03 ^{d}	292.80 ± 28.70 ^{c}	450.70 ± 28.12 ^{a}	3.54 ± 0.39 ^{b}
	Ternstroemiabrasiliensis	1.8 ± 0 ^{f}	6.5 ± 0 ^{c}	0.65 ± 0 ^{e}	49.23 ± 5.26 ^{b}	48.37 ± 7.81 ^{c}	528.86 ± 116.86 ^{d}	830.51 ± 64.63 ^{d}	3.55 ± 0.35 ^{b}
	Varroniacurassavica	1.2 ± 0 ^{a}	5.0 ± 0 ^{a}	0.63 ± 0 ^{d}	95.34 ± 14.28 ^{e}	30.83 ± 5.33 ^{b}	204.89 ± 13.97 ^{a}	749.87 ± 37.76 ^{c}	3.39 ± 0.30 ^{b}
Community	Species	PH (F=8.226)	STD (F=9.311)	WD (F=1.567)	VD (F=88.94)	VF (F=543)	VL (F=706.5)	FL (F=207)	FWT (F=155.3)
5	*Guapira opposita*	1.7 ± 0 ^{d}	6.0 ± 0 ^{c}	0.47 ± 0 ^{a}	71.98 ± 12.48 ^{c}	11.33 ± 2.62 ^{a}	529.48 ± 59.42 ^{c}	800.66 ± 127.70 ^{b}	4.25 ± 0.54 ^{e}
	Myrsineguianensis	2.1 ± 0 ^{f}	8.5 ± 0 ^{f}	0.58 ± 0 ^{d}	66.55 ± 8.78 ^{bc}	53.70 ± 6.34 ^{d}	208.59 ± 5.11 ^{a}	963.22 ± 56.43 ^{c}	3.66 ± 0.29 ^{c}
	Myrcia pulchra	1.5 ± 0 ^{c}	5.5 ± 0 ^{b}	0.86 ± 0 ^{f}	40.23 ± 5.63 ^{a}	60.73 ± 7.13 ^{e}	195.95 ± 25.64 ^{a}	778.69 ± 40.43 ^{b}	3.12 ± 0.45 ^{b}
	Psidiumcattleianum	2.0 ± 0 ^{e}	6.5 ± 0 ^{d}	0.64 ± 0 ^{e}	40.26 ± 5.65 ^{a}	93.10 ± 11.63 ^{f}	352.91 ± 34.44 ^{b}	1000.12 ± 67.83 ^{c}	2.58 ± 0.19 ^{a}
	Senna bicapsularis	0.8 ± 0 ^{a}	2.5 ± 0 ^{a}	0.58 ± 0 ^{d}	64.89 ± 7.22 ^{b}	17.17 ± 4.62 ^{b}	601.27 ± 24.51 ^{d}	1217.07 ± 113.16 ^{d}	3.23 ± 0.26 ^{b}
	Solanumpseudoquina	2.0 ± 0 ^{e}	7.5 ± 0 ^{e}	0.56 ± 0 ^{c}	71.98 ± 7.48 ^{c}	33.87 ± 6.03 ^{c}	369.91 ± 21.76 ^{b}	802.20 ± 47.52 ^{b}	4.16 ± 0.44 ^{d}
	Schinus terebinthifolius	1.2 ± 0 ^{b}	6.0 ± 0 ^{c}	0.50 ± 0 ^{b}	70.95 ± 9.30 ^{bc}	64.77 ± 5.62 ^{e}	369.94 ± 15.21 ^{b}	580.02 ± 32.42 ^{a}	5.08 ± 0.38 ^{f}

Principal Component analysis (PCA) was performed. Statistical analyses were performed in the R environment (Crawley, 2007), version 3.1.2. For the functional analysis of the *restinga* shrub communities, three different data matrices were generated: (i) Matrix Bcontained species described by the means of selected functional attributes; (ii) Matrix W contained the abundance values for each species per community; and (iii) Matrix E considered nutrient and soil salinity data (previously selected by PCA) of water availability, litter thickness and incident light (Pillar, 1999).

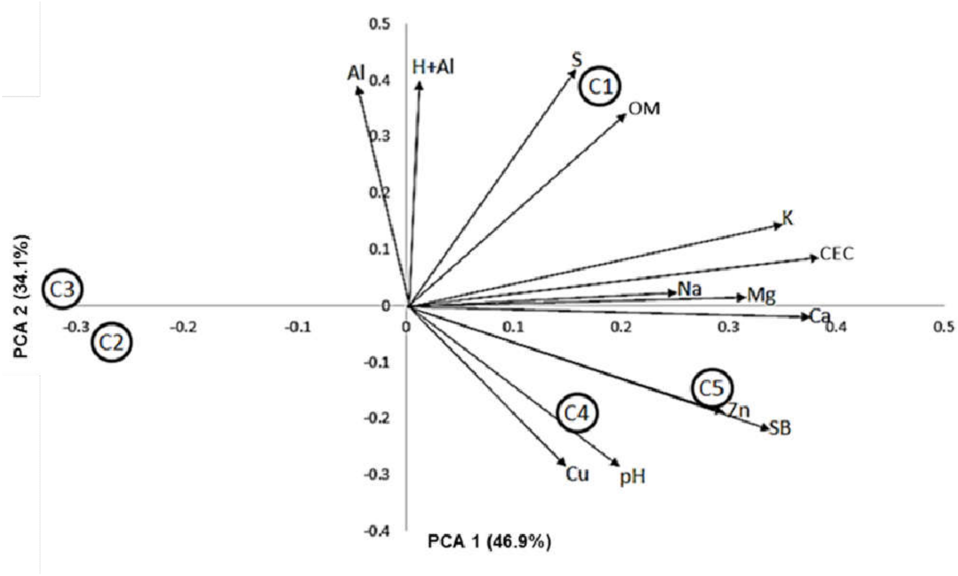

Figure 2. Principal components analysis of edaphic variables of the soils of the *restinga* shrub communities studied inParqueEstadualAcaraí, São Francisco do Sul, Santa Catarina, Brazil.

Table 4. Qualitative functional attributes of wood species of the *restinga* shrub communities of Parque EstadualAcaraí, São Francisco do Sul, Santa Catarina, Brazil

Species	Community					Blade	Phyllotaxis	Trichomes	Glands	Hypoderm	Mesophyll	Porosity
	C1	C2	C3	C4	C5							
Baccharisdracunculifolia		X	X	X		simple	alternate	absent	absent	absent	dorsiventral	diffuse
Clusia criuva		X		X		simple	opposite	absent	absent	present	dorsiventral	diffuse
Guapira opposita	X	X	X	X	X	simple	opposite	absent	absent	absent	dorsiventral	diffuse
Myrcia pulchra	X	X	X	X	X	simple	opposite	absent	absent	absent	dorsiventral	diffuse
Myrsineguianensis	X			X	X	simple	alternate	absent	absent	absent	dorsiventral	diffuse
Myrsineparvifolia	X	X				simple	alternate	absent	absent	absent	dorsiventral	diffuse
Psidiumcattleianum					X	simple	opposite	absent	absent	present	dorsiventral	diffuse
Schinus terebinthifolius	X	X	X	X	X	composite	alternate	present	absent	present	isobilateral	diffuse
Senna bicapsularis	X				X	composite	alternate	absent	absent	absent	dorsiventral	diffuse
Solanumpseudoquina			X		X	simple	alternate	absent	absent	absent	dorsiventral	diffuse
Swartzialangsdorffii	X					composite	alternate	absent	absent	absent	dorsiventral	diffuse
Ternstroemiabrasiliensis	X		X	X		simple	alternate	absent	absent	absent	dorsiventral	diffuse
Varroniacurassavica			X	X		simple	alternate	present	present	absent	dorsiventral	diffuse

Table 5. Indices of the five *restinga* shrub communities analyzed in ParqueEstadualAcaraí, São Francisco do Sul, Santa Catarina, Brazil

Indices	Communities				
	C1	C2	C3	C4	C5
Wood attributes *vs* Soil water availability					
Gini-Simpson (SD)	0.54	0.85	0.67	0.85	0.83
Functional diversity (FD)	0.25	0.42	0.32	0.43	0.42
Functional redundancy (FR)	0.29	0.43	0.35	0.42	0.41
Leaf attributes *vs* Soil water availability, PAR, edaphic nutrition and litter thickness					
Gini-Simpson (SD)	0.81	0.80	0.79	0.84	0.78
Functional diversity (FD)	0.45	0.46	0.40	0.46	0.42
Functional redundancy (FR)	0.36	0.34	0.39	0.38	0.36

The functional attributes that maximize the convergence between the species that make up the communities (trait convergence assembly patterns – TCAP), Gini-Simpson function of the environmental variables, given by the quadratic entropy of Rao (quadratic entropy index of diversity – FD Rao: Rao, 1982), and the functional redundancy (RF, obtained by SD – FD) were evaluated using the software SYNCSA (Pillar andOrlóci, 2004).

RESULTS

Thirteen woody species, belonging to 10 families, of the five rstingashrub communities were selected for analysis: *Baccharis longiattenuata*A. S. Oliveira (Asteraceae), *Clusia* (Nyctaginaceae), *Myrciapulchra* (O.Berg) Kiaersk., *Psidiumcattleianum* Sabine (Myrtaceae), *Myrsineguianensis* (Aubl.) Kuntze, *Myrsineparvifolia* A.DC. (Primulaceae), *bicapsularis* (L.) Roxb., *Swartzialangsdorffii*Raddi (Fabaceae), *Solanumpseudoquina* A.St.-Hil. (Solanaceae), *Ternstroemia brasiliensis* Cambess. (Pentaphylacaceae) and*Varroniacurassavica*Jacq. (Boraginaceae). Chemical analysis of the soil (Table 1) of the shrub communities of the studied *restinga*revealed minimally acidic soil with variation in all of the nutrients and indexes of fertility analyzed. Salinity, represented by sodium (Na), was similar among the communities, being lower only in Community 3 (C3). The highest values for aluminum (Al), potential acidity (H+Al), organic matter (OM), sulfur (S) and potassium (K) were observed in Community 1 (C1), which resembled Community 5 (C5)with regard to cation exchange capacity (CEC). The lowest values of magnesium (Mg), sulfur (S), copper (Cu) and zinc (Zn) were observed in Community 2 (C2), which had the same level of potassium (K) as Community 3 (C3). The lowest values of calcium (Ca), cation exchange capacity (CEC) and sum of bases (SB) were observed in Community 3 (C3). The lowest value for potential acid H+Al, and the highest value for copper (CU) and zinc (Zn), were observed in Community 4 (C4). The highest values of calcium (Ca), magnesium (Mg) and sum of bases (SB), in addition to the lowest value of aluminum (Al), were observed in Community 5 (C5). The first two components of the PCA explained 81%

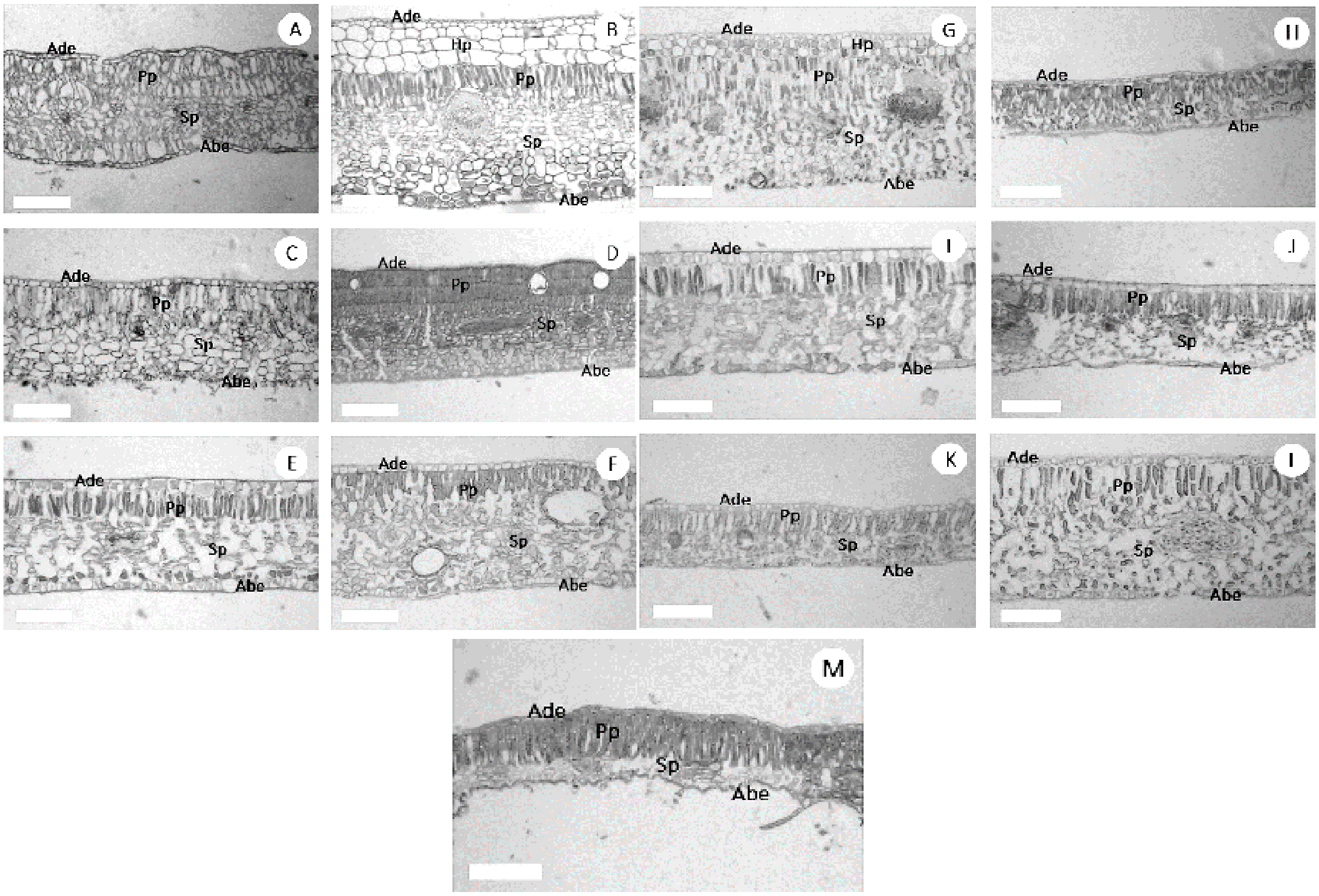

Figure 3. Leafanatomicalstructureof restinga shrubspeciesofParque Estadual Acaraí, São Francisco do Sul, Santa Catarina, Brazil. Legend: A- *Baccharisdracunculifolia* DC. (Asteraceae). B- *Clusia criuva* Cambess. (Clusiaceae). C- *Guapira opposita* (Vell.) Reitz (Nyctaginaceae). D- *Myrcia pulchra* (O.Berg) Kiaersk. (Myrtaceae). E- *Myrsineparvifolia*A.DC. (Primulaceae). F- *Myrsineguianensis* (Aubl.) Kuntze (Primulaceae). G- *Psidiumcattleianum*Sabine (Myrtaceae). H- *Schinus terebinthifolius* Raddi (Anacardiaceae). I- *Swartzialangsdorffii*Raddi (Fabaceae). J- *Senna bicapsularis*(L.) Roxb. (Fabaceae). K- S*olanumpseudoquina* A.St.-Hil. (Solanaceae). L- *Ternstroemia brasiliensis* Cambess. (Pentaphylacaceae). M- *Varroniacurassavica*Jacq. (Boraginaceae)

The first principal component (PCA1) explained 47% of the variance and was represented by magnesium (Mg), calcium (Ca), cation exchange capacity (CEC) and zinc (Zn). The second principal component (PCA2) explained 34% of the variance and was represented by potential acidity (H+Al), copper (Cu), hydrogen ionic potential(pH) and organic matter (OM). The results of the ANOVA indicated significant differences between the average values of most of the functional attributes of the leaves and ofthe wood analyzed, which were able to differentiate the species of each community(Tables2 and 3). Leaf attributes that expressed the greatest variation among communities were dry mass(0.02 – 1.22 g), leaf area (1.36 – 63.99 cm^2) and leaf specific area(30.19 – 520.39 $cm^2.g^{-1}$).For wood, the most significant attributes were vessel frequency (11.33 – 148.70 µm), vessel element length (371.62 – 1350.46 µm) and tangential vessel diameter(29.61 – 104.60µm). On the other hand, certain attributes demonstrated structural convergence among the species of the communities. The optimum subset of leaf attributes that showed the greatest convergence among the species of this study in response to the variables of light, water litter and soil, included simple leaves (SL) alternate phyllotaxis (AP), leaf area (LA), leaf inclination angle (LIA), palisade parenchyma thickness (PP), spongy parenchyma density (SDE). The TCAP level expressed by these attributes was highly significant (ρTE = 0.83, p = 0.03).

The optimum subset of stem attributes that showed the greatest convergence among the species of this study when related to

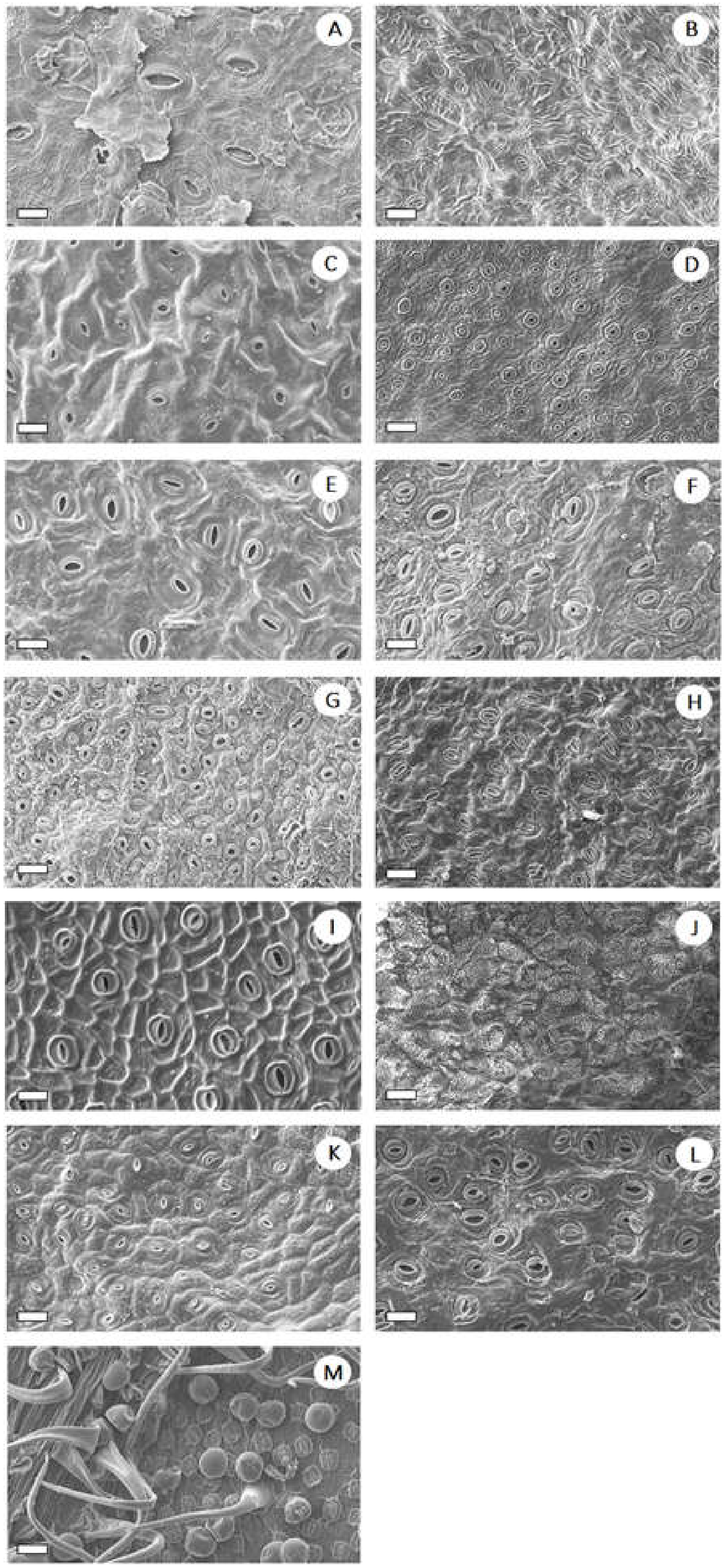

Figure4. Stomataldensityof restinga shrubspeciesof Parque Estadual Acaraí, São Francisco do Sul, Santa Catarina, Brazil. Legend: A- *Baccharisdracunculifolia* DC. (Asteraceae). B- *Clusia criuva* Cambess. (Clusiaceae). C- *Guapira opposita* (Vell.) Reitz (Nyctaginaceae). D- *Myrcia pulchra* (O.Berg) Kiaersk. (Myrtaceae). E- *Myrsineparvifolia*A.DC. (Primulaceae). F- *Myrsineguianensis* (Aubl.) Kuntze (Primulaceae). G- *Psidiumcattleianum*Sabine (Myrtaceae). H- *Schinus terebinthifolius* Raddi (Anacardiaceae). I- *Swartzialangsdorffii*Raddi (Fabaceae). J- *Senna bicapsularis*(L.) Roxb. (Fabaceae). K- S*olanumpseudoquina* A.St.-Hil. (Solanaceae). L- *Ternstroemia brasiliensis* Cambess. (Pentaphylacaceae). M- *Varroniacurassavica*Jacq. (Boraginaceae).

water availability was composed of plant height(PH), wood density (WD), length of vascular elements (VL), fiber wall thickness (FWT) andvessel frequency (VF). The TCAP level expressed by these attributes was also highly significant (ρTE = 0.90, p = 0.001). Among the qualitative attributes evaluated, the diffuse porosity of wood was similar among all species, and the leaf attributesexhibited minimal variation. Since there was no interspecific variation in this category of attributes, table 4 shows the results obtained organized by species. Single leaves were observed in 76.92% of the species, while composite leaves were observed in only 23.08% The absence of trichomes was observed in 84.62% of the species. Glands and isobilateral mesophyll were observed in 92.31% of the species and the absence of hypoderm in 76.92% (Figure 3). The stomatal density was directly proportional to leaf area (Figure 4). The Gini-Simpson index (SD) demonstrated a high diversity of species in the communities with the exception of C1 and C3, which were moderately diverse for stem attributes. The functional diversity (FD), based on leaf and stem attributes, showed low dissimilarity among the 13 *restinga* shrub species analyzed in the five communities. Functional redundancy (FR) showed low functional similarity of the evaluated attributes (Table 5). This means that both the overlap and redundancy of the species are related to a small set of functional attributes (48%).

DISCUSSION

*Restinga*s are represented by plant communities that are subjected to extreme environmental conditions, which repreesnt environmental filters that can exert significantinfluences and contribute to the assembly of these communities. Thus, metrics of diversity and functional redundancy allow the reinterpretation of the processes of community assembly in these environments. The ecological functionality of each attribute that culminated in the functional convergence among the *restinga*species studied is discussed below. Leaf form and number of units and subunits of leaves are explained by the need to for plants to adapt to environmental conditions (Givnish,1987;Popma*et al*., 1992). A simple leaf is considered a primitive characteristic whose formation is entirely conditioned by gene expression that acts in all the physiological process of building the organs of a plant(Taiz *et al*., 2017).Simple leaves may be advantages for plants exposed to high solar radiation since, in association with a reduction in surface area of the leaf, they reduce the surface for transpiration and represent a strategy for water conservation. In environments with water restriction, such as *restinga*, single leaves represent a conservation of resources destined to the production of new aerial structures, due to their perenniality, as opposed to composite leaves (Rollet *et al*., 1990).

Alternate phyllotaxis can be understood by the greater comprehensiveness of the area of light captured by a plant with this type of leaf insertion. It is an attribute associated with other leaf characteristics, such as leaf area and the thickness of chlorophytic parenchyma, in the optimization of light capture (ValladaresandBrites, 2004). Phyllotaxis may influence light uptake, but in general its functional interpretation is still subject to speculation due to the great interaction of various leaf attributes in compensation for the low efficiency of some types of phyllotaxis (Niklas, 1999). Smaller leaf areas may be an advantageous attribute for plants subjected to conditions of high solar incidence and low air humidity, as occurs in the *restinga*, mainly by reducing the area of transpiration and, consequently, minimizing water loss (Boeger *et al*., 2008). Leaves more exposed to direct light and low air humidity tend to have reduced areas and are thicker when compared to leaves that develop under higher levels of shade (Klich, 2000). Several studies carried out in *restinga*s have reported results similar to those of the present study, in which a reduction in leaf area was observed as a function of intense luminosity (Todorovski *et al*., 2015;Bachtold and Melo Júnior, 2015;Silva *et al*., 2016; Melo Júnior and Boeger, 2016; Amorim and Melo Júnior,*in press*). Small leaf inclination angles play an important role in minimizing the effects of excessive solar radiation on leaves (Boeger *et al*., 2007). Vertically oriented leaves, common in plants in environments of high light exposure, allow a greater dispersion of heat when exposed to convective wind currents (Lewis, 1972; Smith *et al*., 1998). Other studies that investigated the effects of luminosity on leaf architecture also found the occurrence of lower leaf angles in leaves exposed to high luminosity (Boeger and Gluzezak, 2006; Melo Júnior and Boeger, 2016).

The increased in thickness of palisade parenchyma observed in the shrub species of *restinga* studied here as a result of greater exposure to light radiation corroborates reports in the literature. This increase may be caused by either to the addition of new cell layers, to cell elongation or to the combination of these two factors (Boeger *et al*.,2009;Lambers*et al*.,2010). The cells of the palisade parenchyma have a columnar shape in order to channel incident light, and it is generally observed that leaves that develop in environments under intense light radiation have thicker palisade parenchyma (Fernandes*et al*.,2014).Other studies that have evaluated differences in palisade parenchyma under varying light intensities showed the same tendency observed in the present study (Mantuano*et al*.,2006;Gyorgy, 2009;Amorim and Melo Júnior,*inpress*). The occurrence of thicker spongy parenchyma indicates greater structural investment in leaves, probably to keep internal temperature low and to optimize photosynthesis (Santiago *et al*.,2001), since the environment where the species are established has high temperatures. Thicker spongy parenchyma enhances the diffusion of light within the leaf, resulting in multiple reflections and greater light path length, increasing the probability of absorption(Vogelmannand Gorton, 2014). This result corroborates the study ofAragão*et al*. (2014), who also observed an increase in spongy parenchyma in some species present in areas of intense solar radiation. The increase in cell length and the number of layers of spongy parenchyma is related to the use of light that reaches both sides of leaves (Delucia*et al*., 1991). The greater number of layers of spongy parenchyma can increase CO_2 gain at the level of the whole plant, taking into account the more vertical position of the sun leaves and the efficient processing of light by the abaxial surface when the sun is near the horizon (Falsterand Westoby, 2003).

The occurrence of dorsiventral mesophyll can optimize the uptake of light since most chloroplasts are found in cells of the palisade parenchyma (Souza, 2005). Due to the shape and arrangement of these cells, chloroplasts can be disposed parallel to cell walls, thereby increasing photosynthetic efficiency or reducing damage from excess light (Menezes *et al*., 2010). Stomatal density is evidence of an adaptive response to extreme climatic conditions and is often related to a reduction in leaf area, thus conditioning a greater amount of stomata per unit area. Several studies have reported that an increase in water stress in the environment causes an increase in stomatal density (Boeger *et al*., 2008;Pereira *et al*., 2009;Santos *et al*., 2010). In addition, a greater number of stomata per unit area can be considered a strategy for conserving leaf water in plants thatdevelopunder high luminosity and on soils with less water retention capacity (Pearce *et al*., 2006). The observed relationship between water availability and stem attributes that promoted convergence among the studied *restinga* shrub species is routinely observed in studies with plants that inhabit soils with water scarcityand has been identified as an adaptation to guarantee water flow (Baas *et al*., 1983; Baas and Carlquist, 1985). The convergences among stem attributes observed in the communities evaluated in this study suggestplant strategiesfor dealing with low water availability and risk of embolism (Carlquist, 1984; Caquet *et al*., 2009; Lima *et al*., 2009; Choat *et al*., 2011). The low height of the plants analyzed in this study may be related to low water availability. In a greenhouse study, Albuquerque *et al*. (2013) observed an increase in height of individuals with greater water availability.In a study of*Tibouchina clavata* (Melastomataceae) occurring in different *restinga* formations,Amorim and Melo Júnior, (*in press*) also observed the height of individual plants to be positively related to water availability. Negative effects on plant height development under conditions of water stress occur due to a decline in cell growth (Jaleel *et al*., 2009).

The low values of basic wood density observed for most of the species of the present study may be related to high vessel frequency and fiber wall thickness.Gasson, (1987) and Rao *et al*. (1997) found a relationship between wood density and vessel frequency. Wood density is an important factor of the ecological strategies employed by plants, being directly related to mechanical support, transportation and water storage (Chave *et al*., 2009). Fibers are generally the most abundant cellular elements in wood, and their thickness directly influences the density of wood, which can contribute to the mechanical resistance needed for the tissues to avoid, in the form of safety, the collapse of vessels that support high negative pressures in water transport during periods of drought (Jacobsen *et al*., 2007). Thickening of fiber walls is related to genetic and environmental factors, as well as tree age (Shimoyama and Barrichello, 1989). When related to low soil nutritional status and low water availability, woody plants tend to synthesize more simple sugars by photosynthesis and, in the cambial layer, increase the biosynthesis of cellulose molecules that are then incorporated as microfibrils, resulting in thickening of the secondary wall (Freitas *et al*., 2015). Fibers with thicker walls are commonly observed in drier environments, ensure greater vessel safety (Luchi *et al*., 2005) and are considered to be ecological tendencies of species in xeric environments (Alves and Angyalossy-Alfonso, 2002).
Vessel length may be related to greater safety in water transport since longer vessels, although less efficient in conducting water, are safer (Zimmermann and Milburn, 1982).

The data observed in the present study corroborate the studies of Bachtold and Melo Júnior (2015) and Silva *et al*. (2016), who verified longer vessels in association with lower soil water availability, however, Marques *et al*. (2012) observed an opposite relationship in*Eugenia uniflora* (Myrtaceae). The frequency of vessels is an extremely sensitive indicator ofxeromorphism and mesomorphism(Carlquist, 2001). The convergence of this functional attribute among the species of the present study illustrates the proposal of Baas *et al*. (2004), who stated that structural adjustments of xylem tend to ensure efficiency and safety in water transport, such that smaller vessels with associated high frequency per unit area occur in dry environments. Studies performed on tree species inhabiting dry soils of *restinga*have shown the same trend observed for most of the shrub species treated here (Bachtold and Melo Júnior, 2015; Melo Júnior *et al*., 2016a; Melo Júnior *et al*., 2016b). On the other hand, the species *Ilex theezans* (Aquifoliaceae) exhibited a relationship opposite of that expected, while *Andira fraxinifolia* (Fabaceae) exhibited channeling of the frequency of vessels, which may be related to the influence of the spatial microscale of the distribution of the populations of these species in the *restinga* environment (Liberatoand Melo Júnior, 2016; Silva andMelo Júnior, 2016).
The functional attributes of leaves and wood responsible for shortening the phylogenetic distance between the*restinga* shrub species studied here and their functional overlap within communities, are indicative of the existence of an expressive environmental filter that regulates both the assembly and diversity of species of the communities. For the attributes analyzed, edaphic nutrition cannot be considered the most influential variable on the convergence of attributes of the species of *restinga* shrubs studied, but together with light radiation and water availability serves to select species and act on their functional strategies to optimize their use of resources.

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