

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

Ilhas lenhosas em campos litorâneos sul-brasileiros: efeitos de variações espaciais sobre a estrutura de comunidades vegetais

Ana Boeira Porto

Porto Alegre, março de 2018

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Ana Boeira Porto

Dissertação apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul como parte dos requisitos para a obtenção do título de Mestre em Botânica.

Orientador: Prof. Dr. Jorge Luiz Waechter

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Resumo

A costa arenosa brasileira (restingas) é amplamente conhecida por seus muitos tipos de vegetação, frequentemente devido a pequenas variações de relevo que, por sua vez, causam condições de solo bastante distintas. Uma fisionomia interessante e ainda pouco conhecida são as moitas ou ilhas dispersas em matrizes herbáceas escassas e densas. Nosso principal objetivo neste trabalho foi avaliar como as variáveis espaciais, como área e volume, afetam a composição florística e a estrutura da comunidade de ilhas lenhosas nos campos costeiros do sul do Brasil. Analisamos 48 ilhas lenhosas em quatro locais de estudo no litoral médio do Rio Grande do Sul. Em cada local, foram amostrados 12 moitas seguindo o método dos pares aleatórios. Cada moita foi medida e todas as espécies de plantas vasculares acima de 30 cm foram registradas e quantificadas de acordo com uma escala de abundância de um a cinco. As ilhas lenhosas variaram aproximadamente entre 4 e 204 m². O inventário florístico resultou em 102 espécies em 49 famílias, sendo as Myrtaceae e Bromeliaceae as mais diversificadas, com oito e sete espécies, respectivamente. Um total de 12 formas de vida foram reconhecidas, sendo as mais diversificadas árvores ou árvores potenciais (27 espécies), ervas subarborescentes (17), trepadeiras (20) e epífitas (15). A riqueza de espécies aumentou significativamente com o tamanho das ilhas lenhosas, corroborando uma das premissas básicas da Teoria da Biogeografia de Ilhas. A diversidade e a abundância de formas de vida, pelo contrário, não foram significativamente diferentes ao longo dos diferentes tamanhos. A comparação de todas as ilhas lenhosas dos quatro locais de estudo indicou uma maior similaridade em cada local, sugerindo variação regional nas propriedades do solo ou distúrbios pretéritos. Mais estudos sobre estas variáveis, especialmente sobre o efeito do pastoreio ao longo do tempo, devem contribuir para uma melhor compreensão das variações espaciais e temporais na paisagem de ilhas lenhosas nos campos litorâneos.

Palavras-chave Composição florística, Formas de vida, Restinga, Sul do Brasil, Diversidade de espécies, Vegetação em mosaico

Abstract

Brazilian coastal sand plains (*restingas*) are widely known for their many vegetation types, often responding to small landform variations which in turn cause quite distinct soil conditions. One interesting and still poorly known physiognomy is the woody patches or islands dispersed over sparse to dense herbaceous matrixes. Our main objective in this paper was to assess how spatial variables, as area and volume, affect the floristic composition and the community structure of woody patches in south Brazilian coastal grasslands. We analysed 48 woody patches in four study sites in central coastal Rio Grande do Sul. In each site we sampled 12 woody patches following the random-pairs method. Each woody island was measured and all vascular plant species above 30 cm were registered and quantified according to a one to five abundance scale. Woody patches varied roughly between 4 and 204 m². The floristic inventory resulted in 102 species in 49 families, the Myrtaceae and Bromeliaceae being the most diversified, with eight and seven species, respectively. A total of 12 life-forms were recognized, the most diversified being trees or potential trees (27 species), herb-subshrub (17), climbers (20) and epiphytes (15). Species richness increased significantly with the size of woody islands, corroborating one of the basic premises of Theory of Island Biogeography. Diversity and abundance of life-forms in the contrary were not significantly different along the different sizes. The comparison of all woody islands from the four study sites indicated a higher similarity within each site, suggesting regional variation in soil properties or past disturbances. Further studies of these variables, especially the effect of grazing over time, are expected to contribute to a better understanding of spatial and temporal variations in coastal woody island landscapes.

Keywords Floristic composition, Life-forms, Restinga, South Brazil, Species diversity, Vegetation mosaics

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Introdução geral

A ocorrência de espécies lenhosas organizadas em formações mais ou menos hemisféricas e descontínuas na vegetação herbácea é comumente denominada de moitas de restinga ou de ilhas lenhosas (Araujo 1992). Assim, as moitas dispersas no espaço formam uma vegetação em mosaico (Araujo et al. 1998). Esta vegetação intriga os pesquisadores desde o início do século passado, tendo sido descrita pela primeira vez por Ule (1901), em uma restinga no Rio de Janeiro.

A vegetação de restinga encontrada na Planície Costeira do Rio Grande do Sul é composta por uma matriz de campos e florestas intercaladas por expressivos corpos d'água (Villwock & Tomazelli 2007). Os campos litorâneos inseridos nesta formação quando comparados com campos de outras formações se caracterizam por apresentar uma riqueza comparativamente baixa de espécies de plantas, grande porcentagem de solo desnudo e alta dominância de espécies (Menezes et al. 2015). Estes campos representam um dos tipos de matrizes ambientais nas quais se encontram as comunidades de moitas ou ilhas lenhosas ao longo da planície. As moitas também ocorrem em matrizes de dunas costeiras (Fernandez 2012), campos pastejados na região do Planalto (Duarte et al. 2006) e em morros graníticos próximos de Porto Alegre (Forneck 2007).

O Sudeste do Brasil é a região onde há mais registros de trabalhos com este tipo de formação (Araujo 1992; Ribas 1992; Araujo et al. 1998), especialmente sobre a composição florística (Pereira 1990; Pereira & Araujo 1995; Pereira & Araujo 2000) e papel de espécies do gênero *Clusia* como plantas focais nas formações abertas de moitas (Zaluar 1997; Zaluar & Scarano 2000; Dias & Scarano 2007; Monteiro et al. 2014). Variações espaciais, como volume (Ribas 1992), índices de diversidade (Pimentel 2002)

e atributos funcionais de plantas subordinadas (Garbin et al. 2012, 2014) também foram relatados para esta região.

Matrizes ambientais que apresentam características xerofíticas, como dunas ou campos com vegetação rasteira, podem ser desfavoráveis para a germinação e o estabelecimento de espécies vegetais menos tolerantes (Maun 1994). Dessa forma, plantas focais ou *nurse plants* (Callaway 1995; Archer et al. 1988), podem favorecer a colonização nestes ambientes e originar as formações de moitas. Porém, nem toda planta pioneira que se estabelece em um ambiente aberto será uma focal, para isso o indivíduo precisará manter um balanço positivo nas interações com as outras espécies (Zaluar & Scarano 2000). Após a estabilização da planta focal, o micro-habitat ao redor começa a ser modificado, proporcionando condições para a colonização de espécies menos tolerantes a condições extremas (Callaway 1995).

Teorias ecológicas como Teoria da Sucessão Ecológica (Clements 1916) e a Teoria da Biogeografia de Ilhas (MacArthur & Wilson 1967) podem ser aplicadas para compreender e acompanhar a dinâmica na comunidade de moitas. Considerando a Teoria da Biogeografia de Ilhas, as moitas lenhosas estão isoladas de maneira similar às ilhas oceânicas, pois estão em uma matriz com características fisionômicas distintas e desfavoráveis para colonização, como areia exposta (Ribas 1992) ou campos pastejados (Duarte et al. 2006). Dessa forma, conforme o aumento na disponibilidade de habitat há o incremento de novas espécies na ilha. Esta teoria também foi aplicada para compreender formações similarmente isoladas como topos de montanhas e fragmentos florestais (Diamond 1975; Pickett & Thompson 1978).

Nesse contexto, o artigo a seguir estabelece alguns objetivos relacionados aos fatores espaciais que afetam a estrutura comunitária das ilhas lenhosas localizadas em

campos litorâneos do Rio Grande do Sul. A redação foi estruturada nas normas do periódico *Brazilian Journal of Botany*.

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**Woody islands in South Brazilian coastal grasslands: effects of spatial variations
on the structure of plant communities**

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Abstract

Brazilian coastal sand plains (restingas) are widely known for their many vegetation types, often responding to small landform variations which in turn cause quite distinct soil conditions. One interesting and still poorly known physiognomy is the woody patches or islands dispersed over sparse to dense herbaceous matrixes. Our main objective in this paper was to assess how spatial variables, as area and volume, affect the floristic composition and the community structure of woody patches in south Brazilian coastal grasslands. We analysed 48 woody patches in four study sites in central coastal Rio Grande do Sul. Each woody island was measured and all vascular plant species above 30 cm were registered and quantified according to a one to five abundance scale. Woody patches varied roughly between 4 and 204 m². The floristic inventory resulted in 102 species in 49 families, the Myrtaceae and Bromeliaceae being the most diversified, with eight and seven species, respectively. A total of 12 life-forms were recognized, the most diversified being trees or potential trees (27 species), herb-subshrub (17), climbers (20) and epiphytes (15). Species richness increased significantly with the size of woody islands, corroborating one of the basic premises of Theory of Island Biogeography. Diversity and abundance of life-forms in the contrary were not significantly different along the different sizes. The comparison of all woody islands from the four study sites indicated a higher similarity within each site, suggesting regional variation in soil properties or past disturbances.

Keywords: Floristic composition, Life-forms, Restinga, South Brazil, Species diversity, Vegetation mosaics

1. Introduction

Coastal vegetation along the extensive Brazilian Atlantic region is commonly characterized as mosaic of many distinct physiognomies, varying from open herbaceous formations to closed woody formations (Rizzini 1979; Eiten 1983; Veloso et al. 1991). Since many different plant formations often occur together in a small-scale geographic space, the vegetation mosaic is generally called collectively as restinga, and has been described under this designation by many authors (Araujo et al. 1998; Giaretta et al. 2013; Scarano and Ceotto 2015). Araujo (1992) provided a comprehensive description of the several habitats and plant physiognomies occurring in Rio de Janeiro, which can also be recognized in most tropical and subtropical Brazilian coastal plains (Waechter 1990; Silva and Britez 2005; Sacramento et al. 2007). Structure and composition of coastal vegetation is strongly affected by rather small variations in landform, which in turn affect soil drainage and temporary to permanent inundation (Waechter 1990; Magnago et al. 2013).

One interesting plant formation in restinga-vegetation consists of relatively small patches or islands with woody vegetation dispersed over a sparse to dense herbaceous layer. This particular physiognomy has been reported from all over coastal Brazil, from northern to southern latitudes (Sacramento et al. 2007; Meira-Neto et al. 2005; Silva and Britez 2005). Woody patches or islands mostly occur on well-drained white sand deposits and develop around some pioneer species able to germinate and establish on open sandy areas or grassy meadows. These species are recognized as focal species or nurse-plants, calling attention for their capacity to start a succession process in which other species are favored by less stressful environments (Callaway 1995). Among important focal species are tank-bromeliads, palms of the genus *Allagoptera*, and shrubs or trees of the genus *Clusia* (Leite 1990; Sampaio et al. 2005; Dias and Scarano 2007).

Woody patches in coastal environments can be regarded as terrestrial island systems in a local or regional scale. As woody vegetation clumps are more or less isolated one from another, they represent an interesting study field to test the premises of the Theory of Island Biogeography (MacArthur and Wilson 1967). This theory predicts that species diversity in islands increases with the size of the isolated area and decreases with the distance from continents or other main sources of dispersal units. As a whole, the theory combines geographic patterns with biological processes, the later consisting essentially by immigration and extinction. It is assumed that species diversity results from a dynamic balance between these two processes, being higher in nearer islands by favouring immigration, and in larger islands by avoiding extinction. As plant immigration succeeds basically through spore and seed dispersal mechanisms, all adaptive features and interactive processes involving dispersion are in fact important aspects towards the understanding of island ecology and biogeography (Duarte et al. 2007).

The increasing size of the woody islands interferes in the composition of floristic heterogeneity (Cabral et al. 2003). Small patches are mostly composed by independent self-supporting life-forms, such as trees, shrubs and succulents (cacti), which are able to establish in open sun-exposed areas. As the size of patches increases, greater habitat heterogeneity develops and allows the occurrence of several subordinate life-forms, including shade-adapted geophytes (terrestrial herbs), and mechanically dependent plants as climbers and epiphytes (Cogliatti-Carvalho et al. 2001; Garbin et al. 2012; Garbin et al. 2014). All these independent and subordinate life-forms are commonly reported for coastal white sand woodlands (Ribas 1992; Pereira and Araujo 1995; Araujo et al. 1998).

The coastal plain of Rio Grande do Sul, the southernmost Brazilian state, stands out for its broad inland extension, encompassing the large Patos and Mirim lagoons. The vegetation of the coastal plain comprises many of the same plant physiognomies as elsewhere in Brazil, from relatively dry dune fields and woodlands to periodically or permanently inundated marshes and peat forests (Waechter 1985, 1990). Differently from other states in tropical and subtropical Brazilian latitudes, Rio Grande do Sul has extensive coastal grasslands, generally related to the Pampas biogeographic province (Boldrini 2009). In comparison to the more inland regions, the coastal grasslands show relatively low species richness and thus high species dominance (Menezes et al. 2015). In some places the coastal plain grasslands also exhibit more or less dispersed woody islands with different sizes. These vegetation mosaics were not included in former descriptions of restingas in Rio Grande do Sul (Waechter 1985, 1990), possibly because they show a restricted distribution in space and time due to disturbance.

The community structure and floristic composition of woody patches in coastal subtropical grasslands remains practically unknown to present times. Since most grassland in the Pampas region is extensively and more or less intensively used for cattle raise, it is also unknown how grazing affects the natural expansion and eventually coalescence of woody islands. In this paper our main objective was to provide evidences for how spatial variables affect the structure of woody patches in coastal grasslands. Our main hypotheses are: (1) the increasing sizes of woody islands, expressed as area or volume, increases species richness of vascular plants; (2) higher diversity and structural complexity of woody patches increases the diversity and abundance of plant life-forms; and (3) smaller distances between woody patches promote higher floristic similarity than larger distances between study areas.

2. Methods

2.1 Study site

We analysed four areas with woody islands immersed in grasslands in the central coastal plain of the state Rio Grande do Sul: Bacupari, Cidreira, Palmares do Sul and Tramandaí (Table 1). Only the first area is somewhat distant from the main city of the municipality (Mostardas), all others are only a few kilometres from the cities with the same names. The four areas are roughly located between 29 and 30°S, and between 6 and 25 km from the coastline, more or less eastwards to the northern region of the Patos Lagoon (Fig. 1).

Table 1. Geographical coordinates and climatic parameters of the studied areas. DCL = distance from coastline; MAT = Mean annual temperature; MAR = Mean annual rainfall.

Study site	Latitude S	Longitude W	Elevation m	DCL km	MAT °C	MAR mm
Bacupari*	30.533446°	50.426730°	9	6	18.1	1573.0
Palmares	30.249532°	50.491866°	8	25	18.5	1601.7
Cidreira	30.144688°	50.251143°	10	6	18.6	1656.7
Tramandaí	29.990450°	50.194886°	10	7	18.7	1673.4

(*) Climatic data are those from Mostardas, the main city in the municipality.

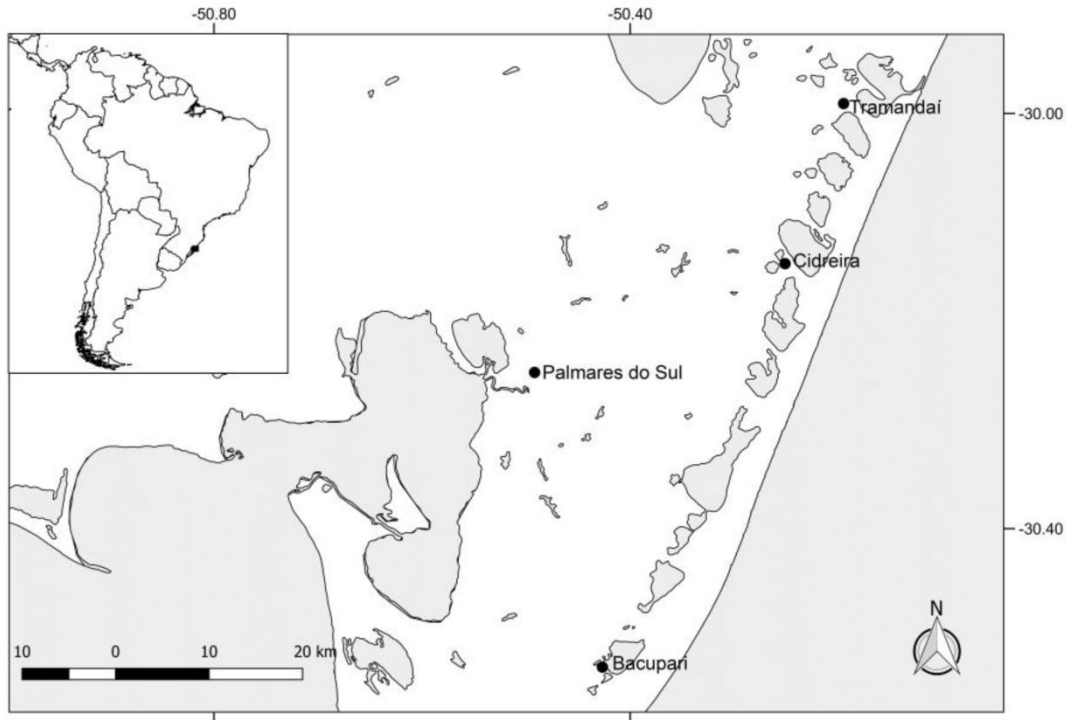


Fig 1 Geographic location of the four study sites in coastal Rio Grande do Sul.

The Coastal Plain of Rio Grande do Sul is one of the main geomorphologic regions (Justus et al. 1986) or geological domains (Kaul 1990) in South Brazil, formed by several types of continental and marine trans-regressive sediments accumulated during Cenozoic times. The surface is mostly Quaternary in origin and is only rarely interrupted by older rocky outcrops, as Mesozoic basalts and sandstone in the northern part and Pre-Cambrian granites in the southern part (Tomazelli and Villwock 2000). In comparison with more northern Brazil, the coastal plain of Rio Grande do Sul has a very broad inland extension between 30 and 34°S (more than 100 km), comprising the three largest coastal lagoons: Patos, Mirim and Manguieira.

The climate in this region is of the Cfa type according to the Köppen classification system, defined as subtropical without a dry season and with hot summers (Peel et al. 2006). The regional mean annual temperature varies between 18 and 19 °C and the mean annual rainfall varies between 1500 and 1700 mm (Alvares et al. 2014). Within the studied region both temperature and rainfall show a slightly decreasing

tendency with increasing latitude (Table 1). Winds are common and constant throughout the year, blowing mostly from northeast (subtropical high pressure cell) during spring and summer, and secondarily from southwest (cold fronts from the southern polar region) during autumn and winter (Nimer 1979; Waechter 1985).

Despite its uniformly flat landform, the soils of the Coastal Plain of Rio Grande do Sul are quite variable, mostly influenced by small geomorphologic variations which in turn influence drainage conditions and soil-forming processes. Two contrasting types are represented by well-drained sandy soils on small hills or trans-regressive barriers, the Planosols, and those poor-drained soils on slacks or inter-dune depressions the Gleisols, Arenosols or Dunes (EMBRAPA 2009; Castro and Mello 2013). All our four studied sites were located on relatively flat areas with well-drained sandy soils. In all areas we also observed white sand dunes appearing in nearby disturbed places or among short-grass vegetation, probably due to overgrazing. In this way we a priori considered soil variations as less important factors acting on floristic and structural variations of woody islands.

Vegetation in the coastal plain is often described as a mosaic ranging from herbaceous to woody types (Waechter 1985; 1990), sometimes collectively referred as restinga vegetation in Brazilian vegetation systems (Scarano 2002). Coastal salinity (salt marshes) and flooding regimes strongly affect the composition and structure of both the herbaceous and woody vegetation, distinguishing between well-drained (sandy) and poor-drained (peaty) grasslands and woodlands. Fresh-water marshes are also common, often dominated by a single species of tall grasses or tall sedges. Areas combining an herbaceous or grassland matrix and relatively small patches of shrubby or woody vegetation (moitas) are widespread in coastal Brazil, where they were often described as a distinct physiognomy of restinga vegetation (Scarano 2002; Silva and Brites 2005).

2.2 Sampling methods

The sampling of woody patches or islands followed the random-pairs method (Cottam and Curtis 1956; Mueller-Dombois and Ellenberg 1974). In each study site we established a linear transect with six sample points separated by 30m one from another, and at each point we surveyed the two nearest woody islands on the two sides of a 180° exclusion angle (in the original description of the method this design was applied to tree sampling). In this way we sampled 12 woody patches in each study site and a total of 48 vegetation patches in all four areas. Each woody island containing at least three woody plants was considered as sample unit. Field work was performed from March 2016 to April 2017.

In order to estimate patch sizes (area and volume) we measured the largest diameter, a smaller diameter perpendicular to the largest, and the maximum height. We also measured the distance between each pair of woody islands, taking the central points of each patch as the extremities. Area and volume were estimated according to the formulas of the circle and the hemisphere, respectively (Ribas et al. 1994). In all our four study sites the woody patches were quite distinct from the surrounding meadows, probably due to the effect of cattle grazing.

Our aim in this study was to include all life-forms of vascular plants. We registered all woody plant species (trees and shrubs) with a minimum height of 30 cm. The same criterion was adopted for succulents-xerophyte (terrestrial cacti). For herbaceous and sub-shrubby species we included only those species not found or at least not visible in the surrounding grassland formation. All other usually dependent or subordinate life-forms (climbers, epiphytes etc.) were also included in the survey.

Aiming to facilitate and standardize a common abundance measure for very different life-forms we attributed an estimate in a scale from one to five, according to

the occurrence of each species in five segments of each woody patch: one central (where usually the highest or dominant species occur) and four marginal (peripheral), according to cardinal quadrants – northern, southern, eastern, and western. The central dominant species, whether one, two or more, always received the maximum abundance value, i.e., five.

Most species occurring in the woody patches are widely known and more or less easy to be identified directly in the field. Despite of this we collected plant fragments for a voucher collection, now available in the Plant Ecology and Plant Geography Lab (<http://fitoecologiaufrgs.wix.com/fitogeografia>) at the Department of Botany of the Federal University of Rio Grande do Sul. Several unknown species were sent to expert plant taxonomists who helped us with identification problems (see acknowledgements). Two apparently very similar species pairs sometimes seemed difficult to distinguish in the field, so we decided to maintain only one of two possible names, attributable to the most common and widespread species: *Eugenia hyemalis* Cambess. (possibly including *E. uruguayensis* Cambess.) and *Myrsine guianensis* (Aubl.) Kuntze (possibly including *M. umbellate* Mart.).

2.3 Data analysis

We organized data matrixes of species per study sites and woody islands (sample units) for the analyses of abundance, richness, and similarity. Species composition and distribution in the four studied areas were compared and represented by a Venn diagram, using the software Venny (Oliveros 2015). Linear, non-linear and multiple linear regressions were used to analyse the relation between areas, volumes and species richness of the patches. For these analyses we pooled pairs of study sites with similar mean and total species richness.

We also pooled island areas into three size classes for comparisons between this spatial variable and the abundance and richness of different life-forms. Size classes were defined as small (less than 10 m², n = 16); medium-sized (between 10 and 18 m², n = 19); and large (more than 20 m², n = 13). The Kruskal-Wallis test and Mann Whitney test was applied to detect differences between sizes classes and richness. A small gap between 18 and 20 m² influenced the separation between medium-sized and large patches.

We defined life-forms in a somewhat detailed way to provide a better description and analysis of spatial variations. Our classification comprised 12 different life-forms, most of them commonly recognized and defined in several publications dealing with this subject (Mueller-Dombois and Ellenberg 1974). Our classification also considered the potential life-form achieved by adult plants, which was not always the case in the field, especially for potential tree species (appearing mostly in a shrubby state). For some analyses we also pooled life-forms into two main categories, namely those independent (self-supporting woody and succulent plants) and those subordinate (plants dependent on physical anchorage, living nutrients, or shadowy environments).

Non-metric multi-dimensional (NMDS) ordination was employed in order to visualize the effect of distances between woody islands (small distances) and study sites (large distances). For this comparison we used a matrix of species' abundances in all 48 woody islands. The Bray-Curtis index, weighted by percent abundance per patch, was used to construct matrices of pairwise distances among plots for the ordinations. Statistical analyses were performed using the R environment (R Core Team 2015) with the package `vegan` `Vegan` (Oksanen et al. 2017) and program `PAST` (Hammer et al. 2001).

3. Results

We sampled a total area of 1028.69 m², including all 48 patches in the four study sites (Table 2). The area of single patches roughly varied between four and 205 m² (precisely between 3.98 and 203.58 m²). All single study sites had one or two relatively large outliers in either area or volume, standing far away from the majority smaller and more clumped woody islands. Maximum height of each island varied from 0.50 to 7.00 m, and seven islands had true trees, measuring between five and seven meters in height. These trees occurred in all areas except Bacupari, where two patches achieved a maximum height of 3.00 m. *Myrsine guianensis* and *Daphnopsis racemosa* Griseb. were the two most common dominant species in the centre of patches (Table 3), the former often appearing as a true tree (at least 5.00 m in height) and the second mostly as a typical shrub (ramified from the base and not exceeding 3.00 in height).

Table 2. Structural variables and species richness of woody islands in each study site. MBDI = Mean distance between islands. S_{mean} = mean species richness, S_{max} = maximum species richness in a single island, S_{total} = total species richness in all 12 islands of each study site.

Study site	Area m ²	Volume m ³	MDBI m	Species Richness		
				S_{mean}	S_{max}	S_{total}
Bacupari	249.63	1611.82	10.08	9.67	16	27
Palmares	173.52	1658.99	21.20	8.75	15	24
Cidreira	451.73	5932,52	14.57	20.75	45	65
Tramandaí	153.81	1501.37	29.10	20.83	41	62

Table 3. Floristic composition, life-form and frequency (number of occurrences) of dominant species according to woody island area in all four studied sites. LF = life-form. See Table 6 for life-form abbreviations. Species are displayed according to decreasing total abundance. Small islands measured less than 10 m², medium islands between 10 and 18 m², and large islands more than 20 m².

Species \ Island Size	LF	Small	Medium	Large	Total
<i>Myrsine guianensis</i>	T	3	6	4	13
<i>Daphnopsis racemosa</i>	S	5	5	2	12
<i>Myrcia palustris</i>	T	1	5	2	8
<i>Opuntia monacantha</i>	SS	3	2	2	7
<i>Eugenia uniflora</i>	T	1	1	3	5
<i>Eugenia hyemalis</i>	ST	2	1	1	4
<i>Psidium cattleianum</i>	T	1	0	2	3
<i>Dodonaea viscosa</i>	ST	1	0	1	2
<i>Guapira opposita</i>	T	1	0	1	2
<i>Myrsine parvifolia</i>	T	1	0	1	2
<i>Sapium glandulosum</i>	T	0	2	0	2
<i>Sideroxylon obtusifolium</i>	T	0	2	0	2
<i>Vitex megapotamica</i>	T	1	0	1	2
<i>Allophylus edulis</i>	T	1	0	0	1
<i>Celtis iguanaea</i>	SC	0	1	0	1
<i>Cereus alacriportanus</i>	SS	0	1	0	1
<i>Chrysophyllum marginatum</i>	T	0	0	1	1
<i>Cupania vernalis</i>	T	0	0	1	1
<i>Erythroxylum argentinum</i>	T	1	0	0	1
<i>Gymnanthes klotzschiana</i>	T	0	0	1	1
<i>Lithraea brasiliensis</i>	T	0	1	0	1
<i>Ocotea pulchella</i>	T	0	0	1	1
<i>Schinus terebinthifolius</i>	T	0	1	0	1

Our floristic inventory resulted in 102 species, belonging to 88 genera and 49 families (complete list as supplementary material S2). Myrtaceae, with eight species, was the most diversified family when all studied sites are pooled. Three other families contributed with a relatively high number of species, namely the Bromeliaceae (seven species), Asteraceae (six species) and Rubiaceae (five species). Additionally, a set of five families appeared with four species each, the Apocynaceae, Cactaceae,

Commelinaceae, Euphorbiaceae and Sapindaceae. All other families had three or fewer species.

The floristic comparison among all four study sites by a Venn diagram (Fig. 2), showed a relatively high number of species restricted and shared between the northern study sites Cidreira and Tramandaí (around 20 species), and a relatively low number of species occurring in all areas (7 species). The two southern sites Palmares and Bacupari, had no species in common, and the same occurred when comparing Bacupari, Palmares and Tramandaí.

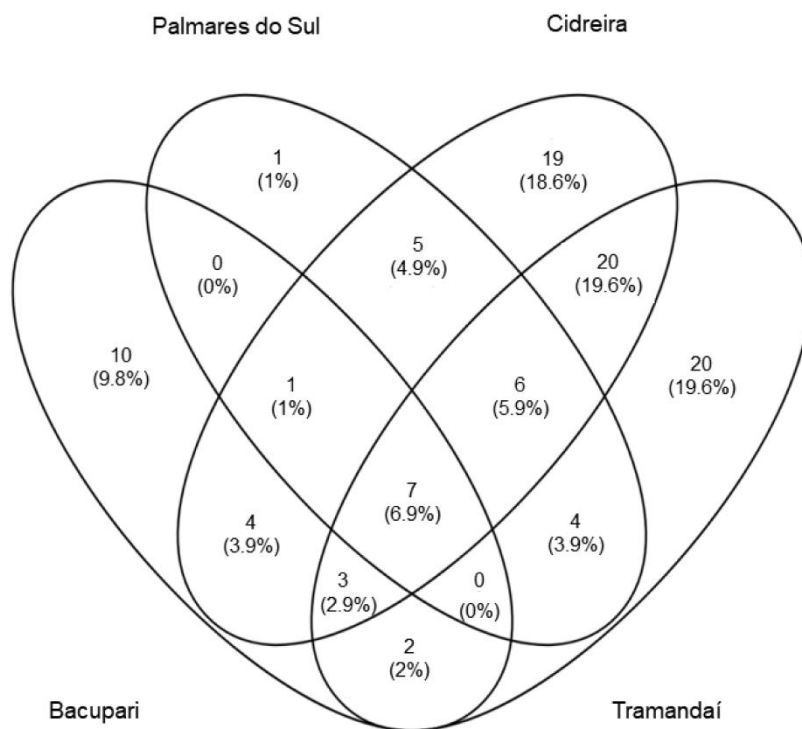


Fig. 2 Venn diagram resulting from species composition and distribution in the four studied areas with woody islands. The figure evidences the relatively low number of species occurring in all the four areas (seven), and the relatively high number of species restricted and shared between Cidreira and Tramandaí, the two most diversified study sites.

Table 4. Floristic composition, life-form (LF) and mean abundance estimation of the most common (abundance higher than 1.00) species in the three area classes of woody islands of coastal grasslands in Rio Grande do Sul, South Brazil. See Table 6 for life-form abbreviations. Small islands measured less than 10 m², medium islands between 10 and 18 m², and large islands more than 20 m².

Plant Categories	Family	LF	Small	Medium	Large	Total
Independent Species						
<i>Daphnopsis racemosa</i>	Thymelaeaceae	S	3.31	2.79	1.77	7.87
<i>Myrsine guianensis</i>	Primulaceae	T	1.63	1.95	2.00	5.58
<i>Opuntia monacantha</i>	Cactaceae	SS	1.06	1.53	1.77	4.36
<i>Myrcia palustris</i>	Myrtaceae	T	0.44	2.00	1.23	3.67
<i>Eugenia hyemalis</i>	Myrtaceae	ST	1.31	0.79	1.31	3.41
<i>Eugenia uniflora</i>	Myrtaceae	T	0.94	0.32	1.69	2.95
<i>Lithraea brasiliensis</i>	Anacardiaceae	T	1.00	0.68	1.08	2.76
<i>Lantana camara</i>	Verbenaceae	SC	0.75	0.79	1.00	2.54
<i>Erythroxylum argentinum</i>	Erythroxylaceae	T	0.63	0.47	0.92	2.02
<i>Myrsine parvifolia</i>	Primulaceae	T	0.56	0.63	0.77	1.96
<i>Guapira opposita</i>	Nyctaginaceae	T	0.69	0.21	1.00	1.90
<i>Varronia curassavica</i>	Boraginaceae	S	0.81	0.68	0.31	1.80
<i>Sideroxylon obtusifolium</i>	Sapotaceae	T	0.19	0.58	0.62	1.39
<i>Schinus terebinthifolius</i>	Anacardiaceae	T	0.25	0.68	0.38	1.31
<i>Psidium cattleianum</i>	Myrtaceae	T	0.38	0.00	0.85	1.23
<i>Annona maritima</i>	Annonaceae	ST	0.00	0.21	1.00	1.21
<i>Lantana fucata</i>	Verbenaceae	SC	0.13	0.47	0.54	1.14
<i>Vitex megapotamica</i>	Lamiaceae	T	0.44	0.00	0.62	1.06
Subordinate Species						
<i>Smilax campestris</i>	Smilacaceae	C	4.44	3.21	3.38	11.03
<i>Tillandsia aeranthos</i>	Bromeliaceae	E	0.81	2.16	2.77	5.74
<i>Microgramma vacciniifolia</i>	Polypodiaceae	E*	0.31	0.58	2.08	2.97
<i>Peperomia glabella</i>	Piperaceae	E*	0.44	0.53	1.62	2.59
<i>Dalechampia micromeria</i>	Euphorbiaceae	C	0.81	0.47	0.77	2.05
<i>Vriesea procera</i>	Bromeliaceae	E	0.38	0.74	0.92	2.04
<i>Passiflora suberosa</i>	Passifloraceae	C	0.56	0.26	0.85	1.67
<i>Dicliptera squarrosa</i>	Acanthaceae	G	0.19	0.37	0.85	1.41
<i>Rumohra adiantiformis</i>	Dryopteridaceae	G	0.38	0.53	0.31	1.22
<i>Asparagus setaceus</i>	Asparagaceae	C	0.19	0.16	0.77	1.12

(*) also observed as herb-subshrub (HS)

Abundance estimations evidenced the same dominant species in the patches, but here *Daphnopsis racemosa* was more important than *Myrsine guianensis* among the independent species (Table 4). A quite different life form appeared as the third species, the stem succulent cactus *Opuntia monacantha* Haw. Among the so defined subordinate species, the climber *Smilax campestris* Griseb. appeared as the most common species, followed by the epiphytic bromeliad *Tillandsia aeranthes* (Loisel.) L.B.Sm. The relatively high abundance of *Microgramma vacciniifolia* (Langsd. & Fisch.) Copel. and *Peperomia glabella* (Sw.) A.Dietr. is probably related to their capacity of occurring both as epiphytes and herb-subshrub.

Species richness variations, estimated both as a mean and a maximum per island, and the total number of species per study site, evidenced a great similarity between two pairs of study sites, the southern Bacupari and Palmares and the northern Cidreira and Tramandaí (Table 2). These areas were statistically identical within the pairs ($p > 0.05$) and statistically different between the pairs ($p > 0.05$). The relationship between area of woody islands and species richness (Fig. 3 and 4) was significant for both the less diversified study sites ($r_s = 0.7472$) as for the more diversified study sites ($r_s = 0.3049$), although the relationship was better explained in the former. The multiple linear regression (Table 5) showed that area was not significant when compared to volume ($p = 0.2675$), but when this parameters were analysed together the relation was significant ($p = 0.030$).

Table 5. Multiple regression coefficients and associated t-tests for the area and volume related to the woody islands in the coastal grasslands. Bold numbers represent a significant difference ($p < 0.05$).

Variable	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	12.1190	1.4951	8.106	0.0001
Area	-0.1651	0.1470	-1.123	0.2675
Volume	0.0383	0.0148	2.585	0.0131
Area : Volume	-0.0001	0.0001	-2.238	0.0303

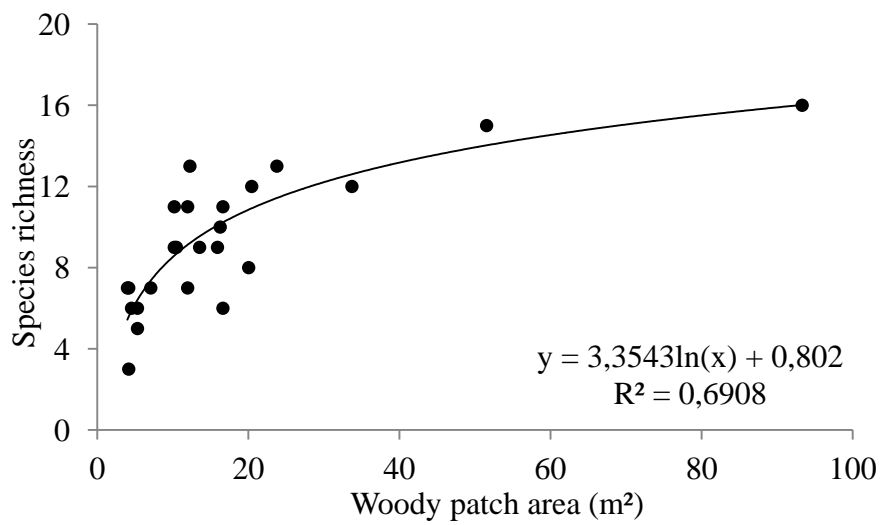


Fig. 3 Regressions between area of woody islands and species richness in the two least diversified study sites: Bacupari (mean richness = 9.67 ± 3.23) and Palmares (mean richness = 8.75 ± 3.41).

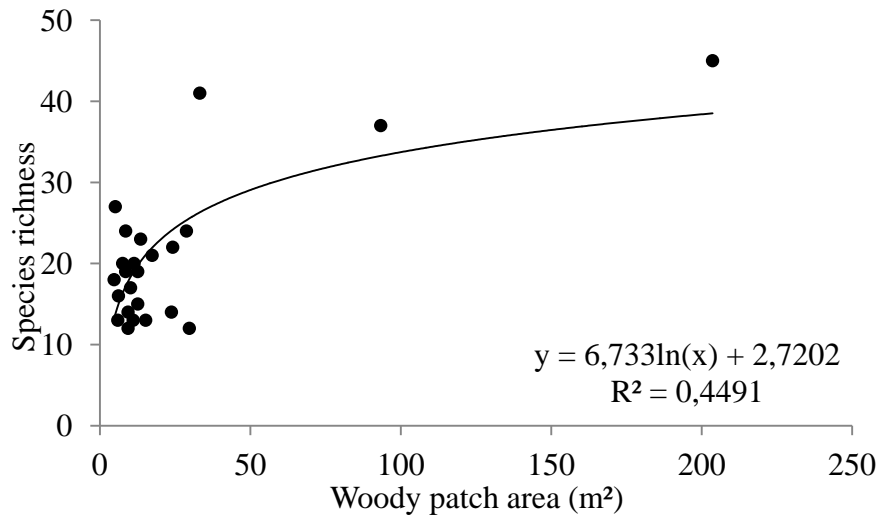


Fig. 4 Regressions between area of woody islands and species richness in the two most diversified study sites: Cidreira (mean richness = 20.75 ± 10.68) and (Tramandaí (mean richness = 20.83 ± 7.28)).

The spatial evolution of life-form diversity and abundance according to patch size categories (Table 6, Fig. 5) evidenced potential tree species as the most important adaptation in woody islands, followed by epiphytes and climbers. However, epiphytes became more diverse and abundant only in large islands, leaving climbers from second to third position in relation to small and medium-sized islands. All 12 recognized life-forms appeared only in large islands, taken as a reference for the decreasing ordination of categories. In small islands four less abundant and less diversified life-forms were absent, as those defined as hemiparasites (*Phoradendron*, *Tripodanthus*), rosette-xerophytes (*Bromelia*), hemiepiphytes (*Thaumatococcus*) and palm-trees (*Euterpe*). Among these four categories, only hemiparasites already appeared in medium-sized islands. A statistical analysis indicated no significant difference among the comparison of life-form abundances according to increasing area categories ($p = 0.2382$).

Table 6. Mean species richness and total abundance for different life-forms in three size classes of woody islands in coastal Rio Grande do Sul. Life-forms are arranged according to decreasing species richness in large islands. Small islands measured less than 10 m², medium islands between 10 and 18 m², and large islands more than 20 m². Life-forms assigned with (*) were classified as independent, all others as subordinate, including one shade-tolerant palm-tree (*Euterpe edulis*).

Life form	Code	Mean Species Richness			Total Abundance		
		Small	Medium	Large	Small	Medium	Large
Tree*	T	1.19	1.00	1.77	8.25	9.32	15.00
Epiphyte	E	0.38	0.26	1.15	2.06	4.42	9.85
Climber	C	0.88	0.58	1.08	7.63	5.16	7.54
Herb-Subshrub	HS	0.75	0.58	1.00	2.38	2.47	3.00
Shrub*	S	0.31	0.32	0.46	4.88	4.00	2.85
Shrub-Climber*	SC	0.19	0.32	0.38	1.25	2.00	2.38
Shrub-Treelet*	ST	0.19	0.21	0.31	1.69	1.16	2.77
Succulents-Xerophyte*	SX	0.13	0.11	0.15	1.25	1.95	2.08
Hemiparasite	HP	0.00	0.11	0.15	--	0.11	0.46
Rosette-Xerophytes *	RX	--	--	0.08	--	--	0.38
Hemiepiphyte	HE	--	--	0.08	--	--	0.15
Palm-Tree	PT	--	--	0.08	--	--	0.08

Obs.: shrub-climbers were classified as independent plants because they commonly occur without mechanical support in the patches; xerophytes because they tolerate high sun exposure at the margins of the patches, despite also occurring in the understory.

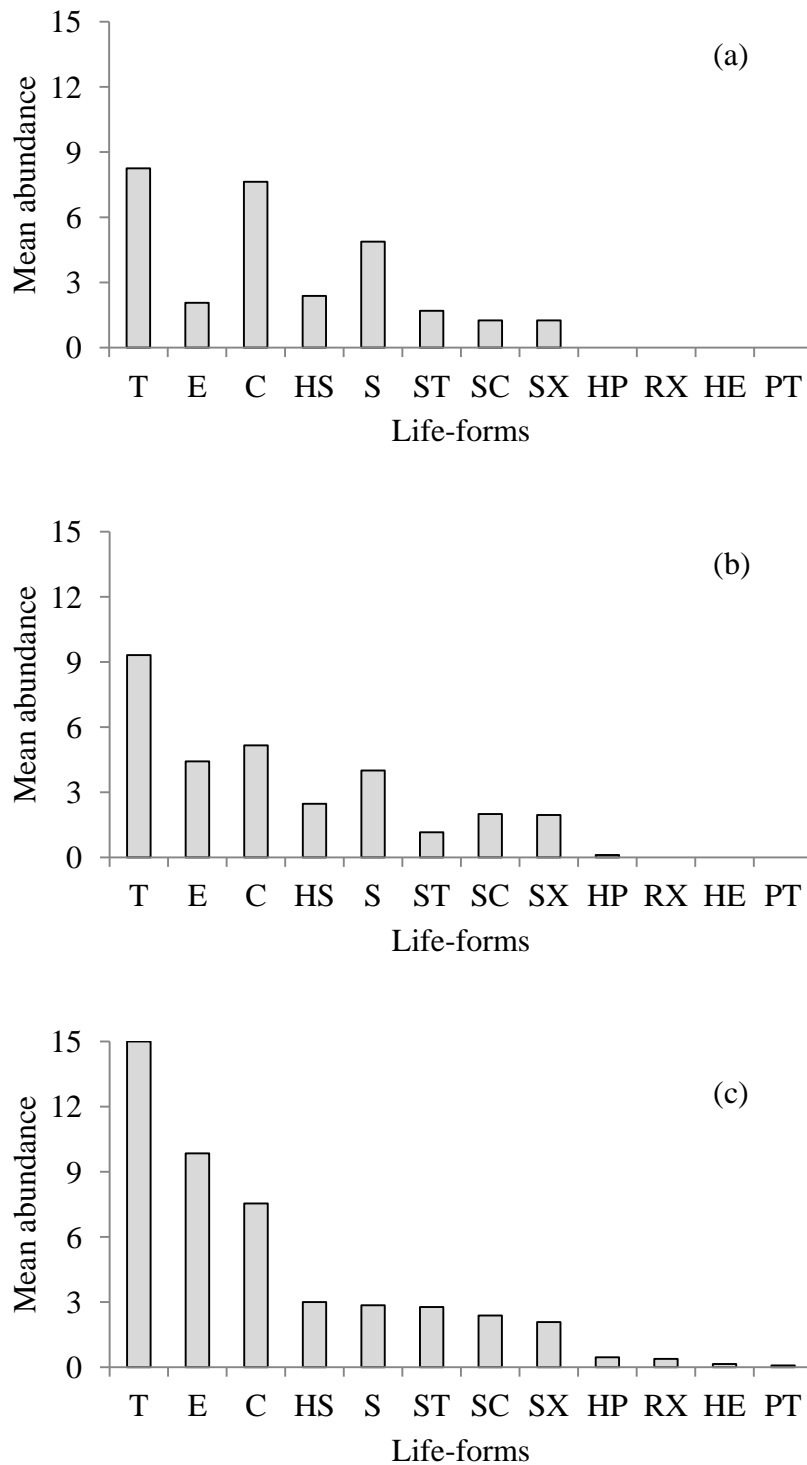


Fig. 5 Effect of woody island area on life-form diversity and abundance in coastal Rio Grande do Sul: (a) small islands with less than 10 m²; (b) medium islands between 10 and 18 m²; and (c) large islands with more than 20 m². Life-forms were ordered in a decreasing sequence according to the values obtained in large islands. See Table 6 for life-form abbreviations.

The grouping of all life-forms into two main categories, i.e., independent and subordinate plants (Fig. 6) showed no significant differences in species richness among island areas when considering independent plants ($p > 0.05$), neither for subordinate plants in small and medium-sized islands ($p = 0.5292$), but alternatively showed significant differences between these two categories and large islands ($p = 0.0213$; $p = 0.0156$). Mean species richness of independent and subordinate achieved very similar values in large islands: 10.615 versus 10.231, respectively.

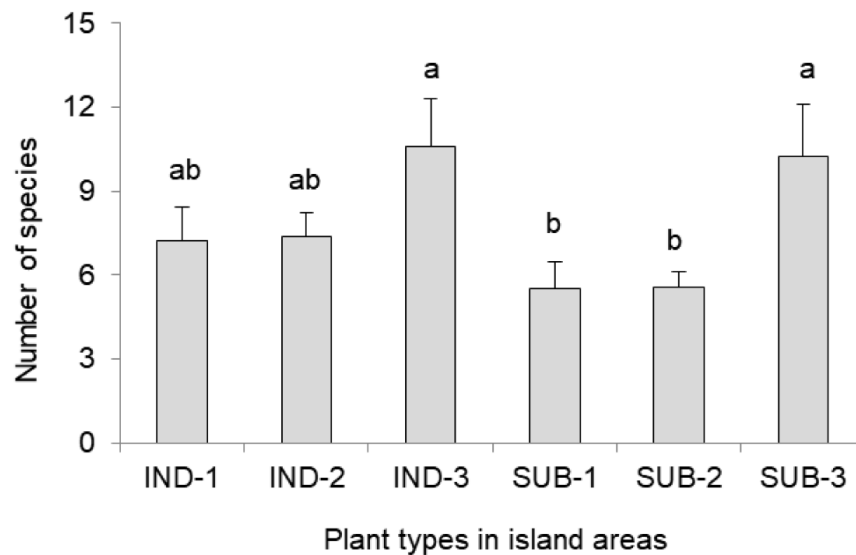


Fig. 6 Effect of patch sizes on the mean number of species in the two main plant types: IND = independent species; SUB = subordinate species. Patch sizes: 1 = small (area less than 10m²); 2 = medium-sized (area between 10 and 18 m²), and 3 = large (area more than 20 m²). Error bars indicate the standard error of the mean. Different letters indicate statistical differences for a significance level = 0.05.

The ordination analysis of all 48 sample units (woody islands) showed a clear separation of the four study sites, indicating that larger distances among study sites are more important than smaller distances among woody patches (Fig. 7). Additionally, the

size (area) of islands was also a lesser factor of floristic differentiation within the study sites, despite a relatively great variation and the presence of outliers in this spatial estimation (see also Fig.3 and 4). One single sample unit from Cidreira showed to be relatively distant from all others in this study site, and thus more similar with those from Tramandaí (Fig. 7). This discrepancy was probably not due to the effect of island size, but rather to floristic composition and abundance.

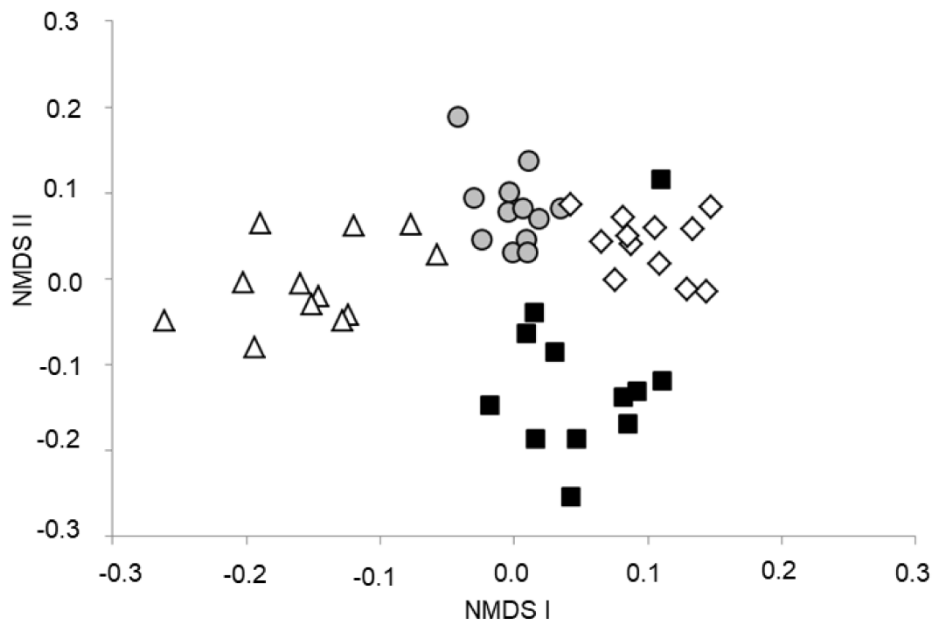


Fig. 7 Ordination diagram of sample units (woody patches) resulting from non-metric multidimensional scaling (NMDS) analysis, distinguishing the four study sites sampled in the coastal plain of Rio Grande do Sul. Stress = 0.2506. Symbols represent the study sites: open triangles = Bacupari, gray circles = Palmares, black squares = Cidreira and open diamonds = Tramandaí.

4. Discussion

Our study evidenced the Myrtaceae as the most diversified family when the entire flora of woody islands is considered. This family is also commonly the most speciose in several different tropical and subtropical forest formations, where the

species occur mostly as trees and sometimes as shrubs (Oliveira-Filho and Fontes 2000; Lucas and Bunker 2015). The Myrtaceae are also an important family in coastal woodlands, often standing out for the relatively high number of species or the high abundance in a single species (Jarenkow and Waechter 2001; Marques et al. 2015). With the exception of *Campomanesia aurea* O.Berg, a small heliophytic shrub, all other species in our list also occur in closed forests, suggesting these environments both as an origin of diaspores and a direction of woody patch temporal evolution. The emblematic family Clusiaceae, which is often mentioned for tropical coastal woodlands (Dias and Scarano 2007; Zaluar and Scarano 2000), was completely absent in our inventories, possibly as a result of the subtropical climate. *Clusia criuva* Cambess., the southernmost species of the genus, occurs mostly as a hemiepiphyte in the Atlantic forest of Rio Grande do Sul (Orihuela et al. 2014), but also appears as a shrub in coastal dunes near the border with Santa Catarina (Beduschi and Castellani 2008).

The Bromeliaceae was the second most diversified family in the woody islands, but differently from tropical woody patches in our study they occurred mostly as epiphytes. *Bromelia antiacantha* Bertol, the single terrestrial species occurred in only one woody island in Tramandaí, despite being a quite common species in the understory and the margins of well-drained dune forests (Smith and Downs 1979). The species has probably little importance as a nurse plant in open coastal habitats, since no isolated rosettes or clumps were observed in the grasslands during field work. The absence of tank-forming bromeliads as pioneers or focal species in our study might be an interesting difference in comparison with the more tropical restingas, where species of *Aechmea* and *Neoregelia* are commonly referred in this condition (Zaluar and Scarano 2000).

The floristic comparison between study sites evidenced the relatively high

number of species both restricted and shared between the northern areas, suggesting a latitudinal influence despite the areas are not much apart one from another (Morawetz 1983). The latitudinal influence is in fact an important spatial variable along the coastal plain of Rio Grande do Sul, mostly reducing the occurrence of tropical species as the temperature and rainfall decrease from north to south (Rambo 1951). These changes affect the species diversity in most life-forms, but are especially outstanding when regarding palms, large-leaved monocotyledons (Heliconiaceae, Marantaceae) and vascular epiphytes (Svenning et al. 2008; Leitman et al. 2015; Machado et al. 2016). In our study twice as many epiphytes occurred in the northern areas when compared with the southern ones (14/7), but this difference can also be attributed to the presence of a few relatively large trees. The lower number of species shared and restricted between the southern study sites indicates regional differences, such as lagoon proximity and the more hilly landform in Bacupari, but possibly also to minor changes in soil properties of the sandy deposits.

Only 17 species occurred in three or four study sites, contrasting with 85 species restricted to one or two study sites. Among the former more widespread species several are typical trees often sampled in phytosociological studies performed in coastal white sand woodlands, such as *Myrcia palustris* DC., *Lithraea brasiliensis* Marchand, *Erythroxylum argentinum* O.E.Schulz, *Myrrhinium atropurpureum* Schott, and *Chrysophyllum marginatum* (Hook. & Arn.) Radlk. (Scherer et al. 2005; Marques et al. 2014). The occurrence of these species in small woody islands indicates a wide ecological tolerance, an effective dispersal mechanism, and a potential development into forest vegetation. A few additional widespread species are remarkable for their high abundance (*Smilax campestris* and *Daphnopsis racemosa*) or otherwise for their physiognomic importance, as the two species of terrestrial cacti (*Opuntia monacantha*

and *Cereus hildmannianus* *Cereus hildmannianus* K.Schum.). The later are among the most striking species distinguishing well-drained white dune forests from water-logged peat or swamp forests.

As expected by our first hypothesis, species richness increased significantly with the size of woody islands, and thus agrees with one of the basic premises of Theory of Island Biogeography (MacArthur and Wilson 1967). The presence of one or two outliers in terms of large area (Bacupari, Palmares and Cidreira), or in terms of high species richness (Tramandaí) probably reduces the level of correlation or explication (R^2), but otherwise indicates a further stage of possible successional development. Other possible factors affecting species richness variation along the increasing tendency when compared to island area is the presence of real trees (not potential tree species), which certainly favour the occurrence of subordinate life-forms, particularly of vascular epiphytes. Nevertheless, our findings reinforce similar studies carried out in Argentinian savannas (Cabral et al. 2003), and South-Brazilian montane grasslands (Duarte et al. 2007).

Diversity and abundance of life-forms was not significantly different along the three area categories of woody patches, thus contradicting our second hypothesis. Despite this result, at least two interesting structural variations became evident. The most striking is the appearance of four quite distinct life-forms, despite their rare occurrence and low species richness: hemiparasites, hemiepiphytes, rosette-xerophytes and palm-trees. The former two are strongly linked to the occurrence of trees and are in a similar abundance-diversity condition as in floristic or ecological studies carried out in mature coastal forests (Dettke and Waechter 2014; Orihuela et al. 2014). The latter two can be defined as accidental occurrences of two very common species in mature coastal forests, the rosette-xerophytes (*Bromelia antiacantha* Bertol.) in the understory of dune

woodlands (Smith and Downs 1979) and the palm-tree (*Euterpe edulis*) in the tree layer of tall rainforests (Fantini et al. 2007; Soares et al. 2014). The other interesting evidence is the abundance inversion between climbers and epiphytes from small to large woody patches. Some species of climbers commonly grow at the margins of patches of any size, where they often start creeping on the ground (e.g. *Oxypetalum tomentosum* Wight ex Hook. & Arn.) or as erect rigid herbs (e.g. *Smilax campestris*), and latter leaning or climbing on nearby shrubs or treelets. Most species of vascular epiphytes otherwise require more developed patches or closed woodlands, where they become much more abundant and diversified (Benzing 1990).

The comparison between all woody islands in all four study sites indicated a higher similarity within each site, as expected by our third hypothesis. One alternative idea was that larger woody patches might converge towards a similar regional type of coastal white-sand woodland, as described by several authors (e.g. Dillenburg et al. 1992). The overall clear separation of the four study sites on the ordination diagram possibly indicates regional differences in soil properties, but the differences may also be due to variation in disturbance, particularly the distinct grazing intensities as hindering the natural expansion of woody patches. During our field work we did not observe recent human interferences, such as cutting of trees or shrubs, but these activities possibly occurred in past times. We neither observed any heavy cattle load in the four study areas, although the grassy vegetation between woody patches in general appeared as intensively grazed, except perhaps in Bacupari. Further studies are certainly needed to asses more precisely the spatial and temporal changes of woody patches into white-sand woodlands (restinga forests), which we suppose are the most developed vegetation type on well drained coastal plains in South Brazil.

Further studies are certainly needed to assess more precisely the spatial and temporal changes of woody patches into white-sand woodlands (restinga forests), which we suppose are the most developed vegetation type on well-drained coastal plains in South Brazil. The general floristic and structural overview given in this contribution is an important step to carry further ecological studies, especially the comparison with larger forest fragments. Small woody patches are more endangered than larger ones, mostly because they can be easily removed for the maintenance of grasslands, which in turn are essential for cattle raising. However, to achieve these goals, a set of larger forest fragments still needs to be studied, just in order to provide a better understanding of spatial variations, with possible inferences on dynamic processes.

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Considerações finais

Com este estudo abordamos pela primeira vez as variações florísticas e estruturais das ilhas lenhosas de restinga localizadas na Planície Costeira do Rio Grande do Sul. Descrevemos a riqueza e a abundância de todas as espécies lenhosas e herbáceas encontradas em 48 moitas distribuídas em quatro áreas de estudo. Classificamos as espécies em 12 formas vitais facilmente reconhecidas na natureza e amplamente definidas na literatura ecológica, para caracterizar esse ambiente insular da melhor forma possível. Em pouco mais de 1000 m² amostrados verificamos que as áreas mais ao sul (Bacupari e Palmares) se apresentaram mais pobres que as localizadas mais ao norte (Cidreira e Tramandaí). Considerando três classes de tamanhos de áreas de moitas, verificamos que a área mais rica, Cidreira, apresentou maior quantidade de ilhas médias e grandes. Por outro lado, Tramandaí a segunda área mais rica, apresentou na sua maioria moitas pequenas. As duas áreas mais pobres apresentaram maior homogeneidade na distribuição de classes de tamanho.

Classificamos as 12 formas vitais encontradas em duas categorias principais: independentes e subordinadas. As espécies independentes com maior diversidade e abundância foram as árvores e os arbustos, enquanto entre as subordinadas os epífitos, trepadeiras e ervas subarbusivas. Epífitos demonstraram maior riqueza e abundância em moitas grandes, diferentes de trepadeiras e ervas subarbusivas, que mantiveram um padrão semelhante nestes parâmetros nos três diferentes tamanhos de moitas. A maior diversidade de formas de vida foi encontrada em moitas grandes e foi também nesta classe de tamanho onde ocorreram exclusivamente três das 12 formas vitais encontradas, definidas como xerófitos, (*Bromelia*) hemiepífitos (*Thaumatococcus*) e palmeiras (*Euterpe*).

Nosso trabalho deixa em aberto outras questões para serem respondidas em

trabalhos futuros, tais como: (i) Quais atributos funcionais estão envolvidos no estabelecimento e no sucesso das espécies subordinadas nas moitas? (ii) Como a dispersão de sementes atua na estrutura organizacional destas ilhas? (iii) Como se dá a evolução das ilhas ao longo do tempo?

As questões levantadas por nós no artigo, assim como as que surgiram no final do trabalho, mencionadas acima, são fundamentais para o conhecimento e a conservação deste ambiente que está ameaçado com o avanço antrópico na Planície Costeira do Rio Grande do Sul.

Woody islands in South Brazilian coastal grasslands: effects of spatial variations on the structure of plant communities

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Supplementary Material 1. Selected images of woody patches from the four study sites



Plate 1. **Above:** small woody island with an emergent treelet (*Ficus cestrifolia*) strongly shaped by dominant northeastern winds; Lake Bacupari appears in the back. Bacupari – March 18, 2016. **Below:** a perfectly hemispheric woody patch with two cacti (*Cereus hildmannianus* and *Opuntia monacantha*) among the tallest species; the most common shrub (*Daphnopsis racemosa*) appears in the front. Palmares – August 25, 2016.



Plate 2. **Above:** a very small and incipient island almost exclusively characterized by a stem-succulent cactus (*Opuntia monacantha*), probably acting as a nurse plant due to its long spines. Cidreira – April 04, 2017. **Below:** a relatively small shrubby island with a central dead tree (possibly *Myrsine guianensis*) still hosting two epiphytic species (*Microgramma vacciniifolia* and *Tillandsia aeranthos*). Tramandaí – April 12, 2017.

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Supplementary Material 2. Woody patches in all study sites of coastal Rio Grande do Sul with their respective spatial measures: maximum diameter (Dmax), minimum diameter (Dmin), medium diameter (Dmed), and maximum height (Hmax).

Study Site	Code	Dmax m	Dmin m	Dmed m	Hmax m	Area m ²	Volume m ³
Bacupari	B1	2,9	2,3	2,60	1,40	5,31	19,56
	B2	6,7	4,3	5,50	2,00	23,76	120,68
	B3	2,4	2,1	2,25	0,90	3,98	9,50
	B4	3,7	3,5	3,60	1,80	10,18	48,82
	B5	4,0	3,8	3,90	1,70	11,95	54,12
	B6	4,7	4,5	4,60	1,80	16,62	79,73
	B7	4,7	3,6	4,15	2,90	13,53	102,77
	B8	3,0	2,2	2,60	2,00	5,31	27,65
	B9	5,7	4,4	5,05	1,80	20,03	94,55
	B10	6,9	6,2	6,55	3,00	33,70	268,79
	B11	3,90	3,90	3,90	1,30	11,95	41,41
	B12	11,50	10,30	10,90	3,00	93,31	744,24
Palmares	P1	2,60	2,00	2,30	1,20	4,15	13,07
	P2	5,40	4,80	5,10	3,00	20,43	162,86
	P3	4,60	4,60	4,60	2,10	16,62	93,07
	P4	3,70	2,30	3,00	1,80	7,07	32,08
	P5	4,80	4,20	4,50	3,00	15,90	126,67
	P6	8,30	7,90	8,10	5,50	51,53	755,31
	P7	3,30	1,50	2,40	1,80	4,52	18,66
	P8	4,90	4,20	4,55	4,00	16,26	172,41
	P9	2,50	2,10	2,30	1,20	4,15	13,19
	P10	3,70	3,50	3,60	4,00	10,18	108,49
	P11	4,20	3,10	3,65	3,00	10,46	81,81
	P12	4,20	3,70	3,95	2,50	12,25	81,37

Cidreira	C1	6,30	4,70	5,50	2,50	23,76	155,04
	C2	19,80	12,40	16,10	7,00	203,58	3599,51
	C3	6,50	5,80	6,15	3,00	29,71	29,71
	C4	2,70	2,40	2,55	2,50	5,11	5,11
	C5	4,90	3,10	4,00	1,60	12,57	50,90
	C6	13,70	8,10	10,90	5,50	93,31	1278,28
	C7	4,80	3,20	4,00	1,20	12,57	38,60
	C8	3,20	2,30	2,75	1,60	5,94	24,66
	C9	4,90	3,90	4,40	2,50	15,21	100,06
	C10	4,30	2,90	3,60	1,80	10,18	47,01
	C11	4,70	2,80	3,75	6,10	11,04	168,13
	C12	6,20	5,90	6,05	3,00	28,75	229,84
Tramandaí	T1	3,30	3,30	3,30	3,30	8,55	75,27
	T2	4,30	4,00	4,15	6,00	13,53	216,14
	T3	3,70	2,90	3,30	2,50	8,55	56,18
	T4	4,80	4,60	4,70	3,00	17,35	138,73
	T1	3,00	2,60	2,80	3,50	6,16	57,18
	T2	3,60	3,30	3,45	3,00	9,35	74,64
	T3	7,10	5,90	6,50	4,00	33,18	350,94
	T4	4,00	3,60	3,80	3,00	11,34	90,48
	T1	3,70	2,50	3,10	2,50	7,55	48,43
	T2	2,80	2,10	2,45	5,00	4,71	61,58
	T3	3,70	3,20	3,45	0,50	9,35	12,40
	T4	6,10	5,00	5,55	5,00	24,19	319,40

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Supplementary Material 3. Families and species of vascular plants sampled in woody patches in all study sites of coastal Rio Grande do Sul: Bacupari (BAC), Palmares (PAL), Cidreira (CID), and Tramandaí (TRA). Numbers under study sites indicate the total abundance of species. Life form (LF) codes are given at the end of the table.

Family	Species \ Study Site	LF	BAC	PAL	CID	TRA
Acanthaceae	<i>Dicliptera squarrosa</i>	HS	0	0	21	0
Amaranthaceae	<i>Gomphrena perennis</i>	HS	0	0	13	0
	<i>Pfaffia tuberosa</i>	HS	0	1	0	2
Anacardiaceae	<i>Lithraea brasiliensis</i>	T	13	0	2	28
	<i>Schinus terebinthifolius</i>	T	7	0	0	15
Annonaceae	<i>Annona maritima</i>	ST	0	0	15	2
Araceae	<i>Thaumatococcus bipinnatifidum</i>	HE	0	0	1	1
Apocynaceae	<i>Forsteronia glabrescens</i>	C	0	0	3	7
	<i>Forsteronia leptocarpa</i>	C	5	0	5	0
	<i>Oxypetalum banksii</i>	C	0	0	0	2
	<i>Oxypetalum tomentosum</i>	C	0	0	2	0
Arecaceae	<i>Euterpe edulis</i>	PT	0	0	0	1
Asparagaceae	<i>Asparagus setaceus</i>	C	0	3	13	0
Asteraceae	<i>Baccharis longiattenuata</i>	T	3	0	0	0
	<i>Elephantopus mollis</i>	HS	0	0	0	5
	<i>Mikania parodii</i>	C	3	0	0	0
	<i>Mikania involucreta</i>	C	0	1	1	1
	<i>Mutisia speciosa</i>	C	0	0	0	3
	<i>Trixis praestans</i>	S	0	1	7	0
Bignoniaceae	<i>Dolichandra unguis-cati</i>	C	0	0	4	0
Blechnaceae	<i>Telmatoblechnum serrulatum</i>	HS	1	0	0	0
Boraginaceae	<i>Varronia curassavica</i>	S	4	0	4	22
	<i>Varronia polycephala</i>	SC	0	0	0	14

Bromeliaceae	<i>Aechmea recurvata</i>	E	0	0	1	1
	<i>Bromelia antiacantha</i>	RX	0	0	0	5
	<i>Tillandsia aeranthos</i>	E	27	20	30	13
	<i>Tillandsia geminiflora</i>	E	0	0	1	0
	<i>Tillandsia stricta</i>	E	13	0	0	0
	<i>Tillandsia usneoides</i>	E	0	1	4	0
	<i>Vriesea procera</i>	E	16	0	16	0
Cactaceae	<i>Cereus hildmannianus</i>	SX	0	11	2	2
	<i>Lepismium cruciforme</i>	E	0	0	1	1
	<i>Opuntia monacantha</i>	SX	2	46	21	0
	<i>Rhipsalis teres</i>	E	0	0	2	1
Commelinaceae	<i>Callisia repens</i>	HS	0	0	2	0
	<i>Commelina erecta</i>	HS	0	0	13	0
	<i>Commelina obliquoa</i>	HS	0	0	0	6
	<i>Tradescantia anagallidea</i>	HS	0	0	1	0
Cannabaceae	<i>Celtis iguanaea</i>	SC	0	0	8	0
Caryophyllaceae	<i>Drymaria cordata</i>	HS	0	0	0	1
Convolvulaceae	<i>Ipomea bonariensis</i>	C	0	0	0	1
Dioscoreaceae	<i>Dioscorea multiflora</i>	C	0	0	1	0
Dryopteridaceae	<i>Rumohra adiantiformis</i>	HS	0	13	0	7
Erythroxylaceae	<i>Erythroxylum argentinum</i>	T	0	3	8	20
Euphorbiaceae	<i>Alchornea triplinervia</i>	T	0	0	0	1
	<i>Dalechampia micromeria</i>	C	0	0	27	5
	<i>Gymnanthes serrata</i>	T	0	0	9	0
	<i>Sapium glandulosum</i>	T	0	0	0	13
Fabaceae	<i>Centrosema virginianum</i>	C	0	0	5	2
	<i>Senna corymbosa</i>	ST	0	0	3	1
Lamiaceae	<i>Vitex megapotamica</i>	T	0	0	0	15
Lauraceae	<i>Ocotea pulchella</i>	T	8	0	0	0
Loranthaceae	<i>Tripodanthus acutifolius</i>	HP	1	0	2	0
Malpighiaceae	<i>Janusia guaranitica</i>	C	0	0	4	4
Malvaceae	<i>Sida urens</i>	HS	0	0	0	14
Melastomataceae	<i>Miconia hyemalis</i>	T	0	0	0	4
	<i>Tibouchina asperior</i>	HS	9	0	0	0
Myrtaceae	<i>Blepharocalyx salicifolius</i>	T	3	0	0	0
	<i>Campomanesia aurea</i>	S	0	0	3	0
	<i>Eugenia hyemalis</i>	ST	4	20	8	21
	<i>Eugenia uniflora</i>	T	0	0	28	15
	<i>Myrcia glabra</i>	T	0	0	0	1
	<i>Myrcia palustris</i>	T	37	13	1	10
	<i>Myrrhinium atropurpureum</i>	T	0	2	5	3
	<i>Psidium cattleianum</i>	T	16	0	0	1
Nyctaginaceae	<i>Guapira opposita</i>	T	0	0	6	22
Orchidaceae	<i>Cattleya intermedia</i>	E	1	0	0	0

	<i>Lankesterella ceracifolia</i>	E	0	0	1	0
	<i>Trichocentrum pumilum</i>	E	0	0	1	0
Passifloraceae	<i>Passiflora suberosa</i>	C	0	1	10	14
Piperaceae	<i>Peperomia catharinae</i>	E	7	0	1	0
	<i>Peperomia glabella</i>	E	0	0	30	8
	<i>Peperomia pereskiifolia</i>	E	0	0	5	0
Poaceae	<i>Oplismenus hirtellus</i>	HS	0	0	0	2
	<i>Panicum sellowii</i>	HS	0	0	0	6
	<i>Pseudechinolaena polystachya</i>	HS	0	0	5	1
Polypodiaceae	<i>Microgramma vacciniifolia</i>	E	16	3	19	5
	<i>Serpocaulon catharinae</i>	HS	0	1	0	0
Primulaceae	<i>Myrsine guianensis</i>	T	0	36	12	41
	<i>Myrsine parvifolia</i>	T	31	0	0	0
Rhamnaceae	<i>Scutia buxifolia</i>	T	1	0	0	0
Rubiaceae	<i>Chiococca alba</i>	SC	0	0	2	5
	<i>Galium hypocarpium</i>	C	0	0	0	2
	<i>Guettarda uruguensis</i>	SC	0	0	2	0
	<i>Psychotria carthagenensis</i>	S	0	0	0	16
	<i>Randia ferox</i>	T	0	0	2	0
Rutaceae	<i>Zanthoxylum fagara</i>	T	0	0	10	1
Salicaceae	<i>Casearia sylvestris</i>	T	0	0	0	10
Santalaceae	<i>Phoradendron piperoides</i>	HP	0	0	3	2
Sapindaceae	<i>Allophylus edulis</i>	T	0	0	7	3
	<i>Cupania vernalis</i>	T	0	5	1	0
	<i>Dodonaea viscosa</i>	ST	0	0	5	6
	<i>Paullinia trigonia</i>	C	0	3	0	7
Sapotaceae	<i>Chrysophyllum marginatum</i>	T	1	0	6	3
	<i>Sideroxylon obtusifolium</i>	T	0	0	22	0
Smilacaceae	<i>Smilax campestris</i>	C	36	48	35	57
Solanaceae	<i>Cestrum strigillatum</i>	S	0	0	1	4
	<i>Solanum laxum</i>	C	0	1	0	1
Thymelaeaceae	<i>Daphnopsis racemosa</i>	S	20	45	22	42
Tropaeolaceae	<i>Tropaeolum pentaphyllum</i>	C	0	0	1	0
Verbenaceae	<i>Lantana camara</i>	SC	1	7	13	19
	<i>Lantana fucata</i>	SC	0	4	14	0

Life forms: Trees (T), Epiphytes (E), Climbers (C), Herb-Subshrub (HS), Shrubs (S), Shrub-Climbers (SC), Shrub-Treelets (ST), Succulents-Xerophyte (SX), Hemiparasites (HP), Rosette-Xerophytes (RX), Hemiepiphytes (HE), and Palm-Trees (PT).