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Desvendando o efeito da proximidade da costa na estrutura e diversidade da vegetação herbácea nas dunas de areia costeiras[1]

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RESUMO

A restinga é um tipo de ecossistema costeiro, moldada por intricadas interações entre fatores bióticos e abióticos limitantes. Eles desempenham um papel vital na manutenção da biodiversidade global e fornecem serviços ecossistêmicos essenciais. A vegetação em dunas costeiras se adapta de maneira distinta às variações ambientais, mas continua altamente vulnerável às atividades humanas e às mudanças climáticas, exigindo uma compreensão abrangente de suas respostas a diferentes condições ambientais. Nossa investigação concentrou-se na vegetação herbácea de restinga dentro de micro-habitats potenciais e escalas de distância da praia, buscando revelar sua influência na composição e distribuição das espécies vegetais. O objetivo é aprimorar nossa compreensão dos padrões de dunas costeiras, ao mesmo tempo identificar possíveis espécies indicadoras e micro-habitats. Avaliamos a cobertura de espécies em 156 parcelas de amostra distribuídas ao longo de seis transectos em 26 escalas de distância, considerando micro-habitats e fatores ambientais. Nossa análise considerou a cobertura, riqueza e composição de espécies em relação à distância da praia dentro de cada micro-habitat. Os resultados sugerem que a riqueza de espécies está mais fortemente relacionada com os tipos de micro-habitats do que com a distância da praia. O reconhecimento de alguns dos micro-habitats específicos foi facilitado pela cobertura e espécies indicadoras. A análise de redundância destacou que a inclinação do terreno, exposição ao solo e alagamento como contribuintes significativos para as variações na composição da comunidade vegetal. Áreas de dunas frontais e baixadas alagadas se destacaram distintamente em comparação com demais micro-habitats. Nossos resultados enfatizam o papel das condições locais, como alagamento, inclinação do terreno e exposição ao solo, na estruturação das comunidades de plantas costeiras e na seleção de espécies. Este estudo oferece insights valiosos sobre esses ecossistemas, na identificação de micro-habitats e de espécies indicadoras, visando enfrentar os desafios da conservação da biodiversidade diante das mudanças climáticas globais.

Palavras-chave: Restinga, Ecossistemas costeiros, Cobertura de vegetação, Espécies indicadoras, Micro-habitat.

Unraveling the effect of proximity to the shore on the structure and diversity of herbaceous vegetation on coastal sand dunes

ABSTRACT

Restinga is a type of coastal ecosystem, shaped by intricate interactions between limiting biotic and abiotic factors. They play a vital role in global biodiversity maintenance and provide essential ecosystem services. Vegetation in coastal dunes adapts distinctly to environmental variations yet remains highly vulnerable to human activities and climate change, warranting a comprehensive understanding of its responses to diverse environmental conditions. This investigation focused on herbaceous restinga vegetation within potential microhabitats and beach distance scales, seeking to unveil their influence on plant species composition and distribution. The aim was to enhance our understanding of coastal dune patterns while identifying potential indicator species and microhabitats. We evaluated species coverage across 156 sample plots distributed over six transects at 26 distance scales, considering microhabitats and environmental factors. The analysis encompassed species coverage, richness, and composition concerning beach distance within each microhabitat. Results suggest that species richness correlated more strongly with microhabitat types than beach distance. Identification of specific microhabitats was aided by coverage and indicator species. Redundancy analysis highlighted terrain, soil exposure, and flooding as significant contributors to variations in plant community composition. Frontal dune areas and humid slack dunes stood out distinctly compared to other microhabitats. Our findings underscore the crucial role of local conditions—like flooding, terrain slope, and soil exposure—in shaping coastal plant communities and species selection. This study offers valuable insights into these ecosystems, pivotal for identifying microhabitats and indicator specie and for effectively addressing biodiversity conservation challenges amid global climate change.

Key words: Restinga, Coastal ecosystems, Vegetation cover, Species indicator, Microhabitats.

Introduction

Coastal ecosystems, present on every continent, are shaped by a complex interaction of biotic and abiotic factors, such as climate, sea level, ocean currents, geomorphology, and human activities (Hesp, 1991; Burke et al., 2001; Psuty, 2008). These ecosystems perform essential functions that support global biodiversity and contribute to climate change mitigation through nutrient cycling, carbon sequestration, and coastal erosion prevention. Additionally, they provide support for artisanal fisheries and the promotion of sustainable ecotourism (Martínez et al., 2007; Richardson & Nicholls, 2021; Du & Hesp, 2020). Notably, vegetation in these coastal areas plays a crucial role in soil fixation and stabilization through root and stem systems that aggregate soil particles, thereby reducing wave and storm impacts, while also providing organic matter vital for vegetation nourishment and maintenance (Feagin et al., 2015).

However, due to anthropogenic pressures from urban expansion and unsustainable tourism, which also lead to improper land use, coastal plant communities are subjected to intense degradation of their natural status, compromising ecosystem services (Alessandrini et al., 2024; Hernández-Cordero et al., 2018; Cabrera-Vega et al., 2013). These communities are highly vulnerable to the climatic changes of the Anthropocene, particularly sea-level rise, which leads to soil salinization and habitat submersion, as well as to catastrophic events, which have become more frequent and intense (Kuhn et al., 2023; Li et al., 2009). Evidence of these changes includes the increase in green cover in dune areas, a direct result of increased rainfall that favors the establishment of more resilient and adapted plant species, many of which are ruderal and invasive species (Marciniak et al., 2022; Mendes & Giannini, 2015; Jackson et al., 2019). Furthermore, there is a global trend toward reduced dune mobility due to urban development activities that alter sediment dynamics, including interventions such as the installation of physical barriers that impact vegetation and sediment transport (Gao et al., 2020). These transformations directly affect the structure and functionality of coastal ecosystems, compromising their resilience and adaptive capacity to future disturbances.

A better understanding of the factors structuring vegetation patterns is essential for predicting how these ecosystems will respond to future environmental pressures, especially regarding climate change and human activities. This knowledge can not only enhance our understanding of the ecological dynamics of these systems but also support the formulation of effective management and conservation strategies aimed at ensuring the continuity of the ecosystem services they provide (Weidemann et al., 2023). A conservation measure involves recognizing indicator species that perform critical functions in coastal ecosystems. Besides identifying species that contribute to dune stabilization (Ciccarelli et al., 2012; Feagin et al., 2019), examples also include species that are more resistant to increased salinity on foredunes, essential for withstanding the extreme conditions resulting from rising sea levels (Greaver & Sternberg, 2010), or species that exhibit greater tolerance to extreme droughts, thereby ensuring ecosystem resilience to seasonal water variations (Antunes et al., 2018; Prisco et al., 2016). These approaches can provide more targeted direction for ecological restoration actions and sustainable management of coastal areas.

Vegetation zonation is a well-defined characteristic in coastal ecosystems worldwide (Doing, 1983; Acosta et al., 2007; Ruocco et al., 2014; Torca et al., 2019; Stešević et al., 2020). In this directional distribution pattern, factors such as soil properties and morphological variations of the dunes influence the distribution of plant communities. Vegetation organization along sea-to-land gradients reflects not only species' adaptation to environmental conditions but also the influence of variables such as elevation, slope, and distance from the sea, which shape habitats along the dunes (Acosta et al., 2009; Bazzichetto et al., 2014). Zonation is characterized by a transition from annual pioneer herbaceous communities at the drift line to shrubs on more stable inland dunes, revealing a complex ecological gradient. Species richness peaks in intermediate sectors of the zonation, while the upper parts of the beaches present more extreme environmental conditions, favoring the survival of a few specialized species with morphological and physiological adaptations to high salinity and substrate instability (Du & Hesp, 2020; Acosta et al., 2009). These conditions make these ecosystems heterogeneous and dynamic, with frequent changes in physical conditions over relatively short periods; such constantly shifting ecosystems act as selectors of species based on their adaptations, interrupting the successional processes of the communities (Tissier et al., 2013).

Spatial heterogeneity in coastal dunes is a significant factor influencing the composition and diversity of vegetation over time, causing population fluctuations that impact community stability (Bar et al., 2023). This heterogeneity and environmental variability give the dunes a mosaic-like appearance, with different plant formations coexisting, such as areas covered by psammophytic plants, bare soil regions, and areas subject to groundwater table fluctuations, which may be flooded, moist, or dry over short distances (Waechter, 1985; Scarano, 2002; Santos Filho et al., 2013; Andrade et al., 2019). The diversity of microhabitats promotes an uneven distribution of resources, directly influencing species presence and abundance (Yu et al., 2008; 2009). Subtle topographic variations, such as elevation and slope, affect critical environmental factors like wind exposure, drainage, and moisture retention, which, in turn, influence the colonization of plant species adapted to these conditions (Cordeiro, 2005). Additionally, elevation and slope control sun exposure and water retention capacity, essential for plants sensitive to water and temperature variations (Moeslund et al., 2013). Thus, the heterogeneous structure of limiting ecosystems fosters the formation of various microhabitats, which at a certain scale can increase species richness, while on the other hand, influencing population dynamics by facilitating or limiting the establishment of other species (García-Chávez et al., 2014).

Soil is an important indicator of the environmental heterogeneity of ecosystems, as it directly influences vegetation distribution, being the product of complex interactions between climate, parent material, and type of vegetation cover (García-Palacios et al., 2012). External factors such as temperature and precipitation affect leaching and decalcification processes, determining soil fertility and consequently plant growth rates, especially in dune systems (Sevink, 1991). Vegetation also plays a fundamental role, as the chemical composition of litter, such as the carbon/nitrogen (C/N) ratio and the presence of recalcitrant compounds, influences decomposition and mineralization rates (O'Neill & Norby, 1996). In dune soils, nutrient limitations, such as nitrogen and phosphorus, are common, and nitrogen input increases plant productivity, altering the C/N ratio and accelerating decomposition (Jones et al., 2004). Additional factors, such as height above the water table, carbonate content in the sand, and disturbance frequency, also affect soil development and, consequently, vegetation structure and composition (Wang et al., 2019; Aggenbach et al., 2017).

In this regard, soil organic matter content and its chemical composition, such as the presence of essential nutrients, also play a role in determining which species can establish in specific dune locations, influencing local vegetation richness and diversity (Melo Júnior & Boeger, 2015; Opolski-Neto et al., 2022). Generally, pioneer species are predominant in the arid soils of mobile dunes, while shrub species occupy more stable dune areas (Wu et al., 2020; Yan & Liu, 2010). Over time, stabilization and organic matter accumulation increase available nutrients and stimulate the growth of shrubs and tree species (Gunster, 1994). Additionally, groundwater table emergence in lower dune areas creates favorable conditions for the presence of hydrophilic or moisture-tolerant plants, creating microhabitats where species with specific adaptations can thrive (Dwyer et al., 2021; Hernández-Cordero et al., 2022). Wind-borne sediment deposition, or aeolian deposition, is another significant factor, as it constantly modifies the soil surface and creates new microenvironments by burying or exposing seeds and roots, influencing plant development (Hernández-Cordero et al., 2015). Alongside sediment deposition, substrate mobility due to wind and tides affects species stabilization, favoring those with root systems adapted to unstable conditions. Moreover, biotic interactions, such as plant competition for limited resources or facilitation among species that protect each other from extreme environmental conditions, also significantly influence the structure of these complex and dynamic habitats (Sarika et al., 2023).

In Brazil, coastal dune ecosystems are known as "restingas" and are notable for their distinct and complex vegetation cover. These ecosystems feature a mosaic landscape of varied phytophysiognomies, ranging from herbaceous to shrubby and arboreal zones, reflecting significant ecological diversity. The formations are defined by edaphic conditions and maritime influences, which contribute to the structuring of plant communities (Falkenberg, 1999; Scarano, 2002; IBGE, 2012). Due to this structural complexity, restinga vegetation has been the focus of extensive research in Brazilian studies over the past decades. Floristic and structural surveys of arboreal plant communities are prominent (Assumpção and Nascimento, 2000; Pereira and Assis, 2000; Scherer et al., 2005; Rocha et al., 2007; Guedes et al., 2006; Menezes et al., 2010; Assis et al., 2011; Melo-Júnior et al., 2017; Santos et al., 2022), alongside studies investigating the ecological plasticity and structural morphology of species in restinga environments (Novaes et al., 2010; Santos et al., 2010; Aguiar-Dias et al., 2012; Reinert et al., 2013; Bachtold et al., 2015; Lemos et al., 2018), as well as approaches that address functional aspects of restinga in response to environmental factors (Melo Júnior and Boeger, 2016; Kuster et al., 2018; Bona et al., 2020).

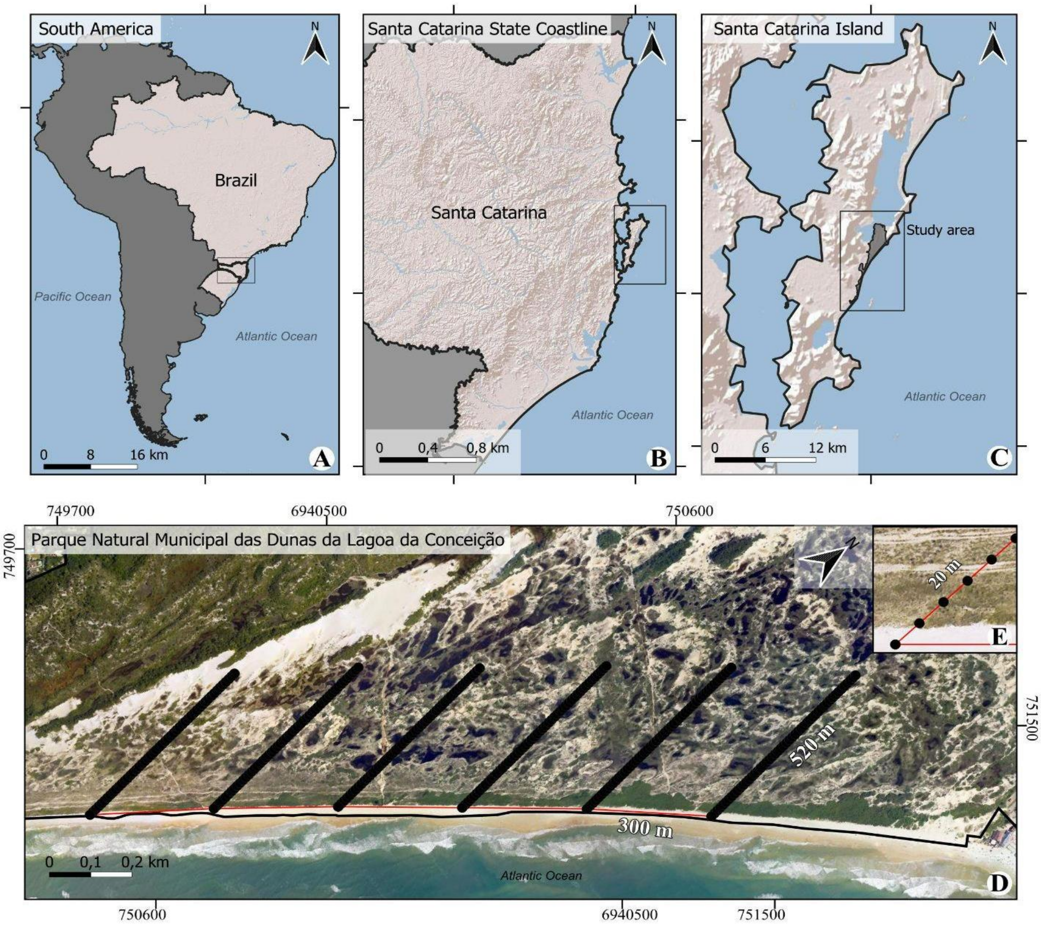
Although restingas share characteristics with adjacent ecosystems, such as nearby forests, they display unique and regional profiles, revealing significant biological diversity along the Brazilian coast (Scherer et al., 2005). From a biogeographical perspective, the structural complexity of restingas has shown a high degree of floristic uniqueness across different regions of Brazil, forming distinct groupings. These groupings reflect a mosaic aspect, resulting from the variety of habitats created by micro-relief along with other abiotic factors (Rabelo et al., 2024). Thus, local studies can enhance the understanding of restinga vegetation, and collectively, these studies are crucial for a comprehensive understanding of these ecosystems, with the aim of better understanding their richness, structure, and organization. Multidisciplinary approaches that explore the variability among microhabitats are equally important for understanding processes occurring within plant communities on a smaller scale within dune fields (Bar et al., 2023).

Understanding the influence of microenvironmental conditions on coastal herbaceous vegetation is essential for analyzing ecological processes on small scales in dune environments. In this study, we analyze the cover, richness, diversity, and species composition in a coastal dune area in southern Brazil, in Florianópolis, assessing how different microhabitats and the distance from the coastline influence these patterns. We also identify the abiotic variables that affect plant composition and indicator species associated with each microhabitat, providing a basis for the development of management and conservation strategies. This study contributes to a deeper understanding of the factors structuring coastal vegetation and to the formulation of protective actions in ecosystems threatened by anthropogenic pressures and climate change. The main research questions addressed in this study are as follows: (1) In this restinga environment, do microenvironmental conditions influence vegetation richness and structure more significantly than the distance from the beach? (2) Are there significant differences in floristic composition among the evaluated microhabitats? (3) Which abiotic variables are most determinant for plant composition in each microhabitat? (4) Which species are indicators of different microenvironments?

Materials and methods

Study area

The study area is located in the Parque Natural Municipal das Dunas da Lagoa da Conceição (PNMDLC), Florianópolis, Southern Brazil (Map 1A-E). The vegetation in the area is referred to as "restinga," a term used in Brazil to define the various forms of vegetation found in sandy deposits in coastal ecosystems (Rizzini, 1963). The study area falls within the herbaceous shrub physiognomy (Falkenberg, 1999), as observed in Figure 1A-C. The climate in the region is classified as Cfb on the Köppen scale, with an average annual temperature of 21°C and average annual rainfall of 1.500 – 1.700 mm (Pandolfo et al., 2002). The predominant winds are from the northeast, while the dominant winds typically blow from the south-southwest and are associated with the passage of cold fronts (Hesp et al., 2007). The average tidal range is 0,8 m, with a maximum of 1,2 m. During storms, water levels can rise to about 1 m above the astronomical tide (Carvalho et al., 1996). The experimental design for sampling was conducted using the ArcGIS mapping program, with six transects established, each 520 m in length and equidistant 600 m apart, oriented approximately 40º relative to the beach coastline. Within each transect, 26 sampling points were allocated, spaced 20 m apart, where vegetation sampling plots were installed (Map 1D-E).



Map 01: Location map of the study area and sampling design: A- South America with emphasis on Brazil and the state of Santa Catarina, B- Coastal region of the state of Santa Catarina, C- Santa Catarina Island, with emphasis on the Parque Natural Municipal das Dunas da Lagoa da Conceição (PNMDLC), D- Sampling design in the study area, displaying the distribution of sampled transects; E- Detail of the sampled plots.

Sampling design and data collection

The vegetation was sampled for 12 months, from December 2019 to December 2020. At each sampling point, the present species were identified to the lowest taxonomic level possible within 1m² plots (1 x 1 m). The coverage of each species was estimated using the relevé method with seven scales (Braun-Blanquet, 1979), along with the percentage area without vegetation cover, assessed by a single observer. For each plot, categorical variables related to terrain slope were also considered: flat, inclined, or depressed (low-lying), and whether the location is prone to flooding or not.

The microhabitat of each plot was defined based on field observations and satellite images and categorized as follows (Figure 1A-J): Embryo Dunes (ED): the first dunes positioned at the coastal edge exposed to high tide or storm surges (Figure 1D); Dry Slack Dune (DSD): flat areas without signs of periodic flooding (Figure 1E); Dune Toe (DT): areas with reduced slope, at the base of the dunes (Figure 1F); Dune Frontal Side (DFS): inclined areas positioned on the frontal side of internal dunes relative to the coastline (Figure 1G); Dune Crest (DC): locations positioned at the highest part of the dunes, excluding the frontal dune (Figure 1H); Dune Dorsal Side (DDS): inclined areas positioned on the dorsal side of internal dunes relative to the coastline (Figure 1I); Humid Slack Dune (HSD): flat areas with signs of periodic or perennial flooding due to groundwater emergence (Figure 1J).

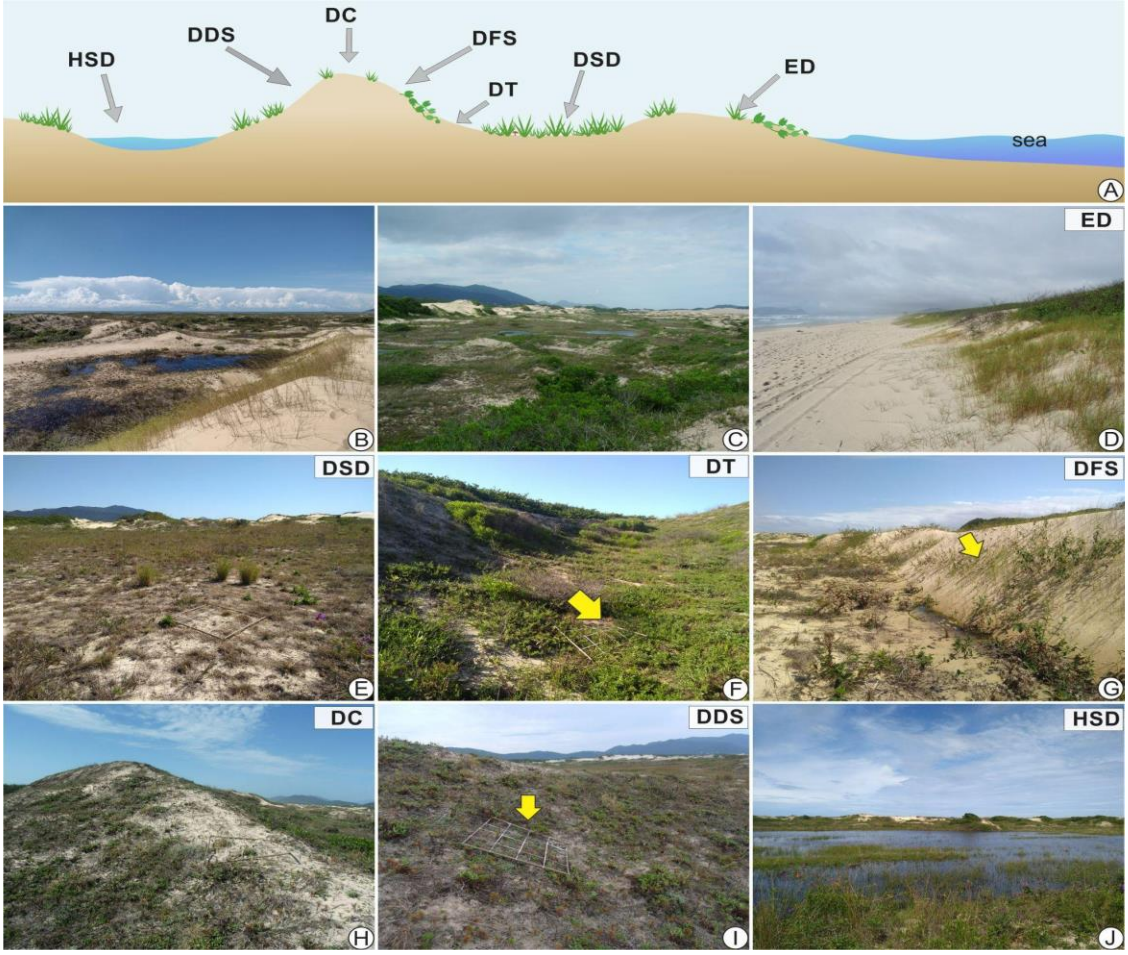


Figure 1: Characterization of the study area's profile diagram and respective microhabitats. A - Profile diagram; B - Different relief aspects; C - Mosaic aspect in the study area, D- Embryo dunes (ED); E- Dry slack dunes (DSD); F- Dune Toe (DT); G - Dune Frontal Side (DFS); H - Dune Crist (DC); I - Dune Dorsal Side (DDS); J - Humid Slack Dune (HSD).

Statistical analysis

To evaluate potential differences in species richness among microhabitats and distance profiles from the beach, species richness values per plot were log-transformed and tested for normality and homoscedasticity. Subsequently, two-way ANOVA analyses were performed, considering the distance factor in five classes: frontal (0m to 40m), near (60m to 120m), mid (140m to 260m), distant (280m to 400m), and very distant (420m to 500m), and the microhabitat factor (seven classes: DC, DDS, DFS, DSD, DT, ED, HSD). We considered organizing the species richness data into distance classes in order to comprehend a smaller number of intervals and enhance the robustness of the analysis. The classes were defined based on field observations concerning the effects of high tides and changes in vegetation profile. When a significant difference (p < 0,05) was identified between variables, a Tukey post-hoc test was conducted to explore differences between group means and identify which groups showed significantly different species richness.

The investigation into the relative contribution of microhabitats, terrain relief, flooding, and distance from the beach in shaping herbaceous community composition was conducted through redundancy analysis (RDA). The species abundance matrix underwent Hellinger transformation to reduce asymmetry and enhance differences between species composition data. Simultaneously, the environmental variable matrix containing distance and exposed soil area was standardized to ensure all variables were on the same scale. The categorical variables matrix consisted of parcel characteristics (relief: flat/slope/depression; floodable/unfloodable; microhabitats: DC, DDS, DFS, DSD, DT, ED, HSD). These were directly included in RDA without additional transformations, as RDA accommodates categorical variables (Legendre e Gallagher, 2001). Variable collinearity was tested using the Variance Inflation Factor (VIF), with values between 3 and 5, following recommendations (Borcard et al., 2011). The significance of correlations obtained by RDA was tested using a Monte Carlo test with 1000 permutations, and the significance level adopted was p < 0,05.

We used the "*iNEXT*" package (Chao et al., 2014) to estimate species richness and diversity in seven microhabitats within the study area. Species abundance data was converted into presence and absence, and Hill numbers (q=0; 1; 2) were extrapolated and rarefied for each microhabitat, allowing estimation of expected richness to identify differences between them. Richness and diversity curve graphs were generated for visualization purposes. Additionally, bar graphs were created to assess species coverage in each microhabitat. Percentage coverage data per species were compiled for each microhabitat and visualized in bar graphs to observe species composition and relative abundance in each environment, providing information on plant community structure.

The Indicator Species Value was calculated for each microhabitat to recognize indicator species. The two components of the indicator value (i.e., specificity and fidelity) were examined, and when the specificity value equaled 1, it was used to assign exclusive species to each type of vegetation. Analyses were conducted using the "*indval*" function (= multipatt) from the *indicspecies* package in R software (Cáceres and Legendre, 2009). This function identifies indicator species for each microhabitat and possible combinations thereof, allowing the identification of conditions or combinations of conditions that host characteristic plant species communities. Analyzing all possible combinations is informative, as spatially discontinuous environmental conditions might harbor common indicator and exclusive species due to unexplored factors (soil physicochemical composition, litter content, historical processes, shading, etc.). All analyses were performed in the R environment using packages vegan and ggplot2 (Dixon, 2003; Wickham, 2009; R Core Team, 2022).

Results

Species-habitat coverage relationships

The survey identified 94 plant species, classified into 35 families, comprising 33 angiosperms, two ferns, and one bryophyte (Table 1). All species are native and commonly found in Brazilian coastal ecosystems. From the coverage data, it can be observed that six species contribute significantly to the total area coverage (>50%), occurring in either a few (2) or many (4-7) microhabitats. More than half of the species (73) showed a coverage of less than 1% of the total, and among these, 40% were sampled in only one of the environmental conditions, suggesting some level of rarity in the area (Table 1 and detailed Supplementary Material I).

Table 1: Species cover sampled in the study respective family and authorship.

Family	Species	Cover (%)
Amaranthaceae	*Alternanthera brasiliana* (L.) Kuntze	0,03
Amaranthaceae	*Alternanthera littoralis* P.Beauv.	1,05
Amaranthaceae	*Dysphania ambrosioides* (L.) Mosyakin & Clemants	0,26
Anacardiaceae	*Schinus terebinthifolius* Raddi	0,13
Apiaceae	*Centella asiatica* (L.) Urb.	0,62
Apocynaceae	*Oxypetalum tomentosum* Wight ex Hook. & Arn.	0,06
Araliaceae	*Hydrocotyle bonariensis* Lam.	0,15
Asteraceae	*Achyrocline satureioides* (Lam.) DC.	0,44
Asteraceae	*Baccharis gnaphalioides* Spreng.	0,43
Asteraceae	*Baccharis trimera* (Less.) DC.	0,03
Asteraceae	*Barrosoa betonicaeformis* (DC.) R.M. King & H. Rob.	0,24
Asteraceae	*Chrysolaena flexuosa* (Sims) H.Rob.	0,03
Asteraceae	*Gamochaeta americana* (Mill.) Wedd.	0,02
Asteraceae	*Noticastrum hatschbachii* Zardini	6,85
Asteraceae	*Porophyllum ruderale* (Jacq.) Cass.	0,03
Asteraceae	*Pterocaulon angustifolium* A.DC.	0,16
Asteraceae	*Pterocaulon lorentzii* Malme	0,00
Asteraceae	*Symphyopappus casarettoi* B.L.Rob.	0,53
Asteraceae	*Senecio platensis* Arechav.	0,26
Blechnaceae	*Telmatoblechnum serrulatum* (Rich.) Perrie, D.J. Ohlsen & Brownsey	0,29
Bromeliaceae	*Vriesea vagans* (L.B.Sm.) L.B.Sm..	0,13
Campanulaceae	*Lobelia hederacea* Cham.	0,13
Caryophyllaceae	*Cardionema ramosissima* (Weinm.) A.Nelson & J.F.Macbr.	0,01
Convolvulaceae	*Evolvulus pusillus* Choisy	0,07
Convolvulaceae	*Ipomoea imperati* (Vahl) Griseb.	0,49
Cucurbitaceae	*Melothria pendula* L.	0,00
Cyperaceae	*Cyperus liguaris* L.	0,65
Cyperaceae	*Cyperus obtusatus* (J.Presl & C.Presl) Mattf. & Kük.	0,02
Cyperaceae	*Cyperus pedunculatus* (R.Br.) J.Kern	0,97
Cyperaceae	*Cyperus rigens* C.Presl	0,00
Cyperaceae	*Cyperus trigynus* Spreng.	2,02
Cyperaceae	*Eleocharis laeviglumis* R.Trevis. & Boldrini	0,51
Cyperaceae	*Rhynchospora barrosiana* Guagl.	1,55
Cyperaceae	*Rhynchospora holoschoenoides* (Rich.) Herter.	2,54
Cyperaceae	*Rhynchospora tenuis* Link.	0,17
Cyperaceae	*Scleria distans* Poir.	0,13
Droseraceae	*Drosera brevifolia* Pursh.	0,06
Eriocaulaceae	*Actinocephalus polyanthus* (Bong.) Sano	1,76
Eriocaulaceae	*Eriocaulon modestum* Kunth	0,15
Eriocaulaceae	*Syngonanthus chrysanthus* (Bong.) Ruhland	0,39
Euphoriaceae	*Euphorbia hyssopifolia* L.	0,01
Euphoriaceae	*Microstachys corniculata* (Vahl) Griseb.	0,23

Family	**Species**	**Cover (%)**
Fabaceae	*Canavalia rosea* (Sw.) DC.	0,13
Fabaceae	*Dalbergia ecastaphyllum* (L.) Taub.	2,56
Fabaceae	*Desmodium adscendens* (Sw.) DC.	0,31
Fabaceae	*Indigofera sabulicola* Benth.	0,13
Fabaceae	*Stylosanthes viscosa* (L.) Sw.	8,42
Haloragaceae	*Laurembergia tetrandra* (Schott) Kanitz.	0,10
Hypoxidaceae	*Hypoxis decumbens* L.	0,05
Juncaceae	*Juncus microcephalus* Kunth	0,30
Lamiaceae	*Vitex megapotamica* (Spreng.) Moldenke	3,29
Melastomataceae	*Pleroma urvilleanum* (DC.) P.J.F.Guim. & Michelang.	0,45
Ochnaceae	*Sauvagesia erecta* L.	0,27
Onagraceae	*Oenothera mollisima* L.	0,04
Orchidaceae	*Epidendrum fulgens* Brongn.	0,75
Plantaginaceae	*Plantago catharinea* Decne	0,01
Plantaginaceae	*Scoparia dulcis* L.	0,03
Poaceae	*Andropogon bicornis* Benth.	0,13
Poaceae	*Andropogon leucostachyus* Kunth.	1,21
Poaceae	*Andropogon selloanus* (Hack.) Hack.	1,12
Poaceae	*Aristida circinalis* Lindm.	0,14
Poaceae	*Cenchrus echinatus* L.	0,39
Poaceae	*Chloris retusa* Lag.	0,00
Poaceae	*Dichanthelium sabulorum* (Lam.) Gould & C.A. Clark	1,68
Poaceae	*Eragrostis bahiensis* Schrad. ex Schult.	0,13
Poaceae	*Eragrostis cataclasta* Nicora	1,19
Poaceae	*Eustachys distichophylla* (Lag.) Nees	0,01
Poaceae	*Gymnopogon legrandii* Roseng. et al.	1,65
Poaceae	*Imperata brasiliensis* Trin.	0,03
Poaceae	*Ischaemum minus* J.	10,43
Poaceae	*Panicum dichotomiflorum* Michx.	0,54
Poaceae	*Panicum racemosum* (P. Beauv.) Spreng.	0,52
Poaceae	*Paspalum arenarium* Schrad.	0,81
Poaceae	*Paspalum pumilum* Nees	0,54
Poaceae	*Paspalum ramboi* Barreto.	0,38
Poaceae	*Paspalum vaginatum* Schrad.	0,26
Poaceae	*Schizachyrium microstachyum* (Desv.) Roseng., B.R.Arrill. & Izag.	0,75
Poaceae	*Spartina ciliata* Brongn.	1,16
Poaceae	*Sporobolus virginicus* (L.) Kunth	0,26
Poaceae	*Steinchisma decipiens* (Nees ex Trin.) W.V.Br.	0,04
Poaceae	*Trichanthecium parvifolium* (Lam.) Zuloaga & Morrone	1,09
Polygalaceae	*Senega cyparissias* (A. St.-Hil. & Moq.) J.F.B.Pastore & Agust. Martinez	0,15
Polypodiaceae	*Pleopeltis lepidopteris* (Langsd. & Fisch.) de la Sota	0,42
Rubiaceae	*Coccocypselum capitatum* (Graham) C.B.Costa & Mamede.	0,67
Rubiaceae	*Hexasepalum apiculatum* (Willd.) Delprete & J.H. Kirkbr	0,04
Rubiaceae	*Hexasepalum radula* (Willd.) Delprete & J.H. Kirkbr.	0,33
Rubiaceae	*Oldenlandia salzmannii* (DC.) Benth. & Hook. f. ex B.D. Jacks.	0,67
Sapindaceae	*Dodonaea viscosa* Jacq.	1,28
Smilacaceae	*Smilax campestris* Griseb.	2,13
Solanaceae	*Petunia integrifolia* (Hook.) Schinz & Thell	0,22
Solanaceae	*Solanum americanum* Mill.	0,00
Solanaceae	*Solanum pelagicum* Bohs	0,00
Sphagnaceae	*Sphagnum* sp. L.	0,01
Xyridaceae	*Xyris jupicai* Rich	0,03
Soil exposed area		29,19

Family	**Species**	**Cover (%)**
Total cover (%)		100

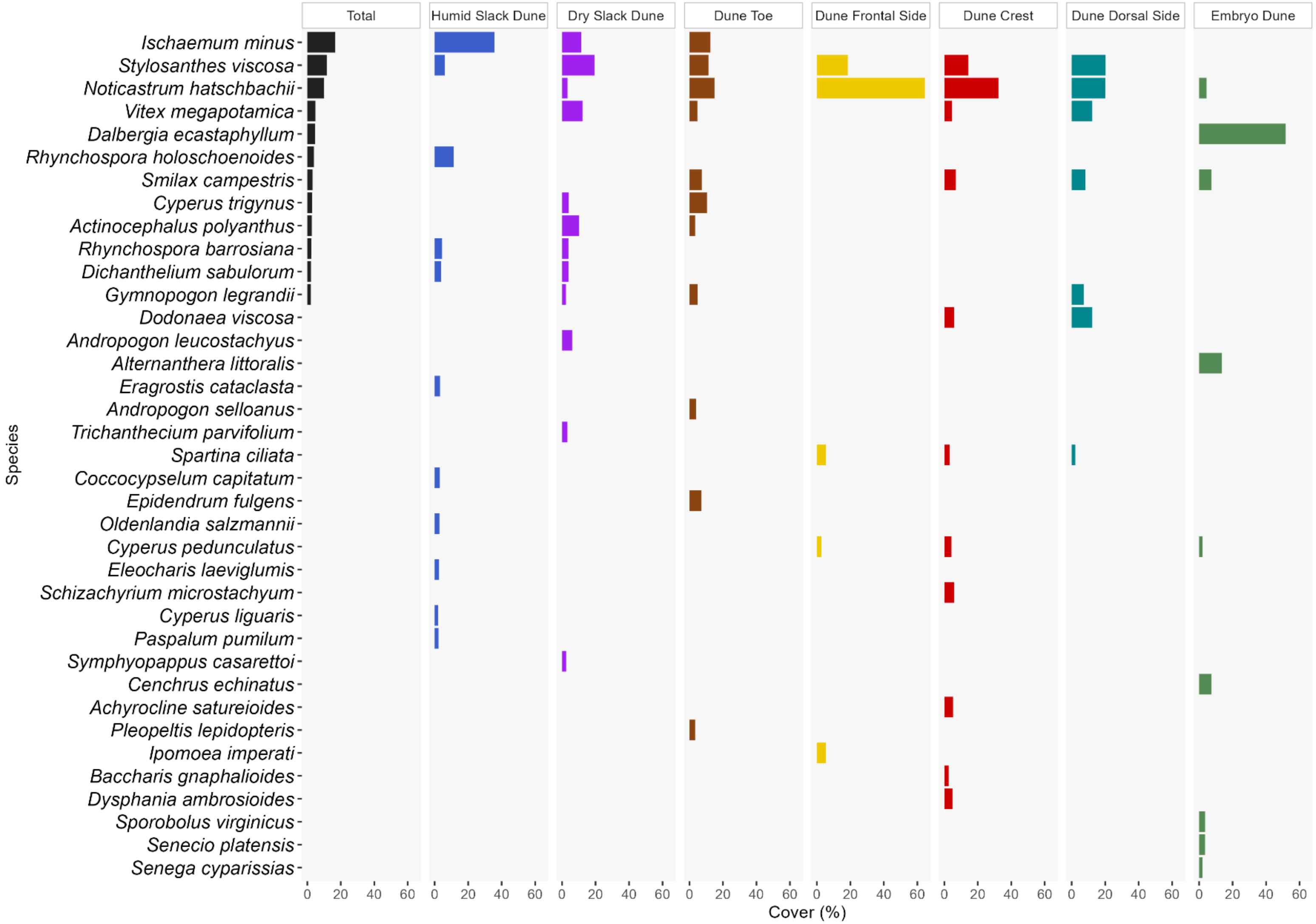


Figure 2: Coverage values of species with proportional coverage greater than 2% considering the entire area and within each type of environment. Species are arranged by occurrence in the total area, based on the highest coverage values. (all values in Supplementary Material I).

The Humid Slack Dune (HSD) areas presented many exclusive species (16) with low coverage, while simultaneously being the environment with the highest number of shared species (37) with the others. It can be observed that the Dry slack dunes (DSD) and Dune Toe (DT) areas share some species with similar coverage values, whereas the Dune Dorsal Side (DDS), Dune crist (DC) and Dune Frontal Side (DFS) locations have more species in common but with low coverage. On the other hand, Embryo dunes (ED) did not present much richness, but it did have some exclusive species with significant coverage. Regarding the most prominent species, we can observe that I. minus made a significant total contribution, with high values in the HSD, DT, and BSE environments, while showing very low values in DDS. On the contrary, *S. viscosa* was found in all environments, with high coverages, except in ED, where it was not sampled. In contrast, *N. hatshbachii* exhibited high values in the DFS, DDS, and DC areas and very low coverage in HSD and ED.

Determining factors for the richness of sampled species

Species richness was more influenced by the type of microhabitat (F = 3,85, p = 0,00014) than by the distance from the beach (F = 1,64, p = 0,168); and by the interaction between environment and distance (F = 1,33, p = 0,189) (Table 2; Figure 3). The Tukey post-hoc test identified significant differences in species richness between some pairs of levels in the environment factor, notably ED-HSD (p = 0,015), ED-DT (p = 0,006), ED-DSD (p = 0,001), DC-DSD (p = 0,03), and DFS-ED (p = 0,008) (Figure 4).

Table 2: Two-way analysis of variance (ANOVA) table for parameters studied

Variable	df	SSq	MSq	F - value	p(>F)
Microhabitat	6	3,86	0,64	3,85	0,000145**
Beach distance	4	1,09	0,27	1,64	0,168
Microhabitat : Beach distance	16	3,55	0,22	1,33	0,189
Residuals	127	21,21	0,167		

df: degree of freedom (*n*-1); SSq: Sum of squares; MSq: Mean of squares; ** significant (<0,001).

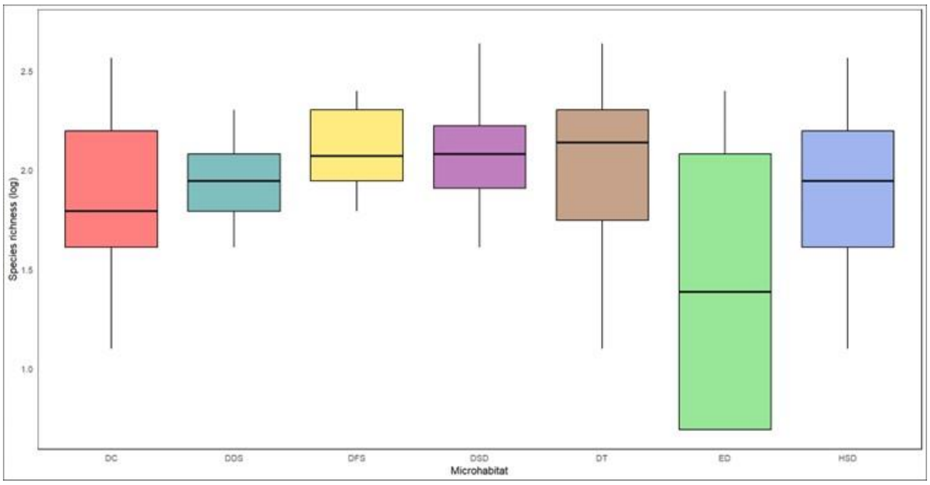


Figure 3: Variation of species richness (in log) for each evaluated microhabitat. Embryo dunes (ED); Dry slack dunes (DSD); Dune Toe (DT); Dune Frontal Side (DFS); Dune Crist (DC); Dune Dorsal Side (DDS); Humid Slack Dune (HSD).

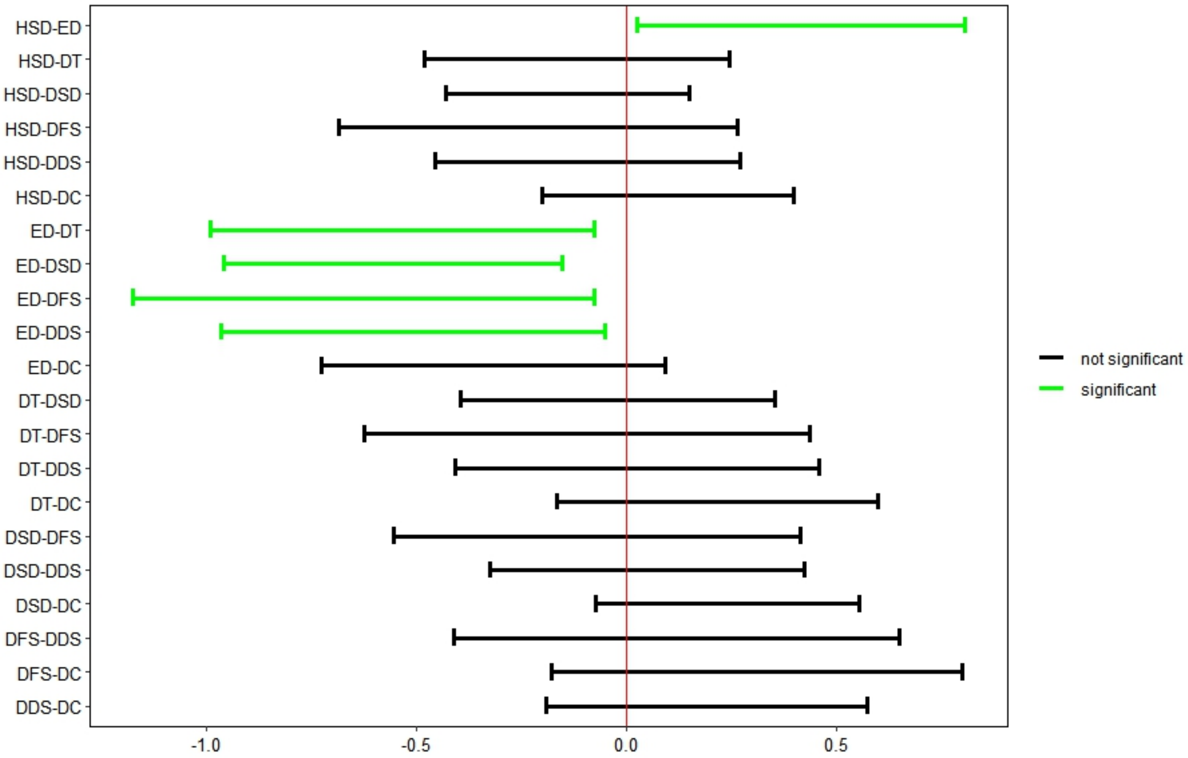


Figure 4. Post-hoc ANOVA analysis using Tukey HSD with 95% confidence for species richness among different microhabitats. Paired comparisons of means between all microhabitats. Lines close to zero are conditions that had no difference in their mean richness, while lines close to zero are conditions that had different mean richness. Green sequencing libraries show the largest differences at average levels above zero.

Community structuring factors

The RDA analysis revealed that 22,7% (0,19) of the total variation (0,86) was explained by the variables considered in the study, while 78.0% (0,67) represented unrestricted variation. All Monte Carlo permutation tests (999 permutations) confirmed the significance of the variables (p < 0,001). The non-flooded condition contributed 6% to the explained variation (31,80% of the total explained variation; F = 12,90), as did the microenvironments (6% of the explained variation; 31,43% of the total explained variation; F = 2,55) (Figure 5) (Table 3).

The main ordination axes, RDA1 and RDA2, jointly explained 61,46% of the total variation (RDA1: 43,64% and RDA2: 17,82%). A weak and negative association was observed between the distance from the beach and RDA1 axes (biplot score = -0,23, p = 0,001) and RDA2 axes (biplot score = -0,17, p = 0,001), indicating that the influence of this variable decreases with increasing distance. On the other hand, the non-flooded condition showed a strong and positive association with RDA1 axis (biplot score = 0,76, p = 0,001), while the percentage of exposed soil showed a moderate and positive association with RDA1 axis (biplot score = 0,51, p = 0,001). The microhabitats (DDS, DFS, DSD, DT, and ED) also contributed to the variation in RDA1 and RDA2 axes, although with relatively moderate associations. These results suggest that these variables play relevant roles in the structure of ecological data.

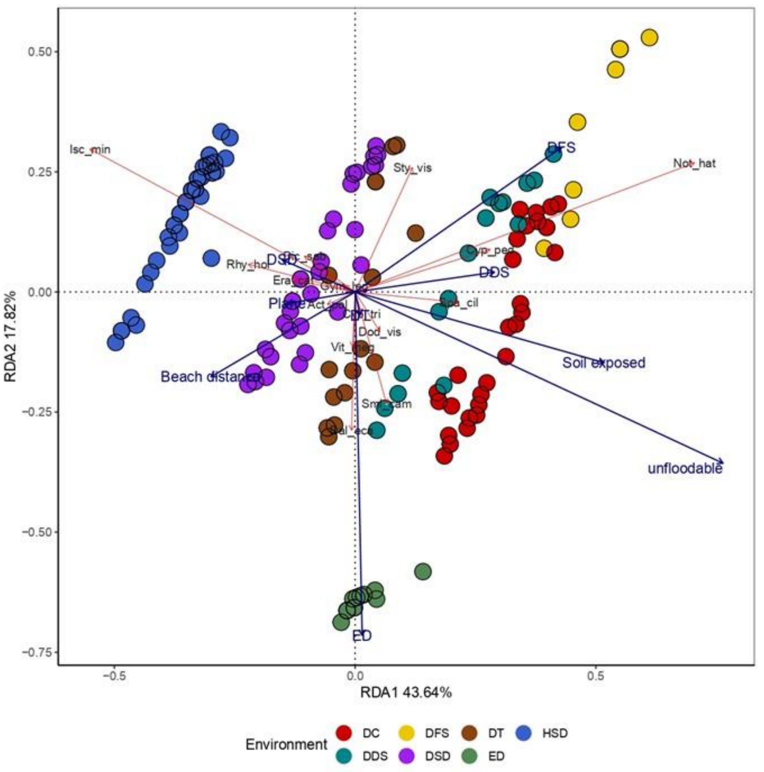


Figure 5: Redundancy analysis illustrating the relationships of the major axis of restinga vegetation observed in the PNDLC with environmental variables. Blue arrows represent structural variables: soil exposed, Beach Distance, Plane relief, unflooded condition; microhabitats include Embryo Dune (ED), Dry Slack Dune (DSD), Dune Toe (DT), Dune Dorsal Side (DDS), Dune Frontal Side (DFS); amostral units: colors points. Major scores species: Act_pol: *Actinocephalus polyanthus*, Cyp_tri: *Cyperus trigynus*, Cyp_ped: *Cyperus pedunculatus*, Dal_eca: *Dalbergia ecastaphyllum*, Dic_sab: *Dichanthelium sabulorum*, Dod_vis: *Dodonaea viscosa*, Era_cat: *Eragrostis cataclasta*, Gym_leg: *Gymnopogon legrandii*, Isc_min: *Ischaemum minus*, Not_hat: *Noticastrum hatschbachii*, Rhy_hol: *Rhynchospora holoschoenoides*, Smi_cam: *Smilax campestris*, Spa_cil: *Spartina ciliata*, Sty_vis: *Stylosanthes viscosa*, Vit_meg: *Vitex megapotamica*. (R^2: 0,2253 R^2 adjust: 0,1769). Graphical results for all species can be seen in Supplementary Material II.

Table 3: Effects of environmental factors on species composition (% of explained variance)

Effect and main variable	**% Explained**	**F**	**Pr(>F)**
Condition	6,99%	12,90	0,001***
Distance	2,84%	5,25	0,001***
Reliev	3,45%	6,37	0,001***
Soil exposed	1,78%	3,29	0,001***
Microhabitat	7,45%	2,77	0,001***

The analysis indicates that the species composition in sample units was better explained by microhabitats and non-flooded conditions than by the distance from the beach. The set of relief and exposed soil variables encompasses the main gradient that shapes the composition patterns in the ordination diagram.

The first axis, RDA1, describes the change in soil conditions, represented by the non-flooded condition and an increase in exposed sand and steeper slope condition. This axis contributed to the distribution of species in actual dune environments (DDS, DFS, and DC) such as*: I. imperati*, *S. ciliata*, *C. pedunculatus*, *S. microstachyos*, *A. circinalis*, and *N. hatschbachii*. Contrary to this axis, the flat relief condition, along with reduced exposed area and flooding conditions, grouped the sample units of the microhabitats DSD and HSD. From the information, it can be observed that flat areas have higher vegetation coverage, with a predominance of species with extensive coverage. The HSD microhabitat did not show significant variation in the model; however, in the diagram, the sample units with this condition formed a unique grouping contrary to RDA1 axis, with strongly related species: *I. minus*, *R. holoschoenoides*, *D. sabul*orum (Figure 5).

Although the distance from the beach contributed significantly to the variation (2,84% p < 0,0001), it did not demonstrate a clear influence on species composition, being negatively related to the environmental condition of DFS, and closely related to flat relief, indicating that as the distance from the beach increases, flat conditions favor the development of some species. In this regard, it is worth noting that the species A. polyanthus has a positive relationship with this variable, while *N. hatschbachii* has a strong negative relationship, indicating different habitat tolerances with proximity to the beach (Figure 5).

The second axis of RDA had a lower contribution to the total explained variation (17,82%) and was strongly related to the conditions of ED and DT. The first condition formed a unique grouping of sample units, distant from the others, with the species *S. virginicus*, *D. ecastaphyllum*, and *A. littoralis*. The second condition was more related to the species *V. megapotamica*, *C. trigynus*, and *E. fulgens* (Figure 5).

Species richness and diversity through rarefaction curves

The analysis of richness and diversity interpolation and extrapolation (Inext) showed low variation in species richness and diversity between microhabitats, with HSD and DSD exhibiting the highest total species richness (53 and 49) and lower values in DFS (25) and ED (22). Extrapolation also demonstrated that the analyzed microhabitats were far from sufficient sampling and with a high overlap of confidence intervals, indicating uncertainties in the estimates. However, it can be observed that, with increased sampling effort, the microhabitats DT and HSD emerge as the richest communities in species, followed by DSD, DDS, and DC (Figure 6).

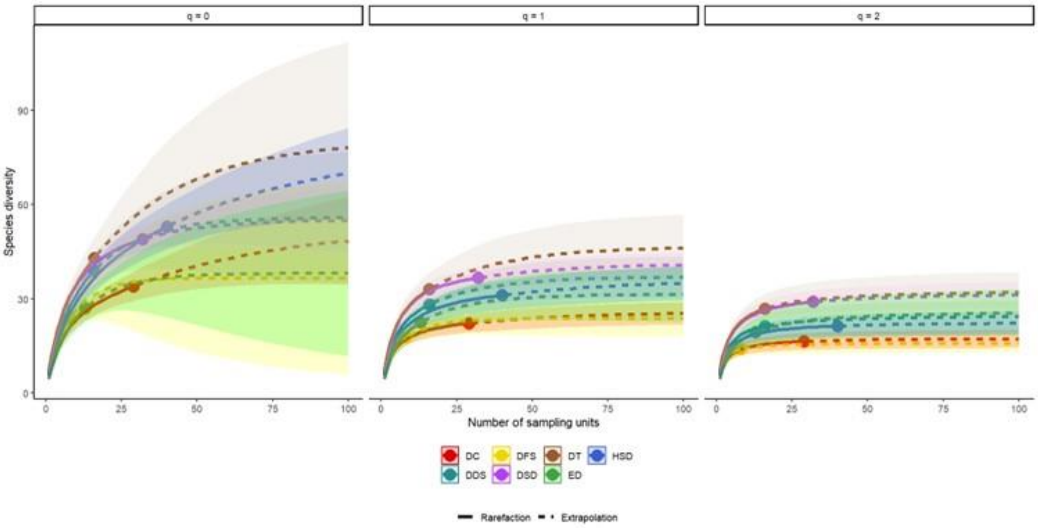


Figure 6: Species richness estimated by iNEXT through extrapolation and rarefaction of Hill numbers (q = 0; 1; 2) for the seven types of herbaceous dune vegetation environments (Embryo Dune (ED), Humid slack Dune (HSD), Dune Crist (DC), Dry Slack Dune (DSD), Dune Toe (DT), Dune Dorsal Side (DDS), Dune Frontal Side (DFS)). Each point represents the observed species richness in that habitat type. Solid lines depict rarefactions based on sample size conducted by iNEXT. Dashed lines are the extrapolated curves produced by iNEXT up to a projection of 100 sample units. The 95% confidence interval (shaded regions) was obtained using the bootstrap method.

Indicator species

The number of indicator species in each type of vegetation, and in different combinations of types, is presented in Table 4 and Supplementary Material III. The data indicates that, independently, the environments Humid slack Dune (HSD) and Embryo Dune (ED) each have seven indicator species, while Dry Slack Dune (DSD) and Dune Dorsal Side (DDS) exhibit two species, Dune Toe (DT) has four, and Dune Frontal Side (DFS) has three. The DC environment did not show any exclusive indicator species. The data demonstrates that *Centella asiatica*, *Ischaemum minus*, and *Rhynchospora holoschoenoides* are important elements in the composition of floodable lowland areas. In areas at the base of dunes, species like *Cyperus trigynus*, *Microstachys corniculata*, and *Epidendrum fulgens* are pointed out as indicators. Non-floodable lowland areas are well represented by the species *Actinocephalus polyanthus* and *Andropogon leucostachyus*, while in the frontal dune regions, the species *Dalbergia ecastaphyllum*, *Sporobolus virginicus*, and *Senecio platensis* stand out. Although they exhibit lower specificity values, on the frontal sides of the dunes, we find species like *Ipomoea imperatii*, *Noticastrum hatschbachii*, and *Spartina ciliata*, while in the dorsal areas, *Petunia integrifolia* and *Dodonaea viscosa* are prominent elements.

Table 4. Indicators species for each one microhabitat: Embryo Dune (ED), Humid slack Dune (HSD), Dry Slack Dune (DSD), Dune Toe (DT), Dune Dorsal Side (DDS), Dune Frontal Side (DFS). The data is presented in descending order of significance value, grouped by microhabitat. The Dune Crist (DC) microhabitat does not exhibit any individual species indicators.

Microhabitat	Specie	Specificity	Fidelity	IndVal	p-value
HSD	*Centella asiatica*	0,89	0,55	0,70	0,001
HSD	*Ischaemum minus*	0,64	0,65	0,64	0,001
HSD	*Rhynchospora holoschoenoides*	1	0,35	0,59	0,001
HSD	*Laurembergia tetrandra*	1	0,25	0,5	0,003
HSD	*Eragrostis cataclasta*	0,70	0,27	0,44	0,023
HSD	*Juncus microcephalus*	1	0,15	0,38	0,042
HSD	*Oldenlandia salzmannii*	1	0,12	0,35	0,048
DT	*Microstachys corniculata*	0,64	0,47	0,55	0,01
DT	*Cyperus trigynus*	0,58	0,47	0,52	0,012
DT	*Epidendrum fulgens*	0,79	0,23	0,43	0,016
DT	*Imperata brasiliensis*	1	0,17	0,42	0,017
DSD	*Actinocephalus polyanthus*	0,75	0,37	0,53	0,006
DSD	*Andropogon leucostachyus*	0,77	0,28	0,46	0,007
ED	*Dalbergia ecastaphyllum*	1	0,45	0,67	0,001
ED	*Sporobolus virginicus*	1	0,27	0,52	0,001
ED	*Senecio platensis*	0,99	0,27	0,52	0,001
ED	*Alternanthera littoralis*	0,86	0,27	0,48	0,005
ED	*Senega cyparissias*	1	0,18	0,42	0,013

Microhabitat	Specie	Specificity	Fidelity	IndVal	p-value
ED	*Canavalia rosea*	0,99	0,18	0,42	0,017
ED	*Oenothera mollisima*	0,96	0,18	0,42	0,048
DDS	*Petunia integrifolia*	0,56	0,37	0,46	0,023
DDS	*Dodonaea viscosa*	0,74	0,18	0,37	0,026
DFS	*Ipomoea imperati*	0,60	0,55	0,58	0,003
DFS	*Noticastrum hatschbachii*	0,43	0,77	0,58	0,004
DFS	*Spartina ciliata*	0,37	0,88	0,57	0,012

When analyzing indicator species considering the formation of groups of up to two species per environmental condition, it is observed that the DFS condition presents the highest number of combinations (22), followed by DT (14) and ED (10). Observations reveal that the DC condition demonstrates two combinations of species that exhibit significant indication, emphasizing the importance of Smilax campestris in conjunction with *Noticastrum hatschbachii*, and *Schizachyrium microstachyum* along with *Ipomoea imperati*, as pivotal indicator elements of the dune's summit condition. The other conditions exhibited the same indicative species as the main element, followed by combinations with each other and other elements, as can be appreciated in the Supplementary Material III.

Discussion

Our study provides crucial insights into the richness of herbaceous and shrubby vegetation in the southern Brazilian restinga and the potential factors affecting plant community structure. Despite our study design not encompassing the entire study area, we identified patterns concerning the species richness and composition, aligning with observations made in smaller areas of nearby regions (Cordeiro, 2005; Menezes et al., 2015; Silva e Melo Junior, 2016; Bonilha et al., 2017; Pereira-Silva et al., 2019; da Silveira et al., 2022) and previous floristic surveys conducted in the area (Falkenberg, 1999; Guimarães, 2006). However, these earlier studies did not focus on herbaceous vegetation nor consider the same environmental variables. Additionally, we observed that the species richness variation is more related to different habitat types than to the distance classes from the beach considered in our study. This observation aligns with our initial hypothesis and is consistent with studies in coastal ecosystems from various regions worldwide (Pimentel et al., 2007; Fenu et al., 2013), challenging patterns observed elsewhere, where richness changes with distance (Abdelaal et al., 2019; Yu et al., 2023).

Contrary to our expectations, the variation in richness among microhabitats was not as distinctive. Changes in the relative abundance of sampled species (incidence data) suggest that the concentrations of some species vary between microhabitat types, potentially influencing the outcomes. The data also indicate lower heterogeneity among certain microhabitats compared to others, reflecting the irregular distribution of resources at a fine scale, indicating the presence of more homogeneous microsites that provide specific conditions, impacting the composition and distribution of species across different microhabitats. This scenario reinforces the understanding of the complexity of the interaction between environmental factors and the ecology of communities at very small scales (Price et al., 2014). Furthermore, the observed patterns may be associated with more discrete factors in coastal ecosystems, such as the occurrence of annual and short-lived species (Isermann, 2011), events triggering long-scale successional processes (Álvarez-Molina et al., 2012), or biotic interactions (e.g., facilitation and competition within and between species (Martínez, 2003; Maltez-Mouro et al., 2010; Vaz et al., 2015) not accounted for in our study.

However, upon observing the species coverage in each microhabitat, we can identify distinct and specific compositions among the microhabitats, primarily highlighted by species with greater coverage and indicative species. We observed that Embryo Dunes (ED) areas presented a lower number of species and exclusive indicators, forming a unique and isolated grouping (Figure 5), associated with the distance from the beach and non-flooded areas. This highlights that those pressures along the marine coast are more significant on vegetation in these conditions than in other microenvironments (Bazzichetto et al., 2020; Nordstrom et al., 2007). Marine-origin pressures increase soil salinity and plant burial by sand, selecting more specialized taxa, known as psammophytes and halophytes, to inhabit these conditions (our case: *D. ecastaphyllum*, *S. virginicus*, *S. platensis*, *A. littoralis*, *S. cyparissias*, and *C. rosea*) (Arruda et al., 2009). Among psammophytes, some species require burial to maintain high vigor (Maun, 1998).

In HSD areas, which presented higher species richness and a greater number of exclusive species, they formed an isolated and well-defined grouping, contrary to the non-flooded condition, inclined relief, and low coverage. This reinforces the influence of flooding and water table level as factors conducive to the growth of species that adapted to total or partial submersion (e.g., *C. asiatica*, *I. minus*, *R. holoschoenoides*, *L. tetrandra*, and *J. microcephalus*). Additionally, this condition is limiting for other species (Pimentel et al., 2007; Vaz et al., 2015; da Silveira et al., 2022). Seasonally wet lowlands require adaptations enabling plants to deal with anoxic conditions followed by periods of extreme aridity, demonstrating the complexity of survival strategies in this environment (Grootjans et al., 2008). Moreover, the size of lagoons, intermittent flooding, and phosphorus concentration are indicated as determining factors in the species composition richness in humid coastal regions (Rolon et al., 2008).

We observed that Dry Slack Dune (DSD) and Dune Toe (DT) presented a lower number of indicative species, with species coverage data similar to what was observed in Dune Crist (DC), Dune Frontal Side (DFS) and Dune Dorsal Side (DDS) but forming distinct groupings (Figure 5). This differentiation is justified by the relationship between terrain slope variables (less predominant in DT and DSD) and more exposed soils (more evident in DC, DFS, and DDS). Vegetation coverage plays a fundamental role in reducing exposed sand and sediment transport by wind. Locations with more exposed soils have greater substrate mobility due to aeolian accretion and erosion dynamics, affecting vegetation through burial (Okin, 2008; Álvarez-Molina et al., 2012). In the study region, aeolian dynamics have produced transversal inversion of dune fields, influencing sediment movement and direction across the dune field (Hesp et al., 2007). As Maun (2009) points out, burial in sand is an important factor in plant establishment in dunes. Species adapted to accretion exhibit distinct strategies to emerge, such as internode elongation and shoot growth (in our case: *S. viscosa*, *N. hatshbachii*, *S. campestris* from DDS and DFS), whereas rhizomatous and stoloniferous species exhibit adaptations like vertical meristem growth and activation of dormant buds allowing an emergence above the sand surface (as in grasses *S. ciliata*, *C. pedunculatus*, *P. arenarium*, or stoloniferous species: *P. integrifolia*, *I. imperati* from DSD, DFS, and DC). In shrub species, there is also a strategy of sprouting through the production of new roots and shoots to replace parts that were suffocated by burial (such as in: *D. viscosa*, *V. megapotamica* from DSD and DFS).

While the role of proximity to the sea in forming selective pressure gradients and its influence on coastal plant community patterns is widely recognized (Angiolini et al., 2013; Houle and Gilles, 2008; Purvis et al., 2015; Ruocco et al., 2014; Tirgan et al., 2022; Tissier et al., 2013; Torca et al., 2019; Wiser et al., 2010), our investigation demonstrated that, in the presented context, abiotic conditions in the microhabitats (relief, floodable, beach distance, microhabitats) played a more significant role in structuring the communities. Despite explaining less than half of the total variation, we infer that the species composition follows a moisture gradient, soil exposure, and terrain slope, leading to the formation of distinct groupings. These observations align with other studies in coastal ecosystems (Lortie and Cushman, 2007; Nordstrom et al., 2007; Pimentel et al., 2007; da Silveira et al., 2022; Hernández-Cordero et al., 2015, Hernández-Cordero et al., 2022) and reinforce the fundamental role of other abiotic variables in vegetation structure at local scales. Especially, soil characteristics play a crucial role in explaining coastal vegetation structure, particularly concerning vegetative influence mechanisms (Feagin et al., 2015; Melo Júnior and Boeger, 2015; Kutbay and Sürmen, 2022; Opolski-Neto and Melo-Júnior, 2022).

The results of the present study revealed distinct groupings, notably the Humid slack Dune (HSD), characterized by the flooding condition, and a second group formed by ED (Embryo Dunes), whose main characteristic is related to the proximity to the sea and its respective influence. Alternatively, we observed a set composed of Dune

Crist (DC), Dune Frontal Side (DFS) and Dune Dorsal Side (DDS), which configure the proper dune condition. Alternatively, we observed a set composed of Dune Crest (DC), Dune Frontal Side (DFS), and Dune Dorsal Side (DDS), which together define the characteristic dune condition. Based on their composition and the presence of indicator species, these areas should be considered as a single unified Dune condition. Among these, an intermediate presence of the Dry Slack Dune (DSD) and Dune Toe (DT) groupings was noted, with the former more associated with HSD due to high vegetation cover and species sharing, while the latter showed similarity with DC, DDS, and DFS due to shared soil conditions and inclined terrain leading to burial processes and, consequently, species sharing (see Supplementary Material III). The groupings DC, DDS, and DFS formed a broader and less distinctly differentiated set, possibly due to greater soil exposure and more inclined terrain in these conditions. In areas with higher relief variability, topography emerges as an essential element in the structuring of coastal communities (Dwyer et al., 2021; Hernández-Cordero et al., 2022). For DC, DDS, and DFS, the analyzed variables in the present study influence a profile of shared indicator species composition (Table 4; Supplementary Material III.) and similar coverage percentages (Figure 2). Both indicators represent different facets of a proper dune condition (Figure 1A, G-I), implying analogous environmental pressures among them, culminating in the absence of a clear demarcation between the frontal and dorsal regions of the dune, addressed in this study. This scenario points to the possibility of further investigations considering also: wind direction (Hernández-Cordero et al., 2015; Muñoz-Reinoso, 2018), salinity (Du and Hesp, 2020), burial (Dech and Maun, 2005; Frosini et al., 2012;), and grain size (Lortie and Cushman, 2007; Fenu et al., 2013).

Conclusions

Although conducted at a local scale, our study provides a comprehensive and detailed analysis of herbaceous and shrub vegetation within the restinga, revealing some of the determining factors in structuring the investigated plant community. The study advances our understanding by indicating that species richness variation was closely linked to different types of microhabitats, challenging patterns observed in other coastal regions where distance from the beach is a predominant factor in community structuring. Additionally, the variation in richness among microhabitats was less distinctive than initially expected, highlighting the complexity of interactions between abiotic variables and species richness. Pressures from the marine environment emerged as a predominant factor for vegetation near the coast, leading to the selection of specialized taxa and distinct structuring, allowing the recognition of the Embryo Dune (ED) microhabitat. Conversely, in more distant areas, flooding related to groundwater table fluctuations proved more influential in community structuring and species selection, configuring the Humid Slack Dune (HSD) microhabitat. However, different dune areas (Dune Frontal Side, Dune Dorsal Side, and Dune Crest) showed similar species structure and composition, suggesting they represent a single microhabitat. Nonetheless, the influence of more subtle factors, such as edaphic (physicochemical) factors and biotic interactions among species, along with their functional aspects, was not considered by this approach. Dry Slack Dune (DSD) areas emerge as transitional zones, sharing a similar composition between Dune Toe (DT) areas and distinct from HSD. Regarding indicator species, we observed that microhabitats feature a selection of specialized taxa reflecting adaptation to specific conditions at local scales. At the same time, we verified that many species are shared among microhabitats, suggesting other environmental factors may be involved in the structuring and selection of species in the herbaceous restinga communities. These results reinforce the importance of the interaction between abiotic factors and floristic composition, which not only supports the specific structuring of each microhabitat but also highlights the complexity of restinga ecosystems. The inferences presented here provide an important foundation for future investigations that may broaden our understanding of similar dune ecosystems. This study represents a significant step towards a deeper understanding of coastal ecology and serves as a valuable resource for researchers and environmental managers seeking effective strategies to conserve and manage these ecosystems, essential to address challenges posed by global climate change.

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