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Original Article

Diversity and floristic uniqueness of non-arboreal *restingas* of the Northern Coast of Bahia, Brazil

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ABSTRACT

The Northern Coast of Bahia state (NCB) encompasses the northernmost stretch of the state coastline and harbors *restinga* ecosystems of exceptional biodiversity, ecological, and cultural importance. Despite previous floristic surveys, non-arboreal *restingas* remain under-sampled, limiting the understanding of their composition and ecological dynamics. This study aimed to document angiosperm diversity in these habitats and assess the distinctiveness of their floristic communities. Field surveys were conducted in the non-arboreal *restingas* of Mata de São João and Entre Rios municipalities. Specimens were collected, photographed, and deposited at the ALCB Herbarium. Data from nine other Brazilian *restingas* were included in similarity (ANOSIM) and clustering (UPGMA) analyses using beta diversity indices. A total of 245 species, 174 genera, and 76 families were recorded, with Fabaceae (28 spp.), Rubiaceae (18 spp.), and Myrtaceae (16 spp.) being the most representative families. The genera *Chamaecrista*, *Myrcia*, and *Cyperus* were the most species-rich. While Bahia's floristic communities showed general similarity, the NCB *restingas* were markedly distinct from the southern coast, showing stronger affinities with Sergipe state *restingas*. This pattern suggests a phytogeographic block shaped by shared climatic and geomorphological conditions, as well as endemic species. Despite their richness, NCB's non-arboreal *restingas* remain insufficiently studied and increasingly threatened by rapid anthropogenic expansion.

Keywords: Atlantic Forest, Beta diversity, Checklist, Dune vegetation, Floristic similarity, Litoral Norte da Bahia, Plant conservation

[†]In memory of Nádia Roque, our mentor and an extraordinary botanist with an admirable career in systematic research. Beyond her remarkable work in systematics, she also played a pivotal role in numerous studies on conservation and biogeography. This study stemmed from her curiosity and recent interest in the *restingas* of the Northern Coast of Bahia, where she was deeply involved in every stage of research and manuscript preparation. Although Nádia left us too soon, her legacy will live on forever.

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Introduction

Restinga corresponds to a peculiar set of vegetational and edaphic characteristics found along coastal terrestrial areas that are influenced by abiotic factors related to maritime action, such as wind and salinity (Brasil, 1999; Falkenberg, 1999; Brasil, 2002). Geologically, *restingas* are characterized as sedimentary deposits of Quaternary origin (Dominguez, 2000), and in a more integrative approach, they can be treated as a vegetational complex, where physical factors cannot be dissociated from biological ones (Rizzini, 1997). Regarding vegetation, these areas may display different physiognomic profiles, with diverse life forms and community structures, including *restinga* forests, scrub formations, and herbaceous meadows (Ule, 1901; Silva & Britez, 2005; Dias & Soares, 2008).

The Brazilian coastline exhibits remarkable variation in the vegetation types of its coastal plains, with several studies proposing the zoning or subdivision of *restinga* vegetation along its extent (Araújo, 1992; Scarano, 2002; Silva & Britez, 2005; Magnago *et al.*, 2007; Dias & Soares, 2008; Araújo & Pereira, 2009; Cantarelli *et al.*, 2012; Pereira & Menezes, 2023). Consequently, the distribution of *restinga* vegetation throughout the Brazilian coast is fragmented (Martin *et al.*, 1980), and its floristic composition is influenced by a complex interplay of geomorphological, edaphic, and climatic factors (Mather & Yoshioka, 1968; Almeida Jr *et al.*, 2009).

From a geomorphological perspective, the Brazilian coastline is classified into units based on geological, hydrological, and sedimentary dynamics (Villwock *et al.*, 2005). These foundational factors are key influencers of the floristic composition of *restinga* communities (Rabelo *et al.*, 2024). The coastline of Bahia state, for example, encompasses two distinct geomorphological regions, the Northeast and East Coasts, which are demarcated by *Todos os Santos* Bay (Villwock *et al.*, 2005). Changes in floristic composition at these geomorphological boundaries have been frequently observed in prior surveys conducted in Bahia (Menezes *et al.*, 2012; Fernandes & Queiroz, 2015) and Maranhão (Lima & Almeida, 2018). Broader coastal comparisons also reveal a north–south differentiation in Atlantic Forest floras, strongly correlated with rainfall and temperature gradients (Leitman *et al.*, 2015).

Therefore, floristic studies play a fundamental role in determining such patterns, especially regarding physiognomies and phytogeography (Kier *et al.*, 2005; Magnago *et al.*, 2011). Many of these studies have revealed the remarkable richness of Brazilian *restingas* (Magnago *et al.*, 2007; Sacramento *et al.*, 2007; Marques *et al.*, 2015; Martins *et al.*, 2008; Almeida Jr *et al.*, 2009; Araújo & Pereira, 2009; Silva *et al.*, 2008; Queiroz *et al.*, 2012; Gomes & Guedes, 2014; Oliveira *et al.*, 2014), providing essential data for assessing biodiversity.

Measuring biodiversity at the community level is a straightforward and useful way to understand biological patterns (Magurran, 2004), which can be done by using several diversity indices, such as alpha and beta diversity (Whittaker *et al.*, 2001). While alpha diversity reflects the richness of a specific site, beta diversity evaluates the differences in species composition between multiple sites (Whittaker *et al.*, 2001). The latter is commonly used for assessing assemblage similarities (Chao *et al.*, 2005) and thus aiding in understanding the uniqueness and factors driving heterogeneity among communities (Baselga, 2010; Yang *et al.*, 2021; Mori *et al.*, 2018), including those in *restinga* formations (Massante & Gerhold, 2020; Inague *et al.*, 2021).

Comprehensive species inventories are fundamental to enabling these diversity measurements and overcoming the biodiversity shortfalls that impede robust ecological analysis (Hortal *et al.*, 2015). As cornerstones for assessing biodiversity, these inventories directly tackle both taxonomic and distributional knowledge gaps. By systematically documenting species occurrences, checklists help resolve the Linnean shortfall (Lomolino, 2004)—the disparity between the number of formally described species and the higher number estimated to exist (Mora *et al.*, 2011; Caley *et al.*, 2014). Concurrently, they provide valuable distributional data that address the Wallacean shortfall (Lomolino, 2004), which arises from geographically biased sampling and the limited resolution of species range data (Hortal *et al.*, 2007; Boakes *et al.*, 2010). This dual role is especially significant in ecosystems like non-arboreal *restingas*, where both species richness and distribution remain poorly documented. Systematic inventories in these environments not only enhance the taxonomic foundation but also refine spatial data, thereby enabling more accurate assessments of alpha and beta diversity and facilitating ecological, biogeographical, and conservation research (Rodrigues *et al.*, 2010; Meyer *et al.*, 2015).

To directly address these critical data shortfalls and contribute the necessary analytical insight for a threatened and understudied ecosystem, this study aims to characterize the angiosperm diversity of non-arboreal *restinga* remnants on the Northern Coast of Bahia by: (i) documenting species composition; (ii) identifying endemic and threatened species of conservation concern; and (iii) analyzing beta diversity patterns of similarities and their environmental drivers. Supporting such botanical cataloging initiatives is crucial for advancing a comprehensive understanding of plant diversity and for addressing the complex challenges in conserving Brazil's threatened ecosystems (Forzza *et al.*, 2012). Furthermore, the quantitative assessment of floristic similarity provides a powerful tool to evaluate the relationship between plant communities, generating critical insights for guiding ecosystem conservation and restoration efforts. These analytical methods establish a robust scientific foundation for developing informed management strategies and effective biodiversity protection policies (Kunz *et al.*, 2009; Bonfim *et al.*, 2016; Mota *et al.*, 2017).

Material and methods

Study Area

Bahia is the state with the longest coastline in Brazil, spanning approximately 1,120 km (Martin *et al.*, 1980). Its northernmost portion is commonly known as Litoral Norte (Northern Coast), and it encompasses the entire coastal plain located between the municipal boundary of Salvador and Lauro de Freitas (12°54'37.05" S, 38°18'17.31" W) up to the state boundary with Sergipe (11°26'33.42"S, 37°20'28.70" W), covering approximately 200 km (Nunes & Matos, 2017).

Considering the five Brazilian Climatic Zones, four cover the Northeast coastline: Equatorial Zone, Equatorial Tropical Zone, Oriental Northeastern Tropical Zone (ONTZ), and Central Brazil Tropical Zone (IBGE, 2002). The ONTZ characterizes the eastern coastal areas of northeastern Brazil with distinct climatic features, encompassing the study area (IBGE, 2002). The region's climate is classified as Tropical Humid, with annual temperatures ranging from 20 °C to 29 °C and total annual rainfall between 1,200 and 1,900 mm (1991–2020; INMET, 2023).

From a hydrographic perspective, this coastal stretch is part of a broader territorial framework defined by the National Hydrographic Division, which compartmentalizes Brazil into 12 Hydrographic Macroregions. These regions are established as territorial units composed of a basin, or a set of contiguous basins and sub-basins, that share homogeneous or similar natural, social, and economic characteristics (CNRH, 2003; IBGE, 2021). In the Northeast, notable regions include the Occidental Northeast Atlantic Region, Parnaíba Region, Oriental Northeast Atlantic Region (ONAR), São Francisco Region, and the East Atlantic Region (EAR)—the latter being the predominant region along the coast of Bahia (CNRH, 2003; IBGE, 2021).

The *restingas* of the Northern Coast of Bahia are part of the Atlantic Forest phytogeographic domain and are characterized by the presence of a foredune, unique to this region of the state (Martin *et al.*, 1980; Minervino Netto, 2017). The areas selected for this study correspond to *restinga* remnants located in the municipalities of Mata de São João (Jauara Lagoon, 12°31'03.2" S, 37°58'39.8" W; Santo Antônio Dunes, 12°27'34.9" S, 37°56'23.4" W) and Entre Rios (Massarandupió, 12°19'15.1" S, 37°50'14.9" W; Porto Sauípe, 12°20'59.9 "S, 37°51'23.0 " W) (Fig. 1).

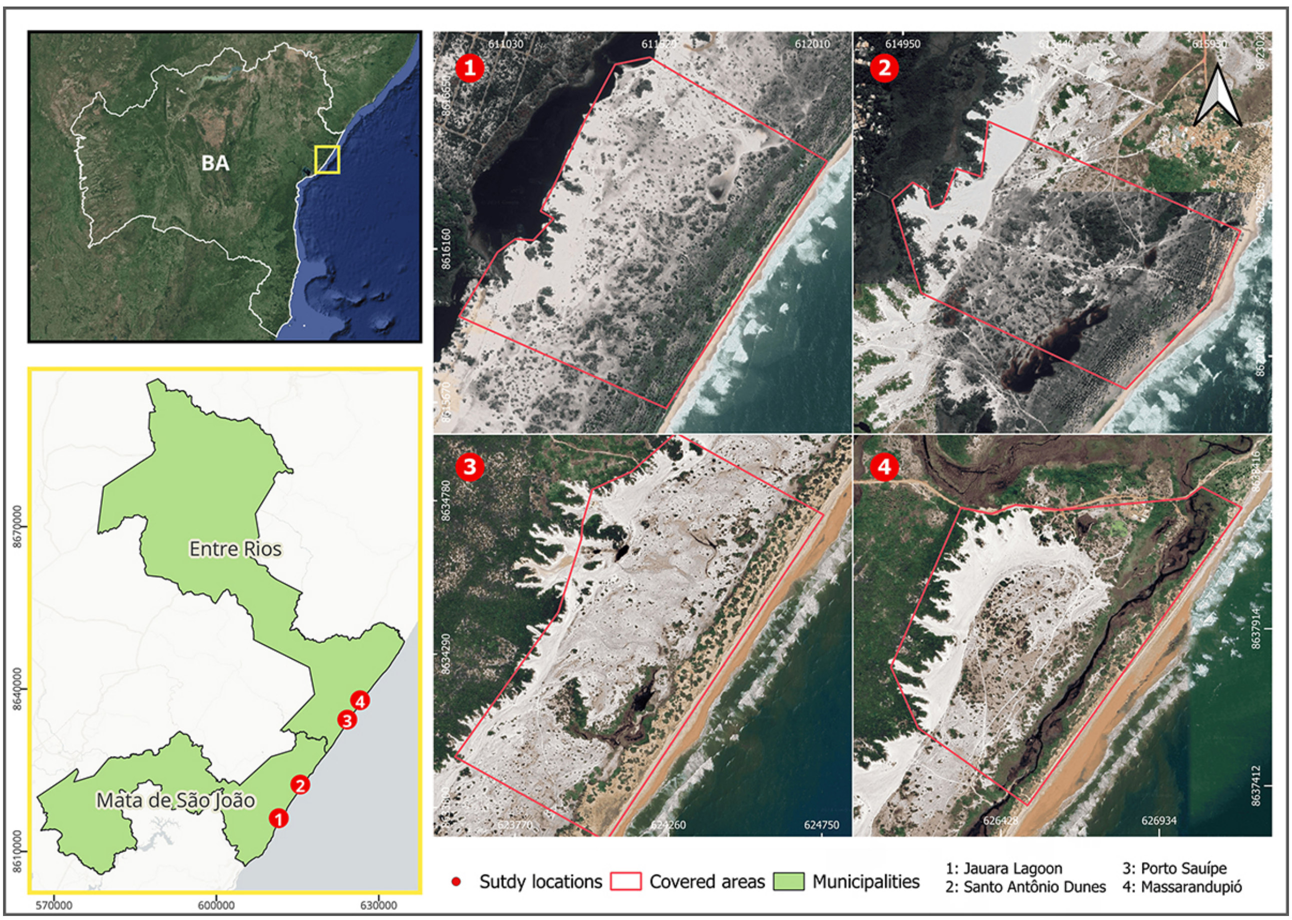

Figure 1. Location maps of the studied *restingas*.

Delimitation of Restingas Vegetation Types

The classification of physiognomies was adapted from the proposal by Silva & Britez (2005), considering local specificities. Meadow formations (Fig. 2, A-B) correspond to predominantly herbaceous psammophilous vegetation, either erect or creeping, that can be open or closed, floodable or non-floodable. Scrub physiognomies (Fig. 2, D-F) are characterized by the predominance of shrubby plants, with occasional arboreal individuals, and may also be open or closed, floodable or non-floodable. The criterion for determining open physiognomies, as brought forth by Silva & Britez (2005), was the degree of soil cover, which must be less than 60%. *Restinga* forests were not evaluated in this study.

Collection and Processing

Six field expeditions were conducted between August 2022 and August 2023, each lasting three days, with one day of sampling for each area. The locality of Porto Sauípe was added later, and thus only one field trip was carried out in August 2023.

The collections were performed using the random-walk method, following parallel and perpendicular paths to the beach line, aiming to cover as much diversity of physiognomies as possible. Only fertile individuals (with flowers and/or fruits) were collected. The collected specimens were pressed, dried at 60°C, and mounted on exsiccate following traditional herbarium techniques, then deposited in the ALCB Herbarium.

Family identifications were based on Souza & Lorenzi (2019). For genus and species identifications, keys from Flora e Funga do Brasil (2025) were used when available. For groups not yet completed in the FFB, specialized taxonomic literature was consulted. Visits to the Alexandre Leal Costa Herbarium (ALCB) and consultations to speciesLink and the Virtual Herbarium Reflora were conducted to compare doubtful specimens with vouchers previously identified by specialists. Field images of species with uncertain identification were sent to taxonomists. Information about the origin and endemism of species was obtained from Flora e Funga do Brasil (2025). To assess the conservation status of the identified species, the reference scale and classification from the International Union for Conservation of Nature (IUCN, 2024) and data from CNCFlora were considered.

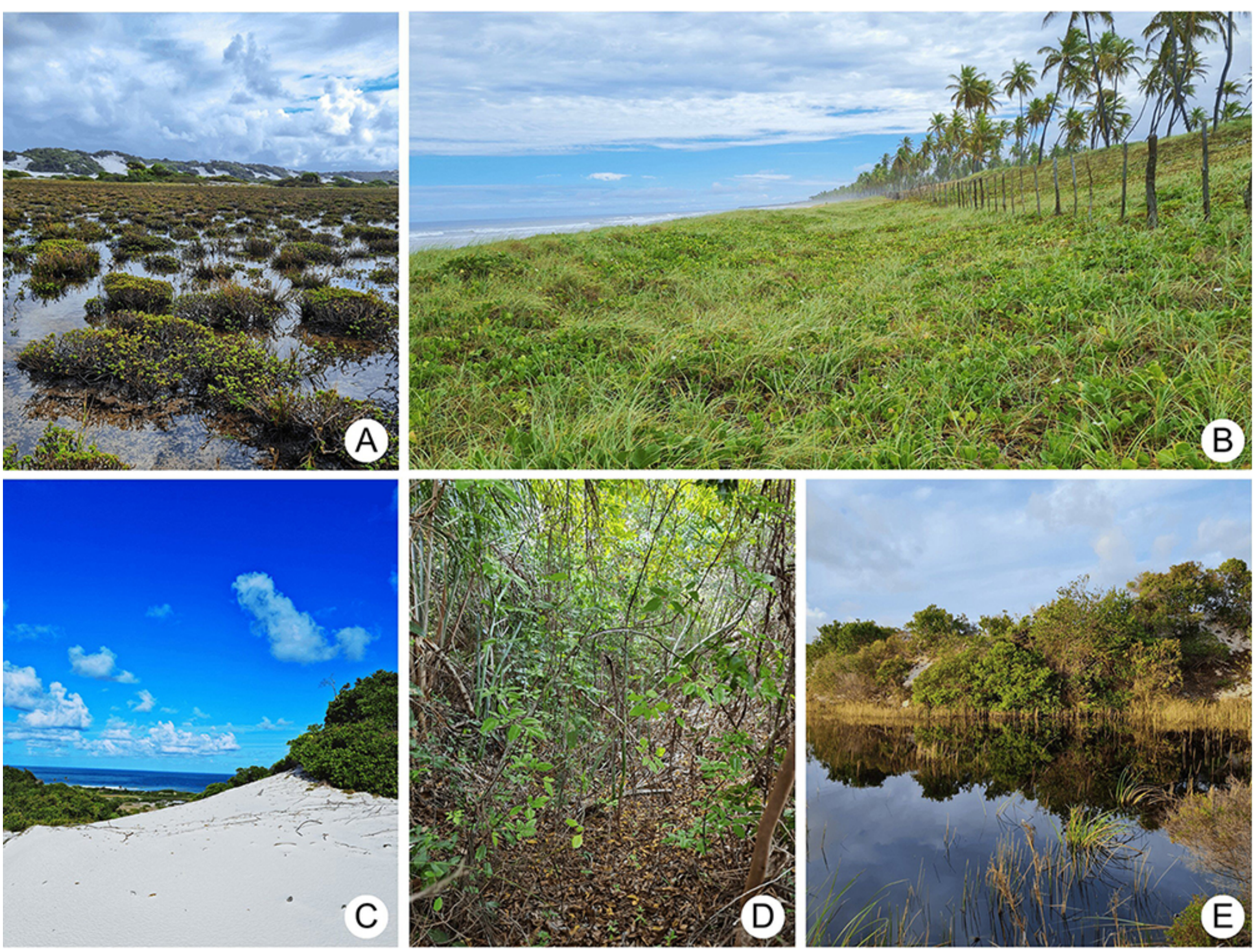

Figure 2. Non-arboreal *restingas* of the North Coast of Bahia: Porto Sauípe (A), Santo Antônio (B), Massarandupió (C, D), and Jauara Lagoon (E)

Consultations in Flora e Funga do Brasil (2025) were conducted to confirm species endemism. As defined by Flora e Funga do Brasil (2025), a species is considered endemic if its distribution is limited to the Brazilian territory, with occurrences recorded in one or more of the six official phytogeographic domains (such as Amazonia, Caatinga, Cerrado, Atlantic Forest, Pampa, and Pantanal) and various vegetation designations (including *restinga*). The assessment of endemism is applied primarily at the national level, followed by domain, state, and vegetation levels.

Data Compilation

In addition to primary field data, secondary data were incorporated into the species checklist to strengthen the analytical foundation of the study and to expand its representativeness. Searches were carried out in virtual databases (speciesLink.net, Reflora, and JABOT) using filters for state and municipal locations, along with keywords in portuguese such as "*restinga*", "*dunas*", "*praia*", and "*areia branca*". Only vouchers containing geographic coordinates, collection area descriptions, and specialist-confirmed identifications were included. The integration of secondary data enhanced taxonomic reliability and spatial coverage, complementing field records.

For the similarity analysis, a review of floristic studies focused on non-arboreal *restingas* along the Northeastern and Southeastern coasts of Brazil was conducted. Studies that did not provide clear occurrence data regarding the vegetational formations of the reported *taxa* were excluded; however, studies conducted in areas known for lacking forest physiognomies were included. To minimize sampling effort bias, we reviewed survey methodologies and included only studies conducted for at least one year. Nine studies were selected for the analysis (Tab. 1). Taxonomic synonyms, non-native taxa (exotic, cultivated, or naturalized), and those without specific identification (cf., aff., or sp.) were excluded. A final list of 778 species was generated, from which a presence-absence matrix was produced for each studied locality (Supplementary Material S1).

Table 1. Selected studies for similarity analyses. Richness values after data processing.

ID	Studies locations	Acronym	Richness	Reference
1	São João da Barra (RJ)	saoj-RJ	62	Assumpção and Nascimento (2001)
2	Presidente Kennedy (ES)	pres-ES	76	Braz *et al.* (2013)
3	Jaguaripe (BA)	jagu-BA	169	Costa *et al.* (2018)
4	Salvador / Abaeté (BA)	salv-BA	326	Britto *et al.* (1993)
5	Camaçari (BA)	cama-BA	321	Queiroz *et al.* (2012)
6	Entre Rios e Mata de São João (BA)	mata-BA	237	Current study
7	Pirambu e Pacatuba (SE)	pira-SE	88	Oliveira and Landim (2014)
8	Sirinhaém (PE)	siri-PE	107	Cantarelli *et al.* (2012)
9	Cabo de Santo Agostinho (PE)	cabo-PE	92	Sacramento *et al.* (2007)
10	Jericoacoara (CE)	jeri-CE	73	Matias and Nunes (2001)

Analysis of Diversity and Similarity

Total beta diversity was assessed using the Sørensen index (βsor), which evaluates dissimilarity between communities based on species presence and absence, disregarding abundance (Sørensen, 1948). βsor was calculated for multiple communities and pairwise between community, allowing its partitioning into nestedness (βsne) and turnover (βsim) components. Partitioning was conducted using the *betapart* R package (Baselga *et al.*, 2012), which generates matrices for each component (Supplementary Material S2). The turnover component, βsim, corresponds to the Simpson dissimilarity index (Simpson, 1960) and was used for hierarchical clustering via UPGMA (Unweighted Pair-Group Method using Arithmetic Averages) using the "*hclust*" function in R. The dendrogram was constructed using the *factoextra* package (Kassambara & Mundt, 2017), with the cut-off point determined based on Mojena's (1977) method.

Non-parametric analyses were also performed, including exploratory NMDS (Non-metric Multidimensional Scaling; Clarke, 1993) to assess spatial ordination of samples, and ANOSIM (Analysis of Similarities) to evaluate whether dissimilarities align with known hydrographic patterns (Macroregions; IBGE, 2021) and climatic zones (IBGE, 2002).

To examine the influence of climatic variables and geographical distance on floristic community composition, Mantel tests using the Spearman correlation method were performed (Mantel, 1967). The tests incorporated data on mean annual temperature (°C), temperature seasonality (standard deviation × 100), annual precipitation (mm), precipitation seasonality (coefficient of variation), and wind speed (m/s), obtained from the WorldClim database (Fick & Hijmans, 2017). Geographical coordinates were extracted from the selected studies. These analyses were conducted using the *vegan* (Oksanen *et al.*, 2013) and *geopackage* (Karney, 2013) packages in R.

All data analysis was carried out using R statistical software version 4.4.1 (R Core Team, 2025) implemented through RStudio version 2025.05.1+513 (Posit Team, 2025)

Methodological Limitations and Potential Bias

Although floras and floristic surveys are a cornerstone of biodiversity assessment, they are inherently prone to undersampling, as comprehensive species inventories are rarely attainable (Hortal *et al.*, 2015). This poses a significant challenge for comparative analyses, since disparities in recorded richness can artifactually influence beta diversity patterns and lead to biased ecological interpretations (Baselga *et al.*, 2007; Beck *et al.*, 2013). With sampling effort difficult to estimate, standardization unfeasible for this type of data, and the exclusion of discrepant studies resulting in substantial information loss, this bias must be regarded as unavoidable.

To help minimize the effects of richness bias, the recommendation of Baselga & Leprieur (2015) was followed by applying the Simpson dissimilarity index (βsim), which is less sensitive to variations in species richness (Koleff *et al.*, 2003). In addition, Mantel tests were performed to quantitatively assess how richness variation affects both turnover and nestedness components, by comparing the matrix of absolute richness differences (Supplementary Material S3) with the matrices of turnover (βsim) and nestedness (βsne). This approach enabled a statistical evaluation of the relationship between richness gradients and beta diversity patterns, while accounting for the structural constraints of inventory-based data.

Results

Floristic Diversity, Endemism and Conservation

A total of 245 species were identified, distributed across 174 genera and 76 families (Tab. 2). The most diverse families were Fabaceae (28 species), Rubiaceae (18), and Myrtaceae (16), followed by Cyperaceae (14) and Asteraceae (eight species). Poaceae and Apocynaceae each contained seven species, while Euphorbiaceae, Malpighiaceae, Orchidaceae, Eriocaulaceae, and Melastomataceae each accounted for six species. The 12 most diverse families collectively accounted for 52% of the total species diversity. The most representative genera were *Chamaecrista* (L.) Moench and *Myrcia* DC., each with seven species, followed by *Cyperus* L. and *Eugenia* L., with five species each, and *Byrsonima* Rich. ex Kunth with four species.

Regarding their origin, 237 species (97%) are considered native, with 124 endemic to Brazil (51%), 52 to the Northeast Region (21%), 20 to Bahia (8%), and, among these, 10 are endemic to the state's *restinga* ecosystems (*Brassavola ceboletta*, *Chamaecrista salvatoris*, *Comolia abaetensis*, *Doliocarpus sellowianus*, *Hohenbergia littoralis*., *Leiothrix restingensis*, *Macrolobium rigidum*, *Manilkara decrescens*, *Microtea bahiensis*, and *Mitracarpus anthospermoides*). In terms of conservation status, only 52 species (21%) have been assessed, of which 15 are classified under threat categories (VU and EN). Species *Allagoptera brevicalyx*, *Calycolpus legrandii*, *Eriope blanchetii*, *Manilkara decrescens*, *Melocactus violaceus*, *Ouratea robusta*, and *Poecilanthe itapuana* are listed as vulnerable (VU), while species *Byrsonima microphylla*, *Hohenbergia littoralis*, *Microtea bahiensis*, *Mitracarpus anthospermoides*, *Protium bahianum*, *Swartzia arenophila*, *Swartzia revoluta*, and *Vanilla phaeantha* are considered endangered (EN).

The growth habits showed considerable variation, with a predominance of shrub (40%) and herbaceous species (36%), followed by subshrubs (9%) and trees (7%). Together, climbers and palms accounted for 8% of the inventoried species.

Scrub formations exhibited the highest richness, with 162 species, with non-floodable scrub physiognomies being the most representative (Fig. 3a). The families Myrtaceae, Rubiaceae, and Fabaceae were more frequent in these formations, particularly in open non-floodable areas (Tab. 2). The genera *Myrcia*, *Byrsonima,* and *Davilla* Vand. stood out as the most diverse within these physiognomies. Shrubs were the predominant growth habit, accounting for approximately 52% of the species found, followed by herbaceous species (18%) and trees (10%). The remaining comprised subshrubs, palms, climbers, and parasites, which collectively represented 22%. Families with significant representation in Bahia's *restinga* ecosystems showed an exclusive distribution in these physiognomies, such as Malpighiaceae (six spp.), Dilleniaceae (five spp.), Loranthaceae (four spp.), and Anacardiaceae (three spp.).

Meadow formations showed lower species richness (88 spp.) compared to scrub formations. The families Cyperaceae, Fabaceae, and Poaceae were the most representative within these physiognomies, with the genera *Cyperus*, *Rhynchospora* Vahl, and *Chamaecrista* being the most diverse. Herbaceous physiognomies were dominated by herbs (69%), followed by shrubs (17%) and subshrubs (11%). Climbers accounted for only 2% of the species, while tree species were absent. *Cocos nucifera* L. was commonly found in non-floodable meadows of the Mata de São João *restingas*, being the only palm species recorded in this vegetation stratum. However, this name was excluded from the checklist, as the region was found to have a history of cultivation of this species, which was confirmed by observed evidence of recent management.

Alpha and Beta Diversities Across Sites

Floristic inventories demonstrated considerable heterogeneity in species richness among the studied non-arboreal *restinga* sites, with values ranging from 62 to 326 angiosperm species (mean = 155.1 ± 103.3 SD). This nearly five-fold variation in alpha diversity provided a robust gradient for evaluating potential sampling bias effects. Results from the Mantel test showed that absolute differences in richness do not significantly impact total beta diversity (βsor; R = 0.204, p = 0.131). Similarly, there was no significant effect on the turnover component (βsim; R = -0.554, p = 0.991); however, richness positively and strongly influenced nestedness (βsne; R = 0.972, p = 0.0001), which is both anticipated and commonly reported (Soininen *et al.*, 2018).

Table 2. Checklist of angiosperms from Northern Coast of Bahia non-arboreal restingas. Growth habits (Hab): herb (he); subshrub (su); shrub (sh); tree (tr); climbing herb or liana (li); palm tree (pm). Conservation status (Cs): data deficient (dd); least concern (lc); endangered (en); near threatened (nt); vulnerable (vu). Endemism (End): endemic to Brazil (br); to Northeast region (ne); to Bahia (ba); to restinga vegetations (r). Vegetation physiognomies (Phy): closed floodable meadow (cfm); closed non-floodable meadow (cnm); closed floodable scrub (cfs); closed non-floodable scrub (cns); open floodable meadow (ofm); open non-floodable meadow (onm); open floodable scrub (ofs); open non-floodable scrub (ons).

Family / Species	Hab.	Cs	End.	Phy	Voucher
Acanthaceae					
Aphelandra nitida Nees & Mart.	su	lc	br	cns	ALCB 149238
Amaranthaceae					
Blutaparon portulacoides (A.St.-Hil.) Mears	he	lc	r	onm	ALCB 149306
Froelichia humboldtiana (Roem. & Schult.) Seub.	sh			onm	ALCB 149369
Gomphrena duriuscula Moq.	su	dd	ne, r	onm, ons	ALCB 149198
Anacardiaceae					
Anacardium occidentale L.	tr			cns	ALCB 149246
Schinus terebinthifolia Raddi	sh			cns	ALCB 149348
Tapirira guianensis Aubl.	tr			cns	ALCB 149340
Apocynaceae					
Catharanthus roseus (L.) Don ex	he			cnm	ALCB 149257
Ditassa crassifolia Decne.	li		br	ons, cns	ALCB 149347
Hancornia speciosa Gomes	tr			cns	ALCB 149289
Mandevilla microphylla (Stadelm.) M.F.Sales & Kin.-Gouv.	li		ba	ons, cns	ALCB 149377
Mandevilla moricandiana (A.DC.) Woodson	li		br	cns	ALCB 149334
Mandevilla scabra (Hoffmanns. ex Roem. & Schult.) K.Schum.	li			ons	ALCB 028677
Oxypetalum banksii R.Br. ex Schult.	li		br	cfs, cns	ALCB 50692
Aquifoliaceae					ALCB 149266
Ilex blanchetii Loes.	sh		ba, r-d	ons	ALCB 149266
Ilex theezans Mart. ex Reissek	sh			ofs	ALCB 149395
Araceae					
Anthurium affine Schott	he		br	cns	ALCB 149135
Philodendron acutatum Schott	he			cfm, cnm, cns	ALCB 149359
Arecaceae					
Allagoptera brevicalyx Moraes	pm	vu	ne	ons	ALCB 149190
Syagrus schizophylla (Mart.) Glassman	pm	lc	br, r	ons, ofs	ALCB 149237
Asteraceae					
Acritopappus confertus (Gardner) R.M.King & H.Rob.	su		br	cns	ALCB 149245
Calea angusta S.F.Blake	su		ne, r	ons, cns	ALCB 149189
Conocliniopsis prasiifolia (DC.) R.M.King & H.Rob.	su	lc	ne	onm, cnm	ALCB 149307
Elephantopus hirtiflorus DC.	he	lc	br	cnm, ons	ALCB 149330
Lepidaploa mucronifolia (DC.) H.Rob.	su		ne	ons	ALCB 149242
Litothamnus nitidus (DC.) W.C.Holmes	sh		ne, r	ons, cns	ALCB 149239
Prolobus nitidulus (Baker) R.M.King & H.Rob.	su		ba, r-d	ons	ALCB 149380
Sphagneticola trilobata (L.) Pruski	he			cfm	ALCB 149310
Balanophoraceae					
Langsdorffia hypogaea Mart.	he			cns	ALCB 149450
Bignoniaceae					
Tabebuia elliptica (DC.) Sandwith	sh	lc	br, r	cns	HUEFS 77505

Table 2. Cont.

Family / Species	Hab.	Cs	End.	Phy	Voucher
Bonnetiaceae					
Bonnetia stricta (Nees) Nees & Mart.	sh		br, r-d	cfm	ALCB 149213
Bromeliaceae					
Aechmea aquilega (Salisb.) Griseb.	he	lc	br	ofs, ons	ALCB 149367
Hohenbergia littoralis L.B.Sm.	he	en	ba, r	ons	ALCB 149166
Burseraceae					
Protium bahianum Daly	sh	en	ne, r	ons, cns	ALCB 149243
Protium heptaphyllum (Aubl.) Marchand	tr			cns	ALCB 149295
Cactaceae					
Cereus fernambucensis Lem.	su		br	cnm, ons	ALCB 149156
Melocactus violaceus Pfeiff.	he	vu	br	ons	ALCB 149451
Calophyllaceae					
Kielmeyera neglecta Saddi	tr	lc	ba, r-d	cns	ALCB 149249
Capparaceae					
Cynophalla hastata (Jacq.) J.Presl	sh			ons	ALCB 149389
Celastraceae					
Monteverdia erythroxyla (Reissek) Biral	sh	lc	ne	ons	ALCB 149373
Chrysobalanaceae					
Chrysobalanus icaco L.	sh		r	cnm, ofs, ons	ALCB 149443
Hirtella ciliata Mart. & Zucc.	tr	lc		cns	ALCB 149308
Parinari littoralis Prance	tr	lc	ne		CEPEC 80352
Cleomaceae					
Dactylaena microphylla Eichler	he		br		HUEFS 78027
Clusiaceae					
Clusia hilariana Schltdl.	sh		br	ons, cns	ALCB 149396
Clusia panapanari (Aubl.) Choisy	sh			cns	ALCB 149448
Commelinaceae					
Commelina erecta L.	he			onm	ALCB 149274
Convolvulaceae					
Daustinia montana (Moric.) Buril & A.R. Simões	li		br	cns	ALCB 149420
Evolvulus imbricatus Mart. ex Colla	sh		br	ofs	ALCB 149412
Ipomoea imperati (Vahl) Griseb.	he			onm	ALCB 149297
Ipomoea pes-caprae (L.) R.Br.	he		r	onm	ALCB 149302
Jacquemontia glaucescens Choisy	li		br	cns	ALCB 149383
Cordiaceae					
Cordia pilosa M.Stapf & Taroda	sh		ne, r	cns	ALCB 028676
Varronia johnstoniana J.I.M. Melo & D.D. Vieira	sh		ne	cfm	ALCB 149233
Varronia multispicata (Cham.) Borhidi	sh		br	ons	ALCB 149387
Cyperaceae					
Abildgaardia baeothryon A.St.-Hil.	he		br	ofm	ALCB 149170
Bulbostylis fasciculata Uittien	he			ofm, cfm	ALCB 149399
Cyperus ligularis L.	he			ofm	ALCB 14932
Cyperus crassipes Vahl Natu	he			onm	ALCB 149210
Cyperus meyenianus Kunth	he			ofm	ALCB 149136
Cyperus pedunculatus (R.Br.) J.Kern	he		r	onm, cnm	ALCB 149301

Table 2. Cont.

Family / Species	Hab.	Cs	End.	Phy	Voucher
Cyperus polystachyos Rottb.	he			ofm, cfm	ALCB 149318
Eleocharis geniculata (L.) Roem. & Schult.	he			ofm	ALCB 149426
Eleocharis mutata (L.) Roem. & Schult.	he			cfm	ALCB 149366
Fimbristylis cymosa R.Br.	he			ofm	ALCB 149384
Fuirena umbellata Rottb.	he			cfm	ALCB 149384
Rhynchospora gigantea Link	he			cfm	ALCB 149406
Rhynchospora holoschoenoides (Rich.) Herter	he			cfm	ALCB 149254
Rhynchospora riparia (Nees) Boeckeler	he			ofm	ALCB 149382
Dilleniaceae					
Davilla flexuosa A.St.-Hil.	li		br	ons, cns	ALCB 149441
Davilla sessilifolia Fraga	su		ba	ons	ALCB 028674
Doliocarpus sellowianus Eichler	sh		ba, r	ons, cns	ALCB 149253
Tetracera boomii Aymard	li		br, r		ALCB 038031
Tetracera breyniana Schltdl.	sh		br	ons, cns	ALCB 149349
Ebenaceae					
Diospyros gaultheriifolia Mart. ex Miq.	sh		br	ons	ALCB 149403
Ericaceae					
Agarista revoluta (Spreng.) J.D. Hook. ex Nied.	sh	lc	br, r-d	ons, cns	HUEFS 206329
Eriocaulaceae					
Comanthera imbricata (Körn.) L.R.Parra & Giul.	he		ne, r-d	ons	ALCB 149446
Leiothrix flavescens (Bong.) Ruhland	he				ALCB 018422
Leiothrix restingensis (Moldenke) Giul.	he		ba, r	ofm	ALCB 149195
Paepalanthus sessiliflorus Mart. ex Körn.	he		ba, r-d	ons	ALCB 149205
Paepalanthus tortilis (Bong.) Mart.	he		br	ofm	ALCB 149445
Syngonanthus gracilis (Bong.) Ruhland	he		r-d	ofm	ALCB 149196
Euphorbiaceae					
Croton heliotropiifolius Kunth	sh			cnm	ALCB 149182
Croton polyandrus Spreng.	sh		br, r	cns	ALCB 149244
Croton sellowii Baill.	sh		ne, r	ons	ALCB 149142
Euphorbia bahiensis (Klotzsch & Garcke) Boiss.	he		r	onm, cnm	ALCB 149155
Maprounea brasiliensis A.St.-Hil	sh			ons	ALCB 149258
Microstachys corniculata (Vahl) Griseb.	sh			ons	ALCB 149256
Fabaceae					
Bauhinia corifolia L.P.Queiroz	sh		ne, r	cns	ALCB 149291
Canavalia rosea (Sw.) DC.	he		r	onm	ALCB 149153
Centrosema brasilianum (L.) Benth.	li			ons, cns	ALCB 149263
Chamaecrista absus (L.) H.S.Irwin & Barneby natu	su			cnm	ALCB 149260
Chamaecrista cytisoides (DC. ex Collad.) H.S.Irwin & Barneby	sh		br		UEC 156508
Chamaecrista desvauxii (Collad.) Killip	he			cfm	ALCB 149430
Chamaecrista flexuosa (L.) Greene	he			cfm, cnm	ALCB 149400
Chamaecrista pascuorum (Benth.) H.S.Irwin & Barneby	sh		br		MBM 235482
Chamaecrista ramosa (Vogel) H.S.Irwin & Barneby	sh			ons	ALCB 149129
Chamaecrista salvatoris (H.S.Irwin & Barneby) H.S.Irwin & Barneby	sh		ba, r	ons	ALCB 149415
Crotalaria holosericea Nees & Mart.	su		ne	ons	ALCB 149192

Table 2. Cont.

Family / Species	Hab.	Cs	End.	Phy	Voucher
Crotalaria stipularia Desv.	su				ALCB 047222
Dalbergia ecastaphyllum (L.) Taub.	sh			cfs	ALCB 149316
Desmodium barbatum (L.) Benth.	su			cnm	ALCB 149336
Indigofera microcarpa Desv.	sh		br	cnm	ALCB 149309
Inga laurina (Sw.) Willd	sh	lc		cns	ALCB 149218
Macrolobium latifolium Vogel	sh	lc	br	cns	ALCB 149433
Macrolobium rigidum R.S.Cowan	sh	lc	ba, r	cns	ALCB 149216
Macropsychanthus violaceus (Mart. ex Benth.) L.P.Queiroz & Snak	li			ofs	ALCB 149432
Macroptilium atropurpureum (Sessé & Moc. ex DC.) Urb. Natu	he			onm	ALCB 149177
Mimosa caesalpiniifolia Benth.	sh	lc	br	cns	ALCB 149374
Mimosa lewisii Barneby	sh		ne	cns	ALCB 149241
Periandra mediterranea (Vell.) Taub.	sh			ons	ALCB 149416
Poecilanthe itapuana G.P.Lewis	sh	vu	ba	ons	ALCB 149356
Stylosanthes viscosa (L.) Sw.	sh			ons	ALCB 149128
Swartzia apetala Raddi	tr		br	ons	ALCB 149414
Swartzia arenophila R. B. Pinto, Torke & Mansano	sh	en	ba	cns	UEC 156038
Swartzia revoluta R. B. Pinto, Torke & Mansano	sh	en	ba	cns	UEC 155688
Gentianaceae					
Schultesia guianensis (Aubl.) Malme	he	lc		ofm	ALCB 149215
Heliconiaceae					
Heliconia psittacorum L.f	he			cfm	ALCB 149344
Heliotropiaceae					
Myriopus subsessilis (Cham.) J.I.M.Melo	li		r	ons	ALCB 149187
Euploca polyphylla (Lehm.) J.I.M.Melo & Semir	su			ofm	ALCB 149379
Humiriaceae					
Humiria balsamifera (Aubl.) A.St.-Hil.	sh			ofs, ons	ALCB 149397
Krameriaceae					
Krameria bahiana B.B.Simpson	su		ne	ofs, ons	ALCB 149184
Lamiaceae					
Eplingiella fruticosa (Salzm. ex Benth.) Harley & J.F.B. Pastore	sh		ne	ons	ALCB 028675
Eriope blanchetii (Benth.) Harley	he	vu	ne, r	cns	ALCB 047231
Hypenia salzmannii (Benth.) Harley	sh			cns	CEPEC 72617
Marsypianthes chamaedrys (Vahl) Kuntze	he			onm, cnm, ons	ALCB 149293
Lauraceae					
Cassytha filiformis L.	li			ofm, onm, ons	ALCB 149157
Ocotea notata *(Nees & Mart.) Mez*	sh		br	cns	ALCB 149352
Lecythidaceae					
Lecythis ibiriba (Miers) N. P. Sm., S. A. Mori & Popovkin	sh	nt	ne		CEPEC 80994
Lentibulariaceae					
Utricularia gibba L.	he			cfm	ALCB 149321
Utricularia myriocista A.St.-Hil. & Girard	he			ofm	ALCB 149338
Utricularia subulata L.	he			ofm	ALCB 149212
Loranthaceae					
Psittacanthus dichroos (Mart.) Mart.	he		br	cns	ALCB 149240
Psittacanthus excrenulatus Rizzini	he		ne	cns	ALCB 149365

Table 2. Cont.

Family / Species	Hab.	Cs	End.	Phy	Voucher
Struthanthus polyrrhizus (Mart.) Mart.	he			cns	ALCB 149410
Struthanthus uraguensis (Hook. & Arn.) G.Don	he			ofs, ons	ALCB 149140
Lythraceae					
Cuphea antisyphilitica Kunth	su		br	cfm	ALCB 149207
Cuphea flava Spreng.	su		br	ofm, ons	ALCB 149236
Lafoensia pacari A.St.-Hil.	sh	lc		cns	ALCB 149390
Malpighiaceae					
Byrsonima bahiana W.R.Anderson	sh	lc	br	cns	ALCB 149353
Byrsonima crassifolia (L.) Kunth	sh			ons, cns	ALCB 149282
Byrsonima microphylla A.Juss.	sh	en	br, r	ofs, ons	ALCB 149269
Byrsonima sp.	sh			ons	ALCB 149393
Peixotoa hispidula A.Juss.	sh		br	cns	ALCB 149434
Stigmaphyllon paralias A.Juss.	sh		br	ons, cns	ALCB 149191
Malvaceae					
Sida plumosa Cav.	sh		br	cnm	ALCB 149188
Waltheria cinerascens A.St.-Hil.	sh	lc	br, r-d	ons	ALCB 149262
Marantaceae					
Maranta divaricata Roscoe	he			cns	ALCB 149418
Melastomataceae					
Comolia abaetensis D.Nunes & P.J.F.Guim.	sh		ba, r	ofm, ons	ALCB 149354
Comolia ovalifolia (DC.) Triana	sh	lc	br, r	ofm, ons	ALCB 149209
Marcetia taxifolia (A.St.-Hil.) DC.	sh			cfm	ALCB 149173
Noterophila bivalvis (Aubl.) Kriebel & M.J.R.Rocha	he			cfm	ALCB 149211
Pleroma urceolare (Schrank et Mart. ex DC.) Triana	sh	lc	ba	cfm	ALCB 149343
Pterolepis glomerata (Rottb.) Miq.	su	lc			HUEFS 101767
Menyanthaceae					
Nymphoides humboldtiana (Kunth) Kuntze	he			ofm	ALCB 149319
Metteniusaceae					
Emmotum affine Miers	sh		br	ofs, ons	ALCB 149264
Microteaceae					
Microtea bahiensis Marchior. & J.C.Siqueira	su	en	ba, r	ons	ALCB 149165
Microtea celosioides Moq. ex Sennikov & Sukhor.	su			cnm, ons	ALCB 149437
Molluginaceae					
Mollugo verticillata L.	he			ons	ALCB 149288
Myrtaceae					
Calycolpus legrandii Mattos	sh	vu	ne, r	cns	ALCB 149286
Eugenia astringens Cambess.	sh	lc	br	cnm, ons	ALCB 149313
Eugenia candolleana DC.	sh	lc	br	ons	ALCB 052615
Eugenia hirta O.Berg	sh		br	ons	UB 191668
Eugenia punicifolia (Kunth) DC.	sh	lc	br		ALCB 038013a
Eugenia sp.	tr			cns	ALCB 149312
Myrcia bergiana O.Berg	tr		br	ons	UB 236255
Myrcia guianensis (Aubl.) DC.	sh	lc		cnm, ons	ALCB 149226
Myrcia hirtiflora DC.	sh		ne	ons	ALCB 149281
Myrcia neoobscura E.Lucas & C.E.Wilson	tr		br	cns	UPCB 92831

Table 2. Cont.

Family / Species	Hab.	Cs	End.	Phy	Voucher
Myrcia neuwiedeana (O.Berg) E.Lucas & C.E.Wilson	tr		br, r	ons	UB 236254
Myrcia ramuliflora (O.Berg) N.Silveira	sh		ne, r-d	ons	ALCB 52649
Myrcia salzmannii O.Berg	sh		ne	cns	UB 196895
Myrciaria floribunda (H.West ex Willd.) O.Berg	tr	lc		ons	HUEFS 65451
Psidium bahianum Landrum	sh		br, ba	ons	HUEFS 65452
Psidium oligospermum Mart. ex DC.	tr			ons	ALCB 126970
Nyctaginaceae					
Guapira pernambucensis (Casar.) Lundell	sh		br, r	cnm, ons	ALCB 149268
Ochnaceae					
Ouratea robusta F.O.Silva & M.R.V.Barbosa	tr	vu	ne, r	ofs, ons	ALCB 149227
Sauvagesia erecta L.	he			cfm	ALCB 149305
Sauvagesia sprengelii A.St.-Hil.	he		ba		ALCB 15097
Orchidaceae					
Brassavola ceboletta Rchb.f.	he	lc	ba, r	cns	ALCB 149378
Catasetum discolor (Lindl.) Lindl.	he			ofm	ALCB 149220
Catasetum gardneri Schltr.	he		br	ofm	ALCB 149180
Epidendrum cinnabarinum Salzm.	he		ne	ofs, ons	ALCB 149364
Habenaria pratensis (Salzm. ex Lindl.) Rchb.f.	he			ofm	ALCB 149447
Vanilla phaeantha Rchb.f.	he	en		ons	ALCB 149363
Passifloraceae					
Passiflora foetida L.	li			onm	ALCB 149176
Passiflora silvestris Vell.	li		br	ons	ALCB 149225
Pentaphylacaceae					
Ternstroemia brasiliensis Cambess.	sh	lc	br	ons	ALCB 149255
Peraceae					
Chaetocarpus echinocarpus (Baill.) Ducke				cns	MBM 238759
Chaetocarpus myrsinites Baill.	tr			cns	ALCB 149423
Plantaginaceae					
Angelonia cornigera Hook.f.	he		ne	cnm, ons	ALCB 149149
Bacopa monnieri (L.) Pennell	he			ofm	ALCB 149320
Matourea pratensis Aubl.	he		r-d	cnm	ALCB 149311
Poaceae					
Panicum racemosum (P.Beauv.) Spreng.	he			cfm	ALCB 52653
Pappophorum pappiferum (Lam.) Kuntze	he			cns	ALCB 149341
Paspalum arenarium Schrad	he			ofm, cnm	ALCB 149332
Paspalum sp.	he			ofm	ALCB 149342
Schizachyrium microstachyum (Desv. ex Ham.) Roseng., B.R.Arrill. & Izag.	he			cfm	ALCB 149345
Stenotaphrum secundatum (Walter) Kuntze	he			onm	ALCB 149327
Trichanthecium schwackeanum (Mez) Zuloaga & Morrone	he			ofm	ALCB 149362
Polygalaceae					
Asemeia martiana (A.W.Benn.) J.F.B.Pastore & J.R.Abbott	he			cnm	ALCB 149323
Senega appressa (Benth.) J.F.B.Pastore	he			ofm	ALCB 149186
Senega cyparissias (A. St.-Hil. & Moq.) J.F.B.Pastore & Agust. Martinez	he		br, r	onm, cnm	ALCB 149304
Senega trichosperma (Jacq.) J.F.B.Pastore	he			ofm, ons	ALCB 149436

Table 2. Cont.

Family / Species	Hab.	Cs	End.	Phy	Voucher
Polygonaceae					
Coccoloba laevis Casar.	sh		br	ons, cns	ALCB 149202
Coccoloba ramosissima Wedd.	sh		br, r	ons	ALCB 149350
Portulacaceae					
Portulaca mucronata Link	he			cnm	ALCB 149275
Portulaca umbraticola Kunth	he			cnm	ALCB 149279
Primulaceae					
Myrsine parvifolia A.DC.	sh			cns	ALCB 149375
Rubiaceae					
Borreria verticillata (L.) G.Mey.	su			cnm, ons	ALCB 149439
Borreria virgata Cham. & Schltdl.	he		br, r	cfm	ALCB 149252
Chiococca alba (L.) Hitchc	sh			cnm, cfs	ALCB 149337
Cordiera obtusa (K.Schum.) Kuntze	sh		br	ons	ALCB 149232
Eumachia chaenotricha (DC.) C.M. Taylor & Razafim.	sh		br	cns	ALCB 149417
Guettarda sp.	sh			ons	ALCB 149273
Guettarda platypoda DC.	sh		br, r	ons	ALCB 149134
Hexasepalum apiculatum (Willd.) Delprete & J.H. Kirkbr.	he	lc	br	ofs, ons	ALCB 149438
Hexasepalum teres (Walter) J.H.Kirkbr.	sh			ons	ALCB 149126
Mitracarpus anthospermoides K.Schum.	he	en	ba, r	ons	ALCB 149440
Mitracarpus eichleri K.Schum.	he		br, r	onm, cnm	ALCB 149208
Mitracarpus frigidus (Willd. ex Roem. & Schult.) K.Schum	he			ons	ALCB 149161
Perama hirsuta Aubl.	he			ofm	ALCB 149171
Salzmannia nitida DC.	sh	lc	ne, r	ons	CEPEC 106608
Salzmannia plowmanii (Delprete) Paudyal & Delprete	sh		br, r	ons	ALCB 149272
Staelia virgata (Link ex Roem. & Schult.) K.Schum.	he			ofs	ALCB 149148
Tocoyena formosa (Cham. & Schltdl.) K.Schum	sh			ofs, ons	ALCB 149221
Tocoyena sellowiana (Cham. & Schltdl.) K.Schum.	sh	lc	br		HUEFS 78009
Rutaceae					
Esenbeckia grandiflora Mart.	sh			ons, cns	ALCB 149355
Salicaceae					
Casearia javitensis Kunth					ALCB 38012
Sapindaceae					
Matayba discolor (Spreng.) Radlk.	sh		br	cns	ALCB 149228
Serjania paradoxa Radlk.	li		br	cns	ALCB 149292
Sapotaceae					
Manilkara decrescens T.D.Penn.	sh	vu	ba, r		MBM 235462
Manilkara salzmannii (A.DC.) H.J.Lam	sh		br	ons, cns	ALCB 149385
Pouteria venosa (Mart.) Baehni	sh			cns	ALCB 149351
Sideroxylon obtusifolium (Roem. & Schult.) T.D.Penn	sh	lc		ons	ALCB 149422
Schoepfiaceae					
Schoepfia brasiliensis A.DC.	sh			cns	ALCB 149402
Simaroubaceae					
Homalolepis bahiensis (Moric.) Devecchi & Pirani	sh	lc	ne	cns	ALCB 149235
Smilacaceae					
Smilax rufescens Griseb.	li		br	cns	ALCB 149247

Table 2. Cont.

Family / Species	Hab.	Cs	End.	Phy	Voucher
Solanaceae					
Schwenckia americana Rooyen ex L.	sh			ons	ALCB 149324
Trigoniaceae					
Trigonia nivea Cambess	li			cns	ALCB 149435
Verbenaceae					
Lantana lucida Schauer	sh		ne	cns	ALCB 149265
Lantana salzmannii Schauer	sh		br, r	ons	ALCB 149193
Violaceae					
Pombalia calceolaria (L.) Paula-Souza	he			cnm, ons	ALCB 149206
Vochysiaceae					
Vochysia lucida C.Presl	tr	lc	ne	cns	UEC 185063
Xyridaceae					
Xyris jupicai Rich.	he			ofm	ALCB 149405

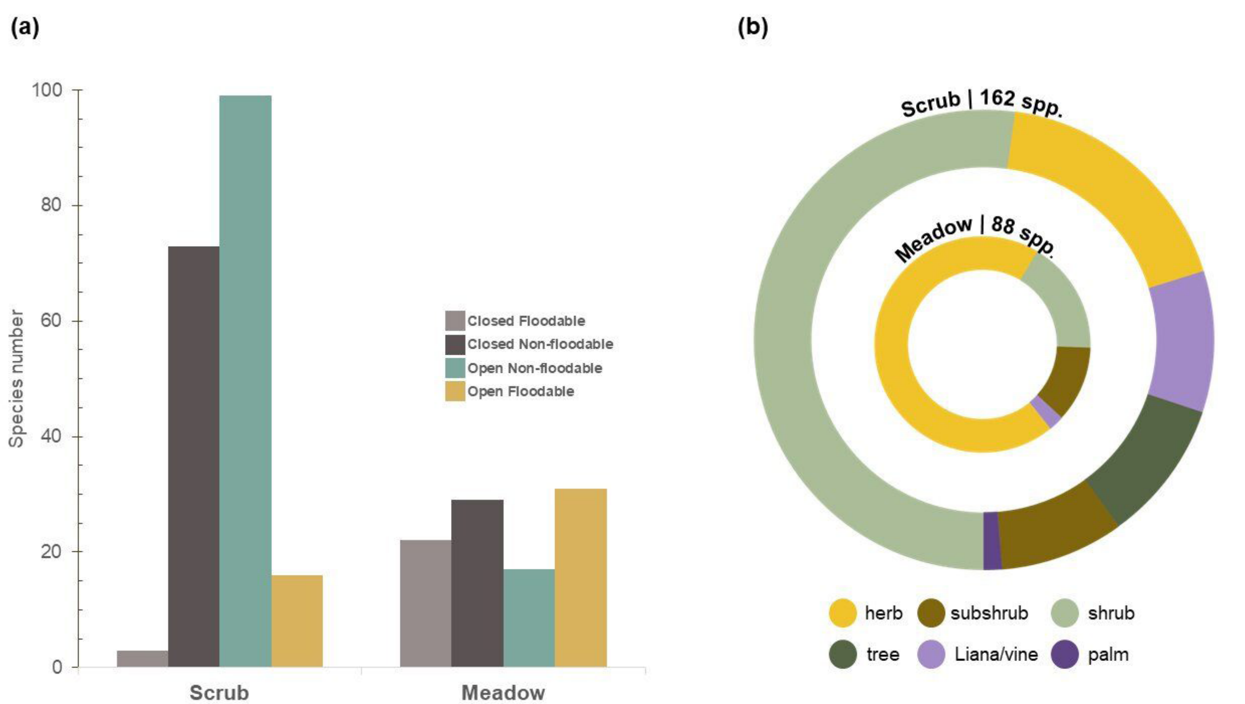

Figure 3. Distribution of diversity among vegetation types (a) and growth habit (b).

The high beta diversity observed (βsor = 0.87) indicates marked spatial variation in species composition across the study area. The turnover component (βsim) reached 0.78, accounting for 90% of βsor, while the nestedness component (βsne) contributed only 10% (0.09). In the pairwise analysis (Fig. 4), most pairs showed higher βsim values compared to βsne, indicating that turnover is the predominant factor. The lowest values of total beta diversity were observed at three main points: 1) between saoj-RJ and pres-ES with βsor=0.64 (Fig. 4a); 2) among the communities of Bahia, with mean βsor= 0.61 (Fig. 4b); and 3) within siri-PE and cabo-PE, with βsor=0.58 (Fig. 4c). The βsim values ranged from 0.46 to 0.89, with the highest indices of turnover resulting from the pairings of jagu-BA with the Southeast Coast (SC) *restingas* (Fig. 4d), SC with the Northeast Coast (NEC) *restingas* (Fig. 4e), and jeri-CE with jagu-BA and NEC together (Fig. 4f). The βsne values ranged from 0.003 to 0.27, with the highest nestedness indices derived from the pairings between the Northern Coast of Bahia (NCB) with SC (Fig. 4g) and NEC (Fig. 4h). However, these βsne values closely reflect the differences in species richness observed between NCB × SC and NCB × NEC, suggesting that they are likely artifacts resulting from richness bias, as previously highlighted by the Mantel test.

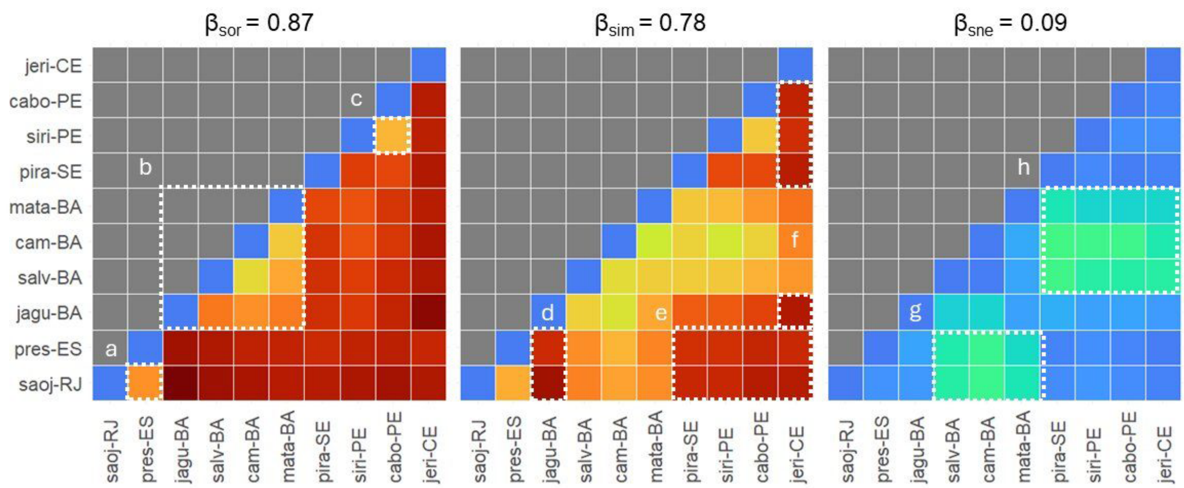

Figure 4. Heatmap of dissimilarities based on the result of the beta diversity partitioning (βsor).

Similarities and Environmental Drivers of Beta Diversity

From the UPGMA clustering (Fig. 5), three main clusters were identified: the outermost group (Fig. 5C), represented exclusively by Jericoacoara (jeri-CE); a group comprising the *restingas* of São João da Barra (saoj-RJ) and Praia das Neves (pres-ES) (Fig. 5B); and a larger group (Fig. 5A) encompassing the *restingas* of Sergipe (pira-SE), Bahia (jagu-BA, salv-BA, cama-BA, mata-BA), and Pernambuco (PE; cabo-PE, siriPE).

The spatial arrangement provided by the NMDS plot (Fig. 6I, II) showed the separation of clusters B (saoj-RJ and pres-ES) and C (jeri-CE), corroborating the UPGMA result. However, cluster A, comprising the communities of Bahia, Sergipe, and Pernambuco, was not evident. In turn, the grouping of the NCB communities (4, 5, and 6) was well represented. Considering the distribution within Brazilian Climatic Zones and Hydrographic Macroregions, the arrangement was more informative (Fig. 6 I). All the communities of cluster A are in the same climatic zone, the Oriental Northeast Tropical Zone (ONTZ), but they are situated in two distinct hydrographic regions; the communities of Bahia and Sergipe are part of the East Atlantic Region (EAR), while those in Pernambuco are in the Oriental Northeast Atlantic Region (ONAR).

To evaluate the significance of these patterns, ANOSIM tests (999 permutations) were performed under four hypothetical groupings: (1) communities within the same hydrographic region ($R = 0.58$, $p = 0.0003$); (2) communities within the same climatic zone ($R = 0.79$, $p = 0.0029$); (3) communities defined by climatic/hydrographic intersections ($R = 0.78$, $p = 0.0004$); and (4) the same intersections with an additional north–south division of Bahia's coastline ($R = 0.79$, $p = 0.001$). As expected, climate appeared to best explain floristic differentiation among *restinga* communities. Mantel tests supported these findings, revealing strong correlations between floristic dissimilarities and environmental parameters, particularly rescaled climatic variables ($R = 0.83$, $p = 0.0001$) and geographic distance ($R = 0.81$, $p = 0.0001$). Among individual variables, temperature seasonality showed the highest correlation ($R = 0.75$, $p = 0.0005$), followed by total precipitation ($R = 0.72$, $p = 0.0001$) and mean annual temperature ($R = 0.67$, $p = 0.0029$). By contrast, wind speed ($R = 0.16$, $p = 0.16$) and precipitation seasonality ($R = 0.37$, $p = 0.06$) were not significantly correlated with floristic composition. Based on these analyses, five floristic groups were identified: Southeast Coast (SC; saoj-RJ + pres-ES), Upper South Coast of Bahia (USCB; jagu-BA), North Coast of Bahia and Sergipe (NCBS; salv-BA + cama-BA + mata-BA + pira-SE), Oriental Northeast Coast (ONC; siri-PE + cabo-PE), and Septentrional Northeast Coast (SNC; jeri-CE) (Fig. 6 II).

Discussion

Floristic Composition, Richness, and Endemism

The richness among botanical families is a crucial aspect in assessing floristic communities. Regarding *restinga* ecosystems, the predominance of Fabaceae is a consistent finding across various northeastern states, including Bahia (Britto *et al.*, 1993; Cunha *et al.*, 2003; Fernandes & Queiroz, 2015; Queiroz *et al.*, 2012; Costa *et al.*, 2018), Sergipe (Dantas *et al.*, 2010; Oliveira *et al.*, 2014; Oliveira & Landim, 2020; Oliveira *et al.*, 2023), and Rio Grande do Norte (Freire, 1990). In Pernambuco, however, Myrtaceae stands out as the most diverse family (Sacramento *et al.*, 2007; Cantarelli *et al.*, 2012), whereas in Ceará and Paraíba, Poaceae is the most frequently represented (Cunha *et al.*, 2003; Matias & Nunes, 2001).

The relationship between species richness, growth habits, and associated vegetation types is frequently discussed in the literature (Assumpção & Nascimento, 2001; Cantarelli *et al.*, 2012; Queiroz *et al.*, 2012; Gomes & Guedes, 2014; Fernandes & Queiroz, 2015; Costa *et al.*, 2018). The lower diversity observed in meadow formations compared to scrub formations has been noted in this and other studies of Brazilian *restingas* (Silva & Britez, 2005; Martins *et al.*, 2008; Almeida Jr. *et al.*, 2009). The higher richness in shrubby formations may indicate less severe environmental conditions, with more consolidated and nutrient-rich soils, as highlighted by Silva & Britez (2005).

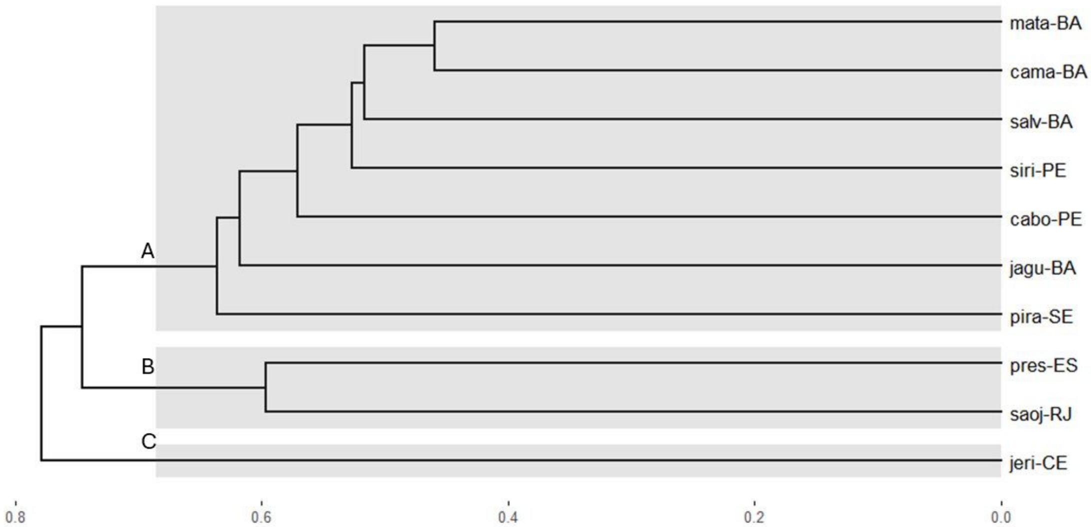

Figure 5. UPGMA cluster created based on the Simpson Similarity (βsim), highlighting four groups with a 0.73 cut-off point. Created with RStudio 2024.04.1+748

Despite local variations, the ranking of the ten most diverse families in the *restingas* of the Northern Coast of Bahia (NCB) shows a composition similar to those of the Caatinga and Atlantic Forest biomes (BFG, 2015). This suggests that these biomes significantly contribute to the floristic diversity of coastal ecosystems. Such findings support the conclusions of Freire (1990) and Scarano (2002), who noted that the young geological age of these environments, combined with low endemism rates (6% in the present study), provides evidence of species provision from adjacent vegetation. This phenomenon has also been observed in floristic studies of Ceará's coastal formations (Fernandes, 1985; Matias & Nunes, 2001; Castro *et al.*, 2012) and in the analysis of life forms on Sergipe's dunes by Oliveira & Landim (2020).

In the non-arboreal *restingas* of the NCB, approximately 88% of the recorded species are naturally distributed in the Atlantic Forest (AF), and one-third of them are endemic to this biome (Fig. 7). That finding highlights the AF influence on the floristic composition of these environments and underscores the importance of their conservation. Nonetheless, some taxa cataloged are commonly associated with other phytogeographic domains, such as *Froelichia humboldtiana, Conocliniopsis prasiifolia, Mimosa caesalpiniifolia, Mimosa lewisii*, and *Lafoensia pacari*, which are typical of the Cerrado and/or Caatinga (Fig. 8 A–C). Similarly, disjunct distributions are frequent between the Amazon and AF (Ledo & Colli, 2017), which share several species, such as *Borreria virgata*, *Coccoloba ramosissima*, *Dalbergia ecastaphyllum*, *Noterophila bivalves*, *Pouteria venosa*, and *Sauvagesia sprengelii*, identified in the studied *restingas* (Fig. 8D–F). Another noteworthy observation is the simultaneous occurrence of species between rocky outcrops ("*campos rupestres*") and *restingas* (e.g. *Agarista revoluta*, *Bonnetia stricta*, *Comanthera imbricata*, *Ilex blanchetii*, *Matourea pratensis*, *Paepalanthus sessiliflorus*, *Syngonanthus gracilis*, *Waltheria cinerascens*) (Fig. 9), often showing disjunct distributions between these environments (Giulietti & Pirani, 1987; Alves *et al.*, 2007).

Diversity Patterns and Floristic Uniqueness

Contrary to the idea that *restinga* formations merely act as species reservoirs of adjacent forests, many species are restricted exclusively to these environments, suggesting a unique floristic composition, as observed by Rabelo *et al.* (2024). This study identifies 40 species as exclusive to Brazilian *restingas*, with 13 of them occurring solely in Bahia (Fig. 10). The distinctiveness of Bahia's *restingas* is evident, given the apparent discrepancy in the number of endemic species recorded in the state (Britto *et al.*, 1993; Costa *et al.*, 2018; Queiroz *et al.*, 2012) compared to other regions (Scarano, 2002; Sacramento *et al.*, 2007; Castro *et al.*, 2012). According to Flora e Funga do Brasil (2025), Bahia ranks first in endemic angiosperms in *restingas*, likely due to both the length of its coastline and the floristic uniqueness of the Northeastern Atlantic Forest (NEAF). This region, bounded by the Rio Doce to the south and extending to Pernambuco, has been highlighted as a center of endemism (Fiaschi & Pirani, 2009; Santos *et al.*, 2017; Lins-e-Silva *et al.*, 2021). Several studies support this notion (Prance, 1982; Thomas *et al.*, 1998; Carnaval & Moritz, 2008; Thomas *et al.*, 2009; Rocha & Amorim, 2012; Moreira *et al.*, 2020), recognizing NEAF as a center of endemism. This region includes the ombrophilous forest of Southern Bahia, commonly referred to as the *Hileia Baiana*, which is renowned for its exceptional biological diversity (Reginato & Michelangeli, 2020).

The northern region of Bahia's coastline usually exhibits lower rates of endemism compared to its southern coast, as noted by Menini Neto *et al.* (2016) in their evaluation of epiphytic diversity in the Atlantic Forest. However, limited sampling efforts in the region may introduce collection biases (Araújo & Ramos, 2021; Werneck *et al.*, 2011), potentially affecting phytogeographic analyses. The similarity analyses conducted in this study highlight the unique floristic characteristics of the NCB, aligning with other floristic studies in the region (Costa *et al.*, 2018; Fernandes & Queiroz, 2015;

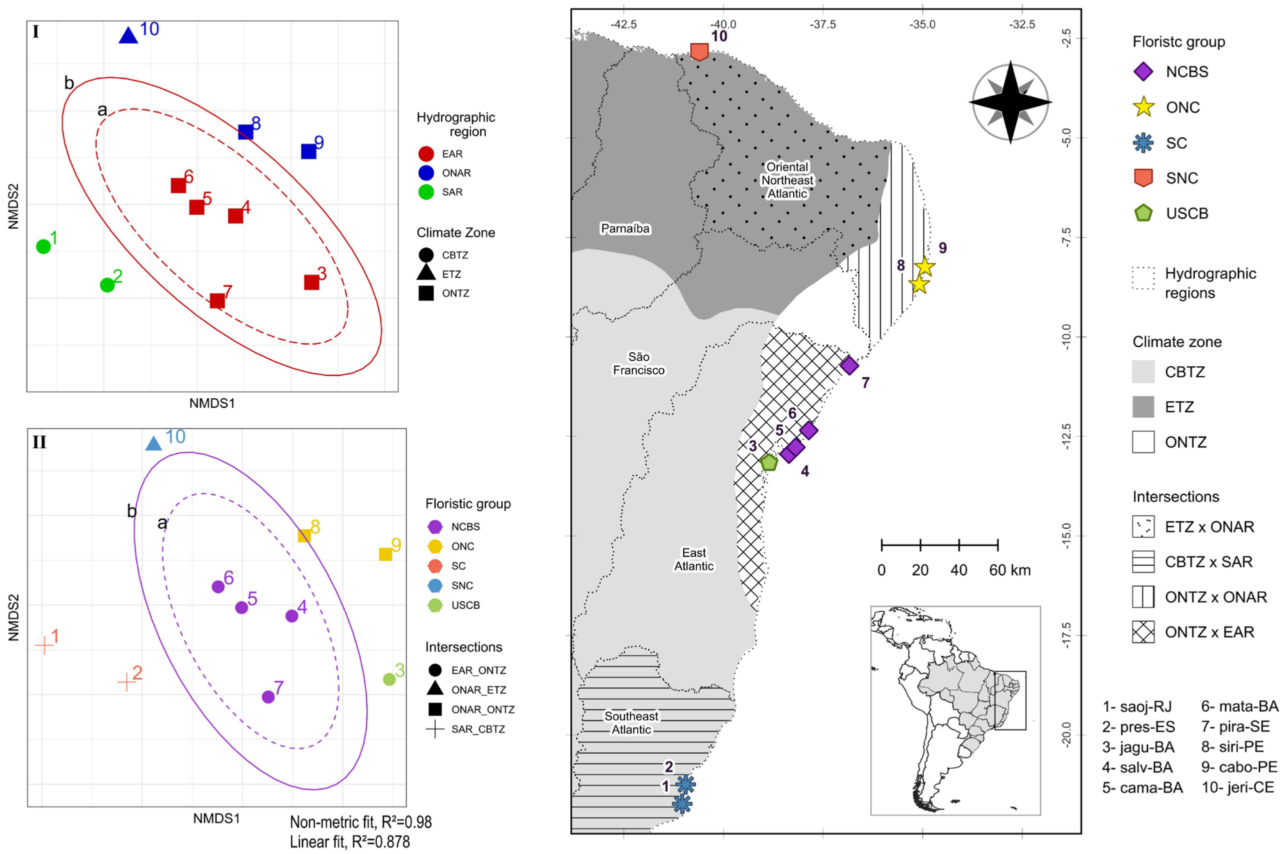

Figure 6. Spatial ordination plots (NMDS) of the samples based on the βsim similarity matrix (Supplementary Material S2) and Bray-Curtis distances. Stress=0.14. The colors represent the hypothetical floristic groups, and the shapes represent the climatic zones (I) and hydrographic regions (II) of Brazil. SC: Southeast Coast; USBC: Upper South Coast of Bahia; NCBS: North Coast of Bahia and Sergipe; ONC: Oriental Northeast Coast; SNC: Septentrional Northeast Coast. CBTZ: Central Brazil Tropical Zone; ETZ: Equatorial Tropical Zone; ONTZ: Oriental Northeast Tropical Zone; EAR: East Atlantic Region; ONAR: Oriental Northeast Atlantic Region; SAR: Southeast Atlantic Region. a: 0,95 confidence level ellipse; b: 0,8 confidence level ellipse. Graphs created with R 4.4.0, maps and final layout with QGIS 3.36.3-Maidenhead.

Melo *et al.*, 2023; Rabelo *et al.*, 2024) and supporting the formation of a large group encompassing the *restingas* of the NCB, Sergipe, and Pernambuco. Environmental features such as a dry summer season, proximity to fragments of semideciduous forests, and the presence of a continuous foredune near the shoreline (Martin *et al.*, 1980; Matos *et al.*, 2017) further distinguish the NCB from the rest of the state coast. Several species have already been described as endemic to the NCB, some of which were recorded in this study, such as *Hohenbergia littoralis*, *Chamaecrista salvatoris*, *Comolia abaetensis*, and *Microtea bahiensis* (Fig. 10 E-F), reinforcing the region's uniqueness.

The evaluation of patterns derived from the partitioning of beta diversity, as well as the environmental and evolutionary factors driving it, has been the focus of several recent studies in Brazilian *restinga* ecosystems (Massante & Gerhold, 2020; Inague *et al.*, 2021; Oliveira *et al.*, 2024). A recurring finding is the greater contribution of the turnover component (Soininen *et al.*, 2018; McFadden *et al.*, 2019) also observed in this study, indicating that dissimilarities are primarily due to the occurrence of species with restricted distributions, rather than biased sampling of widespread species (Mori *et al.*, 2018). This emphasizes that diversity in non-arboreal *restinga* communities is heterogeneous, influenced by environmental variables and geographical distance between communities.

Based on these analyses, floristic groups with substantial distinctions were identified, such as the Northern Coast of Bahia and Sergipe (NCBS), which merges the NCB with the coastline of Sergipe. This grouping aligns with the delimitation proposed by Carnaval & Moritz (2008) for the Atlantic Forest refuge in Bahia, a climatically stable area with the São Francisco River marking its northern boundary. Although the refuge also encompasses Bahia's southern coast, the pronounced floristic distinction between the northern and southern coasts results in a stretch that aligns with the proposed NCBS group, further corroborating the findings of Rabelo *et al.* (2024). The sharing of endemic species between Bahia and Sergipe strengthens the distinction of this region, including *Allagoptera brevicalyx*, *Bauhinia corifolia*, *Calea angusta*, *Comanthera imbricata*, *Eriope blanchetii*, *Gomphrena duriuscula*, *Krameria bahiana*, *Myrcia hirtiflora*, *Poecilanthe itapuana*, *Psittacanthus excrenulatus*, and *Vochysia lucida*, all listed in the present study (Fig. 11).

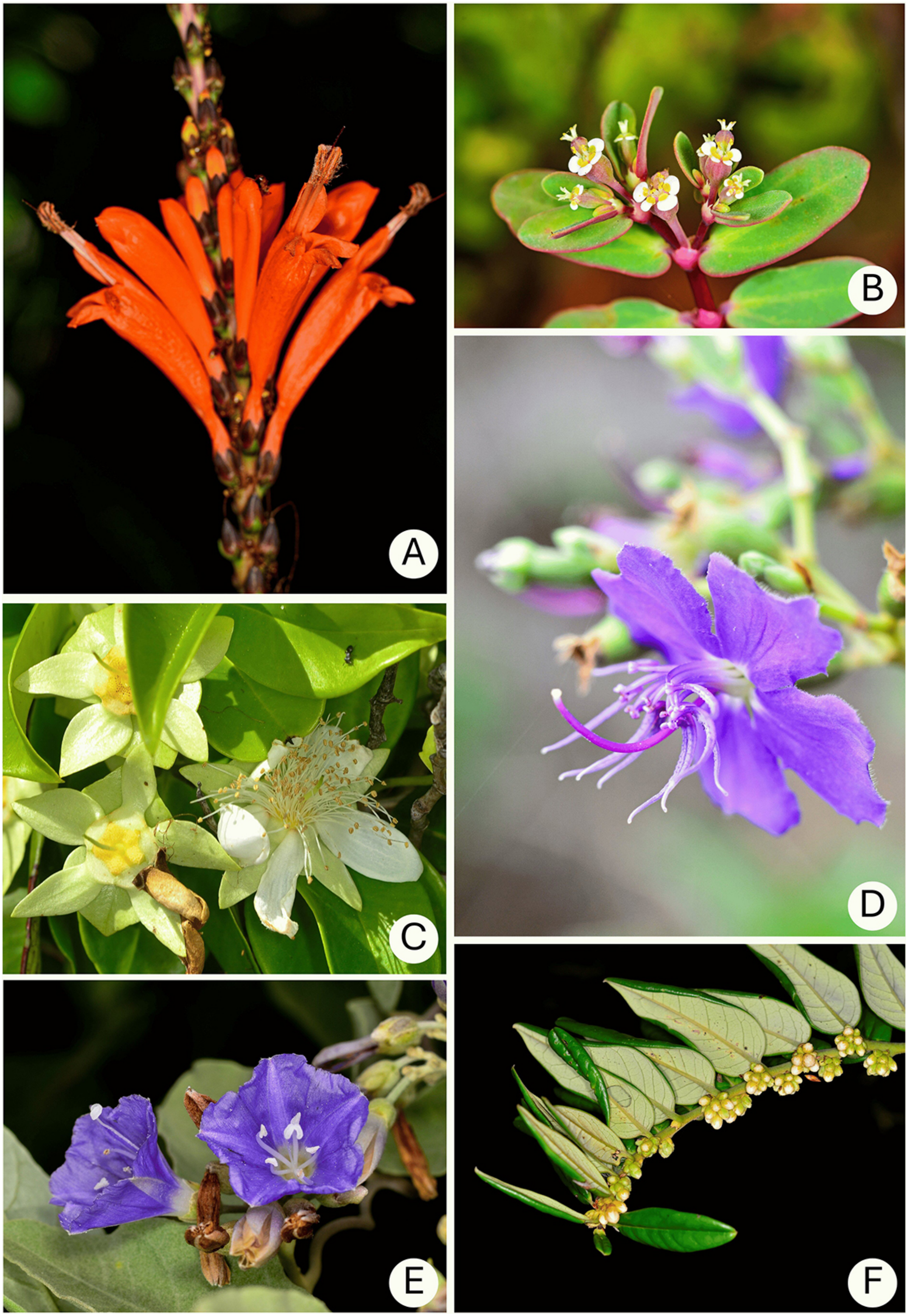

Figure 7. Species endemic to the Atlantic Forest. A – *Aphelandra nitida*; B – *Euphorbia bahiensis*; C – *Calycolpus legrandii*; D – *Pleroma urceolare* (Schrank et Mart. ex DC.) Triana; E – *Evolvulus imbricatus*; F – *Diospyros gaultheriifolia*.

Figure 8. Species from other phytogeographical domains found in the restinga of the Northern Coast of Bahia: Caatinga and Cerrado (A–C), Amazon (D–F). A – *Mimosa lewisii*; B – *Froelichia humboldtiana*; C – *Conocliniopsis prasiifolia*; D – *Pouteria venosa*; E – *Coccoloba ramosissima*; F – *Dalbergia ecastaphyllum*.

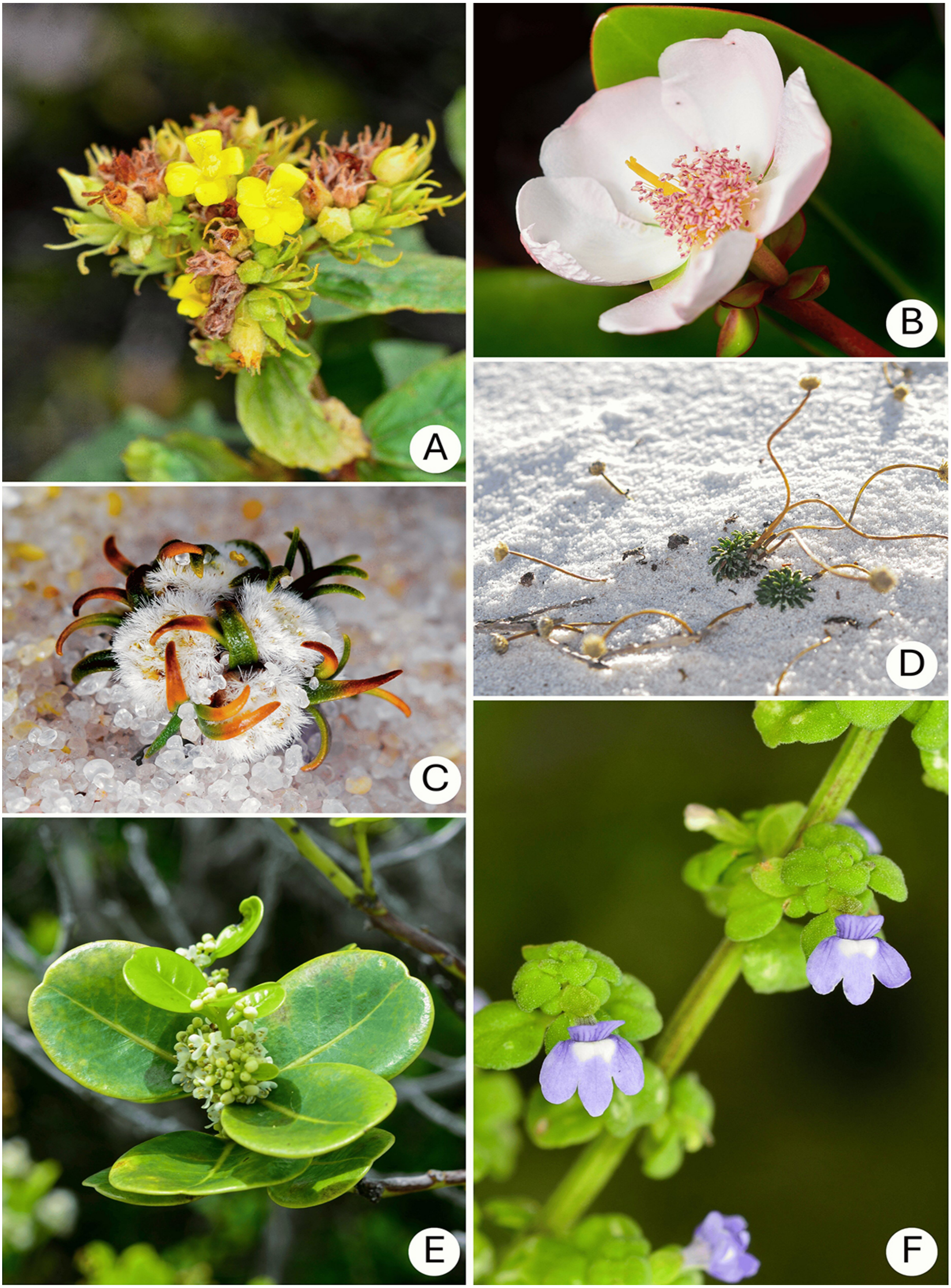

Figure 9. Species with disjunct distribution between *campos rupestres* and *restinga* areas of Bahia. A – *Waltheria cinerascens*; B – *Bonnetia stricta*; C – *Paepalanthus sessiliflorus*; D – *Comanthera imbricata*; E – *Ilex blanchetii*; F – *Matourea pratensis*.

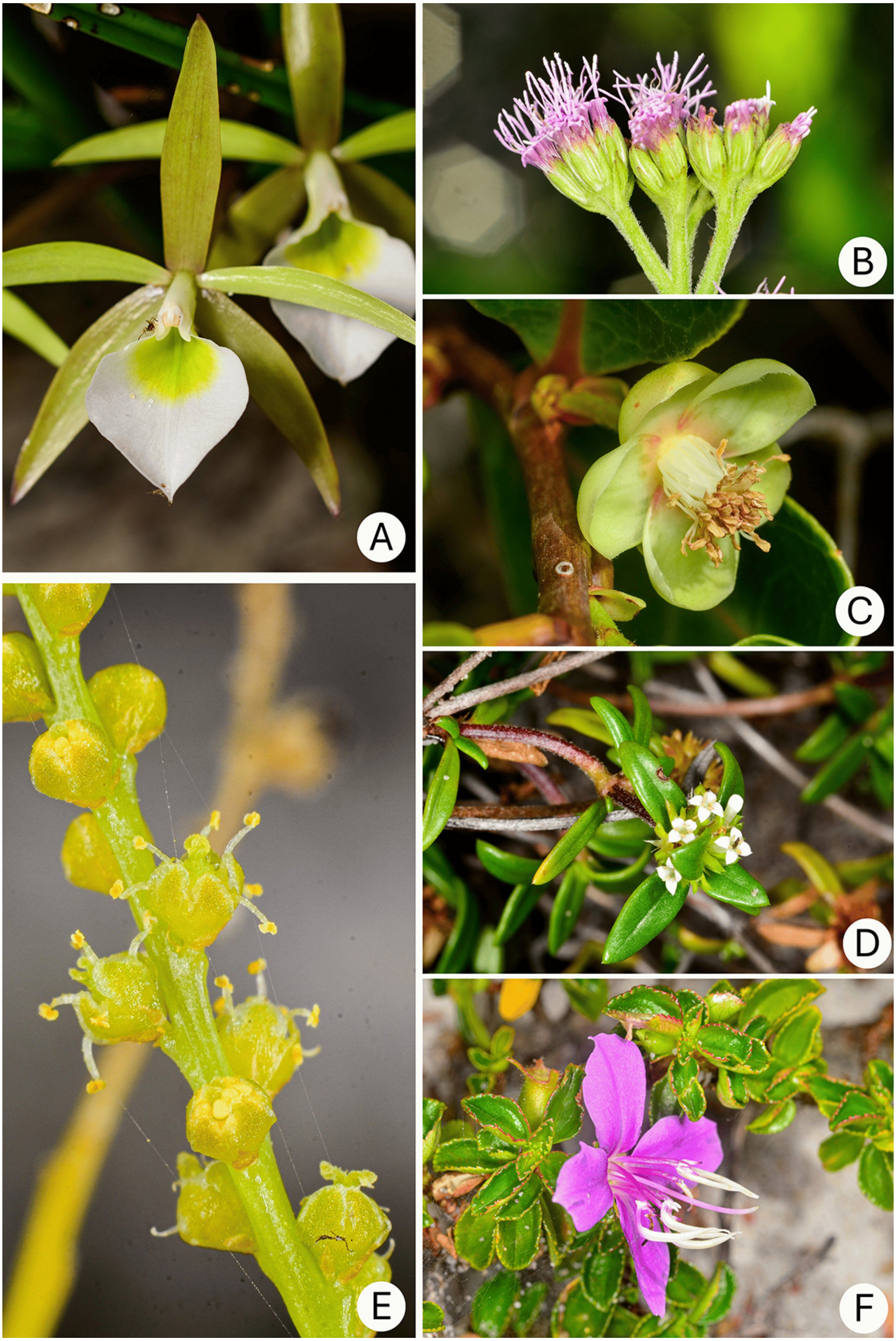

Figure 10. Endemic species of the *restinga* of Bahia (A-D) and those with restricted distribution to the Northern Coast (E-F). A – *Brassavola ceboletta*; B – *Prolobus nitidulus* C – *Doliocarpus sellowianus*; D – *Mitracarpus anthospermoides*; E – *Microtea bahiensis*; F – *Comolia abaetensis*.

Figure 11. Species with exclusive occurrence in Bahia and Sergipe. A – *Allagoptera brevicalyx*; B – *Calea angusta*; C – *Krameria bahiana*; D – *Bauhinia corifolia*; E – *Myrcia hirtiflora*; F – *Gomphrena duriuscula*.

Similarly, the occurrence of *Varronia johnstoniana*, originally described for the state of Sergipe, constitutes the first record of this species for Bahia and highlights the flow of species between the *restinga* ecosystems of these states.

These results reveal the striking floristic heterogeneity of Bahia's *restinga*, particularly between its northern and southern coasts, divided by the Salvador peninsula. The non-arboreous *restingas* of the northern coast, along with those in Sergipe, form a unique phytogeographic block characterized by notable levels of endemic species and distinct climatic influences. Despite previous surveys, critical gaps remain—especially in dune vegetation—limiting our understanding of these ecosystems. This study underscores the urgent need for their conservation, as these *restingas* harbor exceptional and irreplaceable floristic diversity. Ensuring their protection is therefore crucial to safeguard both the unique species they host and the long-term resilience of Bahia's coastal ecosystems.

Supplementary Material

The following online material is available for this article:

Supplementary Material S1. Consolidated species presence/absence matrix, including environmental and categorical variables for each inventory.

Supplementary Material S2. Dissimilarity matrices derived from beta diversity partitioning.

Supplementary Material S3. Matrix of absolute richness differences between inventories.

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Authors' contributions

The study was conceptualized and designed with contributions from all authors. Material preparation, including the collection and identification of specimens, was carried out primarily by Gabriel Costa Guerra (GCG) and Renato Silva da Silva. Data compilation and statistical analyses were performed by GCG. The initial draft of the manuscript was written by GCG, with all authors providing critical feedback on earlier versions. The final version was reviewed and approved by all authors.

Conflict of Interest

The authors declare that they have no conflicts of interest.

Data Availability

All raw data supporting the findings of this study are provided in the article's supplementary materials. Climatic datasets used in the analyses are publicly available from the WorldClim repository at https://www.worldclim.org/data/worldclim21.html.

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