



## ECOSYSTEMS

# Biogeography of restinga vegetation in Northern and Northeastern Brazil and their floristic relationships with adjacent ecosystems

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**Abstract:** Restinga formations are defined as the vegetation covering sandy coastal sediments deposited during the Quaternary period, regardless their physiognomy. They are usually characterized as areas of confluence between plant species associated with diverse phytogeographical domains. However, detailed floristic and biogeographic studies are still required to better define their distribution patterns, the origins of their plant species, and their biogeographical affinities. In this study, we investigate the floristic similarities among restingas in Northern and Northeastern Brazil and diverse ecosystems from different Brazilian phytogeographical domains (Caatinga, Cerrado, Atlantic Forest and Amazonia). We employed multivariate analyses to investigate differences in species composition and identify floristically similar groups. While sharing species with other ecosystems, restingas exhibit unique floristic composition, representing a coastal flora. Furthermore, the restingas of Northern and Northeastern Brazil are biogeographically subdivided according to previously recognized sectors of the coast of the country. These findings underscore the complex nature of restinga ecosystems, influenced by environmental factors such as geographic distance, geology and climate. These insights contribute to a nuanced understanding of the complex relationships between restingas and their surrounding ecosystems, facilitating informed conservation efforts in the face of escalating urban and industrial expansion along the Brazilian coast.

**Key words:** Coastal Vegetation, Floristic, Phytogeography, Restinga.

## INTRODUCTION

A diverse array of vegetation types occurs along the Brazilian coastline, encompassing grasslands, savannas, and forests that grow on sandy coastal sites or muddy estuary areas (Ab'Saber 2001, 2006, Overbeck et al. 2022). The term “restinga vegetation” has been employed in both scientific literature and Brazilian legislation to refer to the plant cover on sandy substrates. However, its use has been inconsistent, leading to significant variations and generating discussions and controversies. Etymologically, the term “restinga” has a Luso-Brazilian origin (Souza et al. 2008), referring

to the sandy sediments that were deposited in coastal zones after repeated processes of marine transgression and regression during the Quaternary period (Suguio & Tessler 1984). That term was later extended to the field of botany to describe the vegetation established on these sandy sediments (Flexor et al. 1984).

In a botanical context, restinga vegetation encompasses a set of plant communities associated with sandy coastal sites (Cerqueira 2000), such as those on beaches, movable, semi-fixed and fixed dunes, as well as coastal forests and savannas (Suguio & Tessler 1984). Rizzini (1997) broadened the term to include all vegetation complexes growing on Holocene

sandy surfaces of marine origin, essentially classifying all the vegetation along the Brazilian coast as “restinga”. While the Radam Brasil project (developed between 1970 and 1985) significantly contributed to classifying Brazilian coastal plains and mapping vegetation types (Veloso & Góes-Filho 1982, Veloso et al. 1991, IBGE 2012), it has faced criticism for oversimplifying the diverse vegetation types occupying sandy coastal areas under a single category. As a consequence, even today, official maps and Brazilian legislation often disregard phytophysiognomic variation within coastal ecosystems, such as forest, savanna or open formations (Correia et al. 2020a), collectively referring to them as “restinga”, “vegetation under marine influence” or “restinga complexes” or “mosaics”. Despite this, restinga vegetation are complex formations that exhibit wide variation in physiognomy and distinct ecological conditions. These formations are exposed to stressful environmental conditions, including high temperatures, elevated salinity, nutrient-poor sandy soils, strong winds, and deep water tables (Almeida-Jr et al. 2009, Moro et al. 2015). However, the vegetation exhibits high adaptability to these conditions, with plants possessing physiognomic, anatomical and physiological adaptations that allow efficient utilization of resources, including obtaining nutrients from poor soils and withstanding salinity from marine aerosols (Lacerda 1984, Júnior & Cuzzuol 2009, Santos-Filho et al. 2013).

Few restinga species are known to be endemic, and most restinga plants can be found in other ecosystems and phytogeographical domains. Rizzini (1963), for example, suggested that most of the plant species growing in restingas originated in the Atlantic Forests, but several species also have their origins in other phytogeographical domains such as Amazonia, Cerrado, and Caatinga (Cerqueira 2000, Scarano 2002). Recent taxonomic studies, however, have

identified new restinga endemic species in different regions of Brazil (e.g., Pacifico & Almeda 2020, Queiroz et al. 2020, Sodr e et al. 2023), indicating that some of its floristic components are exclusive of coastal restingas vegetation.

Despite recent advancements (e.g., Neves et al. 2017, Massante & Gastauer 2023), the lack of comprehensive information regarding floristic composition of the restingas (Martins et al. 2008) makes their classification yet imprecise. Floristic inventories of restinga formations are less common as compared to inventories in other ecosystems of Amazonia, Caatinga, Cerrado, and the Atlantic Forest (Correia et al. 2020). Moreover, botanical studies focused on restinga have been unevenly distributed among the regions of Brazil. More recently efforts were made to enhance sampling in the Northern and Northeastern regions of country (e.g., Silva et al. 2010, Queiroz et al. 2012, Castro et al. 2012, Oliveira & Landim 2014, Fernandes & Queiroz 2015, Correia et al. 2020b, Araujo et al. 2020, Oliveira & Landim 2020). Nevertheless, there is still significant room for improvement in the geographical coverage of botanical surveys conducted in the restingas, with the most of publications concentrated in the Southern and Southeastern regions of Brazil (e.g., Assis et al. 2004, 2011, Scherer et al. 2005, Guedes et al. 2006, Martins et al. 2008, Lima et al. 2011, Marques et al. 2015, J nior & Boeger 2015, Schlickmann et al. 2019, Silveira et al. 2022). Therefore, there is an urgent need for increased floristic studies in the least known Northern and Northeastern regions.

Considering the numerous knowledge gaps regarding the floras of restingas and the escalating degradation of coastal areas due to rapid expansion of urban and industrial areas (Rocha et al. 2007), a more profound understanding of these plant formations is needed to effectively inform conservation efforts. This study focuses on the biogeography of the restinga floras in the

Northern and Northeastern regions of Brazil, where studies are scarce despite severe impacts from anthropic activities. We compiled several floristic publications focused in the restingas of Northern and Northeastern Brazil, comparing their species compositions with those of the other environments within Amazonia, Caatinga, Cerrado and the Atlantic Forest phytogeographical domains. Our comparative analysis aims to determine whether the restingas of the region exhibit floristic identity (e.g., restinga sites are more similar to each other regardless the distance separating them) or align more closely with their surrounding vegetation types.

## MATERIALS AND METHODS

### Datasets

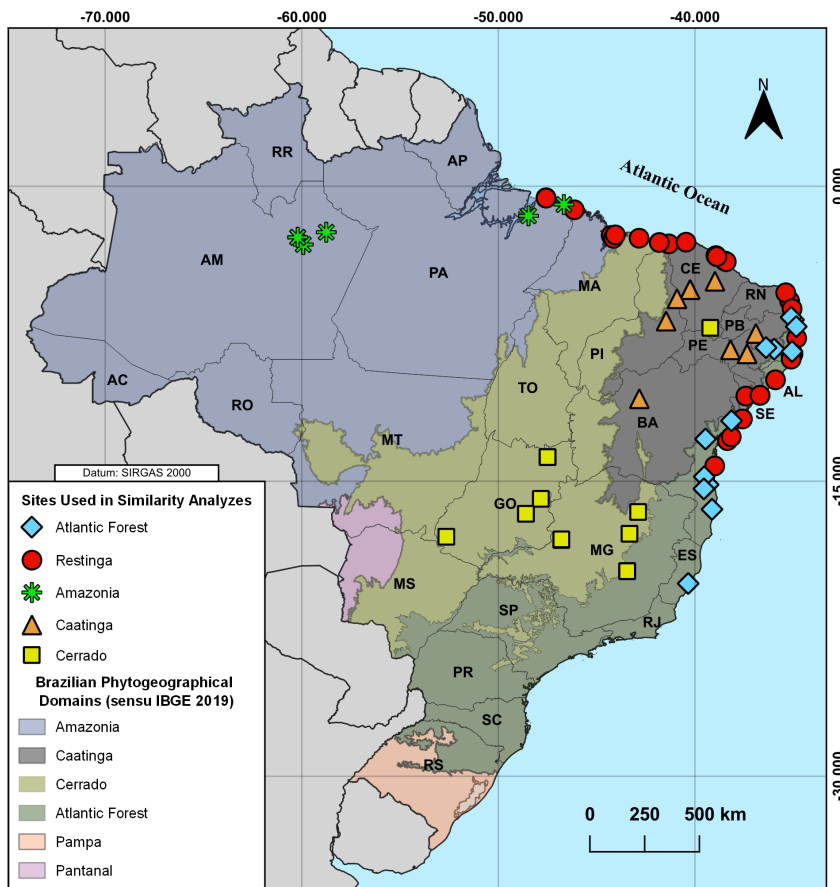
We conducted a literature search for floristic surveys of restinga sites in Northern and Northeastern Brazil, as well as non-restinga environments of Brazilian phytogeographical domains (Amazonia, Caatinga, Cerrado, Atlantic Forests), using the Google Scholar, Scielo and Science Direct bibliographic platforms. We considered studies published in scientific journals, books, dissertations and theses. The bibliographic searches employed keywords in both Portuguese and English, including “floristics” and “restinga”, along with the names of the Northern and Northeastern coastal states of Brazil (in order from north to south): Amapá, Pará, Maranhão, Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, and Bahia (e.g., “floristics, restinga, Amapá”). We also searched for floristic inventories in non-coastal formations of Brazilian phytogeographical domains, using as keywords for each domain (Amazonia, Caatinga, Cerrado or Atlantic Forests) along with the words “floristics” and “vegetation” (e.g., “Amazonia, floristics, vegetation”). Studies

were then selected based on their geographic proximity to our restinga dataset.

Only floristic surveys that included plants from all strata and all habits (herbs, climbing plants, shrubs and trees) were considered. Surveys focusing solely on a single botanical family or specific habits (e.g., only woody plants or only climbing plants) were excluded. The limited number of studies from Amazonia domain (six) largely reflects the scarcity of comprehensive inventories including all vegetation strata as most studies in the region focused on the arboreal stratum. Our final dataset comprised 31 floristic surveys of restinga areas in Northern and Northeastern Brazil, 15 in the Cerrado, 12 in the Caatinga, 13 in the Atlantic Forests, and six in the Amazonia (Appendix 1, Figure 1).

The dataset includes studies of different phytophysiognomies of restinga vegetation, following the classification proposals of authors such as Bastos et al. (1995), Santos-Filho et al. (2010), Moro et al. (2015) and Lima et al. (2017). The concept of restinga used in this study therefore encompasses formations located close to the ocean, growing on Quaternary sandy substrates. These are distinct from vegetation on coastal tablelands (matas de tabuleiro), primarily differing in geological age as the vegetation on coastal tablelands is established on Tertiary surfaces (Sousa & Santos-Filho 2020), but a few studies included areas of restingas and coastal tablelands together without separating their floristic lists.

We used the *Flora do Brasil 2020* database to standardize and clean our taxonomy dataset. We first used *Flora do Brasil 2020* to check the validity of all names in our dataset, replacing synonyms and misspelled names for the accepted species. In cases presenting infraspecific category (e.g., subspecies or variety), we considered only the species category. Taxa identified to genus or family level, along with



**Figure 1.** Map of Brazil indicating the localization of the areas used in the similarity analyses, according to their respective phylogeographical domains. Sites according to Appendix 1.

those with imprecise identifications (*affine* and *confer*) were excluded. Exotic species, according to information of *Flora do Brasil 2020*, were also excluded as their occurrence is not pertinent to biogeographic studies. Finally, we also excluded species restricted to mangrove vegetation as this environment has quite distinct conditions of those in the restingas. Our final database comprised 77 sites and 5,857 species, used to build a presence/absence matrix of species per area (supplementary material at: <<https://doi.org/10.6084/m9.figshare.24002199.v1>>).

**Biogeographic analyses**

The floristic similarities between the areas was compared with cluster analysis using the algorithm Unweighted Pair Group Method with Arithmetic Mean (UPGMA) and the Sorensen similarity index (Bray-Curtis). Cluster analyses

are a set of methods that aim to separate objects into distinct groups based on the number of features they have in common. For biogeography or ecology, we can separate sites with distinct species composition into groups where sites with more shared species in common are grouped into clusters distinct from clusters with sites with less species in common (see Legendre & Legendre 2012, Wildi 2010). Based on the proportion of shared species between two sites, they receive a similarity value (in our case using Sorensen similarity index) for the pair, were sites with a value of 1 share all species between them and sites with similarity of 0 do not share any species (Legendre & Legendre 2012). The general quality of the cluster analysis was evaluated by the cophenetic correlation, that express to what extent the graph correlates with the complex,

multivariate data that is being simplified for plotting (Legendre & Legendre 2012).

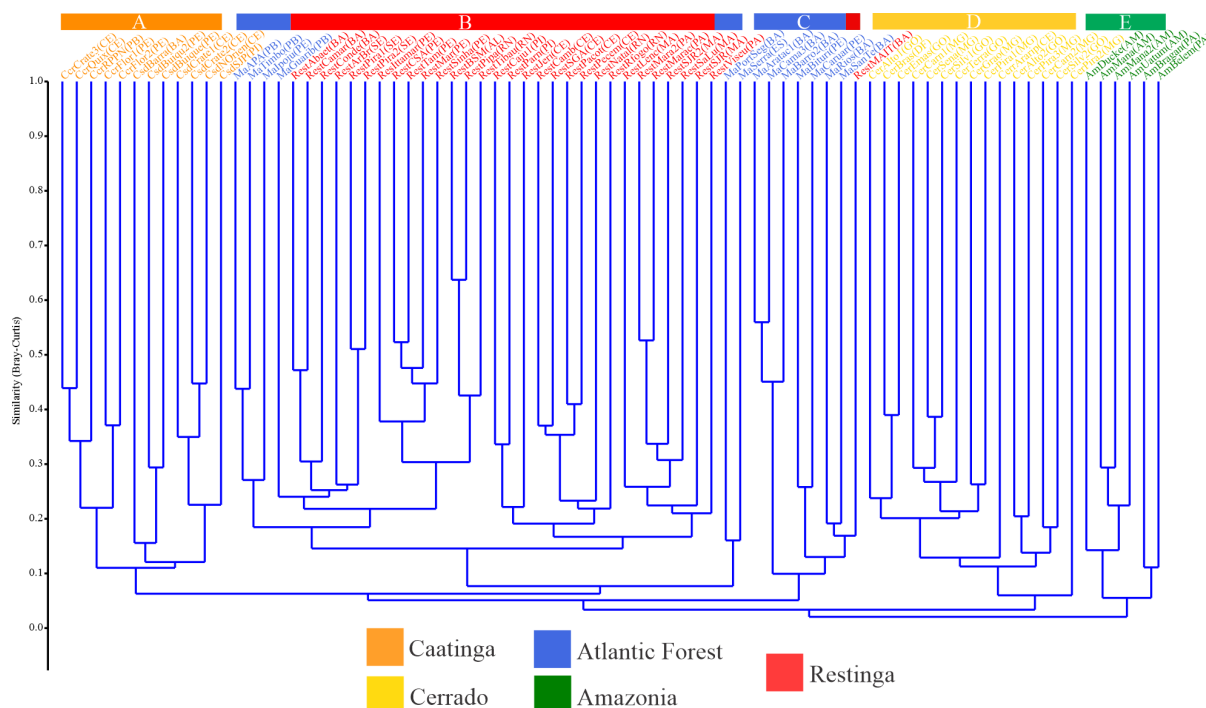
We also conducted an ordination analysis using Nonmetric Multidimensional Scaling (NMDS) with the presence/absence matrix and the Sorensen index (Legendre & Legendre 2012). The multivariate ordination analyses are a group of methods that represent multivariate objects (in our case multiple sites with thousands of species) based on the general similarity (proportion of shared species) between them (Koleff et al. 2003, Legendre & Legendre 2012). NMDS method represent sites (floristic studies) as points on a graph. The method compares the similarity between all pair of sites based on the number of shared species between each pair of sites and organizes all sites on a graph based on the general similarity between sites (Legendre & Legendre 2012, Wildi 2010). Sites that are more similar are placed closer to other similar sites, while sites with distinct plant communities are positioned far apart in the graph. We have labeled the different habitats (restinga, Caatinga, Cerrado, etc) with different symbols to evaluate in the graph how the flora of each habitat is similar or different from the flora of other habitats being compared. Both group and ordination analyses were performed using Past 4.13 software (Hammer et al. 2001). The matrix used in the multivariate analyses is available in our supplementary data.

We also used Venn Diagrams to compare the overlap of floras among different floristic groups using the Bioinformatics & Evolutionary Genomics platform (<http://bioinformatics.psb.ugent.be/webtools/Venn/>), which uses the software Venny 2.1. This aimed to further investigate which species are shared among different vegetation types.

## RESULTS

The examination of the similarity indices among restinga and non-restinga formations of diverse Brazilian phytogeographical domains revealed the emergence of five floristic groups (A–E) (Figure 2). These groups exhibited high coherence with their respective vegetation types, and distinct vegetation types clustered for the Cerrado, Caatinga and Amazonia, with restinga vegetation mixing with the flora of the Atlantic Forest in groups B and C. Nevertheless this result, most of restinga vegetation formed a large group, from restingas in Amazonia (Pará state), to restingas in the semiarid coast bordering the Caatinga (Ceará and Piauí states) and restingas bordering the humid Atlantic Forest (Rio Grande do Norte, Paraíba, Pernambuco, Sergipe and Bahia states). This cluster of restinga sites grouped with a few non-restinga in the Atlantic Forest of Paraíba and Pernambuco. And this larger cluster, grouped to other Atlantic Forest sites (with a small similarity, of less than 0.1). Group A comprised solely Caatinga sites. Group B consisted of restingas in Northern and Northeastern Brazil, along with a few non-restinga sites of the Atlantic Forest domain. Group C comprised areas of coastal and non-coastal Atlantic Forest formations in the states of Bahia, Pernambuco and Espírito Santo, along with a single restinga site in Bahia. Group D included solely Cerrado vegetation sites in the state of Ceará (Chapada do Araripe) and central Brazil (in the Federal District and the states of Goiás and Minas Gerais). Group E was formed by Amazonia (upland and seasonally flooded forests) in the states of Amazonas and Pará. The cophenetic correlation coefficient of grouping was 0.8875, suggesting the analysis is robust.

The formation of these groups was further corroborated by the NMDS analysis (Figure 3). In that ordination, sites within the investigated phytogeographical domains maintained



**Figure 2. Similarity dendrogram (UPGMA) of the restingas in Northern/Northeastern Brazil and other areas in different phytogeographical domains (Caatinga, Cerrado, Amazonia and Atlantic Forests).**

consistent grouping pattern. Greater proximity is only observed among restingas and sites belonging to other environments in the Atlantic Forests (stress 0.2059, considered a good representation of the dataset in a reduced space).

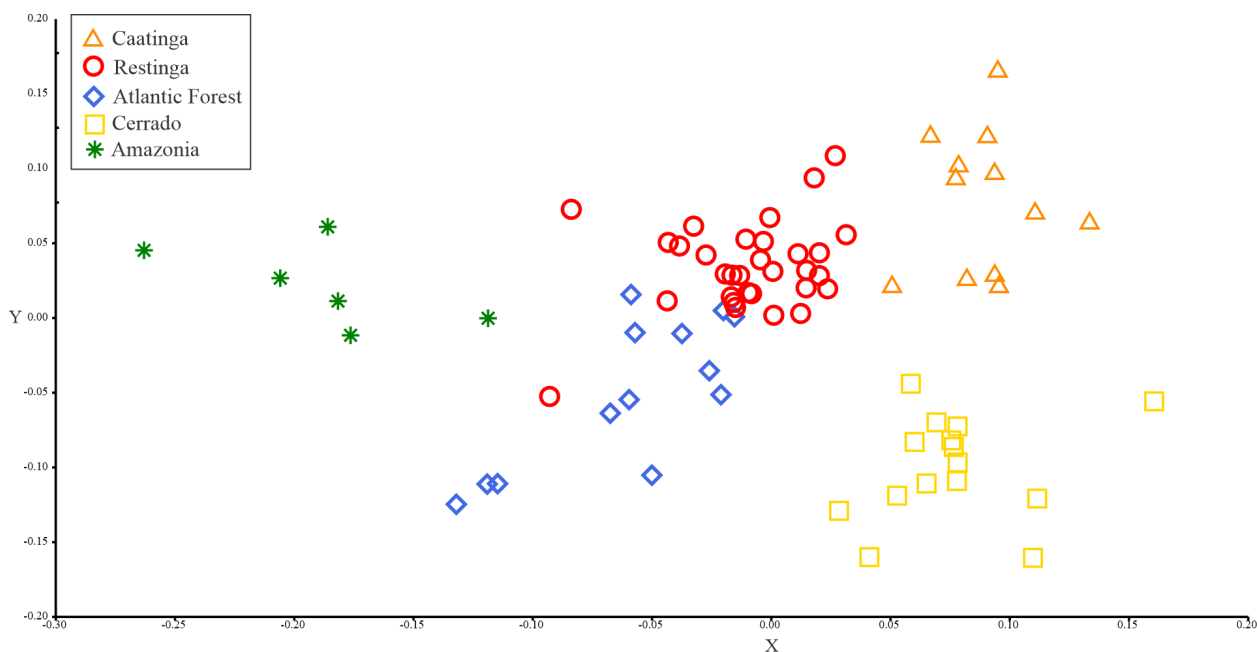
Additional analyses using Venn Diagrams illustrated species overlap among the restingas and other environments within nearby Brazilian phytogeographic domains. The results highlighted the influence of the surrounding phytogeographic domains, especially the Atlantic Forest, which shared the largest number of species (651 spp.) with the restingas of Northern and Northeastern Brazil, followed by the Caatinga (331 spp.), Cerrado (297 spp.) and Amazonia (272 spp.) (Figure 4).

## DISCUSSION

The floristic groups identified in our analyses largely reflect the floras of the respective

phytogeographical domains to which they belong, and the restinga sites do not align to any specific domain. Restingas exhibited a higher number of shared species with formations within the Atlantic Forest – and some Atlantic Forest sites grouped with restinga sites, whereas one restinga site located in Bahia grouped with a mostly Atlantic Forests cluster. However, the majority of restinga sites formed a singular group (group B), displaying low similarity with other vegetation types.

Group B, while dominated by restinga sites, also included some non-restinga sites within the Atlantic Forest domain. The overall similarity within this group was relatively low ( $< 0.3$ ), although subgroups displayed Sorensen values exceeding 0.6 (Figure 2). This overall low value is attributed to the limited number of shared species, in most cases, widely distributed along the coast of Brazil and in more interior formations. These results underscore the singular floristic composition of different restinga sites,



**Figure 3.** Ordination diagram produced by NMDS analysis (Nonmetric Multidimensional scaling) of restinga areas and phytogeographical domains in Brazil (Caatinga, Cerrado, Amazonia and Atlantic Forests). The surveys used are registered in Appendix 1.

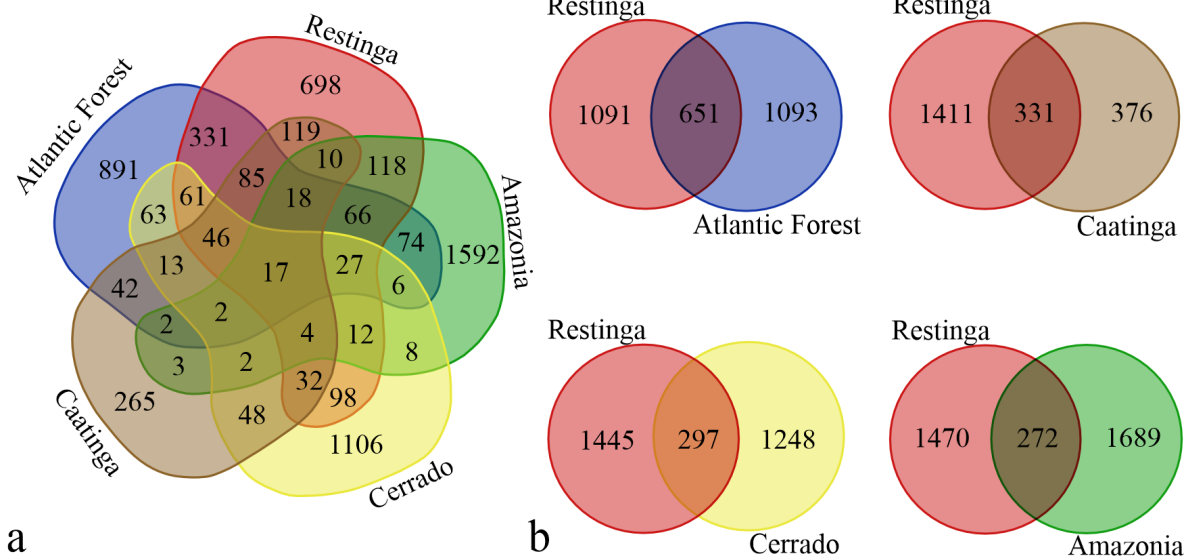
reflecting the environmental heterogeneity of Brazilian coastal regions (Magnago et al. 2011, Correia et al. 2020a). Although some restinga sites grouped with other environments within the Atlantic forests, the fact that most restinga sites grouped together highlights restingas unique floristic identity. Notably, the presence in our dataset of species unique to the restinga, such as *Bacopa cochlearia*, *Canavalia rosea*, *Cyperus pedunculatus*, *Duguetia restingae*, *Eugenia luschnathiana*, *Jacquinia armillaris*, *Myrcia restingae* (see list of species from Venn diagrams that occurred only in restingas in the supplementary material) reinforces the presence of various species restricted to the restinga habitat.

Despite restingas singular identity, putative connection with other formations within the Atlantic Forest should be acknowledge, though in need of more scrutiny. Indeed, previous authors have highlighted the influence of the Atlantic Forest on the patterns of diversity and composition of restinga communities (Rizzini

1963, Fernandes & Queiroz 2015). Our analyses revealed that, regarding the restingas of the Northern and Northeast Brazil, floristic links with the Atlantic Forest may be an outcome of environmental similarities. For example, the non-restinga Atlantic Forest sites (Figure 2) that clustered with the restinga dominated Group B are described as semi-deciduous seasonal forests growing on coastal plateaus dating to the Tertiary Period (Pereira & Alves 2007, Leite et al. 2007, Amazonas & Barbosa 2011, Barbosa et al. 2011, Pinto et al. 2019), meaning they are subjected to regular water-deficit as that experienced in restinga formations due to the low water-retention capacity sandy soils (Souza et al. 2008).

### Restinga and their vegetational mosaics

Our findings support the concept of organizing restinga vegetation in accordance with previously established compartmentalization of the Brazilian coast into distinct sectors (Villwock et al. 2005). Subgroups within Group B, for example,



**Figure 4. a** – Venn diagram demonstrating the overlapping between restingas and the phytogeographic domains analyzed. **b** – Pairs of Venn diagrams demonstrating the number of species shared between restingas and the phytogeographic domains.

closely correspond to the Amazonian Northern sector (encompassing the states of Pará and Maranhão), the semiarid Northeastern sector (covering the states of the states of Piauí, Ceará and the northern region of Rio Grande do Norte), and the Atlantic Forest sector (spanning along the southern coast of Rio Grande do Norte State and Pernambuco, Alagoas, Sergipe and Bahia). This pattern suggests that variations in the floristic compositions of restingas in Northern and Northeastern Brazil may be predominantly influenced by factors associated with climatic and geomorphological variations (see Villwock et al. 2005, Diniz & Oliveira 2016).

Climate and geographic distance, along with additional parameters such as the influence of surrounding phytogeographical domains (Cerqueira 2000, Scanaro 2002, Fernandes & Queiroz 2015, Silva & Souza 2018) may also significant factors influencing the levels of floristic similarity among restinga sites. Plants inhabiting the restingas established over coastal plains of the Amazonian northern sector, with large extensions of estuary zones (Lima &

Almeida-Jr 2018), for example, are exposed to higher amounts of rainfall. Plats inhabiting the Tertiary-Quaternary sandy plains along the semiarid Northeastern coast (Silveira 1964, Moro et al. 2015), on the other hand, tend to experience drier climatic conditions (Nimer 1972, IBGE 2002, Castro et al. 2012, Soares et al. 2021). These environmental differences partially explain why the restingas along the coasts of Pará and Maranhão are mostly dominated by species typical of wetter environments, such as *Abarema cochleata*, *Calycolpus goetheanus*, *Entada polystachya*, *Myrcia cuprea* and *Rhabdadenia biflora* (Cabral-Freire & Monteiro 1993, Amaral et al. 2008, Serra et al. 2016, Lima & Almeida-Jr 2018), whereas restingas areas in the states of Ceará, Piauí and the northern region of Rio Grande do Norte (including the municipalities of Rio do Fogo and Natal) are mostly populated by species typical of those seasonal environments, such as *Anacardium occidentale*, *Cereus jamacaru*, *Croton blanchetianus*, *Curatella americana*, *Himatanthus drasticus*, *Mimosa ophthalmocentra*, *Piptadenia retusa*,



*Stryphnodendron coriaceum* and *Sarcomphalus joazeiro* (Castro et al. 2012, Lima & Almeida-Jr 2018).

Within the Atlantic Forest coastal sector, two subgroups were identified: one in the northern portion of the Atlantic Forest coast of Brazil and another in the southern portion of that area that includes the states of Sergipe and Bahia (north of the *Todos os Santos Bay*). Notably, the restinga site located to the south of *Todos os Santos Bay* in Bahia State (Fernandes & Queiroz 2015) clustered with non-restinga environments of the Atlantic Forest (Group C). Once again, this distinction in floristic composition seems to be explained by distinctive climatic conditions, the coastal region north of Bahia State experiences a seasonal tropical climate with well-defined dry seasons, whereas the southern portion of the state is under a humid tropical climate without dry season (Oliveira-Filho & Fontes 2000, Peel et al. 2007, Alvares et al. 2013).

## CONCLUSIONS

Restingas are complex ecosystems that show diverse floristic composition along its long geographical extension. Our work adds to the knowledge of the restinga formations in Northern and Northeastern Brazil, regions largely neglected by previous studies. We showed that, despite the influence from surrounding ecosystems, the restingas of the regions present some degree of floristic singularity and form their own floristic cluster. The variation in floristic composition within the restinga cluster is linked factors such as geographic distance, geomorphological and climatic variables.

Our analyses revealed that the flora of the restinga of Northern and Northeastern Brazil are distinct from other ecosystems in different phytogeographic domains and that they are subdivided according to previously recognized

sectors of the Brazilian coast (Villwock et al. 2005). These results suggest that current classification adopted by the official Brazilian authorities (e.g., IBGE 2012) is insufficient due to their oversimplification (e.g., Veloso et al. 1991, IBGE 2012). Finally, our study highlights that future biogeographic investigations are critical for understanding restinga plant species composition, in order to provide information relevant for effective conservation and decision making.

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## APPENDIX 1

**Table I. Floristic surveys utilized in the analyses of similarity, indicating Designation, Formation, Municipality, State, Geographic Coordinates (Latitude and Longitude) and Bibliographic References.**

Designation	Formation	Municipality	State	Latitude	Longitude	Reference
Amazon Forest						
AmBelém(PA)	Floodplain Forest	Belém	PA	-0.4167	-48.4167	Maués et al. 2011
AmBragan(PA)	Upland Forest	Bragança	PA	-0.9278	-46.6722	Abreu et al. 2006
AmDucke(AM)	Upland Forest	Manaus	AM	-2.9617	-59.9278	Ribeiro et al. 1999
AmMana(AM)	Upland Forest	Manaus	AM	-2.5958	-60.2111	Oliveira & Amaral 2005
AmMana2(AM)	Upland Forest	Manaus	AM	-2.5958	-60.2111	Oliveira & Amaral 2004

**Table I. Continuation.**

AmUatum(AM)	Upland Forest	Uatumã	AM	-2.3344	-58.7572	Amaral et al. 2000
<b>Caatinga</b>						
CcrCrate3(CE)	Caatinga on Crystalline Basement	Cratêus	CE	-5.2500	-40.2500	Araújo et al. 2011
CcrQuix(CE)	Caatinga on Crystalline Basement	Quixadá	CE	-4.8261	-38.9858	Costa et al. 2007
CsdCrate2(CE)	Caatinga on Sedimentary Substrate	Cratêus	CE	-5.2500	-40.2500	Araújo et al. 2011
CsdCrate1(CE)	Caatinga on Sedimentary Substrate	Cratêus	CE	-5.2500	-40.2500	Araújo et al. 2011
CsdNOrien(CE)	Caatinga on Sedimentary Substrate	Novo Oriente	CE	-5.7167	-40.9167	Araújo et al. 1998
CsdBarra(BA)	Caatinga on Sedimentary Substrate	Barra	BA	-10.8000	-42.8333	Rocha et al. 2004
CsdBuíqu2(PE)	Caatinga on Sedimentary Substrate	Buíque	PE	-8.5158	-37.3497	Figueirêdo et al. 2000
CsdBuíque(PE)	Caatinga on Sedimentary Substrate	Buíque	PE	-8.5158	-37.3497	Andrade et al. 2004
CcrFlor1(PE)	Caatinga on Crystalline Basement	Floresta and Betânia	PE	-8.3125	-38.1953	Costa et al. 2009
CcrFlor2(PE)	Caatinga on Crystalline Basement	Floresta	PE	-8.3125	-38.1953	Santos et al. 2009
CcrRPPN(PB)	Caatinga on Crystalline Basement	Planalto da Borborema	PB	-7.4792	-36.9050	Nascimento et al. 2012
CsdSJP(PI)	Caatinga on Sedimentary Substrate	São José do Piauí	PI	-6.8536	-41.4708	Mendes & Castro 2009
<b>Cerrado</b>						
CerAlto1(GO)	Cerrado	Alto do Paraíso	GO	-13.7667	-47.5000	Munhoz & Proença 1998
CerEmas(GO)	Cerrado	Mineiros and Chapadão do Céu	GO	-17.8167	-52.6500	Batalha & Martins 2007
CerAlto2(GO)	Cerrado	Alto do Paraíso	GO	-13.7667	-47.5000	Munhoz & Proença 1998
CerSilv1(GO)	Cerrado	Silvânia	GO	-16.6500	-48.6000	Francener et al. 2012
CerSilv2(GO)	Cerrado	Silvânia	GO	-16.6500	-48.6000	Francener et al. 2012

**Table I. Continuation.**

CerTerra(GO)	Cerrado	São Domingos	GO	-13,6000	-46,2833	Teixeira 2015
CerGrao(MG)	Cerrado	Grão Mogol	MG	-16.5575	-42.8939	Pirani et al. 2009
CerPira1(MG)	Cerrado	Santana do Riacho	MG	-19.5667	-43.4500	Zappi et al. 2014
CerPira2(MG)	Cerrado	Santana do Riacho	MG	-19.5667	-43.4500	Zappi et al. 2014
CerPira3(MG)	Cerrado	Santana do Riacho	MG	-19.5667	-43.4500	Zappi et al. 2014
CerCarn1(MG)	Cerrado	Lagamar	MG	-17.9500	-46.8000	Siqueira et al. 2006
CerCarn2(MG)	Cerrado	Lagamar	MG	-17.9833	-46.8000	Siqueira et al. 2006
CerSena(MG)	Cerrado	Senador Modestino Gonçalves	MG	-17.6667	-43.3333	Neri et al. 2007
CerBras(DF)	Cerrado	Brasília	DF	-15.8892	-47.8422	Chacon et al. 2014
CerrArarip(CE)	Cerrado	Crato, Jardim and Barbalha	CE	-7.1950	-39.2244	Ribeiro-Silva et al. 2012
<b>Atlantic Forest</b>						
MaRios(BA)	Seasonal Semideciduous Forest	Rios	BA	-11.9222	-38.1450	Alves et al. 2015
MaAratac1(BA)	Montane Ombrophilous	Arataca	BA	-15.1667	-39.3333	Amorim et al. 2009
MaBarro2(BA)	Montane Ombrophilous	Barro Preto	BA	-14.7667	-39.5333	Amorim et al. 2009
MaCama3(BA)	Montane Ombrophilous	Camacan	BA	-15.3833	-39.5500	Amorim et al. 2009
MaPortSeg(BA)	Dense Ombrophilous Lowland Forest	Porto Seguro	BA	-16.4228	-39.1364	Pinto et al. 2019
MaSanTe(BA)	Submontane Ombrophilous	Santa Terezinha and Castro Alves	BA	-12.8500	-39.4667	Sobrinho & Queiroz 2005
MaAPA(PB)	Seasonal Semideciduous Forest	Baía da Traição	PB	-6.7886	-34.9894	Pereira & Alves 2007
MaGuarib(PB)	Seasonal Semideciduous Forest	Mamanguape and Rio Tinto	PB	-6.6631	-35.1128	Barbosa et al. 2011
MaTimbo(PB)	Seasonal Semideciduous Forest	João Pessoa	PB	-7.1358	-34.8500	Amazonas & Barbosa 2011



**Table I. Continuation.**

MaSerra(ES)	Tableland Atlantic Forests	Serra	ES	-20.1942	-40.3475	Leite et al. 2007
Malpoju(PE)	Dense Ombrophilous Forest	Ipojuca	PE	-8.40012	-35.0643	Pereira et al. 2013
MaCaruar(PE)	Montane Ombrophilous	Caruaru	PE	-8.2814	-35.9735	Rodal & Sales 2007
MaBituri(PE)	Semi-Deciduous Seasonal Montane Forest	Brejo da Madre de Deus	PE	-8.2014	-36.3892	Nascimento et al. 2012
<b>Restinga</b>						
RestViseu(PA)	Restinga	Viseu	PA	-1.1967	-46.1400	Santos et al. 2003
RestMara2(PA)	Restinga	Maracanã	PA	-0.6043	-47.5745	Santos & Rosário 1988
RestMarac(PA)	Restinga	Maracanã	PA	-0.5817	-47.5811	Bastos et al. 1995
RestLenç(MA)	Restinga	Barreirinhas	MA	-2.6400	-42.8467	Rodrigues et al. 2019
RestSaLu(MA)	Restinga	São José de Ribamar	MA	-2.5000	-44.2667	Cabral-Freire & Monteiro 1993
RestSJR(MA)	Restinga	São José de Ribamar	MA	-2.6464	-44.1514	Serra et al. 2016
RestSJR2(MA)	Restinga	São José de Ribamar	MA	-2.4731	-44.0539	Lima & Almeida 2018
RestParn(PI)	Restinga	Ilha Grande, Parnaíba and Luiz Correia	PI	-2.8578	-41.8208	Santos-Filho 2009
RestCaju1(PI)	Restinga and Coastal Tableland	Cajueiro da Praia	PI	-2.9278	-41.3358	Santos-Filho et al. 2016
RestJeri(CE)	Restinga	Jijoca de Jericoacoara	CE	-2.8420	-40.4582	Matias & Nunes 2001
RestSGA(CE)	Restinga	São Gonçalo do Amarante	CE	-3.5744	-38.8939	Araujo et al. 2020
RestPecém(CE)	Restinga and Coastal Tableland	São Gonçalo do Amarante	CE	-3.5250	-38.9372	Castro et al. 2012
RestPacot(CE)	Restinga and Coastal Tableland	Fortaleza, Eusébio and Aquiraz	CE	-3.83614	-38.4132	Rabelo 2022
RestCamb(CE)	Restinga and Coastal Tableland	Fortaleza	CE	-3.7986	-38.4861	Moro et al. 2011

**Table I. Continuation.**

RestNatal(RN)	Restinga and Coastal Tableland	Natal	RN	-5.8316	-35.1889	Freire 1990
RestPipa(RN)	Restinga	Tibau do Sul	RN	-6.2258	-35.0638	Almeida & Zickel 2009
RestRfogo(RN)	Restinga and Coastal Tableland	Rio do Fogo	RN	-5.4133	-35.3875	Oliveira et al. 2012
RestTibau(RN)	Restinga	Tibau do Sul	RN	-6.2254	-35.0657	Almeida-Jr et al. 2006
RestCSA(PE)	Restinga	Cabo de Santo Agostinho	PE	-8.1250	-35.0153	Sacramento et al. 2007
RestMar(PE)	Restinga	Maracáipe	PE	-8.5300	-35.0181	Almeida-Jr et al. 2009
RestSinha(PE)	Restinga	Sirinhaém	PE	-8.5908	-35.1158	Cantarelli et al. 2012
RestItamar(PE)	Restinga	Itamaracá	PE	-7.7224	-34.8315	Almeida-Jr et al. 2007
RestTam(PE)	Restinga	Tamandaré	PE	-8.7889	-35.1125	Silva et al. 2008
RestBSM(AL)	Restinga	Barra de São Miguel	AL	-9.8400	-35.9067	Almeida-Jr et al. 2016
RestPira1(SE)	Restinga	Pirambu and Pacatuba	SE	-10.6292	-36.6933	Oliveira & Landim 2020
RestPira2(SE)	Restinga	Pirambu and Pacatuba	SE	-10.6292	-36.6933	Oliveira et al. 2015
RestArBr(SE)	Restinga	Areia Branca, Itabaiana and Laranjeiras	SE	-10.6667	-37.4167	Dantas et al. 2010
RestAbaet(BA)	Restinga	Salvador and Lauro de Freitas	BA	-12.9333	-38.3500	Britto et al. 1993
RestCamar(BA)	Restinga	Camaçari	BA	-12.7417	-38.1583	Queiroz et al. 2012
RestConde(BA)	Restinga	Conde	BA	-11.8303	-37.5888	Menezes et al. 2009
RestMAIT(BA)	Restinga	Maraú and Itacaré	BA	-14.2169	-38.9983	Fernandes & Queiroz 2015

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**Author contributions**

S.T.R. conceived the work, undertook data collection, created the biogeographical database, ran the statistical analyses and wrote the manuscript; M.F.F participated in defining the objectives and structure of the work, discussed the results, and reviewed the manuscript; M.F.M. conceived the work, supported data collection, aided the statistical analysis, discussed the results, and reviewed the manuscript.

