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Spatial structure, diversity, and edaphic factors of an area of Amazonian coast vegetation in Brazil[1]

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Abstract. This study intends to verify whether edaphic factors contribute to the structural arrangement of the woody restinga vegetation in the Northeast region of Brazil, and whether there is similarity between the restingas of the Amazonian and Northeast coasts. To sample the restinga vegetation of Maranhão State, we used the point-quarter method. In each quadrant, we collected soil samples to determine the chemical and physical variables. We built a matrix to correlate the soil variables with the species, using the canonical correspondence analysis, and used cluster analysis for the similarity. The analysis resulted in 32 species and 17 families. *Astrocaryum vulgare*, *Protium heptaphyllum*, *Anacardium occidentale*, *Coccoloba latifolia*, and *Tilesia baccata* presented higher importance value. The Shannon's diversity index was 2.9 nat.ind^{-1}, and Pielou's equality was 0.8. The correlation analysis showed that only *Chioccoca alba* and *Mouriri guianensis* presented positive correlation with magnesium, organic matter, sum of bases, and base saturation. Regarding similarity, the flora of the restinga in the present study resembles the restinga of Alcântara, in Maranhão State, and an area of Ceará State. Finally, we assert that such studies of the Northeast coastal vegetation constitute an important tool to assist in the development of strategies for biodiversity conservation.

Key words: Amazonian coast, edaphic variables, Northeast coast, phytosociology, tropical coast

The Brazilian tropical coastal vegetation (restinga) covers a narrow continental strip of Holocene sands of marine origin (Fernandes 1998), occupying around 80% of the coast (Lacerda, Araujo, and Maciel 1993) and comprising a group of phytophysically distinct plant communities (Sugiyama 1998). Learning about the restingas enables an understanding of how this vegetation behaves and increases the information about coastal plant communities associated with abiotic factors (César and Monteiro 1995).

Araujo and Henriques (1984) highlighted the richness of these plant communities of the Northeast, which is due to the extensiveness of its coastal region, but noted that little is known about them. Despite a considerable increase in the number of studies focused on the Northeast, the data that have been published are still basic and need more robust analyses to assess the distribution and endemism of the species (authors' personal observation). The data on the coastal region of the North of Brazil are preliminary and do not encompass the entire territory. This claim was emphasized by Santos-Filho and Zickel (2013), who observed 30 years later that the analyses are still simplified and that the scarcity of phytosociological data still impedes greater generalizations about the pattern of species in the restingas of the Northeast.

Santos-Filho, Almeida Jr., and Zickel (2013) noted that analyses of the tropical coast vegetation structure must incorporate the chemical and physical characteristics of the soil, and that attributes such as declivity, humidity, and depth of the water table may influence the spatial arrangement of the plants, especially in transition areas, as observed in the Atlantic Forest (Moreno and Schiavini 2001). The authors also mention that the presence of certain nutrients may be a predominant factor in the establishment of plant communities. Therefore, it is possible to ascertain which nutrients limit the presence of certain groups of plants (Lima *et al*. 2003).

Araujo and Scarano (2007) stressed that the flora of the Atlantic Forest is similar to the

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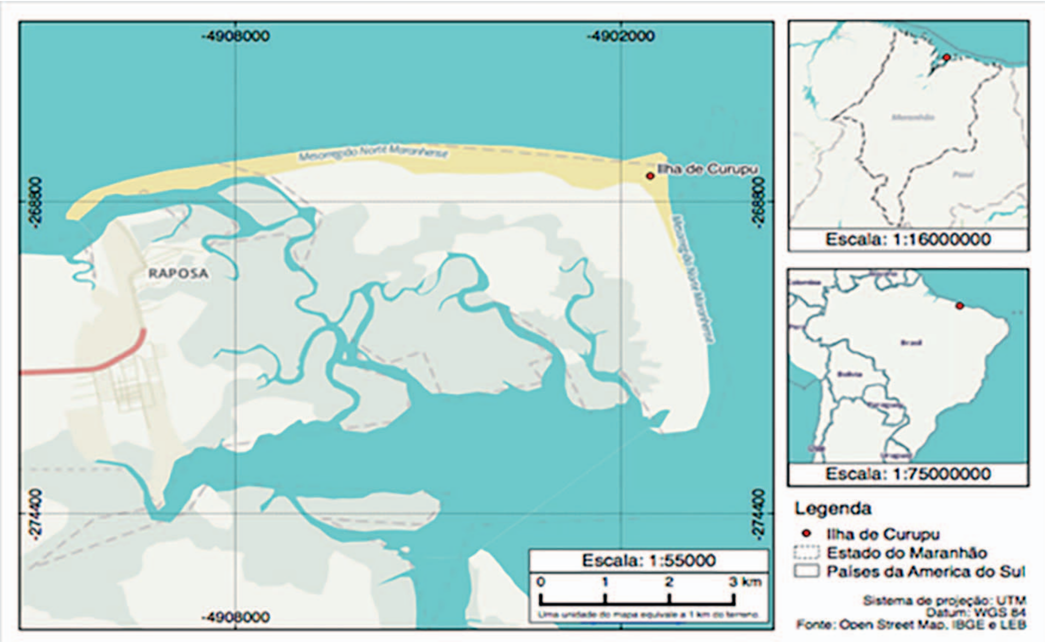

FIG. 1. Map of the study area location: Curupu, Raposa, Maranhão State, Brazil. Adapted by D. B. Muniz.

vegetation of restingas in Rio de Janeiro State. The same sort of similarity is believed to occur between Amazonian flora and the restingas of Maranhão on account of their geographic proximity and the costal vegetation being influenced by adjacent vegetation. However, the deficiency of data on the flora of Maranhão prevents further comparison or confirmation.

Nevertheless, the works that analyze restinga plant communities of the Brazilian coast, especially those focused on the Amazonian coast (the region between the Oiapoque River falls and eastern Maranhão) and the Northeast coast (from eastern Maranhão to Recôncavo Baiano), are still preliminary in terms of similarities of the flora and environmental attributes (Silveira 1964, Villwock *et al*. 2005, Ab'Saber 2006). Such studies are crucial for answering questions related to the functional dynamics of these coastal ecosystems; they are valuable sources of data that can be used to determine the degree of fragility of these environments (Moreno, Schiavini, and Haridasan 2008).

Through the contribution of knowledge about restinga vegetation of the Maranhão coast, data on the structural arrangement of woody vegetation provides important support for management and conservation projects. Based on studies of restinga areas in the Northeast, Almeida *et al*. (2011) and Santos-Filho, Almeida Jr., and Zickel (2013) indicated that various abiotic factors may contribute to the structural arrangement of the woody vegetation.

In this context, we will test two hypotheses: (a) edaphic factors are related to the composition and structural distribution of the woody species in the coastal region of Maranhão and (b) the composition of woody vegetation of the North coast is similar to that of the Amazonian coast. To this end, we will answer the following questions: (a) What is the structural arrangement of vegetation on the Curupu coast? (b) What is the relationship between the edaphic factors and the vegetation structure? (c) Is the woody vegetation composition of the Maranhão coast similar to that of the coasts of Ceará, Piauí, and Pará?

Material and Methods. STUDY AREA. Curupu Island (02°24′09″S, 44°01′19″W) is located in the municipality of Raposa, Maranhão, Brazil (Fig. 1). Characterized by extensive sandy beaches, restinga vegetation, mangroves, and dunes (Barreto, Lima, and Barbosa 2009), Curupu Island is part of the Golfão Maranhense, which comprises an estuarine system of Pleistocene-Holocene formation (Ab'-Saber 1960). The lithostratigraphy of the study area sits on the Coastal Sedimentary Basin of São Luís, consisting of the Itapecuru Formation (Cretaceous), Barreiras Group (Tertiary), and recent sediments (Quaternary) (Rangel 2000).

The coastal vegetation of Curupu presents grassland, shrub, and forest physiognomies, according to the classification of Silva and Britez (2005). The grassland is found in lower areas of the sandy strands and is characterized by the presence of herbs or subshrubs, with isolated and sparse shrubs. The grassland can be flooded, due to the accumulation of groundwater, or non-flooded, whose substrate is found on the beaches' upper stretches that the tides or water table rarely reach.

The shrub physiognomy consists of small shrubby and subshrub by formations reaching 1–3 m in height. Its vegetation is denser in areas farther from the shoreline, which is sometimes associated with more open areas of herbaceous vegetation. The forest physiognomy features a canopy that varies from 4 to 15 m, with areas farther from the beach becoming denser and abundant in trees and shrubs, forming a more closed environment (Silva and Britez 2005).

Data Collection and Species Identification. Phytosociological sampling took place in the forest physiognomy through the point-quarter method (Cottam and Curtis 1956). We made five transections, 10 m apart and perpendicular to the coastline. Each transection had 10 point-centered quadrants set 10 m apart (total of 50 points). In each point-centered quadrant, we analyzed the four living woody individuals that were closest to the center of the quadrant and had a diameter at ground level $\geq$ 3 cm. For branched individuals, all of the branches were measured then summed and converted into the average diameter of the plant. Once measured, we collected the individuals in accordance with Peixoto and Maia (2013) and identified the material through bibliographic resources and comparison with herbarium material. The organization of the species followed the proposed classification of the Angiosperm Phylogeny Group (2016). After herborization, the vouchers were incorporated into the archive of the Maranhão Herbarium, Department of Biology, at Universidade Federal do Maranhão.

Data Analysis and Structure of the Woody Community. For the phytosociology, we analyzed the values of basal area, absolute density, absolute frequency, absolute dominance, importance value (IV), and cover value. We also calculated Shannon's diversity index (H′), Pielou's equality (J′), and total richness (S). All data were calculated using the package Fitopac 2.0 (Shepherd 2010).

To analyze the diametric distribution, we created a histogram of the number of individuals per diameter class (10-cm interval). To characterize the vertical space, we made another histogram of the number of individuals per height class (1-m interval), with a right-open interval.

Collection and Analysis of Edaphic Data. We collected a total of 25 soil samples (at depths of 0–20 cm), using a soil auger (Meira Neto *et al.* 2005) according to the recommendations of Embrapa (2017). For this sampling, a prior random draw of points determined where samples would be collected, totaling five soil samples from each transection (Almeida *et al.* 2011). The collected samples were analyzed at the Soil Laboratory of the State University of Maranhão (Universidade Estadual do Maranhão) to obtain the chemical variables—pH, levels of potassium (K), phosphorous (P), calcium (Ca), magnesium (Mg), aluminum (Al), total acidity (H + Al), sum of bases (SB), base saturation (V), organic matter (OM), cation exchange capacity (CEC)—and the physical variables: proportions of sand, silt, and clay.

For the analysis relating the woody species to the chemical and physical variables of the soil, we performed a canonical correspondence analysis (CCA) (Ter-Braak 1995) in the software MVSP version 3.22 (Multi-Variate Statistical Package Kovach (1998)). This analysis used two matrices: one matrix consisted of species-density values, considering only those species that had two or more individuals in the total sampling (Botrel *et al.* 2002); the second matrix consisted of the chemical and physical variables of the soil (pH, K, P, Ca, Mg, Al, H + Al, SB, V, OM, CEC, sand, silt, and clay). We then ran a preliminary analysis with all the variables. From the total, we eliminated 11 variables that were weakly correlated or highly redundant (Teixeira and Assis 2009). The variables that presented the strongest correlations with the ordination axis were Mg, SB, V, and OM. After processing the final CCA, we applied the Monte Carlo test (1,000 permutations) to verify the significance of the correlations among the environmental variables.

Table 1. List of location, data source and species richness of all plots included in this study.

Location	Region	Source	Richness	No. of woody species
Ilha de Curupu, Maranhão State	Northern coast	This study	32	25
Alcântara, Maranhão State	Amazon coast	Almeida Jr., Correia, and Santos-Filho (u.d.*)	61	22
Ilha Grande, Piauí State	Northern coast	Santos-Filho, Almeida Jr., and Zickel (2013)	12	12
Parnaíba, Piauí State	Northern coast	Santos-Filho, Almeida Jr., and Zickel (2013)	18	17
Luís Correia, Piauí State	Northern coast	Santos-Filho, Almeida Jr., and Zickel (2013)	23	20
Pecém, Ceará State	Northern coast	Castro, Moro, and Menezes (2012)	52	41
Viseu, Pará State	Amazon coast	Santos *et al*. (2013)	141	41
Algodoal, Pará State	Amazon coast	Bastos, Rosário, and Lobato (1995)	224	88

* u.d. = unpublished data.

Similarity Analysis. The Maranhão coast is divided into two slopes: the western side, belonging to the Amazonian coast, and the eastern side, belonging to the Northeast coast. To analyze the similarity between the species in the present study and those of other coastal areas, we created a presence/absence matrix with woody species listed in phytosociological studies conducted in Ceará, Piauí, and Maranhão (Castro, Moro, and Menezes 2012; Santos-Filho, Almeida Jr., and Zickel 2013; Almeida Jr., Correia and Santos-Filho unpublished data). Due to the absence of phytosociological studies for the coast of Pará, we included two floristic studies (Bastos, Rosário, and Lobato 1995; Santos *et al*. 2003), considering only the woody species (Table 1). There are no studies for the stretch of coast along the north of the state of Rio Grande do Norte.

In creating the presence/absence matrix, we considered only the species identified to species level. After creating the matrix, we constructed a cluster dendrogram based on the group average of Jaccard distances. The analyses were run in the Vegan package (Oksanen *et al*. 2015) of the program R version 3.2.0 (R Development Core Team 2015). To validate the dendrogram, we constructed a cophenetic matrix, following Borcard, Gillet, and Legendre (2011).

Results. Structural Arrangement. The sampling resulted in 32 species, 27 genera, and 17 families, totaling 200 individuals (Table 2). Of all the species, seven remained as morphospecies. The families with the highest richness were Rubiaceae (six species), Myrtaceae and Fabaceae (five species each), and Sapindaceae (three species). The other families presented only one species each. In relation to the number of individuals, the most representative families were Burseraceae (45 individuals, represented by *Protium heptaphyllum*), Arecaceae (21 individuals of *Astrocaryum vulgare*), Rubiaceae (22 individuals), Anacardiaceae (20 individuals of *Anacardium occidentale*), Myrtaceae (19), and Fabaceae (16). These families are predominant in the structural arrangement of the restinga, totaling 70.5% of the sample.

The species *Astrocaryum vulgare*, *Protium heptaphyllum*, *Anacardium occidentale*, *Coccoloba latifolia*, and *Tilesia baccata* present the highest IVs (Table 2). The species *Matayba guianensis*, *Cereus jamacaru*, *Pseudima frutescens*, and *Tocoyena* aff. *sellowiana* were considered rare due to low representation in the area, comprising about 2.5% of the sample.

The total density by area was estimated to be 1,520.3 individuals/ha. Shannon's diversity index (H′) was 2.8 nat.ind^{-1}, and equality (J′) was 0.82 when compared to the other areas in the Northeast of Brazil.

The average height among individuals was 4 m, and the maximum was 15 m. The height classes from 0.6 to 4 m had the greatest height frequency among individuals (130 individuals, or 65%), particularly the first height class (0.6–2 m), which included 59 individuals (Fig. 2). The 8th9th, and 10th classes (8–15 m) had the fewest plants (16 individuals). The species *Andira* sp., *Protium heptaphyllum* (12 m), *Mouriri guianensis*, *Anacardium occidentale*, *Ouratea fieldingiana*, and *Guet-*

Table 2. Phytosociological parameters recorded in restinga vegetation, Curupu, Raposa, Maranhão State, Brazil.*

Species	Family	N	AbsFr (%)	AbsD (%)	AbsDo (%)	IV (%)	CV (%)
Astrocaryum vulgare Mart.	Arecaceae	21	38	145.8	21.31	61.56	50.12
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	45	62	312.4	10.11	59.97	41.29
Anacardium occidentale L.	Anacardiaceae	20	34	138.8	11.38	41.4	31.16
Coccoloba latifolia Lam.	Polygonaceae	11	20	76.4	1.22	13.8	7.78
Tilesia baccata (L.f.) Pruski	Asteraceae	11	18	76.4	0.5	11.85	6.43
Myrcia aff. *laruotteana* Cambess.	Myrtaceae	10	18	69.4	0.51	11.36	5.94
Matayba guianensis Aubl.	Sapindaceae	7	14	48.6	0.58	8.8	4.59
Ouratea fieldingiana (Gardner) Engl.	Ochnaceae	7	10	48.6	1.23	8.79	5.78
Alibertia aff. *edulis* (Rich.) A.Rich.	Rubiaceae	6	10	41.7	1.29	8.42	5.41
Solanum paludosum Moric.	Solanaceae	8	14	55.5	0.07	8.35	4.13
Inga sp.	Fabaceae	7	12	48.6	0.44	7.93	4.31
Guettarda angelica Mart. ex Müll.Arg.	Rubiaceae	6	10	41.7	1.02	7.92	4.9
Chloroleucon aff. *acacioides* (Ducke) Barneby & J.W. Grimes	Fabaceae	3	6	20.8	1.36	5.83	4.03
Andira sp.	Fabaceae	4	6	27.8	1.03	5.72	3.91
Chomelia obtusa Cham. & Schltdl.	Rubiaceae	5	8	34.7	0.16	5.21	2.81
Eugenia stictopetala Mart. ex DC.	Myrtaceae	4	6	27.8	0.06	3.92	2.12
Mouriri guianensis Aubl.	Melastomataceae	3	4	20.8	0.52	3.66	2.46
Cynophalla flexuosa (L.) J.Presl	Capparaceae	3	6	20.8	0.14	3.57	1.76
Manilkara bidentata (A.DC.) A.Chev.	Sapotaceae	3	4	20.8	0.12	2.92	1.71
Guettarda spruceana Muil. Arg.	Rubiaceae	2	4	13.9	0.16	2.51	1.3
Chiococca alba (L.) Hitchc.	Rubiaceae	2	4	13.9	0.08	2.36	1.36
Myrcia splendens (Sw.) DC.	Myrtaceae	2	4	13.9	0.06	2.32	1.12
Eugenia biflora (L.) DC.	Myrtaceae	2	4	13.9	0.04	2.27	1.07
Indet.	Indet.	1	2	6.9	0.14	1.36	0.76
Fabaceae 1	Fabaceae	1	2	6.9	0.1	1.29	0.69
Cereus jamacaru DC.	Cactaceae	1	2	6.9	0.08	1.26	0.66
Moraceae 1	Moraceae	1	2	6.9	0.02	1.14	0.54
Pseudima frutescens (Aubl.) Radlk.	Sapindaceae	1	2	6.9	0.02	1.14	0.54
Fabaceae 2	Fabaceae	1	2	6.9	0.01	1.12	0.51
Tocoyena aff. *sellowiana* (Cham. & Schltdl.) K.Schum.	Rubiaceae	1	2	6.9	0.01	1.12	0.52
Myrcia multiflora (Lam.) DC.	Myrtaceae	1	2	6.9	0.01	1.11	0.51

* N = number of individuals, AbsFr = absolute frequency, AbsD = absolute density, AbsDo = absolute dominance, IV = importance value, CV = coverage value. Indet. = indeterminate species

tarda angelica (10 m) stood out as emergent, their height varying from 10 to 15 m.

The average diameter was 15 cm, and the maximum was 132 cm. The greatest number of individuals (128, or 64%) was recorded in the first diameter class (3–10 cm). The fewest individuals were found in the eighth and ninth classes (63–133 cm), corresponding to the highest diameter values

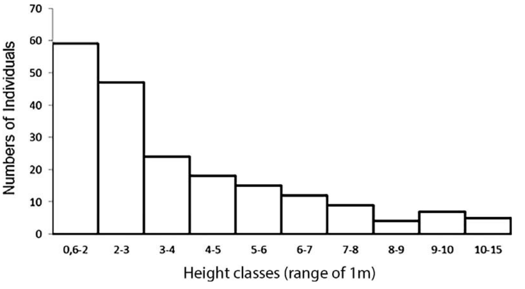

Fig. 2. Distribution of the number of individuals, by height classes (1-m interval), of the woody species in Curupu, Raposa, Maranhão State, Brazil.

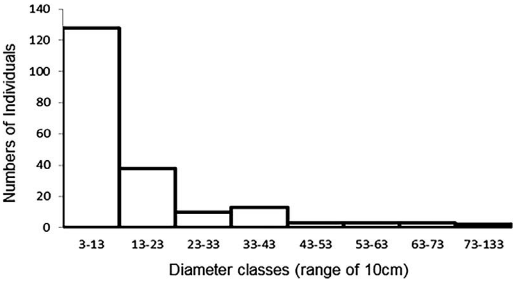

Fig. 3. Distribution of the number of individuals, by diameter classes (10-cm interval), of the woody species in Curupu, Raposa, Maranhão State, Brazil.

Table 3. Physical-chemical variables of soil samples, Curupu, Raposa, Maranhão State, Brazil.

Edaphic variables*	Average ± SE	Standard deviation
pH	4 ± 68	0,23
P (mg/kg)	6 ± 84	1,35
K	37 ± 1	79,88
Ca	13 ± 04	7,04
Na	2 ± 76	1,37
Mg	11 ± 6	2,42
Al	0 ± 16	0,21
SB	28 ± 4	5,64
H	15 ± 24	0,26
CEC	44 ± 79	8,64
Base saturation (%)	63 ± 58	4,65
Na/CEC (%)	6 ± 14	3,08
Al/Al + SB	0 ± 69	1,02
OM	11 ± 6	5,22
Coarse sand	2 ± 8	1,61
Fine sand	94 ± 72	2,25
Silt	0	0
Clay	2 ± 04	0,76
Conductivity/25°C	0 ± 06	0
H_2O saturation (%)	22 ± 91	0,15

* P = phosphorus, K = potassium, Ca = calcium, Na = sodium, Mg = magnesium, Al = aluminum, SB = sum of bases, H = hydrogen, CEC = cation exchange capacity, V = base saturation, OM = organic matter,

(Fig. 3). The present study observed that the diameter distribution followed a similar pattern as native forests: an inverted "J," with the greatest number of individuals in the smallest diameter classes and a gradual decrease in the largest diameter classes.

Edaphic Factors. The physical analysis of the soil showed high levels of sand, with an average of 94.72%; the pH varied between 4.20 and 5.30 (average 4.68 ± 0.23), which is considered moderately acidic (Table 3). The variables correlated with Axis 1 were Mg (–0.034), OM (–0.047), SB (–0.048), and V (–0.036). The eigenvalues for the first two axes were 0.272 and 0.226, respectively. These values are considered low (< 0.5) (Ter-Braak 1995), indicating short gradients in which the majority of species are not influenced by the variables (Fig. 4). The variances for the two axes were 3.251% and 5.950%, indicating the existence of variance not explained by the selected environmental variables. However, we observed a high correlation between species and environmental variables, with values of 0.841 (Axis 1) and 0.751 (Axis 2).

The CCA analysis suggests the formation of three groups (Fig. 4). The first group consisted of

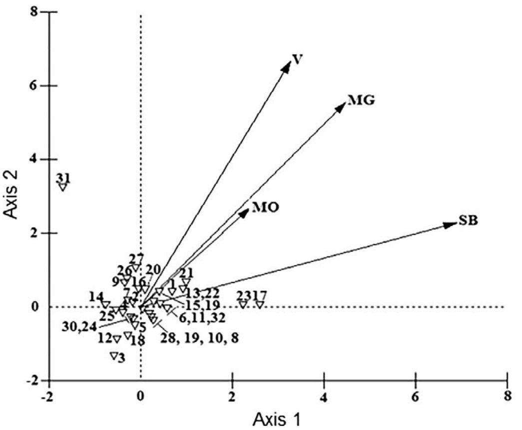

Fig. 4. Schematic diagram of the density of woody species in Curupu, Raposa, Maranhão State, Brazil, and its correlation with magnesium (Mg), organic matter (MO), sum of bases (SB), and saturation by bases (V).

Mouriri guianensis (23) and *Chioccoca alba* (17) and showed a positive correlation with base saturation. The second group contained *Tocoyena sellowiana* (31), which correlated negatively with the variables Mg, OM, SB, and V. The third group comprised the rest of the species, all of which are considered to be generalists; thus, none of the variables could be interpreted as constraints. Therefore, the soil showed no direct influence on the structural arrangement, refuting the hypothesis that proposes the edaphic variables as predominant factors in woody structural arrangement.

Similarity. The similarity analysis considered 266 valid species, compiled from eight studies. The total number of taxa per restinga varied between 13 and 88, reflecting the heterogeneity of the areas. The cophenetic analysis presented a value of 0.923, indicating a strong linear correlation (Hair *et al.* 2005).

The compared areas formed three distinct groups (Fig. 5). The first group comprised the restingas of Piauí, representing the northern coast (Parnaíba, Luiz Correia, and Ilha Grande); the second group comprised the restingas of Maranhão, representing the Amazonian coast (Alcântara), the northern coast (present study), and Ceara (Pecém). The third group comprised the restingas of Pará, representing the Amazonian coast (Viceu, Algodoal). In Maranhão, the municipalities of Alcântara (Amazonian coast) and Curupu (Northeast coast) show a low similarity value of 30%.

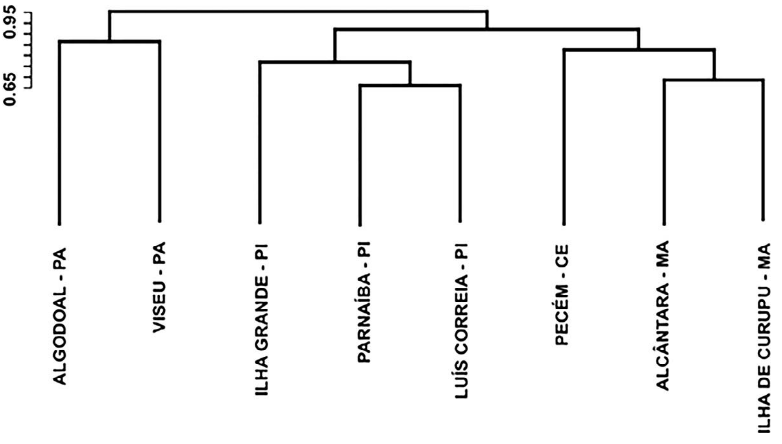

Fig. 5. Dendrogram of similarity between the restinga of the present study (in Curupu, Raposa, Maranhão State), and other areas of restinga (Algodoal, Para State; Viceu, Pará State; Ilha Grande, Piauí State; Parnaíba, Piauí State; Luís Correia, Piauí State; Pecém, Ceará State; Alcântara, Maranhão State).

Maranhão, Pará and Ceará can be consolidated into one clade of low similarity.

Discussion. The species richness found in the present study was lower than that found in Ceará, on the Northeast coast (Castro, Moro, and Menezes 2012), and in areas of the Amazonian coast (Almeida Jr., Correia, and Santos-Filho unpublished data) in Maranhão. However, it was higher in comparison to the first group of areas in Piauí, on the Northeast coast (Santos-Filho, Almeida Jr., and Zickel 2013). The difference in species richness is related to the variation in abiotic factors present in this ecosystem (Vicente *et al*. 2014). Differences in substrate, soil nutrient levels, degree of salinity, water table depth, and the proximity to other ecosystems can contribute to this differentiation (Almeida *et al*. 2009).

The coastal vegetation area in the present study appears to have a selective character, explaining the presence of many *Protium heptaphyllum* and *Astrocaryum vulgare* individuals. Environments marked by extreme conditions, such as low water and nutrient availability, the influence of winds, and salinity tend to increase the ecological dominance of some species (Ashton 1990). The forest physiognomies exhibit these extreme conditions (such as low fertility and low water retention), contributing to the selection of species more able to establish themselves in this type of physiognomy (Silva and Scariot 2003; Gomes *et al*. 2007).

Although the species composition differs, the families Rubiaceae, Myrtaceae, and Fabaceae were recorded in this type of vegetation. In the Southeast of Brazil, Assis, Pereira, and Thomaz (2004) found more than 50% of the species belonging to the abovementioned families. In the restingas of the Northeast, Sacramento, Zickel, and Almeida Jr. (2007) and Almeida Jr. *et al*. (2009) also reported an elevated richness of these families. Rubiaceae, Myrtaceae, and Fabaceae are among the most abundant families in the restingas of Alagoas, Bahia, Pernambuco, and Rio Grande do Norte (eastern coast of the Northeast), which are influenced by the Atlantic Forest vegetation. The species of these families are also abundant in the restingas on the northern coast of the Northeast, particularly Maranhão, due to the phytogeographic influences of the Cerrado biome (Brasil. Instituto 2004). This can be explained by the plasticity, dispersal, and distribution amplitude of these families and/or the conditions for their establishment in the ecosystem (Santos-Filho, Soares, and Almeida Jr. 2013).

Burseraceae, however, is one of the most representative families in terms of number of individuals. Its species have also been recorded in other restingas of the Northeast (Almeida *et al*. 2009, 2011; Cantarelli *et al*. 2012) and are remarkable in both composition and structural arrangement, having developed large populations in low-fertility soils.

Despite the large number of *Protium heptaphyllum* individuals, this species had only the second highest IV (Table 2). The highest IV belongs to the species *Astrocaryum vulgare*, which is considered a pioneer plant and a pasture invader, indicating environments with some type of disturbance (Shanley and Medina 2005), and tends to establish itself easily. The species grows in poor soils of the *terra firme*, with limitations similar to those found in restinga soils, which would explain its adaptation to coastal environments. It is also resistant to fire, owing to its high capacity for resprouting. It is widely distributed in eastern Amazonia, an area considered as a center of genetic diversity for *A. vulgare* (Clement, Lleras Pérez, and Van Leeuwen 2005; Shanley and Medina 2005).

Anarcadium occidentale presented a similar IV in the restinga of Piauí, on the northern coast (Santos-Filho, Almeida Jr., and Zickel 2013). The records of *Coccoloba latifolia*, *Astrocaryum vulgare*, and *Protium heptaphyllum* point to the influence of Amazon forest species on the colonization of the restingas of Maranhão.

The woody community of the Northeast coast reaches heights of 4.25–8 m. On the Maranhão coast, in the Amazonian coastal area, the average height is 4.45 m (Almeida Jr., Correia and Santos-Filho unpublished data), close to the measurement of individuals in the restinga of Ceará (Castro, Moro, and Menezes 2012). When comparing the present study (which found an average height of 4 m), the woody stratum is shorter, and the plants grow in a more clustered formation, imparting a denser aspect to the woody structure.

Various factors are associated with small-sized individuals. In most of the restinga forests, trees have branched and tortuous trunks and sparse crowns that are unilaterally deformed by the wind (Silva and Britez 2005); they develop in heavily leached soils that are poor in nutrients (Guedes, Barbosa, and Martins 2006). These plant formations do not reach great heights relative to the arboreal individuals found in other ecosystems (*e.g.*, Atlantic and Amazon biomes) whose characteristics are favorable for growth. Such characteristics include higher levels of OM, greater plant litter formation, higher water availability (Moreira and Malavolta 2004), and more stable soils that support the growth of large trees.

In relation to the distribution of diameter classes, the smallest values recorded in this study were found for the restingas of the northern coast (Ceará and Piauí). Scolforo *et al*. (1998) reported that this fact can characterize a stock community, owing to greater representation of young individuals, and can be a pattern of mature tropical forests. It should be noted that the diameter value of 132 cm recorded in this study is due to the large-sized individual of *Anacardium occidentale* and also to the branches present in *Chomelia obtusa*, *Guettarda angelica*, *Alibertia edulis*, *Myrcia splendens*, *Eugenia stictopetala*; *Eugenia biflora*, *Pseudima frutescens*, *Matayba guianensis*, and *Protium heptaphyllum*. The quantity of branched individuals can indicate different degrees of anthropization (Cantarelli *et al*. 2012) or the species' capacity to resprout (Araujo *et al*. 1997, Sá 2002).

The H′ value found in the present study (2.9 nat.ind–[1]) is close to the value found in other restingas of the Northeast coast (Piauí and Ceará, which varied from 2.1 to 2.8 nat.ind–[1]). The indexes are equivalent, which indicates uniformity among the communities and a balanced vegetation structure with few dominant groups (Corsini *et al*. 2014).

With pH varying between 4.2 and 5.3, the soil of the restinga under study resembles the soils of Brazilian restingas with medium to high acidity (Almeida *et al*. 2011; Santos-Filho, Almeida Jr. and Zickel 2013). Nutrients such as Mg and OM are available in areas with low to medium pH values. In ecosystems with higher levels of OM or Mg, together with exchangeable Al, they can have an influence on the establishment of seedlings (Ruggiero *et al*. 2006), selecting species typical of forest or cerrado *sensu lato* (*e.g.*, *Mouriri guianensis* and *Chiococca alba*) (Flora do Brasil, 2020 in preparation).

Organic matter increases the retention of humidity in the soil and offers better conditions for the growth of woody species (Oliveira-Filho, Vilela, and Carvalho 1997). Higher OM content on the surface contributes to greater base saturation, owing to higher Mg and lower Al content (Ruggiero *et al*. 2006), which can contribute to the presence of *Mouriri guianensis* and *Chiococca alba* in the area.

Chiococca alba in particular presented positive correlation with Mg, V, SB, and OM. This species grows in shaded locations (Pereira and Barbosa 2004), explaining its occurrence in areas of high OM content, which is due to the plant litter from trees surrounding the species. Unlike species that showed positive correlation with the variables (Mg, V, SB, and OM), *Tocoyena sellowiana* presented a negative correlation. The areas that lacked OM were also deficient in Mg, possibly favoring the emergence of less-demanding species such as *T. sellowiana* (authors' personal observations).

With respect to similarity, the two areas of Maranhão (Curupu and Alcântara) have the highest affinity. This fact was expected because of the geographic proximity (Scarano 2002), which enables a continuity of vegetation. However, this similarity must be interpreted with caution, since there are only two phytosociological samplings for the restingas of Maranhão—one from an area situated in the Amazonian region (Alcântara) and another from the Northeast region (Curupu Island)—which may have interfered with the data analysis.

In this analysis, we also observed similarity between the restingas of the Northeast coast (Maranhão and Ceará), which are about 871 km apart. Despite the distance, this resemblance may be related to factors such as wind, dispersal of diaspores, soil nutrients, and humans that reside in the vicinity of the areas (Vicente *et al*. 2014).

The Ceará and Piauí coasts have areas of mainland wilderness colonized by species of the Caatinga (Castro, Moro, and Menezes 2012; Santos-Filho, Almeida Jr., and Zickel 2013). The Ceará coast is more similar to the Maranhão coast (present study), however, sharing characteristics that contribute to the similarity between the compositions of these two areas, such as higher rainfall and a more equatorial temperature and humidity (Castro, Moro, and Menezes 2012).

Although the Caatinga species successfully exploit coastal environments, the flora tends to be a mixture of species, from different phytogeographic domains (Cerrado, Amazon, Atlantic Forest, and Caatinga), that establish in intermediate conditions (Castro, Moro, and Menezes 2012). This mixture in the Maranhão restingas makes the vegetation easily identifiable through lists of species associated with influences of adjacent ecosystems (Cerrado, Amazon) (Rizzini 1997; Scarano 2002; Serra *et al*. 2016).

Another fact that deserves attention is that, depending on the areas in which the restingas are located, anthropogenic actions can contribute to the maintenance or permanence of certain species (Cantarelli *et al*. 2012). For example, the areas of the northern coast—Curupu Island (Maranhão) and Ceará—presented in this study are similar in the sense that the species of the woody stratum generally have socioeconomic potential, whether for food, construction, or medicinal use (Oliveira et al. 2010; Gualberto *et al*. 2014). This contributes to the permanence of *Anacardium occidentale*, *Protium heptaphyllum*, *Coccoloba latifolia*, *Guettarda angelica*, *Myrcia splendens*, and *Tocoyena sellowiana* individuals in the area.

Thus, the condition of the ecotone on the northern coast provides great potential for testing ecological hypotheses, principally with respect to phytogeography; however, there are only three phytosociological studies of the northern coast (Castro, Moro, and Menezes 2012; Santos-Filho, Almeida Jr., and Zickel 2013; Almeida Jr., Correia, and Santos-Filho unpublished data). The restingas are heterogeneous in terms of their plant composition and ecological importance, which suggests that phytosociological surveys are necessary to broaden the knowledge about the structural arrangement and diversity of the plant community of this coastal ecosystem.

Finally, it should be noted that the restinga of the present study showed a diversity and a richness similar to the restingas of the northern coast, with small-sized, branched, and tortuous plants typical of this type of vegetation. Rubiaceae, Myrtaceae, and Fabaceae are common to the coastal vegetation of the Northeast and are found widely in other restingas in Brazil. We observed that the soil variables contributed directly to the structural arrangement of the woody stratum, and further analyses should be carried out. The woody component of the Maranhão coast and the Ceara coast showed similarity, due to shared climatic characteristics. Therefore, studies on the coast of the Northeast can provide important support for the creation of conservation strategies for these coastal areas. Furthermore, as this is the first study of the woody stratum of the coastal Maranhão restingas, the database needs to be expanded to enable further inferences.

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