Restinga vegetation, which is a vegetation type of coastal zones, are present in two geomorphological features in the North coast of Sergipe state - Brazil: litoraneous dunes (LD) and continental dunes (CD). The objective of the present paper is to record the species composition, Raunkiaer’s life forms, dispersal syndromes and soil fertility differences between both habitats. Furthermore, we compared the life forms spectra of the studied features to the spectra of the main Brazilian phytogeographic domains. We conducted a floristic survey from November 2013 to May 2014 in different Restinga areas in two dune habitats in coastal Sergipe state, Brazil, and compared differences in the two localities. Although the two areas were geographically close, there was low floristic similarity between the two habitats; CD showed higher richness than LD. The spectrum of life forms was more similar to that of Caatinga, probably due to environmental similarities. Life forms and dispersal syndromes proportions significantly differed between features, as well as the pH, organic matter, phosphorus, sodium and base saturation index. Zoochory prevailed in both features, whereas phanerophytes prevailed in CD and chamaephytes and phanerophytes in LD. Despite the influence of historical processes, micro-environmental differences between features, which were amplified by their different distances from the sea, were assumingly responsible for the recorded differences.

Key words: dispersal syndromes, floristic similarity, Raunkiaer’s life forms, Restingas.

Resumo
No litoral norte de Sergipe, a vegetação de Restinga ocorre sobre duas feições geomorfológicas: dunas litorâneas (DL) e continentais (DC). O objetivo do presente trabalho é registrar as diferenças na composição de espécies, formas de vida de Raunkiaer, síndromes de dispersão e fertilidade do solo entre ambos os habitats. Adicionalmente, comparamos os espectros de formas de vida das feições com aqueles espectros dos principais domínios fitogeográficos brasileiros. Conduzimos um levantamento florístico durante o período de novembro/2013 a maio/2014 nas duas feições geomorfológicas analisadas. Embora as duas áreas sejam geograficamente próximas, houve baixa similaridade florística entre os dois habitats, tendo DC apresentado maior riqueza de espécies do que DL. O espectro das formas de vida foi mais similar ao da Caatinga, provavelmente em virtude de semelhanças ambientais. As proporções de formas de vida e síndromes de dispersão diferiram significativamente entre as feições, assim como os parâmetros pH, matéria orgânica, fósforo, sódio e índice de saturação por bases. A zoochoria predominou nas duas feições, enquanto que os fanerófitos predominaram em DC e caméfitos e fanerófitos, em DL. Apesar da influência de processos históricos, diferenças micro-ambientais entre as feições dunares estudadas, amplificadas pelas suas diferentes distâncias do mar, devem ser responsáveis pelas diferenças observadas.

Palavras-chave: síndromes de dispersão, similaridade florística, formas de vida de Raunkiaer, Restingas.
Introduction

Coastal dunes are natural features formed by the transportation of fine-grained beach sand by the wind (Villwock et al. 2005; Cordazzo et al. 2006; Guerra & Guerra 2008; Guerra & Cunha 2009). These features play a fundamental role in maintaining and preserving the integrity of the coast, since they work as dynamic barriers against the action of waves and storms (Cordazzo & Seeliger 1995) and as habitat for numerous plant and animal species (Cerqueira 2000).

The strong winds, high salinity, low soil moisture and low organic matter levels in these habitats are the most constraint factors for plant growth and development (Andrade 1967; Santos et al. 2000). Vegetation presents morphological adaptations in response to these factors, such as salt accumulation in the leaves and the development of special stems (Joly 1970; Rizzini 1997). Furthermore, many perennial plants in the coastal dunes are succulent and/or sclerophyllous (Martin et al. 1992).

Different habitats for plants result from a variety of topographic features associated with different environmental gradients in coastal dunes (Cordazzo et al. 2006). Therefore, dune vegetation is not homogeneous, but rather disposed in bands or patches, whose zonation is responsible for differences in vegetation richness and structure (Waechter 1985; Cordazzo & Seeliger 1995; Falkenberg 1999; Cordazzo et al. 2006; Almeida-Jr. et al. 2016).

These micro-environmental variations are also responsible for vegetation diversity (Brito et al. 1993; Leite & Andrade 2004; Cordazzo et al. 2006). Chamaephytes and geophytes, for instance, often prevail in dunes located closest to the sea, while phanerophytes are the predominant vegetation in dunes more distant to the water (Guara et al. 1992; Martin et al. 1992; Henriques & Carlos-Neto 2002). Greater relative importance of anemochory has been observed in the windward of dunes (Maun 2009) and of zoochory to leeward (Marques & Oliveira 2005).

Coastal dunes are one of the richest Restinga formations; estimates show that they house 31 to 410 angiosperms to species, belonging to 28–283 genera and to 11–88 families (Cordazzo & Seeliger 1995; Amaral et al. 2008). Leguminosae is the family with the largest number of species in these environments, which is followed by families Asteraceae and Poaceae (in decreasing order of importance) in coastal dunes in Northern (Santos & Rosário 1988; Araujo et al. 2016), Northeastern (Brito et al. 1993; Santos et al. 2000, 2011; Leite & Andrade 2004; Viana et al. 2006; Almeida-Jr. et al. 2016), Southeastern (Castelo & Braga 2017) and Southern Brazil (Palma & Jarenkow 2008; Ribeiro & Melo-Jr. 2016).

Besides the dunes in the Coastal Plains, that compose the geomorphological feature of litoraneous dunes (dunas litorâneas) in the North coast of Sergipe State, dunes are also found on the Coastal Tablelands (Tabuleiros Costeiros), which are geomorphological units associated with Barreiras Formation sediments, represent the features of the so-called continental dunes (dunas continentais) (Fontes 1985; Guerra & Guerra 2008; Alves 2010). Quaternary sand dunes or sandy bands over tertiary deposits in the Coastal Tablelands are present in other Northeastern Brazil coastal regions such as Ceará (Moro et al. 2015), Rio Grande do Norte (Freire 1990; Almeida-Jr. et al. 2006), Paraíba (Oliveira-Filho & Carvalho 1993) and Bahia states (Rizzini 1997).

In the Restingas of Sergipe, 831 species of angiosperms have been recorded (Oliveira et al. 2014), being Leguminosae the family with the highest specific richness (Oliveira et al. 2014, 2015; Nascimento-Jr. 2012). The phytophysiognomies found in the Restingas of Sergipe are diverse and similar to other areas of this vegetation in the Northeast Brazil (Oliveira & Landim 2014), presenting rare and endangered species (Oliveira & Landim 2016) despite the intense anthropic degradation (Pergentino & Landim 2014). Floristic and/or taxonomic studies were carried out in the Restingas of the Biological Reserve (REBIO) of Santa Isabel (Oliveira et al. 2015), in the Santo Amaro das Brotas County (Nascimento-Jr. 2012), and in the Coastal Tablelands of the Pirambu County (Silva 2014), all of these located in the north coast of the state.

Despite the scientific importance of and conservation risk faced by dune ecosystems, given the intense anthropic pressure on them (Santos & Rosário 1988; Santos et al. 2000; Leite & Andrade 2004; Melo-Jr. et al. 2017), publications on their flora in Sergipe State remain scarce; unlike observed for Restinga areas in general, where studies have increased recently. Accordingly, the aim of the present paper is to compare the flora of litoraneous and continental dunes in order to assess the composition, richness, frequency of Raunkiaer’s life forms and dispersal syndromes of plant species and the soil fertility of two geomorphological dune
features in the Northern coast of Sergipe state. Furthermore, we compared the life forms spectra of the studied features to the spectra of the main Brazilian phytogeographic domains.

**Material and Methods**

**Study site**

We conducted the study in two different areas, one inside and another in the vicinity, of the Biological Reserve (REBIO) of Santa Isabel, Pirambu County, North coast of Sergipe state, Northeastern Brazil (Figs. 1, 2). According to its creation decree, Santa Isabel Biological Reserve, which is located between Pirambu and Pacatuba Counties, covers 2,766 ha and comprises a 45 km-long coastline (Brasil 1988).

Based on the Köppen’s climate classification system, the region is of the As type, (Alvares et al. 2013). It records mean annual temperature of 26 ºC, and the mean annual rainfall is 1,650 mm; and the rainy season goes from March to August (SEPLAG-SE 2011). The Quartzarenic Neosol soil type prevails in the assessed REBIO, which is acidic and presents high permeability and low fertility (EMBRAPA 2006; Fraga 2010). The soil types Podzolic and Halomorphic are also found throughout this REBIO’s, as well as in its surrounding areas (EMBRAPA/SUDENE 1975).

Santa Isabel Biological Reserve is predominantly covered by Restinga vegetation. It presents seven phytosociological types, like graminous fields, as well as coastal scrubs, flooded and non-flooded forests (Oliveira & Landim 2014). Oliveira et al. (2015) recorded 260 species distributed in 184 genera and 78 families in the area.

According to the limits of each geomorphological habitat (Alves 2010; SEMARH/SRH-SE 2013), we initially assessed the dunes selected for sampling in the REBIO by analyzing their aerial photographs (SEPLANTEC-SE 2003). We selected four sampling sites (Figs. 1, 2); three of them were on the Coastal Plain, in the litoraneous dune (LD) feature, which were located approximately 100 m from the coastline. We also chose a more extensive sampling area of the continental dune (CD) feature located in Coastal Tablelands, approximately 2 km from the coastline. This area was chosen because it holds the only continental dune in the REBIO limits according to a proposal to extend the limits of the REBIO (Santos et al. 2017).

We obtained the geographical coordinates of each sampling site in the field using a GPS (collected in field), and delimited the limits of each dune and their total area using a GIS software. The continental dune is approximately 11,500 m², and this area is equivalent to the three litoraneous dunes sampled, which, together, cover an area of approximately 11,600 m².

**Data collection**

We conducted a floristic sampling through opportunistic collection of plant material during hiking from October 2013 to May 2014 (Filgueiras et al. 1994) in the two studied dune fields in order to search for material, mainly at its reproductive stage. Eight field samplings were carried out in each of the two studied features (sixteen in all), being two campaigns per month. Each field sampling lasted six hours, on average. All four dunes were sampled in every field LD campaign. We deposited the collected material in the ASE Herbarium of Federal University of Sergipe and herborized according to usual methods (Mori et al. 1989).

The collected material was identified based on the specialized literature (Souza & Lorenzi 2012; Prata et al. 2013, 2015; Martins-da-Silva et al. 2014) and on comparisons to the material registered at the ASE Herbarium. We used the floristic survey applied to Santa Isabel Biological Reserve to help identifying non-fertile specimens (Oliveira et al. 2015). Classification of species in families followed the APG IV (2016) classification system and the spelling of name of species was checked in BFG (2018).

Soil collection was based on the methodology by Silva (1999) and carried out in top dune areas in the two assessed dune features: 12 samples (nine in LD and three in CD), in total. We collected three samples in CD under different shrub-tree vegetation islands presenting the best development stage among other islands of that feature. The topsoil was removed (including the litter) and a 0.5 kg fraction of soil was collected from the layer 20-cm down the surface at these sites. The same sampling methodology was adopted for each of the three sampled dunes in LD; three soil samples were collected in areas covered with plants for each of the sampled dunes.

We sent the collected material to the Laboratório de Solos e Química Agrícola do Instituto Tecnológico e de Pesquisas do Estado de Sergipe (Soils and Agricultural Chemistry Laboratory of Sergipe State Technological and
Figure 1 – Sampling points of the dune features sampled, being one inside and another in the vicinity, of the Biological Reserve (REBIO) of Santa Isabel, Pirambu County, North coast of Sergipe state, Northeastern Brazil. Boundaries of REBIO Santa Isabel according ICMBio (2017). Source of polygons and aerial photographs: Atlas Digital - SRH 2013/ SEPLANTEC-SE 2003. Preparation: Eduardo V.S. Oliveira, UTM Projection; Datum Sirgas 2000, Zone 24 S.
Research Institute) in order to be subjected to fertility analysis (pH, organic matter, aluminum, calcium, phosphorus, magnesium, potassium, sodium, exchangeable bases, cation exchange capacity and base saturation index) according to standardized methods (Silva 1999).

Data analysis

A species accumulation (Gurevitch et al. 2009) curve was generated to check the sufficiency of the sample from each feature by taking into consideration that each field campaign was a sampling unit.

Morphological characteristics such as color and size, as well as the accessory structures potentially attractive to dispersing agents were initially analyzed to classify the diaspores of dispersal syndromes. Subsequently, the morphological characterization of fruits (Barroso et al. 2004; Lorenzi et al. 2006) and the classification of their dispersal syndrome (Pijl 1982) were carried out. Dispersal syndrome classification of non-fertile specimens was done by consulting the scientific literature. Finally, the collected species were classified based on Raunkiaer’s life-forms (Martins & Batalha 2011) by using the key classification proposed by Mueller-Dombois & Ellenberg (1974). The floristic similarity between the two dune features was calculated based on the Sørensen Index ($S_s$) (Mueller-Dombois & Ellenberg 1974).

The proportion of Raunkiaer’s life forms of the studied features were compared to the life form spectra of the main Brazilian phytogeographic domains (Costa et al. 2016). We used the life-forms in our sites to compare to a database with the life-form spectra of 21 areas in Ombrophilous and semideciduous Atlantic forests, Amazon Rainforest, Cerrado (Central Brazilian Savanna) and Crystalline and Sedimentary Caatinga (Seasonally Dry Forests) (Costa et al. 2016). The relation between spectra of life forms in each area was evaluated through Non-Metric Multidimensional Scaling (NMDS) by using the Euclidian distances. This analysis was performed in the vegan package of the R software (R Development Core Team 2013; Oksanen et al. 2018).

Figure 2 – Sampled dunes in the studied features of Santa Isabel Biological Reserve, Pirambu County, Northern coast of Sergipe state, Northeastern Brazil. CD = continental dune; LD = litoraneous dunes.
The chi-square test ($x^2$) was applied to assess differences in the proportion of dispersal syndromes and Raunkiaer's life forms in the two analyzed features. The null hypothesis ($H_0$) of equality in the proportion between the analyzed factors was tested. The Mann-Whitney U-Test ($\alpha = 0.05$; $U_{\text{critical}} = 2$), suitable for small samples (Siegel 1977), was used to find whether soil fertility presented significant difference between the two dune features. All statistical tests were performed using the software Past 2.17 statistical (Hammer et al. 2013).

**Results**

We list 91 species of angiosperms distributed in 43 families in the four dunes sampled (Tab. 1). The highest number of species and family richness was observed in CD (Tab. 2). Whereas Leguminosae and Myrtaceae (six species each), and Rubiaceae (five) were the richest families in number of species in CD (Fig. 3a), Leguminosae (six species), Poaceae (four) and Asteraceae and Rubiaceae (three species each) were the richest families in species number in LD.

**Table 1** – Angiosperms collected in dunes studied in the interior and surroundings of Biological Reserve of Santa Isabel, north coast of Sergipe state, Northeastern Brazil. CD = continental dune feature; LD = littoraneous dunes feature; FT = fruit type; Ac = achene; Ba = bacca; Ca = capsule; Cr = caryopsis; Cy = cypsela; Dr = drupe; Sc = schizocarp; Fo = follicle; Le = legume; Lo = lomentum; Nu = nucula (nut type); Py = pyxidium; DS = dispersal syndrome; An = anemochory; Au = autochory; Zo = zoochory; LF = Raunkiaer’s life forms; Ch = chamaephyte; Ph = phanerophyte; Hc = hemicryptophyte; He = hemiepiphyte; Th = therophyte.

| Family / Species | CD | LD1 | LD2 | LD3 | FT | DS | LF | Collector number | Voucher (ASE register number) |
|------------------|----|-----|-----|-----|----|----|----|------------------|-------------------------------|
| **Anacardiaceae** |    |     |     |     |    |    |    |                  |                               |
| *Anacardium occidentale* L. | x | x | x | x | Nu | Zo | Ph | E.V.S. Oliveira 255, 259 | 29411, 29582 |
| **Annonaceae** |    |     |     |     |    |    |    |                  |                               |
| *Duguetia moricandiana* Mart. | x |     |     |     | Ba | Zo | Ph | E.V.S. Oliveira 244 | 29401 |
| **Apocynaceae** |    |     |     |     |    |    |    |                  |                               |
| *Calotropis procera* (Aiton) Dryand.* | x |     |     |     | Ca | An | Ph | E.V.S. Oliveira 100 | 29212 |
| *Hancornia speciosa* Gomes | x | x |     |     | Dr | Zo | Ph | E.V.S. Oliveira 249 | 29405 |
| *Himatanthus bracteatus* (A.DC.) Woodson | x |     |     |     | Sc | Au | Ph | E.V.S. Oliveira 413 | 30872 |
| *Mandevilla moricandiana* (A.DC.) Woodson | x |     |     |     | Fo | Au | Ph | E.V.S. Oliveira 407 | 30587 |
| *Mandevilla scabra* (Hoffmanns. ex Roem. & Schult.) K.Schum. | x |     |     |     | Fo | Au | Ph | E.V.S. Oliveira 277 | 25598 |
| **Arecaceae** |    |     |     |     |    |    |    |                  |                               |
| *Anthurium affine* Schott | x | x |     |     | Ba | Zo | He | E.V.S. Oliveira 410, 424 | 30590, 30860 |
| *Philodendron imbe* Schott ex Kunth. | x | x |     |     | Ba | Zo | He | E.V.S. Oliveira 258 | 29581 |
| **Asteraceae** |    |     |     |     |    |    |    |                  |                               |
| *Allagoptera arenaria* (Gomes) Kuntze | x |     |     |     | Dr | Zo | Ph | E.V.S. Oliveira 414 | 30592 |
| *Syagrus coronata* (Mart.) Becc. | x | x | x |     | Dr | Zo | Ph | E.V.S. Oliveira 274 | 25595 |
| **Rubiaceae** |    |     |     |     |    |    |    |                  |                               |
| *Ageratum conyzoides* L. | x |     |     |     | Cy | An | Ch | E.V.S. Oliveira 419 | 30857 |
| *Conocliniopsis pratifolia* (DC.) R.M.King & H.Rob. | x | x | x |     | Cy | An | Th | E.V.S. Oliveira 271 | 25594 |
| Family / Species                      | CD | LD1 | LD2 | LD3 | FT | DS | LF | Collector number | Voucher (ASE register number) |
|-------------------------------------|----|-----|-----|-----|----|----|----|------------------|-----------------------------|
| Conyza bonariensis (L.) Cronquist   | x  |     |     |     | Cy | An | Ch | E.V.S. Oliveira 406 | 30586                       |
| Elephantopus hirtiflorus DC.        | x  | x   |     |     | Cy | An | Th | E.V.S. Oliveira 122, 268 | 29153, 29591                |
| Bignoniaceae                        |    |     |     |     |    |    |    |                  |                             |
| Landia cordata (Vell.) DC.           | x  |     |     |     | Ca | An | Ph | E.V.S. Oliveira 135 | 29165                       |
| Bonnetiaceae                        |    |     |     |     |    |    |    |                  |                             |
| Bonnetia stricta (Nees) Nees & Mart. | x  |     |     |     | Ca | Au | Ph | E.V.S. Oliveira 413 | 30872                       |
| Bromeliaceae                        |    |     |     |     |    |    |    |                  |                             |
| Aechmea aquarela (Salisb.) Griseb.  | x  |     |     |     | Ba | Zo | Hc | E.V.S. Oliveira A98 | 29138                       |
| Hohenbergia catingiae Ule           | x  | x   |     |     | Ba | Zo | Hc | E.V.S. Oliveira 250 | 29406                       |
| Cactaceae                           |    |     |     |     |    |    |    |                  |                             |
| Melocactus violaceus Pfeiff.        | x  |     |     |     | Ba | Zo | Ch | E.V.S. Oliveira 304 | 30075                       |
| Chrysolalaceae                      |    |     |     |     |    |    |    |                  |                             |
| Hirtella racemosa Lam.              | x  | x   |     |     | Dr | Zo | Ph | E.V.S. Oliveira 425 | 30859                       |
| Clusiaceae                          |    |     |     |     |    |    |    |                  |                             |
| Symphonia globulifera L.f.          | x  |     |     |     | Ba | Zo | Ph | E.V.S. Oliveira 161 | 35638                       |
| Commelinaceae                       |    |     |     |     |    |    |    |                  |                             |
| Commelina erecta L.                 | x  |     |     |     | Ca | Au | Ch | E.V.S. Oliveira 420 | 30862                       |
| Convolvulaceae                      |    |     |     |     |    |    |    |                  |                             |
| Evolvulus pterocaulon Moric         | x  |     |     |     | Ca | Au | Ch | M.F. Landim 1711 | 30500                       |
| Cyperaceae                          |    |     |     |     |    |    |    |                  |                             |
| Cyperus crassipes Vahl              | x  |     |     |     | Ac | An | Hc | E.V.S. Oliveira 415 | 30853                       |
| Cyperus ligularis L.                | x  | x   |     |     | Ac | An | Hc | E.V.S. Oliveira 285 | 29603                       |
| Elocarhis geniculata (L.) Roem. & Schult. | x  |     |     |     | Ac | Au | Th | E.V.S. Oliveira 405 | 30585                       |
| Dileniaceae                         |    |     |     |     |    |    |    |                  |                             |
| Curatella americana L.              | x  |     |     |     | Nu | Zo | Ph | E.V.S. Oliveira 303 | 30047                       |
| Davilla flexuosa A.St.-Hil.         | x  |     |     |     | Ca | Zo | Ph | E.V.S. Oliveira 291 | 30063                       |
| Tetracera breyniana Schltdl.        | x  | x   | x   |     | Ba | Zo | Ph | E.V.S. Oliveira 301, 266 | 30051, 29589                |
| Euphorbiaceae                       |    |     |     |     |    |    |    |                  |                             |
| Cnidoscolus urens (L.) Arthur       | x  | x   |     |     | Sc | Au | Ph | E.V.S. Oliveira 284 | 29602                       |
| Croton sellowii Baill               | x  |     |     |     | Ca | Au | Ph | E.V.S. Oliveira 257 | 29393                       |
| Krameriaceae                        |    |     |     |     |    |    |    |                  |                             |
| Krameria tomentosa A.St.-Hil.       | x  |     |     |     | Nu | Zo | Ph | E.V.S. Oliveira 253 | 29409                       |
| Lamiaceae                           |    |     |     |     |    |    |    |                  |                             |
| Hyphenia salzmannii (Benth.) Harley | x  |     |     |     | Ca | Au | Ch | E.V.S. Oliveira 239 | 29397                       |
| Hyptis fruticos Salzm. ex Benth.    | x  |     |     |     | Sc | Au | Ph | E.V.S. Oliveira 292 | 30303                       |
| Marsypianthes chamaedrys (Vahl)     | x  |     |     |     | Sc | Au | Ch | E.V.S. Oliveira 416 | 30854                       |
| Lauraceae                           |    |     |     |     |    |    |    |                  |                             |
| Family / Species               | CD | LD1 | LD2 | LD3 | FT | DS | LF | Collector number         | Voucher (ASE register number) |
|-------------------------------|----|-----|-----|-----|----|----|----|--------------------------|------------------------------|
| Cassytha filiformis L.        | x  | x   | x   | x   | Ba | Zo | Ph | E.V.S. Oliveira 236, 417 | 29395, 30856                 |
| Lecythidaceae                 |    |     |     |     |    |    |    |                          |                              |
| Eschweilera ovata             | x  |     |     |     |    |    |    | E.V.S. Oliveira 291A     | 30874                        |
| (Cambess.) Mart. ex Miers     |    |     |     |     |    |    |    |                          |                              |
| Lecythis pisonis Cambess.     | x  |     |     |     |    |    |    | E.V.S. Oliveira 412      | 30871                        |
| Leguminosae                   |    |     |     |     |    |    |    |                          |                              |
| Aeschynomene viscidula Michx. | x  |     |     |     | Lo | Zo | Ch | E.V.S. Oliveira 269      | 25592                        |
| Andira fraxinifolia Benth.    | x  |     |     |     | Dr | Zo | Ph | E.V.S. Oliveira 160      | 29184                        |
| Centroseris virginianum (L.) Benth. | x |     |     |     | Le | Au | Th | E.V.S. Oliveira 276, 267 | 25597, 29586                 |
| Centroseris brasilianan (L.) Benth. | x |     |     |     | Le | Au | Th | E.V.S. Oliveira 263      | 25590                        |
| Chamaecrista flexuosa (L.) Greene | x |     |     |     | Le | An | Ch | E.V.S. Oliveira 287, 283 | 30038, 29601                 |
| Chamaecrista hispida (Vahl) H.S.Irwin & Barneby | x |     |     |     | Le | Au | Th | E.V.S. Oliveira 247      | 29404                        |
| Chamaecrista ramosa (Vogel) H.S.Irwin & Barneby | x |     |     |     | Le | Au | Th | E.V.S. Oliveira 240, 264 | 29398, 29587                 |
| Stylosanthes viscasa (L.) Sw. | x  |     |     |     | Lo | Zo | Ch | E.V.S. Oliveira 254, 265 | 29410, 29588                 |
| Lythraceae                    |    |     |     |     |    |    |    |                          |                              |
| Cuphea flava Spreng           | x  |     |     |     | Ca | An | Ch | E.V.S. Oliveira 251      | 29407                        |
| Malpighiaceae                 |    |     |     |     |    |    |    |                          |                              |
| Byrsonima gardnerana A. Juss. | x  |     |     |     | Dr | Zo | Ph | E.V.S. Oliveira 293, 418 | 30064, 30855                 |
| Byrsonima sericea DC.         | x  |     |     |     | Dr | Zo | Ph | E.V.S. Oliveira 270      | 29593                        |
| Stigmaphyllon paralia A.Juss. | x  |     |     |     | Sc | Au | Ph | E.V.S. Oliveira 297      | 30301                        |
| Malvaceae                     |    |     |     |     |    |    |    |                          |                              |
| Sida angustissima A.St.-Hil.  | x  |     |     |     | Sc | Au | Ch | E.V.S. Oliveira 294      | 30065                        |
| Sida spinosa L.               | x  |     |     |     | Sc | Au | Ch | E.V.S. Oliveira 262      | 29585                        |
| Melastomataceae               |    |     |     |     |    |    |    |                          |                              |
| Comolia ovalifolia (DC.) Triana| x  |     |     |     | Ca | Au | Ph | E.V.S. Oliveira 121      | 29152                        |
| Mouri ru pusa Gardner         | x  |     |     |     | Ba | Zo | Ph | E.V.S. Oliveira 299A     | 30578                        |
| Myrtaceae                     |    |     |     |     |    |    |    |                          |                              |
| Calycolpus legrandii Mattos   | x  |     |     |     | Ba | Zo | Ph | E.V.S. Oliveira 302      | 30300                        |
| Eugenia punicifolia (Kunth) DC. | x |     |     |     | Ba | Zo | Ph | E.V.S. Oliveira 298      | 30297                        |
| Marlierea excortiata Mart.    | x  |     |     |     | Ba | Zo | Ph | E.V.S. Oliveira 400      | 30869                        |
| Myrcia guianensis (Aubl.) DC. | x  |     |     |     | Ba | Zo | Ph | M.F. Landim 1708         | 30498                        |
| Myrcia ovina Proenca & Landim | x  |     |     |     | Ba | Zo | Ph | E.V.S. Oliveira 401      | 30582                        |
| Psidium guajava L.            | x  |     |     |     | Ba | Zo | Ph | E.V.S. Oliveira 403      | 30583                        |

Nyctaginaceae
| Family / Species                                      | CD | LD1 | LD2 | LD3 | FT | DS | LF | Collector number               | Voucher (ASE register number) |
|------------------------------------------------------|----|-----|-----|-----|----|----|----|--------------------------------|-------------------------------|
| Guapira pernambucensis (Casar.) Lundell              | x  | x   |     |     | Dr | Zo | Ph | E.V.S. Oliveira 408, 280         | 30588, 29599                  |
| Ochnaceae                                            |    |     |     |     |    |    |    |                                 |                               |
| Ouratea cuspidata St. Hil.                          | x  |     |     |     | Dr | Zo | Ph | E.V.S. Oliveira 157              | 29181                         |
| Sauvagesia erecta L.                                | x  |     |     |     | Ca | Au | Ph | E.V.S. Oliveira 409              | 30589                         |
| Passifloraceae                                       |    |     |     |     |    |    |    |                                 |                               |
| Piriqueta duartean var. duartean (Cambess.) Urb.     | x  | x   | x   |     | Ca | Au | Ch | E.V.S. Oliveira 237, 267A        | 29396, 30293                  |
| Peraceae                                             |    |     |     |     |    |    |    |                                 |                               |
| Chaetocarpus echinocarpus (Baill.) Duche            | x  |     |     |     | Ca | Zo | Ph | E.V.S. Oliveira 296              | 30302                         |
| Plantaginaceae                                       |    |     |     |     |    |    |    |                                 |                               |
| Scoparia dulcis L.                                   | x  |     |     |     | Ca | Au | Ch | E.V.S. Oliveira 286              | 30294                         |
| Poaceae                                              |    |     |     |     |    |    |    |                                 |                               |
| Andropogon selloanus (Hack.) Hack.                   |    |     |     |     |    |    |    |                                 |                               |
| Eragrostis ciliaris (L.)                             | x  |     |     |     | Cr | An | Hc | E.V.S. Oliveira 241              | 29399                         |
| Paspalum maritimum Trin.                             | x  |     |     |     | Cr | An | Hc | E.V.S. Oliveira 218, 241         | 29449, 30861                  |
| Pycress fugax (Liebm.) C.D. Adams                    | x  |     |     |     | Cr | An | Hc | E.V.S. Oliveira 274A             | 30357                         |
| Setaria tenax (Rich.) Desv.                          | x  |     |     |     | Cr | An | Hc | E.V.S. Oliveira 404, 281         | 30584, 29600                  |
| Polygalaceae                                         |    |     |     |     |    |    |    |                                 |                               |
| Asemeia violacea (Aubl.) J.F.B.Pastore & J.R.Abbott  | x  | x   | x   |     | Ca | An | Ch | E.V.S. Oliveira 243, 279         | 30352, 30295                  |
| Polygala cyparissias A.St.-Hil. & Moq.              |    |     |     |     |    |    |    |                                 |                               |
| Polygonaceae                                         |    |     |     |     |    |    |    |                                 |                               |
| Coccoloba laevis Casar.                              | x  |     |     |     | Dr | Zo | Ph | E.V.S. Oliveira 426              | 30865                         |
| Portulacaceae                                        |    |     |     |     |    |    |    |                                 |                               |
| Portulaca halimoides L.                              | x  | x   |     |     | Py | Au | Hc | E.V.S. Oliveira 222              | 29413                         |
| Rubiaceae                                            |    |     |     |     |    |    |    |                                 |                               |
| Borreria capitata (Ruiz & Pav.) DC.                  |    |     |     |     |    |    |    |                                 |                               |
| Borreria verticillata (L.) G.Mey.                    | x  | x   | x   |     | Ca | Au | Ch | E.V.S. Oliveira 245, 260         | 29402, 29583                  |
| Cordiera concolor (Cham.) Kuntze                     | x  |     |     |     | Ba | Zo | Ph | E.V.S. Oliveira 278              | 30868                         |
| Diodella apiculata (Wild. ex Roem. & Schult.) Delprete| x  |     |     |     | Sc | Au | Ch | E.V.S. Oliveira 246              | 29403                         |
| Mitracarpus hirtus (L.) DC.                          | x  | x   |     |     | Ca | Au | Ch | E.V.S. Oliveira 261              | 29584                         |
| Tocoyena bullata (Vell.) Mart.                       | x  |     |     |     | Ba | Zo | Ph | E.V.S. Oliveira 427, 423         | 30864, 30858                  |
| Santalaceae                                          |    |     |     |     |    |    |    |                                 |                               |
Zoochory was the most frequent syndrome in both dune features (Fig. 3b), although the number of species presenting different dispersal syndromes was significantly different ($x^2 = 7.6; \text{d.f.} = 2; p < 0.05$) between the studied dune features; anemocory was proportionally more important in LD.

The proportions of life forms also recorded significant difference ($x^2 = 24.4; \text{d.f.} = 4; p < 0.01$) between the studied dune features. Phanerophytes (54% of the total) were the predominant life form in CD, whereas chamaephytes and phanerophytes (approximately 30% of the total number of species, each) were proportionally more abundant in LD (Fig. 3c).

Both studied features (CD and LD) formed different groups of life form spectra when they were compared to the main Brazilian phytogeographic domains, although they showed greater resemblance to Caatinga (Fig. 4). CD was more similar to the sedimentary Caatinga when the proportion of life forms was analyzed, because both have phanerophytes and chamaephytes as their most important life forms and similar proportion of hemicryptophytes and therophytes in comparison to the total data. On the other hand, LD is more similar to the crystalline Caatinga, since both have lower proportion of phanerophytes, and higher proportion of therophytes and hemicryptophytes in comparison to the total.

The two dune features also showed significant differences in some of the analyzed soil parameters (Tab. 3): pH, organic matter, phosphorus, sodium and base saturation index ($U_{measured} = 0$ to 2; $p < 0.05$). Soil analysis results per sample are available in the supplementary material (<https://doi.org/10.6084/m9.figshare.6671792>).

| Feature                | Species number | Family number | Percentage of exclusive species | Distance from the ocean |
|------------------------|----------------|---------------|--------------------------------|-------------------------|
| Litoraneous dune       | 43             | 26            | 19%                            | ~ 100 m                 |
| Continental dune       | 67             | 39            | 54%                            | ~ 2 km                  |

Table 2 – Richness of species and families in the dune features studied in the interior and surroundings of Biological Reserve of Santa Isabel, north coast of Sergipe state, Northeastern Brazil.
Discussion

Altogether, the recorded richness corresponds to 33% of the number of species found by Nascimento-Jr. (2012) in a Restinga area on the Coastal Tablelands of the Northern Coast of Sergipe state. This number represents 35% of the total number of species and 55% of families already found in Santa Isabel Biological Reserve (Oliveira et al. 2015). This outcome evidences how the studied dune features hold a considerable part of the plant diversity in this protected area. We also highlight the low similarity between the two habitats studied. The Sørensen similarity between the two dune types ($S_\alpha = 0.36$), was less than 0.50 (Felfili et al. 1992; Silva-Jr. 2001) (Tab. 2).

The proximity of litoraneous dunes (LD) to the sea when compared to continental dunes (CD) make them more prone to be influenced by the severity of sea stressing factors (salinity, wind, etc.) than CD (e.g., Cordazzo & Seeeliger 1995; Wilson & Sykes 1999). Assumingly, the proximity to the sea seems to be responsible for differences in the richness and floristic composition between dune features, since this pattern was also observed in other studies (e.g., Waechter 1985; Falkenberg 1999; Amaral et al. 2008). Salt spray, desiccation, wind speed and soil instability and salinity are among the main micro-environmental factors influencing plant settlement in coastal dunes (Wilson & Sykes 1999; Maun 2009). These factors are stronger in LD due to the proximity of the sea, and to their association with lower availability of nutrition resources in the substrate (Vince & Snow 1984; Oliveira-Filho 1993; Cordazzo & Seeeliger 1995).

This clear micro-environmental distinction leads to zonation of species and to significant floristic richness and dissimilarity increase from the sea towards more continental areas (Andrade 1967; Waechter 1985; Oliveira-Filho 1993; Cordazzo & Seeeliger 1995; Melo-Jr. & Boeger 2015). Studies carried out in Paraiba (Oliveira-Filho 1993; Santos et al. 2000), Sergipe (Santos et al. 2011) and Santa Catarina states (Melo-Jr. & Boeger 2015) have shown that the structural and floristic differences among dunes on regions close to the sea within the Coastal Plain (for example, foredunes), and those dunes in further inland in this geomorphological unit (for instance, parabolic dunes) or dunes in the Coastal Tablelands can be attributed to the micro-environmental gradient.

Figure 3 – The most species rich families (a), percentage of species by dispersal syndrome (b) and Raunkiaer’s life forms (c) in the dune features studied in the interior and surroundings of Biological Reserve of Santa Isabel, north coast of Sergipe state, Northeastern Brazil.

Figure 4 – Non-Metric Multidimensional Scaling (NMDS, based on the Euclidian distances) of the relation between the spectra of life forms in the main Brazilian phytogeographic domains and the dune features studied in inlands and in surrounding areas of Santa Isabel Biological Reserve, Northern coast of Sergipe state, Northeastern Brazil. Symbols representing the areas: □ = Ombrophilous and semideciduous Atlantic forests and the Amazonic Rainforest; + = Cerrado (Central Brazilian Savanna); ○ = Sedimentary Caatinga (Seasonally Dry Forests); Δ = Crystalline Caatinga; × = CD (continental dune) and LD (litoraneous dunes). Information about the areas used in the database of life forms spectra of the Brazilian phytogeographic domains were collected in Costa et al. (2016).
However, the role played by historical processes such as the geological history of the studied features (Barthlott et al. 2005) can not be ruled out at the time to explain the recorded results. Although both dune features were formed in the Quaternary period, they differ in Epoch formation: CD was formed in the Pleistocene and LD in the Holocene (Salgado-Labouriau 1994; Alves 2010). At least six major events of Quaternary sea level variation were observed in the Northern coast of Sergipe state: three transgression events and three regression ones (Bittencourt et al. 1983; Suguio & Tesller 1984). Assumingly, dunes in CD were formed prior to the Cananéia Transgression, in the subsequent regression to Mais Antiga Transgression (older than 120,000 years B.P.), which was the first of the three greatest transgressive Quaternary episodes in the Northern coast of Sergipe state. On the other hand, dunes in LD are more recent than 5,100 years B.P., because their formation during the subsequent regression to Santos Transgression, which was the last of the six main sea level variation events in the Quaternary in the North coast of Sergipe State (Bittencourt et al. 1983; Suguio & Tesller 1984). Longer existence times such as that of CD allows more complete colonization than more recent areas (Currie 1991; Diniz-Filho & Bini 2011).

The Leguminosae stands out as one of the richest family in surveys conducted in coastal dunes in many Brazilian states, namely: Santa Catarina (Ribeiro & Melo-Jr. 2016; Melo-Jr. et al. 2017), Bahia (Brito et al. 1993; Viana et al. 2006), Alagoas (Almeida-Jr. et al. 2016), Pernambuco (Leite & Andrade 2004), Rio Grande do Norte (Freire 1990), Maranhão (Araujo et al. 2016) and Pará (Santos & Rosário 1988). Furthermore, this family has high diversity in the dunes and Coastal Tablelands areas of the Northern coast of Sergipe state (Silva 2014). Leguminosae species are very efficient in colonizing sterile environments, such as sand, they prefer dry and warm areas (Carvalho & Oliveira-Filho 1993; Stehmann et al. 2009), fact that may explain the high importance of this family to both analyzed features.

Asteraceae and Poaceae were among the four richest families in species number in LD, besides being the most important in dunes located in the Coastal Plains of Rio Grande do Sul (Palma & Jarenkow 2008), Rio de Janeiro (Castelo & Braga 2017), and Sergipe states (Santos et al. 2011); these families are mostly composed of herbaceous species that colonize open areas. The influence of the wind is of fundamental importance to their pollination and dispersal (Carvalho & Oliveira-Filho 1993; Stehmann et al. 2009), fact that may explain the highest distribution of these families in LD, whose environmental characteristics (e.g., higher wind intensity) may be more favorable than CD.

Table 3 – Results of the soil chemical analysis, with average and standard deviation of the samples in the dune features studied in the interior and surroundings of Biological Reserve of Santa Isabel, north coast of Sergipe state, Northeastern Brazil.

| Parameter                    | Unit     | LD               | CD               |
|------------------------------|----------|------------------|------------------|
| pH*                          | --       | 6.40 ± 0.33      | 5.91 ± 0.28      |
| Organic matter*              | g/dm³    | 3.02 ± 1.44      | 7.97 ± 1.47      |
| Aluminum (Al)                | cmolc/dm³| 0.08 ± 0.00      | 0.10 ± 0.01      |
| Calcium (Ca)                 | cmolc/dm³| 0.24 ± 0.20      | 0.37 ± 0.13      |
| Phosphorus (P)*              | mg/dm³   | 4.60 ± 2.00      | 1.90 ± 0.45      |
| Magnesium (Mg)               | cmolc/dm³| 0.77 ± 0.24      | 0.58 ± 0.15      |
| Potassium (K)                | mg/dm³   | 17.60 ± 7.69     | 8.00 ± 0.90      |
| Sodium (Na)*                 | mg/dm³   | 6.20 ± 2.73      | 3.00 ± 0.75      |
| Exchangeable bases           | cmolc/dm³| 1.09 ± 0.37      | 0.88 ± 0.22      |
| Cation exchange capacity     | cmolc/dm³| 1.46 ± 0.46      | 1.42 ± 0.60      |
| Base saturation index*       | %        | 73 ± 11          | 53 ± 8           |

* = statistically significant difference.
Myrtaceae, which is one of the richest families in CD, presents high diversity in coastal forests (e.g., Pereira & Assis 2000; Lourenço & Barbosa 2012). Their floristic importance is greater in studies carried out in coastal scrubs (arbusais or fruticetos in Portuguese) and Restinga forests in Northeast Brazil: Rio Grande do Norte (Almeida-Jr. & Zickel 2012), Pernambuco (Sacramento et al. 2007) and Alagoas states (Medeiros et al. 2010); in Southeast Brazil: Espírito Santo (Assis et al. 2004), Rio de Janeiro (Sá & Araújo 2009) and São Paulo states (Guedes et al. 2006); and in South Brazil: Rio Grande do Sul state (Scherer et al. 2005; Santos et al. 2012). Myrtaceae diversity in coastal forests (Menezes-Silva 1998; Souza & Lorenzi 2012) can justify their importance in CD.

Significant differences in the proportion of dispersal syndromes and in Raunkiaer’s life forms between LD and CD were attributed to plant adaptive responses to micro-environmental variations between these features. Therefore, these results may be attributed to selective pressures acting on these environments, mainly in LD. A similar pattern was observed in two Restinga formations in Santa Catarina state, whose differences in vegetation were attributed to the selective pressure exerted by environmental factors (Melo-Jr. et al. 2017). Evidences indicate pressure of environmental filters on the region near the sea, which leads to convergent morphological adjustments between plants (Melo-Jr. & Boeger 2017).

Zoochory was the most important dispersal syndrome in both analyzed features, it is one of the most frequent syndromes in coastal dunes, mainly in leeward regions (Marques & Oliveira 2005). Restinga vegetation is structurally more developed in these environments, since it forms scrubs (fruticetos) and coastal forests (Oliveira-Filho & Carvalho 1993; Oliveira & Landim 2014). Anemochory, which is one of the most important syndromes in LD, may be the most efficient along the coast, since most species distributed in dune windwards are wind dispersed (Maun 2009).

The CD distribution in areas more protected from the wind can benefit other syndromes to the detriment of anemochory. The same process can also happen in the LD leeward, fact that justifies the high zoochory proportion in this feature. LD has been colonized by species from adjacent open fields where autochoric and anemochoric species are usually prevalent (Marques & Oliveira 2005). Thus, anemochory should be more advantageous for LD plants than zoochory, which is more advantageous in CD.

Phanerophytes had curved stem and treetops following the prevailing direction of the winds in LD. This outcome is known as wind pruning or anamorphic aspect (Waechter 1985; Almeida-Jr. & Zickel 2009; Castelo & Braga 2017). Phanerophyte, which is the first most expressive life form in CD and LD, was also important for Restinga areas in Maranhão (Serra et al. 2016), Rio Grande do Norte (Almeida-Jr. et al. 2006; Almeida-Jr. & Zickel 2009), Pernambuco (Almeida Jr. et al. 2007, 2009), Alagoas (Almeida-Jr. et al. 2016) and Bahia states (Gomes & Guedes 2014).

Hemicryptophytes and chamaephytes can be branched or clotted to assure protection to the gemstones subjected to stressful environmental conditions such as salt spraying (Begon et al. 2006; Martins & Batalha 2011). Such characteristics may suggest more evolutionary advantages to these life forms than to phanerophytes in LD. This outcome corroborates the higher frequency of these life-forms in studies carried out in beach areas (Almeida-Jr. & Zickel 2009; Araujo et al. 2016).

The ordination analysis revealed that CD and LD present life forms spectra different from other areas within the main phytogeographic domains of Brazil. Periods of low rainfall in coastal dunes, low water retention by the substrate, high sand temperature and high evapotranspiration rates, force plants in this environment to face water deficit (Cordazza et al. 2006). This scenario may justify the high proportion of hemicryptophytes and therophytes (Martins & Batalha 2011) in comparison to the total life form spectra in LD, as observed for crystalline Caatinga (Costa et al. 2016). On the other hand the stress factors causing water deficit in CD, which is farther from the sea, are less intense (Cordazza et al. 2006), fact that explains why its life-form spectrum is more similar to the sedentary Caatinga rather than having potentially more water available in the soil than the crystalline Caatinga (Costa et al. 2016).

Soil chemical characteristics are other factors capable of setting the differences in the distribution, richness, floristic composition and abundance of Restinga vegetation (Almeida-Jr. et al. 2011, 2016; Santos-Filho et al. 2013; Magnago et al. 2012). Some of the soil parameters responsible for these differences are pH, organic matter, P, Na and base saturation index (Santos...
et al. 2000; Almeida-Jr. et al. 2009; Magnago et al. 2010, 2012; Santos-Filho et al. 2013). These parameters differed between the studied dune features.

Organic matter and sodium are some of the main soil attributes responsible for structural differences and floristic composition in Restinga areas among the aforementioned ones. They favor or limit the development of these areas and, consequently, set the phytophysionomic type (Almeida-Jr. et al. 2009; Magnago et al. 2010, 2012; Santos-Filho et al. 2013; Melo-Jr. & Boeger 2015). These two attributes are amid the ones mostly limiting species richness in dune areas at the beginning of the successional process (Santos et al. 2000).

The presence of organic matter modifies the environment by facilitating nutrient absorption and by increasing particle aggregation and moisture retention in the substrate (Silva & Sommer 1984). Most plants are not tolerant to sodium; therefore, high concentrations of it can be very harmful to some species (Epstein & Bloom 2006). The highest amount of organic matter and the lowest sodium content in CD soils may have contributed to its greater richness and subsidized the observed floristic composition differences between the two studied dune features.

The lack of information about the optimal ranges of soil chemical attribute values for Restinga plants impairs the development of more robust explanations about the observed differences. However, data presented in the scientific literature substantiate the conclusion that organic matter and Na are somehow related to the observed differences in the vegetation of both dune features.

Supplementary material
All figures, the list of species and the raw data (e.g., soil data) used to support our analysis are available for download at <https://doi.org/10.6084/m9.figshare.6671792>.

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