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MESTRADO EM SISTEMÁTICA, USO E CONSERVAÇÃO DA BIODIVERSIDADE**

**ANTONIA MIRELLE LOPES MARQUES**

**COMPOSIÇÃO FLORÍSTICA E FATORES ASSOCIADOS AO SOLO QUE  
DETERMINAM TRAÇOS FUNCIONAIS DA VEGETAÇÃO LENHOSA EM DUAS  
FITOFISIONOMIAS DA CAATINGA: CARRASCO VERSUS MATA SECA**

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FITOFISIONOMIAS DA CAATINGA: CARRASCO VERSUS MATA SECA

Dissertação apresentada ao Programa de Pós-Graduação em Sistemática, Uso e Conservação da Biodiversidade da Universidade Federal do Ceará, como requisito parcial à obtenção do título de Mestra em Sistemática, Uso e Conservação da Biodiversidade. Área de concentração: Taxonomia, Sistemática e Evolução Biológica.

Orientador: Prof. Dr. Ítalo Antônio Cotta Coutinho.

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A Deus. Ao meu Marido, Francisco Elton de  
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mas tentei para que o melhor fosse feito. Não  
sou o que deveria ser, mas Graças a Deus, não  
sou o que era antes” (Martin Luther King)

## RESUMO

A Caatinga, bioma de aproximadamente 850.000 km<sup>2</sup>, destaca-se por baixa precipitação e altas temperaturas, abrigando notável diversidade nas Florestas Tropicais Sazonalmente Secas (FTSS), como Carrasco e Mata Seca do Sedimentar. Distintas fitofisionomias surgem devido à vastidão e fatores diversos, como solo, resultando em desafios de preservação devido à exploração inadequada, atividades humanas e mudanças climáticas. O estudo na Reserva Particular de Patrimônio Natural Serra das Almas (RNSA) visou compreender Carrasco e Mata Seca por meio da análise da composição florística e traços funcionais. Utilizou o Manual de Campo para Estabelecimento e Remedição de Parcels - DryFlor, protocolos de análise de solo e conteúdo foliar da Rainfor, e o Manual de medição padronizada de traços funcionais de plantas desenvolvido por Perez -Harguindeguy. A análise fitossociológica com Fitopac 2.1, PCA e LDA destacou diferenças nas propriedades físico-químicas do solo, indicando influência na seleção de espécies. O Carrasco apresentou solo arenoso franco com Neossolo Quartzarênico, enquanto a Mata Seca tinha solo franco-argiloarenoso, Neossolo Litólico, com menor profundidade. Na flora, Carrasco abrigou 708 indivíduos, 13 famílias, 24 gêneros e 31 espécies, com Fabaceae, Myrtaceae, Euphorbiaceae e Apocynaceae em destaque. Já a Mata Seca teve 1057 indivíduos, 19 famílias, 32 gêneros e 41 espécies, sendo Fabaceae, Myrtaceae, Apocynaceae, Euphorbiaceae, Combretaceae, Celastraceae e Rubiaceae mais representativas. O Carrasco exibiu um índice de Shannon 2,124 nats/ind<sup>-1</sup> e uma equabilidade de Pielou 0,61. Enquanto na Mata Seca registrou-se um índice de Shannon de 2,988 nats/ind<sup>-1</sup>, acompanhado por uma equabilidade de Pielou igual a 0,79. PCA não revelou diferenças significativas nos traços funcionais, mas LDA identificou altura média, concentrações de nitrogênio (N) e carbono (C) como discriminantes entre Carrasco e Mata Seca. Ambas as áreas enfrentam filtros climáticos semelhantes, com o solo sendo fator ambiental principal. Apesar da Mata Seca ter maior conteúdo de água, ambas recebem mesma precipitação anual. O estudo observou maior concentração de carbono foliar em Mata Seca, alinhando-se a padrões globais associados a precipitação e temperatura. No entanto, as limitações dos traços analisados indicam necessidade de mais pesquisas sobre anatomia do caule e folhas para compreensão mais detalhada e clara das distintas fitofisionomias de Carrasco e Mata Seca.

**Palavras-chave:** flora; fitofisionomia da caatinga; diversidade; Serra das Almas; solo.

## ABSTRACT

The Caatinga, a biome of approximately 850,000 km<sup>2</sup>, is characterized by low rainfall and high temperatures, and is home to a remarkable diversity of Seasonally Dry Tropical Forests (SDTF), such as Carrasco and Sedimentary Dry Forest. Distinct phytophysiognomies arise due to the vastness and diverse factors, such as soil, resulting in preservation challenges due to inadequate exploitation, human activities and climate change. The study at the Patrimônio Natural Serra das Almas (RNSA) aimed to understand Carrasco and Mata Seca by analyzing their floristic composition and functional traits. It used the Field Manual for Plot Establishment and Remediation - DryFlor, Rainfor's soil and leaf content analysis protocols, and the Manual for Standardized Measurement of Plant Functional Traits developed by Perez-Harguindeguy. Phytosociological analysis using Fitopac 2.1, PCA and LDA highlighted differences in the soil's physical and chemical properties, indicating an influence on species selection. Carrasco had sandy loam soil with Quartzarenic Neosol, while Mata Seca had sandy loam soil, Litholic Neosol, with less depth. In terms of flora, Carrasco was home to 708 individuals, 13 families, 24 genera and 31 species, with Fabaceae, Myrtaceae, Euphorbiaceae and Apocynaceae standing out. The Dry Forest had 1057 individuals, 19 families, 32 genera and 41 species, with Fabaceae, Myrtaceae, Apocynaceae, Euphorbiaceae, Combretaceae, Celastraceae and Rubiaceae being the most representative. Carrasco had a Shannon index of 2.124 nats/ind<sup>-1</sup> and a Pielou equability of 0.61. In the Dry Forest, a Shannon index of 2.988 nats/ind<sup>-1</sup> was recorded, accompanied by a Pielou equability of 0.79. PCA revealed no significant differences in functional traits, but LDA identified average height, nitrogen (N) and carbon (C) concentrations as discriminating between Carrasco and Mata Seca. Both areas face similar climatic filters, with soil being the main environmental factor. Although Mata Seca has a higher water content, both receive the same annual rainfall. The study observed a higher concentration of leaf carbon in Mata Seca, in line with global patterns associated with precipitation and temperature. However, the limitations of the traits analyzed indicate the need for further research into stem and leaf anatomy for a more detailed and clear understanding of the distinct phytophysiognomies of Carrasco and Mata Seca.

**Keywords:** diversity; flora; phytophysiognomy of the caatinga; Serra das Almas; soil.

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## 1 INTRODUÇÃO

A Caatinga possui uma das maiores biodiversidades de espécies vegetais em áreas de Floresta Tropical Sazonalmente Seca (FTSS), cobrindo uma área de aproximadamente 850.000 km<sup>2</sup> (De Queiroz et al., 2017; Moro et al., 2014; Prado, 2003). Este bioma apresenta baixas precipitações e altas temperatura, consequentemente registra baixa disponibilidade de água no solo (Da Silva et al., 2011; Moro et al., 2016). As chuvas ocorrem em um estreito intervalo de tempo, geralmente concentrada em três meses do ano (Viana Santos et al., 2023).

Estas variações sazonais influenciam nas propriedades do solo tornando cada solo único, deste modo existem diferentes tipos de solos na Caatinga (Cambissolos, Luvissolos, Latossolos, Argissolos e Neossolos) (Araújo Filho et al., 2022, 2018). E em uma escala local, um dos melhores preditores para distribuição das espécies são fatores pedológicos e topográficos (Arruda et al., 2015). O solo possui um papel primordial na formação e diferenciação das vegetações, proporcionando uma modificação na diversidade de plantas de cada local (Oliveira et al., 2021; Rodrigues et al., 2018; Rodrigues; Silva; Schaefer, 2019).

As diferentes fitofisionomias se formaram devido a linhagens antigas que foram se diversificando em locais distintos devido a vários fatores abióticos formando núcleos ricos em endemismos elevado o desafio de conservação dessas áreas (De Queiroz et al., 2017; Fernandes; Queiroz, 2018; Moro et al., 2014). Dentre essas fitofisionomias, destacam-se: 1) a caatinga *sensu stricto*, presente na maior parte do bioma e ocorrendo em bacias cristalinas, 2) o carrasco, presente em bacias sedimentares (Araújo; Martins, 1999; De Queiroz et al., 2017) 3) uma vegetação de mata seca, podendo ocorrer tanto na bacia do cristalino como na bacia do sedimentar (de Queiroz et al., 2017; Fernandes; Cardoso; de Queiroz, 2020; Moro et al., 2014). Contudo, aqui o enfoque será dado nas fitofisionomias que ocorrem em áreas sedimentares, carrasco e mata seca.

O Carrasco também chamado de Caatinga do Sedimentar ou Caatinga de Areia (Moro et al., 2014, 2015), encontra-se geralmente em solos arenosos e com baixa fertilidade natural, com predominância de vegetação lenhosa, estruturalmente finas e de pequeno porte (Araújo et al., 1998; Moro et al., 2015). As plantas apresentam múltiplos caules, devido à baixa estatura formam um emaranhado de galhos (Vodonis, 2019).

A Mata Seca do Sedimentar conhecida também como Floresta Estacional Decidual (Veloso et al., 1991), o solo destas áreas possui maior disponibilidade hídrica que os solos de carrasco, contém uma vegetação florestal com espécies de porte mais elevado, consequentemente, são mais volumosas em relação ao seu diâmetro relacionado a vegetação

citada anteriormente (Lima et al., 2007, 2011). Caracterizado como uma riqueza mais elevada de árvores, arbustos e com baixa riqueza de espécies herbáceas (Lima et al., 2007, 2009).

Estas vegetações localizadas em áreas sedimentares apresentam uma riqueza elevada de espécies (Moro et al., 2014), com um número significativo de espécies endêmicas (Fernandes; Queiroz, 2018). Contudo, a utilização inapropriada de parte da vegetação tem gerado enormes problemas quanto a preservação e conservação das espécies (Castelletti et al., 2004; Tabarelli et al., 2018), ocasionados por diversos fatores, desde as intensas modificações climáticas que vem acontecendo ao longo dos últimos anos, até ações antrópicas que transformam as fitofisionomias deixando-as fragmentadas e/ou desertificadas (Alves; De Araújo; Do Nascimento, 2009; Moro et al., 2015).

Além disso, o número de Unidades de Conservação dentro do bioma caatinga são baixíssimos com apenas 7,7% de áreas protegidas, contribuindo assim para a perda de sua biodiversidade e a falta de desenvolvimento de estratégias para conservação (De Oliveira; Da Silva; De Moura, 2019), em que muitas vezes pode levar a extinção das espécies únicas que nem chegaram a ser identificadas e que não ocorrem em outra região do mundo (Fernandes; Queiroz, 2018).

A maioria dos estudos são voltados para composição florística, e ainda assim metade da vegetação de áreas de caatinga não é conhecida (Moro et al., 2014). Conhecer a flora possibilita verificar a diversidades locais, conhecer espécies inéditas e entender a similaridade entre os locais próximos (Da Silva; Carvalho; De Faria, 2017; Santana et al., 2017), além disso, esses dados possibilitam conhecer sobre a estrutura da comunidade e sobre índices taxonômicos (diversidade e equabilidade) (Maestre et al., 2012).

Outro fator importante diante da perda de diversidade é compreender como estas plantas respondem a diferentes processos que ocorrem em cada ecossistema (Roscher et al., 2012). As respostas das espécies são compreendidas através dos traços funcionais que juntas respondem a estresses do meio ambiente, assim como estas espécies contribuem para processos e serviços ecossistêmicos, desde fitofisionomias locais a biomassas (Pérez-Harguindeguy et al., 2016). Uma vez que, as plantas respondem de forma diferente conforme as variações do espaço e do tempo (Díaz; Cabido; Casanoves, 2009).

O termo “traço funcional” foi descrito por diferentes pesquisadores, inicialmente os traços funcionais foram abordados como traços relacionados ao ambiente (Calow, 1987), assim o termo “funcional” correspondia a uma visão mais adaptativa. Posteriormente, os traços funcionais passaram a se referir a uma variedade de traços dos organismos que afetam seu desempenho, performance ou aptidão física (Geber; Griffen, 2003; McGill et al., 2006; Reich et

al., 2003), além disso podem ser definidos através da sua capacidade de crescimento, desenvolvimento e sobrevivência no ambiente (Violle et al., 2007). De acordo com Nock; Vogt; Beisner, (2016), e de modo geral um traço funcional é uma propriedade mensurável dos indivíduos vivos, geralmente medida a nível individual e que seja passível de comparação entre espécies.

Há uma crescente no uso de traços funcionais visando representar características mensuráveis das espécies para caracterizar a função da comunidade e da biodiversidade, tais traços podem ser de vários tipos: contínuos, categóricos, ordinais, binários (Nock; Vogt; Beisner, 2016). Cinco variáveis essenciais foram propostas para monitorar e as variações dentro das populações: fenologia, morfologia, reprodução, fisiologia e movimento (Jetz et al., 2019; Kissling et al., 2018). Isso possibilita a padronização das estimativas de dados sobre os traços funcionais.

A sazonalidade climática influencia ao estresse da planta e induz a diferentes respostas ecofisiológicas que permitirá a sobrevivência das espécies estes ambientes (Araújo; Castro; Albuquerque, 2007). A partir desse conhecimento adquirido por meio dos traços funcionais, questões ecológicas e evolutivas podem ser entendidas.

Em relação aos traços funcionais foliares estes podem responder as diferentes concentrações de nutrientes que as espécies podem apresentar (Wang et al., 2019; Xing et al., 2021a), além disso, estão relacionadas ao clima, absorção e perca de água na planta, o que leva a presença/ausência de espécies com área foliar distintas entre as comunidades (Li et al., 2021; Stanisci et al., 2020; Xing et al., 2021a, 2021b). Quanto à altura das árvores, está fortemente relacionada a sua capacidade de crescimento dos indivíduos (Liu et al., 2016), os traços funcionais de madeira podem responder a questões hídricas das espécies, como a prevenção ou reparação de embolias nos vasos, a estruturação e a sua relação com a arquitetura hidráulica, dentre outras (Carvalho et al., 2023).

Diante disso, é de suma importância estudos em diferentes fitofisionomias de caatinga, com a finalidade de conhecer sua biodiversidade, além de colaborar para demais estudos que venham a traçar metas e estratégias para sua conservação. O conhecimento sobre essa diversidade pode auxiliar com informações importantes sobre a biodiversidade e funções de ecossistema de comunidades da Caatinga.

**2 FLORISTICS AND SOIL-ASSOCIATED DRIVERS OF WOODY  
VEGETATION TRAITS IN TWO CAATINGA PHYTOPHYSIOGNOMIES:  
CARRASCO VERSUS MATA SECA**

A ser submetido para a revista Biotropica (Qualis A2 em Biodiversidade, Fator de impacto: 2.1)

**FLORISTICS AND SOIL-ASSOCIATED DRIVERS OF WOODY VEGETATION  
TRAITS IN TWO CAATINGA PHYTOPHYSIOGNOMIES: CARRASCO VERSUS  
MATA SECA**

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## RESUMO

O bioma Caatinga ocorre em uma Floresta Tropical Sazonalmente Seca com uma flora rica, mas muitas vezes negligenciado e pouco conhecido. Suas diferentes fitofisionomias, influenciadas por fatores abióticos, resultam em estruturas e composições florísticas únicas. Os traços funcionais permitem compreender melhor como estas espécies se adaptam aos diferentes fatores ambientais de cada fitofisionomia. Portanto, o presente trabalho visa compreender as diferenças florísticas entre as duas fitofisionomias, Carrasco e Mata Seca, e relacionar com os traços funcionais das espécies. O estudo foi desenvolvido na Reserva Particular de Patrimônio Natural Serra das Almas (RNSA), em duas fitofisionomias, Carrasco e Mata Seca. O Carrasco, apresentou um Neossolo Quartzarênico, abrigando 708 indivíduos de 31 espécies, enquanto a Mata Seca, com solo Neossolo Litólico, tinha 1057 indivíduos de 41 espécies. As propriedades físico-químicas do solo diferiram, refletindo nas métricas de diversidade vegetal. O índice de Shannon no Carrasco foi  $2,124 \text{ nats/ind}^{-1}$ , com equabilidade de Pielou de 0,61, enquanto na Mata Seca foi  $2,988 \text{ nats/ind}^{-1}$ , com equabilidade de 0,79. Análises fitossociológicas, Análise de Componentes Principais (PCA) e Análise de Discriminante Linear (LDA) revelaram similaridade nos traços funcionais entre as áreas. No entanto, o LDA destacou diferenças significativas, como altura média, teor de N e teor de C, indicando que esses traços distinguem efetivamente as áreas. Possivelmente, outros traços, como a anatomia do caule e da folha, também desempenham papel na adaptação das espécies a esses ambientes distintos.

**Palavras-chave:** análises fitossociológicas, diversidade vegetal, flora, traços funcionais

## ABSTRACT

The Caatinga biome occurs in a Seasonally Dry Tropical Forest with rich flora, but is often neglected and little known. Their different phytophysiognomies, influenced by abiotic factors, result in unique floristic structures and compositions. Functional characteristics allow us to better understand how these species adapt to the different environmental factors of each phytophysiognomy. Therefore, the present work aims to understand the floristic differences between the two phytophysiognomies, Carrasco and Mata Seca, and relate them to the functional characteristics of the species. The study was carried out in the Serra das Almas Private Natural Heritage Reserve (RNSA), in two phytophysiognomies, Carrasco and Mata Seca. Carrasco, presented a Quartzarenic Neossolo, housing 708 individuals of 31 species, while Mata Seca, with Litholic Neossolo soil, had 1057 individuals of 41 species. The physicochemical properties only differed, reflected in the analyzes of plant diversity. Shannon's index in Carrasco was 2.124 nats/ind-1, with Pielou's equability of 0.61, while in Mata Seca it was 2.988 nats/ind-1, with equability of 0.79. Phytosociological analyses, Principal Component Analysis (PCA) and Linear Discriminant Analysis (LDA) revealed similarity in functional characteristics between areas. However, the LDA highlighted significant differences such as average height, N content and C content, showing that these traits effectively distinguish areas. Possibly, other traits, such as stem and leaf anatomy, also play a role in the adaptation of species to these different environments.

**Keywords:** flora, functional traits, phytosociological analyses, vegetal diversity

## 2.1 Introduction

The Seasonally Dry Tropical Forest (SDTF) is a unit that was not long ago identified as a biome (Prado, 2003). Such a biome houses a highly endemic flora, at both generic and species level (Särkinen et al., 2011). The species living at the SDTFs are usually subjected to less than 1,100 mm /year rain fall and face a 5-6 month dry season with rain fall below 100 mm (Särkinen et al., 2011). As a result, evergreen species are indeed present, but most species are prolonged-deciduous, living amongst a shrubby or subshrubby (but often not grassy) vegetation (Machado et al., 1997; Lima & Rodal 2010; Paloschi et al., 2021).

Although many authors recognize the Brazilian Caatinga as the largest and most species rich nucleus of the SDTF, Caatingas have also been largely ignored (Pennington et al., 2000; Fiaschi & Pirani, 2009; Fernandes et al., 2020; 2022; De Souza et al., 2022). The flora of this relatively poorly known biome has a strongly fragmented distribution across South America. The richest Caatinga families in terms of endemic species or diversity are Fabaceae, Euphorbiaceae, Cactaceae, Bromeliaceae, Malvaceae, and Apocynaceae (Fernandes et al., 2022; Fernandes; Queiroz, 2018; Moro et al., 2014; Queiroz, 2009; Sarker et al., 2018).

This flora varies throughout the Caatinga domain and such floristic variations are determined and influenced by the climate, relief and geological basement (Rodal et al., 2008, Silva et al., 2017) The geological basement (crystalline or sedimentary) plays a crucial role in determining plant diversity and influences the distribution of floristic composition (Queiroz 2006, Moro et al. 2016, de Queiroz et al. 2017). The different types of soils, due to their different physicochemical compositions, not only contribute to the diversification of the flora, but also play a significant role in its structuring (Rodrigues et al., 2018; 2019; Oliveira et al., 2021) which gives rise to the different Caatinga phytobiognomies. (Moro et al. 2016; Queiroz et al., 2017).

Among these phytobiognomies, Carrasco and Mata Seca are present in the sedimentary basemen (Fernandes; Queiroz, 2018; Moro et al., 2015). Although the soils are generally poor in nutrients, such phytobiognomies are found above different types of soils (Lemos & Rodal, 2002; Lima et al., 2009, 2011; Moro et al., 2016; Pagano et al., 2013). The relationship between soil and vegetation at local scales plays an essential role in several ecological processes in which conditions and resources influence the attributes of plant communities (Pausas & Austin, 2001; Putten et al., 2016; de Souza et al., 2020). Another important attribute for in-depth knowledge of different such as the Carrasco and Mata Seca is

understanding their respective functioning. This functioning may be understood through functional traits that respond to several environmental factors

The floristic composition and structure of the community allow us to understand in detail the richness and diversity of species and how their distribution occurs, as well as the abundance, dominance and frequency of species in each phytobiognomy (Magurran, 2003; Rodal et al., 2013; Lima & Coelho, 2018; de Souza et al., 2021). Another important attribute for in-depth knowledge of different such as the Carrasco and Mata Seca is understanding their respective functioning. This functioning may be understood through functional traits that respond to several environmental factors (Pérez-Harguindeguy et al., 2016) directly influencing the growth, reproduction and survival of species (Violle et al., 2007).

Understanding the composition and variability of functional traits at the community level represent a major challenge in ecology (Grime 2006; Myers-Smith et al., 2019). The functional traits and measurable properties of living organisms, which encompass both structure and function, make it possible to understand and quantify changes in the community (Reich, 2014). There is an unlimited diversity of functional traits that are relevant to different plant research contexts, however some traits are universally significant because they are tied to the heart of the plant life cycle (Grime et al., 1997; Westoby, 1998; Garnier & Navas, 2012). Examples of these traits are plant size (height) and leaf tissue structure (specific leaf area or leaf dry matter content). These fundamental parameters provide a robust basis for understanding and comparing diverse plant species (Pérez-Harguindeguy et al., 2016). Furthermore, Cornelissen et al. (2003) encourages the inclusion of other traits of plant species, providing an expansion to improve knowledge of different species, as the greater the number of traits studied, the greater the power to test hypotheses. The functional traits of species are crucial in improving their adaptation to the environmental limits of the habitat, whether morphologically, biochemically or phenologically, influencing their contribution to the functioning of the ecosystem (Cadotte et al., 2011).

In this way, the present work aims to understand the floristic differences between two Caatinga phytobiognomies, i.e. Carrasco and Mata Seca, as well as their functional traits in a way to understand whether there are or not different functional traits at play for the species that are living at such phytobiognomies. Thus, it is expected that the pedological characteristics influence the floristic composition of the two phytobiognomies, so that each phytobiognomy presents a distinctive set of functional traits, which will aid the species to deal with the stresses to which they are exposed.

## 2.2 Methods

### 2.2.1 Study areas

The Reserva Natural Serra das Almas (RNSA) is located at the center-south of the Ibiapaba plateau, on the border of the States of Ceará and Piauí, between the municipalities of Crateús (CE) and Buriti dos Montes (PI) at 5°15' and 5°00'S and 40°15'e 41°00'E. The area has a hot semi-arid climate (BSh) (Alvares et al., 2013) at its lowest altitude (~300m) and a mild hot semi-arid climate (As) at its highest altitude (~750 m) (Alvares et al., 2013), throughout the reserve the average annual temperature varies between 26-29°C and a total average annual precipitation of ~800 mm (Associação Caatinga 2023), varying according to the literature between 630m (Menezes, 2010) and ~900m (Menezes et al., 2020). The RNSA houses three Caatinga phytophysiognomies: 1) Caatinga of the crystalline, 2) seasonal deciduous forest (Veloso et al., 1991) known as Mata Seca of the sedimentary and 3) Caatinga of the sedimentary, known as Caatinga Arenosa (Moro et al., 2015) or Carrasco (Araújo & Martins, 1999).

In order to standardize the abiotic factors (rainfall, altitude and climate), two of the three phytophysiognomies occurring at the RNSA, i.e., Carrasco and Mata Seca, on the plateau area and at a similar height, were chosen (Figure 1). Carrasco (5°08'29" S and 40°54'54" W, 640 m altitude) is composed of a dense shrubby vegetation, lacking thorns (Araújo et al., 2011), usually on quartzitic sandy soils quartzosas (Embrapa, 1972). The Mata Seca of the sedimentary (5°08'48" S and 40°55'42" W, 620 m altitude) is composed of an woody (arboreal) vegetation taller than the Carrasco species (Araújo et al., 2005; Lima et al., 2009).

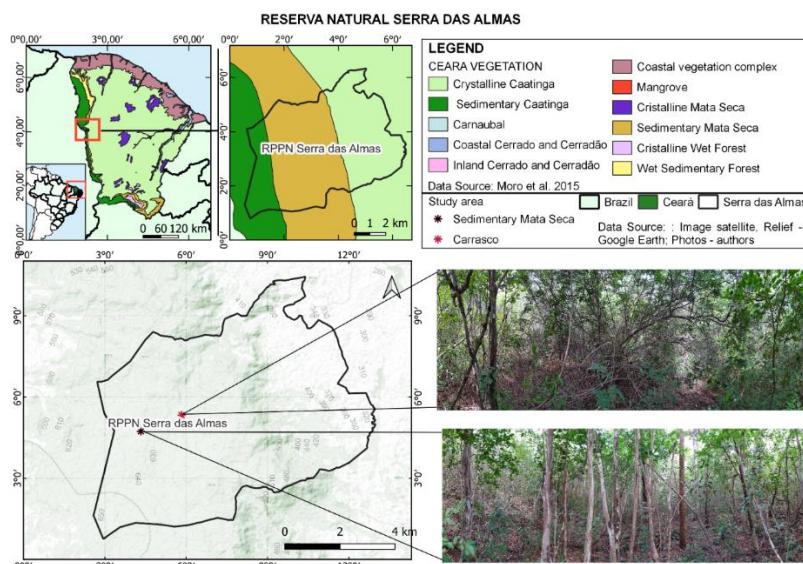


Figure 1 – Location of the study areas at RNSA, Crateús/CE, Brazil.

### **2.2.2 Sample design and soil characterization**

For data collection, we made use of the Field Manual for Plot Establishment and Remeasurement- DryFlor (DryFlor et al., 2022). Thus, the plots in the present study consisted of permanent plots established in 2017. However, the vegetation data collected for the present study were collected in 2022. At each phytophysiognomy (i.e., Carrasco and Mata Seca), a 0.5 ha plot divided into fifty 10x10 m subplots was used. Following the DryFlor protocol, the criteria for inclusion in the sampling were stems with  $\geq 5$  cm diameter. Two diameter measurements were taken, one at 30 cm (D30) and the other at 130 cm from the ground (DBH – diameter at breast height), as well as the total height of the specimen. Samples for all woody species, except lianas, are deposited at the Herbarium of the State University of Feira de Santana (HUEFS).

For soil characterization, soil collection were carried out based on the standard protocol (<https://rainfor.org/wp-content/uploads/sites/129/2022/07/soilandfoliarsampling.pdf>) with specific adjustments to Caatinga areas. Four to seven soil cores were used. Depth for collection was established at 2 m, collecting samples every 0.05 m. It should be kept in mind that in some of the collection spots the soils were shallow, making it possible to collect at a maximum of 1m deep, due to the presence of rock. Soil extractions were carried out with an auger, trench and composite sample Brunello et al. (2024). The samples were sieved in order to remove any non-soil materials, such as stones, roots and animal remains. The analyzes for physical-chemical characterization of the soil were carried out following the description by Brunello et al. (2024).

### **2.2.3 Functional Traits (FTs) and Leaf Nutrients**

A total of 12 functional traits (FT) were selected. Average plant height (H), biomass, leaf area (LA,  $\text{cm}^2$ ), specific leaf area (SLA,  $\text{m}^2/\text{kg}$ ), leaf dry-matter content (LDMC,  $\text{mg/g}^{-1}$ ), Leaf nitrogen concentration (LNC, g), leaf phosphorus concentration (LPC, g), leaf carbon content (LCC, g), wood density (WD,  $\text{g/cm}^3$ ). All collections followed the protocols described by Pérez-Harguindeguy et al. (2016). Besides the FTs described above, type of fruit (dry or fleshy), leaf blade division (simple or compound) and presence/absence of cork on the stem. The species sampled represent ~80% of all individuals in each area, from this

representation only the species that were found in one of the areas were selected (Figure 2), that is, only species specific from the Mata Seca or Carrasco.

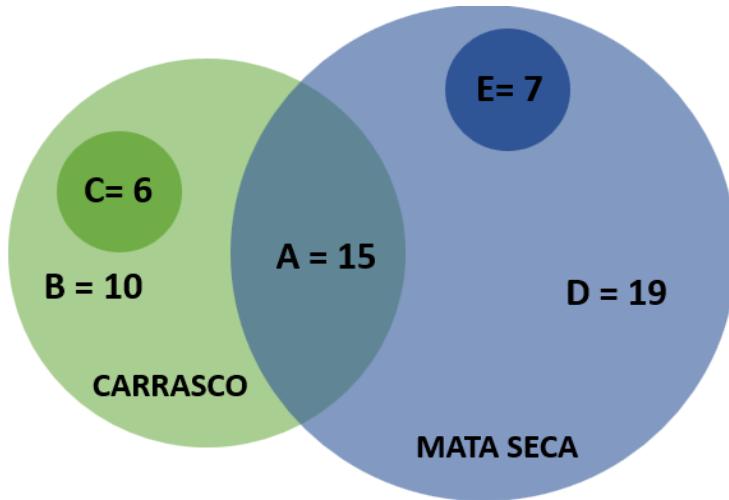


Figure 2 – Total number of species studied at the two phytophysiognomies of the Caatinga: Carrasco and Mata Seca. (A) Number of species co-occurring in the two phytophysiognomies and which made up part of the 80% of total abundance in the areas and whose functional traits were analyzed. (B) Number of species exclusive to the Carrasco that also made up 80% of the total abundance of the area and had their functional traits analyzed. (C) Number of species exclusive to Carrasco, but which did not make up 80% of the area's total abundance and were therefore excluded from functional trait analyses. (D) Number of species exclusive to the Mata Seca that also made up 80% of the area's total abundance and had their functional traits analyzed. (E) Number of species exclusive to the Mata Seca, but which did not make up 80% of the area's total abundance, and were therefore excluded from functional trait analyzes.

Leaf data for each of the predominant species were collected from fully expanded leaves of three individuals. Due to the high temperature at the time of the collection, the leaves were stored in plastic bags with damp paper, and sealed to avoid loss of water. To calculate fresh weight, the leaves were then weighed on a digital scale on the same day. Subsequently, to calculate the LA, the leaves were digitized with the aid of a scanner and the area was calculated using the ImageJ program (Schneider et al., 2012). After being scanned, leaves were then placed in paper bags, oven-dried until reaching constant dry weight and used for nutrient analysis.

For wood collection, we used the same individuals used for the leaf traits. The wood samples were taken from the main trunk at 10cm below the DBH with the aid of an increment borer. After collection, wood samples were stored in tubes filled with distilled water. Samples were left for 48h in the tubes and weighed. Soon after, the wood density was measured by making use of the hydrostatic method, that is, through the variation in the weight of the liquid, according to Vital (1984). After determining the wood density, samples were placed in paper

bags oven-dried and weighed.

Nutrient value was obtained for calculating the concentration of nitrogen (N), phosphorus (P) and carbon (C), the dry leaf material was previously ground in a Willey. For P extraction, dry digestion was carried out according to Embrapa (2009) and the determination was made by colorimetry. For organic N and C, extractions were carried out by digestion with sulfuric acid, according to Tedesco et al. (1995), and potassium dichromate and sulfuric acid in the digester block, respectively. For determining N, steam distillation (Kjeldahl method) was used, (Tedesco et al., 1995; Embrapa 2009). The quantification of organic C content was carried out by titration with ammonium ferrous sulfate (Embrapa, 2009). Biomass was analyzed according to Sampaio e Silva (2005), by using the equation as follows:  $0.1648 * (ABH * H * p)^{0.9023}$ , where ABH, H and p are respectively the stem diameter at the breast height, specimen height, and wood density. This is the best equation we have for Caatinga dry areas (Lima et al., 2017; Castanho et al., 2020).

#### **2.2.4 Statistical analysis**

A matrix with all data was generated in Excel software (2010). The phytosociological analysis was carried out on the Fitopac 2.1 (Shepherd, 2010), which generated the following parameters Absolute Density (AD), Absolute frequency (AF), Absolute dominance (DoA), Relative Density (RD), Relative frequency (RF), Relative dominance (DoR), and importance value (IV). Diversity was measured using the taxonomic diversity of each plot, which is characterized by species richness (Magurran, 2003) by using Shannon-Wiener and Pielou evenness indices.

A Principal Component Analysis (PCA) was carried out to verify the difference between the areas through functional traits. After this analysis, an analysis of similarities (ANOSIM) (Clarke & Ainsworth, 1993) was carried out. This is a non-parametric technique that allowed us to determine whether there are significant differences between the two fragments, which outputs the R value and p-value. Euclidean distance was used and 999 free-form permutations were made.

Upon verifying that there was no distinction of the two areas (i.e., Carrasco and Mata Seca) through functional traits through PCA, a Linear Discriminant Analysis (LDA) was carried out (Tharwat et al., 2017). The LDA examined the data matrix within groups of standardized feature and the Permutation Multivariate Analysis of Variance (PERMANOVA) was performed, testing whether there was a significant difference between groups from different areas.

## 2.3 Results

### 2.3.1 Soil Property

The physicochemical properties of the soil for the two study fragments differed (Table 1), the soil texture at the Carrasco was predominantly sandy loam (Figure 3), with greater amounts of sand (87.68%) and lower amounts of clay (7.26%) and silt (5.06%), with no differences with increasing depth. On the other hand, the Mata Seca soil had a sandy-clay texture (Figure 3), with smaller amounts of sand (58.69%) which decreased with depth (55.02%), significant proportions of clay (22.42%), slightly increasing (26.27%) at a greater depth, and with silt (18.88%) keeping the same amount even with increasing depth. Soil density in Carrasco was 1.288 g/cm<sup>-3</sup> and 1.390 g/cm<sup>-3</sup> in Mata Seca. In both cases, without major variations with increasing the depth.

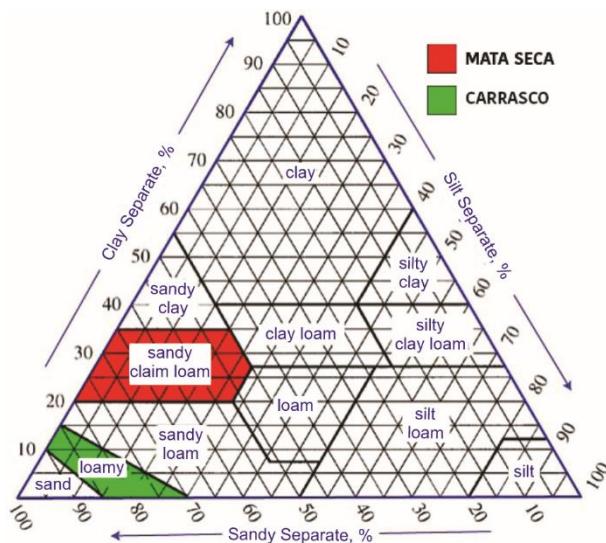


Figure 3 – Grouping of soil texture classes in the studied areas, Carrasco e Mata Seca.

The Carrasco soil (Table 1) showed 0.095% of nitrogen (N) and 1.213% of carbon (C). These concentrations decreased with depth to 0.033% of N and 0.441% of C. The C:N ratio was 12.41, showing a slight increase (13.52) at greater depths, with low amounts of organic matter in the soil. The pH showed acid values, as in water (4.51) and pH in KCl (3.78) of the soil presented values below 7. The amount of exchangeable cations was low such as Calcium (Ca) ( $0.761 \text{ mmolc/kg}^{-1}$ ), Magnesium (Mg) ( $0.734 \text{ mmolc/kg}^{-1}$ ), Potassium (K) ( $0.518 \text{ mmolc/kg}^{-1}$ ), and Sodium (Na) ( $0.001 \text{ mmolc/kg}^{-1}$ ).

mmolc/kg<sup>-1</sup>) and Aluminum (Al) (8.885 mmolc/kg<sup>-1</sup>). 1 1) and Sodium (Na) (0.518 mmolc/kg<sup>-1</sup>). Low total exchangeable cations were found for phosphorus (P) (128.94 mg/kg<sup>-1</sup>), Mg (7.66 mmolc/kg<sup>-1</sup>), K (5.38 mmolc/kg<sup>-1</sup>), Na (7.30 mmolc/kg<sup>-1</sup>), Al (1299.33 mmolc/kg<sup>-1</sup>), Iron (Fe) (11180 mg/kg<sup>-1</sup>), Manganese (Mn) (133 mg/kg<sup>-1</sup>) and Zinc (Zn) (15 mg/kg<sup>-1</sup>), high values were found only for Ca (3.3 mmolc/kg<sup>-1</sup>). The sum of bases (SB) was 2.532 at 30 cm of soil and 1.430 at 2 m depth, and effective cation exchange capacity (ECEC) was 11.417 up to 30 cm and 7.091 up to 2 m depth, and the total reserve in bases (TRB) was 23.655 mmolc/kg<sup>-1</sup>.

The Mata Seca soil (Table 1) showed 0.107% and 1.21% for C and N, respectively. With increasing depth N decreased to 0.072% while C for 0.927%. The ratio C:N was 12.13, with low amounts of organic matter in the soil. The pH in water was 4.21 while 3.90 in KCl. As for the Carrasco, Mata Seca also presented acid soils. The higher values of exchangeable cations were for Mg (1.109 mmolc/kg<sup>-1</sup>), K (0.697 mmolc/kg<sup>-1</sup>) and Al (12.949 mmolc/kg<sup>-1</sup>) while for Ca (0.373 mmolc/kg<sup>-1</sup>) and Na (0.295 mmolc/kg<sup>-1</sup>) showed lower values than Carrasco. Total values for P (180.96 mg/kg<sup>-1</sup>), Mg (25.91 mmolc/kg<sup>-1</sup>), K (31.79 mmolc/kg<sup>-1</sup>), Na (10.26 mmolc/kg<sup>-1</sup>), Al (2719.77 mmolc/kg<sup>-1</sup>), Fe (11180 mg/kg<sup>-1</sup>), Mn (133 mg/kg<sup>-1</sup>) and Zn (15 mg/kg<sup>-1</sup>) were moderate in the Mata Seca in comparison with the Carrasco. The SB was 2.476 mmolc/kg<sup>-1</sup> up to 30 cm and 1.882 mmolc/kg<sup>-1</sup> up to 1 m, ECEC was 15.425 mmolc/kg<sup>-1</sup> up to 30 cm and 18.194 mmolc/kg<sup>-1</sup> up to 1 m, and TBR was de 69.822 mmolc/kg<sup>-1</sup>.

The Carrasco soil was deeper (Table 1), as it was possible to extract soil samples up to 2 m deep, with a sandy texture and low amounts of exchangeable cations corresponding to Quartzarenic Neosol. On the other hand, the Mata Seca soil was shallower (Table 1), as it is possible to extract soil samples up to 1 m deep, and with low amounts of exchangeable cations, sum of bases and with a higher fraction of clay and silt classified as Litholic Neosol.

Table 1 – Summary of the physicochemical properties of the soil for the two study fragments.

Plot Code	SDA-01	SDA-02	Units
<b>Depth</b>	0-30	30-200	cm
<b>Sand</b>	87.67	88.24	58.69
<b>Clay</b>	7.26	7.01	22.42
<b>Silt</b>	5.06	4.75	18.88
<b>Density</b>	1.288	1.442	1.390
<b>N</b>	0.095	0.033	0.107
<b>C</b>	1.213	0.441	1.322
<b>C:N</b>	12.41	13.52	12.13
<b>pH_water</b>	4.51	4.86	4.21
<b>pH_KCl</b>	3.78	4.34	3.90
<b>exchangeable Ca</b>	0.761	0.084	0.373
			0.257
			mmol/kg <sup>-1</sup>

<b>exchangeable Mg</b>	0.734	0.242	1.109	0.658	
<b>exchangeable K</b>	0.518	0.227	0.697	0.488	
<b>exchangeable Na</b>	0.518	0.084	0.295	0.478	
<b>exchangeable Al</b>	8.885	3.145	12.949	16.312	
<b>SB</b>	2.532	0.639	2.476	1.882	
<b>ECEC</b>	11.417	3.784	15.425	18.194	
<b>Total P</b>	128.94	-	180.96	-	mg/kg <sup>-1</sup>
<b>Total Ca</b>	3.3	-	1.85	-	
<b>Total Mg</b>	7.667	-	25.916	-	
<b>Total K</b>	5.385	-	31.794	-	
<b>Total Na</b>	7.304	-	10.261	-	mmol/kg <sup>-1</sup>
<b>TRB</b>	23.655	-	69.822	-	
<b>Total Al</b>	1299,33	-	2719,77	-	
<b>Total Fe</b>	5340	-	11180	-	
<b>Total Mn</b>	124	-	133	-	mg/kg <sup>-1</sup>
<b>Total Zn</b>	11	-	15	-	

Legend: N= Nitrogen, C= Carbon, Ca= Calcium, Mg= Magnesium, K= Potassium, Na= Sodium, Al= Aluminum, P= Phosphorus, Fe= Iron, Mn= Magnesium, Zn= Zinc, SB= Sum of bases, ECEC= Effective Cation Exchange Capacity, TRB= Total Reserve in Base.

### 2.3.2 Floristic composition

In the Carrasco, 708 specimens were sampled. The individuals were distributed into 13 families, 24 genera and 31 species (Table 2). Fabaceae (32.25% – 10 spp.), Myrtaceae (22.58% – 7 spp.), Euphorbiaceae (9.68% – 3 spp.), and Apocynaceae (6.45% – 2 spp.) were the most representative families. The other 29.04% of the species were distributed across 9 families with one species per family: Annonaceae, Burseraceae, Cactaceae, Malpighiaceae, Moraceae, Nyctaginaceae, Opiliaceae, Rhamnaceae and Rutaceae (Figure 4).

In the Mata Seca, 1057 specimens were sampled. The individuals were distributed into 19 families, 32 genera and 41 species (Table 2). Fabaceae (26.82% – 11 spp.), Myrtaceae (9.75% – 4 spp.), Apocynaceae (9.75% – 4 spp.), Euphorbiaceae (7.31% – 3 spp.) and Combretaceae (7.31% – 3 spp.) were the most representative families. Celastraceae and Rubiaceae had two species each (altogether 9.75%) while the remaining families (29.31%) only one: Annonaceae, Bignoniaceae, Cordiaceae, Erythroxylaceae, Lamiaceae, Malpighiaceae, Meliaceae, Moraceae, Nyctaginaceae, Ochnaceae, Opiliaceae and Ximeniaceae (Figure 4).

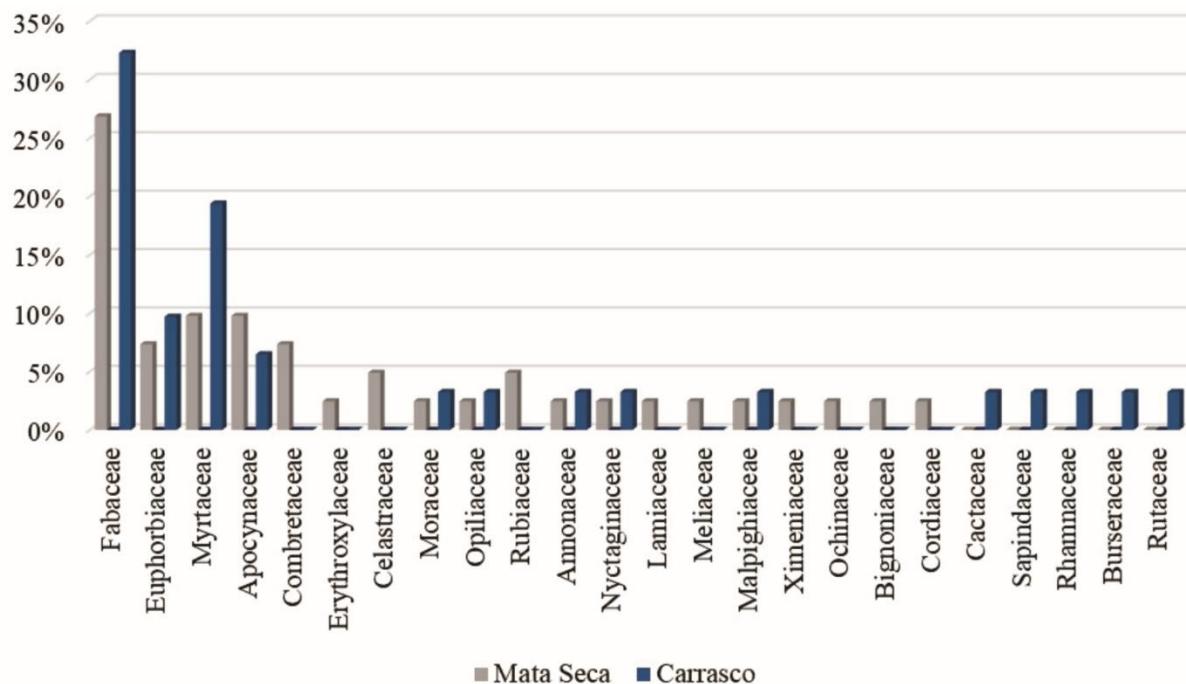


Figure 4 – Percentage of representation of botanical families registered in the two study areas.

Although Myrtaceae is the second most representative family in the Carrasco, it was the most abundant, as the genus *Eugenia*, with the largest number of individuals in the area (366 ind.) (Table 3). *Eugenia* was also the richest genus, presenting four species: *E. flavesrens* DC., *E. nordestina* L.R.V.Santos & I.R.Costa, *E. stictopetala* Mart. ex DC. and one indetermined. *Hymenaea* and *Senegalalia* (both Fabaceae) and *Campomanesia* (Myrtaceae) made up the remaining rich genera (Table. 2).

In the Mata Seca, Euphorbiaceae was the second most representative family. However, the genus *Maprounea* (318 ind.) stood out as the most abundant in the area. *Aspidosperma* is the richest genus, with four species identified (*A. brasiliense* A.S.S.Pereira & A.C.D.Castello, *A. pyrifolium* Mart. & Zucc., *A. subincanum* Mart. and *A. tomentosum* Mart. & Zucc.), followed by *Eugenia*, which had two species identified (*E. flavesrens* and *E. stictopetala*) and one indeterminate (Table 2).

Table 2 – Floristic composition of the two phytophysiognomies of the study.

Species	Voucher HUEFS	Phytophysiognomy Carrasco	Phytophysiognomy Mata Seca
<b>ANNONACEAE</b>			
<i>Annona leptopetala</i> (R.E.Fr.) H.Rainer	233625	X	
<i>Ephedranthus pisocarpus</i> R.E.Fr.	233583		X
<b>APOCYNACEAE</b>			
<i>Aspidosperma brasiliense</i> A.S.S.Pereira & A.C.D.Castello	264740		X
<i>Aspidosperma pyrifolium</i> Mart. & Zucc.	235538	X	X
<i>Aspidosperma subincanum</i> Mart.	264746		X
<i>Aspidosperma tomentosum</i> Mart. & Zucc.			X
<i>Tabernaemontana catharinensis</i> A.DC.	233546	X	
<b>BIGNONIACEAE</b>			
<i>Handroanthus ochraceus</i> (Cham.) Mattos	235524		X
<b>BURSERACEAE</b>			
<i>Commiphora leptophloeos</i> (Mart.) J.B.Gillett	233596	X	
<b>CACTACEAE</b>			
<i>Cereus jamaicaru</i> DC.	233662	X	
<b>CELASTRACEAE</b>			
<i>Monteverdia catingarum</i> (Reissek) Biral	233683		X
<i>Monteverdia distichophylla</i> (Mart. ex Reissek) Biral	264712		X
<b>COMBRETACEAE</b>			
<i>Combretum glaucocarpum</i> Mart.	264734		X
<i>Combretum mellifluum</i> Eichler	235495		X
<i>Terminalia mame luco</i> Pickel	246950		X
<b>CORDIACEAE</b>			
<i>Cordia</i> sp. L.			X
<b>ERYTHROXYLACEAE</b>			
<i>Erythroxylum</i> sp. P.Browne	264725		X
<b>EUPHORBIACEAE</b>			
<i>Cnidoscolus vitifolius</i> (Mill.) Pohl	233577	X	
<i>Croton argyrophyllus</i> Kunth		X	
<i>Croton limae</i> A.P. Gomes, M.F. Sales P.E. Berry	264724		X
<i>Maprounea guianensis</i> Aubl.	264742		X
<i>Sapium glandulosum</i> (L.) Morong	264702	X	X
<b>FABACEAE</b>			
<i>Amburana cearensis</i> (Allemão) A.C.Sm.	246960		X
<i>Apuleia leiocarpa</i> (Vogel) J.F.Macbr.	246947		X
<i>Bauhinia dubia</i> G.Don	233606	X	X
<i>Bauhinia pulchella</i> Benth.	264732		X
<i>Copaifera duckei</i> Dwyer	246958		X
<i>Copaifera luetzelburgii</i> Harms	235494		X
<i>Dalbergia cearensis</i> Ducke	233690		X
<i>Hymenaea eriogyne</i> Benth.	264761	X	X

<i>Hymenaea velutina</i> Ducke	233620	X	
<i>Mimosa verrucosa</i> Benth.	264674	X	
<i>Pityrocarpa moniliformis</i> (Benth.) Luckow & R.W.Jobson	264693	X	X
<i>Senegalia langsdorffii</i> (Benth.) Seigler & Ebinger	264739	X	X
<i>Senegalia polyphylla</i> (DC.) Britton & Rose	264694	X	
<i>Senna catingae</i> (Harms) L.P.Queiroz		X	
<i>Senna splendida</i> (Vogel) H.S.Irwin & Barneby	233602	X	
<i>Swartzia psilonema</i> Harms	233579	X	X
<b>LAMIACEAE</b>			
<i>Vitex pashiniana</i> Moldenke			X
<b>MALPIGHIACEAE</b>			
<i>Byrsonima gardneriana</i> A.Juss	264704	X	X
<b>MELIACEAE</b>			
<i>Trichilia emarginata</i> (Turcz.) C.DC.	233677		X
<b>MORACEAE</b>			
<i>Brosumum gaudichaudii</i> Trécul	233657	X	X
<b>MYRTACEAE</b>			
<i>Campomanesia</i> sp. Ruiz et Pav.	264733	X	X
<i>Campomanesia aromatica</i> (Aubl.) Griseb.	264701	X	
<i>Eugenia</i> sp. L.	235493	X	X
<i>Eugenia flavesrens</i> DC.	233621	X	X
<i>Eugenia nordestina</i> L.R.V.Santos & I.R.Costa	246954	X	
<i>Eugenia stictopetala</i> Mart. ex DC.	233582	X	X
<i>Myrcia</i> sp. DC.		X	
<b>NYCTAGINACEAE</b>			
<i>Guapira graciliflora</i> (Mart. ex Schmidt) Lundell	233568	X	X
<b>OCHNACEAE</b>			
<i>Ouratea parvifolia</i> (A.St.-Hil.) Engl.	235521		X
<b>OPILIACEAE</b>			
<i>Agonandra brasiliensis</i> Miers ex Benth. & Hook.f.	264685	X	X
<b>RHAMNACEAE</b>			
<i>Colubrina cordifolia</i> Reissek	264696	X	
<b>RUBIACEAE</b>			
<i>Cordiera sessilis</i> (Vell.) Kuntze	235523		X
<i>Tocoyena formosa</i> (Cham. & Schltl.) K.Schum.	235501		X
<b>RUTACEAE</b>			
<i>Zanthoxylum stelligerum</i> Turcz.	233535	X	
<b>XIMENIACEAE</b>			
<i>Ximenia americana</i> L.	264753		X

As for the community structure in Carrasco, the total density was 1416 individuals/ha<sup>-1</sup>, being *E. nordestina* (326 ind.), *P. moniliformis* (Benth.) Luckow & R.W.Jobson (93 ind.) and *Hymenaea velutina* Ducke (56 ind.) the most abundant species,

representing more than 50% of the abundance (Table 3). These species also presented the highest importance values (IV). *Eugenia nordestina* stood out for presenting 46.05% for relative density, 17.27% for relative frequency and 33.74% for dominance. *Pityrocarpa moniliformis* showed density, frequency and relative dominance of 13.14%, 12.00% and 23.30%, respectively, while *H. velutina* showed 7.91% for relative density, 8.27% for relative frequency and 10.85% for relative dominance (Table 3).

In the Mata Seca, the total absolute density was 2114 individuals/ha<sup>-1</sup>. The species with the highest number of individuals were *Maprounea guianensis* Aubl. (241 ind.), *Bauhinia pulchella* Benth. (106 ind.), *Erythroxylum* sp. P.Browne (67 ind.), *Croton limae* A.P. Gomes, M.F. Sales P.E. Berry (60 ind.), *E. stictopetala* (51 ind.), *Combretum glaucocarpum* Mart. (49 ind.) and *P. moniliformis* (41 ind.), representing more than 50% abundance (Table. 4). Regarding the Importance Value (IV), *M. guianensis*, *B. pulchella* and *P. moniliformis* were the ones that stood out. *Maprounea guianensis* presented the highest IV, with 22.80 relative density, 8.51 relative frequency and 10.88 relative dominance, followed by *B. pulchella* followed with 10.03, relative density, 6.88 relative frequency and 4.71 relative dominance. *Pityrocarpa moniliformis* recorded 3.88, 4.89 and 10.20 for density, frequency and relative dominance, respectively (Table 4).

Carrasco exhibited 2.124 nats/ind<sup>-1</sup> for the Shannon index and 0.61 for Pielou equability while Mata Seca, 2.988 nats/ind<sup>-1</sup> for the Shannon index and 0.79 for the Pielou equability.

Table 3 - Summary of Phytosociological Parameters of the Carrasco community.

<b>Espécies</b>	<b>N (Ind.)</b>	<b>AD (N/ha)</b>	<b>RD (%)</b>	<b>AF (%)</b>	<b>RF (%)</b>	<b>DoA (m<sup>2</sup>/ha)</b>	<b>DoR (%)</b>	<b>IV (%)</b>
<i>Eugenia nordestina</i> L.R.V.Santos & I.R.Costa	326	652.0	46.05	96.00	17.27	3.34	33.74	97.05
<i>Pityrocarpa moniliformis</i> (Benth.) Luckow &	93	186.0	13.14	72.00	12.95	2.31	23.30	49.39

R.W.Jobson								
<i>Hymenaea velutina</i> Ducke	56	112.0	7.91	46.00	8.27	1.07	10.85	27.03
<i>Campomanesia</i> sp. Ruiz et Pav.	30	60.0	4.24	40.00	7.19	0.27	2.72	14.15
<i>Senegalia polyphylla</i> (DC.) Britton & Rose	30	60.0	4.24	26.00	4.68	0.44	4.42	13.33
<i>Agonandra brasiliensis</i> Miers ex Benth. & Hook.f.	25	50.0	3.53	38.00	6.83	0.27	2.71	13.07
<i>Eugenia stictopetalata</i> Mart. ex DC.	20	40.0	2.82	28.00	5.04	0.38	3.87	11.74
<i>Guapira graciliflora</i> (Mart. ex Schmidt) Lundell	20	40.0	2.82	32.00	5.76	0.21	2.09	10.67
<i>Hymenaea eriogyne</i> Benth.	15	30.0	2.12	16.00	2.88	0.41	4.16	9.16
<i>Mimosa verrucosa</i> Benth.	13	26.0	1.84	24.00	4.32	0.12	1.24	7.39
<i>Sapium glandulosum</i> (L.) Morong	12	24.0	1.69	22.00	3.96	0.13	1.33	6.98
<i>Byrsonima gardneriana</i> A.Juss	10	20.0	1.41	14.00	2.52	0.08	0.79	4.72
<i>Croton argyrophyllus</i> Kunth	7	14.0	0.99	12.00	2.16	0.11	1.14	4.29
<i>Bauhinia dubia</i> G.Don	8	16.0	1.13	14.00	2.52	0.04	0.44	4.09
<i>Annona leptopetala</i> (R.E.Fr.) H.Rainer	6	12.0	0.85	12.00	2.16	0.04	0.45	3.45
<i>Tabernaemontana</i> <i>catharinensis</i> A.DC.	4	8.0	0.56	4.00	0.72	0.19	1.87	3.16
<i>Swartzia psilonema</i> Harms	4	8.0	0.56	8.00	1.44	0.08	0.82	2.82
<i>Cereus jamacaru</i> DC.	4	8.0	0.56	8.00	1.44	0.07	0.76	2.76
<i>Senegalia langsdorffii</i> (Benth.) Seigler & Ebinger	4	8.0	0.56	8.00	1.44	0.06	0.61	2.61
<i>Commiphora</i> <i>leptophloeos</i> (Mart.) J.B.Gillett	3	6.0	0.42	6.00	1.08	0.04	0.42	1.93
<i>Aspidosperma pyrifolium</i> Mart. & Zucc.	4	8.0	0.56	4.00	0.72	0.06	0.62	1.90
<i>Cnidoscolus vitifolius</i> (Mill.) Pohl	2	4.0	0.28	4.00	0.72	0.03	0.33	1.33
<i>Senna splendida</i> (Vogel) H.S.Irwin & Barneby	2	4.0	0.28	4.00	0.72	0.03	0.29	1.29
<i>Zanthoxylum stelligerum</i> Turcz.	2	4.0	0.28	4.00	0.72	0.02	0.20	1.20
<i>Eugenia flavescentis</i> DC.	2	4.0	0.28	2.00	0.36	0.05	0.51	1.15
<i>Brosimum gaudichaudii</i> Trécul	1	2.0	0.14	2.00	0.36	0.01	0.08	0.58

<i>Senna catingae</i> (Harms) L.P.Queiroz	1	2.0	0.14	2.00	0.36	0.01	0.08	0.58
<i>Eugenia</i> sp. L.	1	2.0	0.14	2.00	0.36	0.01	0.08	0.58
<i>Campomanesia aromaticata</i> (Aubl.) Griseb.	1	2.0	0.14	2.00	0.36	0.00	0.05	0.55
<i>Colubrina cordifolia</i> Reissek	1	2.0	0.14	2.00	0.36	0.00	0.05	0.55
<i>Myrcia</i> sp. DC.	1	2.0	0.14	2.00	0.36	0.00	0.04	0.55

Legends: N: Individuals number; AD: Absolute Density, AF: Absolute frequency, DoA: Absolute dominance, RD: Relative Density, RF: Relative frequency, DoR: Relative dominance, and importance value (IV).

Table 4 - Summary of Phytosociological Parameters of the Mata Seca community.

Espécies	N (Ind.)	AD (N/ha)	RD (%)	AF (%)	RF (%)	DoA (m <sup>2</sup> /ha)	DoR (%)	IV (%)
<i>Maprounea guianensis</i> Aubl.	241	482.0	22.80	94.00	8.51	1.81	10.88	42.20
<i>Bauhinia pulchella</i> Benth.	106	212.0	10.03	76.00	6.88	0.78	4.71	21.63
<i>Pityrocarpa moniliformis</i> (Benth.) Luckow & R.W.Jobson	41	82.0	3.88	54.00	4.89	1.69	10.20	18.97
<i>Erythroxylum</i> sp. P.Browne	67	134.0	6.34	68.00	6.16	0.85	5.12	17.62
<i>Combretum glaucocarpum</i> Mart.	49	98.0	4.64	58.00	5.25	1.06	6.40	16.29
<i>Eugenia stictopetala</i> Mart. ex DC.	51	102.0	4.82	62.00	5.62	0.52	3.16	13.60
<i>Croton limae</i> A.P. Gomes, M.F. Sales P.E. Berry	60	120.0	5.68	54.00	4.89	0.46	2.80	13.36
<i>Swartzia psilonema</i> Harms	33	66.0	3.12	50.00	4.53	0.91	5.47	13.12
<i>Campomanesia</i> sp. Ruiz et Pav.	41	82.0	3.88	50.00	4.53	0.75	4.50	12.90
<i>Monteverdia distichophylla</i> (Mart. ex Reissek) Biral	52	104.0	4.92	46.00	4.17	0.63	3.78	12.87
<i>Aspidosperma brasiliense</i> A.S.S.Pereira & A.C.D.Castello	37	74.0	3.50	50.00	4.53	0.71	4.27	12.30
<i>Aspidosperma tomentosum</i> Mart. & Zucc.	32	64.0	3.03	38.00	3.44	0.80	4.80	11.27
<i>Brosimum gaudichaudii</i> Trécul	22	44.0	2.08	38.00	3.44	0.61	3.69	9.22
<i>Terminalia mame luco</i> Pickel	15	30.0	1.42	26.00	2.36	0.64	3.88	7.65
<i>Agonandra brasiliensis</i> Miers ex Benth. &	16	32.0	1.51	20.00	1.81	0.66	3.96	7.28

	Hook.f.							
<i>Copaifera luetzelburgii</i> Harms	15	30.0	1.42	28.00	2.54	0.54	3.22	7.18
<i>Eugenia</i> sp. L.	19	38.0	1.80	32.00	2.90	0.18	1.10	5.80
<i>Hymenaea eriogyne</i> Benth.	16	32.0	1.51	20.00	1.81	0.40	2.42	5.75
<i>Cordiera sessilis</i> (Vell.) Kuntze	20	40.0	1.89	32.00	2.90	0.15	0.91	5.70
<i>Aspidosperma pyrifolium</i> Mart. & Zucc.	12	24.0	1.14	18.00	1.63	0.46	2.77	5.54
<i>Senegalia langsdorffii</i> (Benth.) Seigler & Ebinger	17	34.0	1.61	24.00	2.17	0.24	1.48	5.26
<i>Ephedranthus pisocarpus</i> R.E.Fr.	16	32.0	1.51	26.00	2.36	0.20	1.18	5.05
<i>Guapira graciliflora</i> (Mart. ex Schmidt) Lundell	10	20.0	0.95	18.00	1.63	0.34	2.07	4.65
<i>Vitex pashiniana</i> Moldenke	10	20.0	0.95	18.00	1.63	0.29	1.76	4.34
<i>Dalbergia cearensis</i> Ducke	10	20.0	0.95	20.00	1.81	0.25	1.53	4.29
<i>Trichilia emarginata</i> (Turcz.) C.DC.	15	30.0	1.42	18.00	1.63	0.19	1.16	4.21
<i>Apuleia leiocarpa</i> (Vogel) J.F.Macbr.	6	12.0	0.57	12.00	1.09	0.11	0.68	2.33
<i>Byrsonima gardneriana</i> A.Juss	5	10.0	0.47	10.00	0.91	0.07	0.44	1.82
<i>Eugenia flavescentis</i> DC.	3	6.0	0.28	6.00	0.54	0.08	0.48	1.30
<i>Combretum mellifluum</i> Eichler	4	8.0	0.38	8.00	0.72	0.03	0.16	1.27
<i>Ximenia americana</i> L.	4	8.0	0.38	6.00	0.54	0.04	0.21	1.13
<i>Monteverdia catingarum</i> (Reissek) Biral	2	4.0	0.19	4.00	0.36	0.02	0.13	0.68
<i>Bauhinia dubia</i> G.Don	2	4.0	0.19	4.00	0.36	0.01	0.07	0.62
<i>Copaifera duckei</i> Dwyer	1	2.0	0.09	2.00	0.18	0.02	0.14	0.41
<i>Sapium glandulosum</i> (L.) Morong	1	2.0	0.09	2.00	0.18	0.02	0.14	0.41
<i>Amburana cearensis</i> (Allemao) A.C.Sm.	1	2.0	0.09	2.00	0.18	0.02	0.14	0.41
<i>Tocoyena formosa</i> (Cham. & Schldl.) K.Schum.	1	2.0	0.09	2.00	0.18	0.02	0.13	0.41
<i>Ouratea parvifolia</i> (A.St.- Hil.) Engl.	1	2.0	0.09	2.00	0.18	0.01	0.06	0.33
<i>Handroanthus ochraceus</i> (Cham.) Mattos	1	2.0	0.09	2.00	0.18	0.01	0.05	0.33
<i>Aspidosperma</i> <i>subincanum</i> Mart.	1	2.0	0.09	2.00	0.18	0.01	0.03	0.31
<i>Cordia</i> sp. L.	1	2.0	0.09	2.00	0.18	0.00	0.03	0.30

Legends: N: Individuals number; AD: Absolute Density, AF: Absolute frequency, DoA: Absolute dominance, RD: Relative Density, RF: Relative frequency, DoR: Relative dominance, and importance value (IV).

### 2.3.3 Functional traits (FT)

The PCA based on the functional traits extracted from species both studied areas (i.e., Carrasco and Mata Seca) were performed to confirm whether or not there were differences between the areas (Figure 5). The variance was explained by the first two axes, PC1 explained 33.33% and PC2 explained 16.48%. PC1 had the highest correlation with C content - LCC (-1.183), N content – LNC (-1.167) and P content – LPC (-1.152) while PC2 was strongly correlated with LDMC (1.044), SLA (-0.862), and Cork ( -0.673). ANOSIM test revealed 0.08234 for the R value, suggesting there is a moderate level of similarity between the areas, with an overlap of species based on functional traits. Furthermore, high p-value (0.13) indicated that there was not enough evidence to confirm a significant difference between the areas through functional traits.

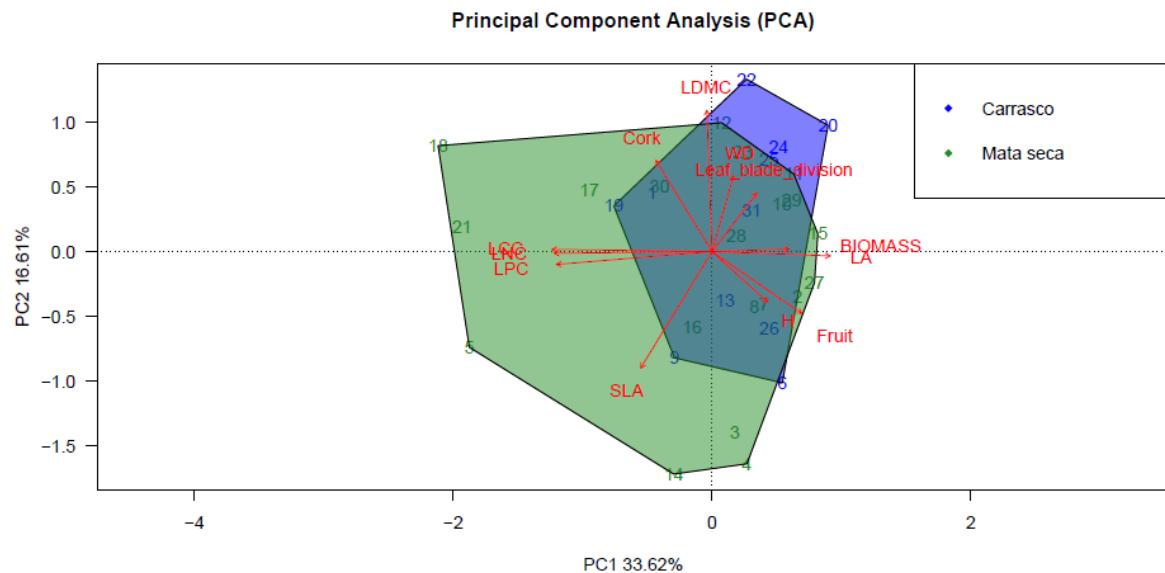


Figure 5 – Principal Component Analysis (PCA) of the functional traits of species that occurred in only one of the two phytobiognomies.

The LDA test highlighted which functional traits were used to make distinction between Carrasco and Mata Seca (Table 5). Using the LDA, the average height, N content and C content were higher, showing that these traits were the ones that would best explain the distinction of both areas (Figure 6). The accuracy was 96.77% and the LDA value with cross-

validation was 83.87%, showing that the groups were effectively separated. Significant differences between the areas was also demonstrated by p value (0.024).

Table 5 – Linear Discriminant Analysis (LDA) of the functional traits of species that occurred in only one of the two phytophysiognomies.

Traços funcionais	Coeficientes obtidos no teste LDA
<b>sa.dataH</b>	1.69361018
<b>sa.dataLA</b>	0.38539241
<b>sa. dataSLA</b>	-0. 35525107
<b>sa.dataLDMC</b>	-0.34640884
<b>sa.dataWD</b>	0.27564636
<b>sa.dataLNC</b>	-1.46090642
<b>sa. dataLPC</b>	0.60746353
<b>sa. dataLCC</b>	1.99832105
<b>sa, dataBiomass</b>	-0.24467010
<b>sa.dataLeaf_blade_division</b>	-0.01202768
<b>sa. dataFruit</b>	-0.48984257
<b>sa.dataCork</b>	-0.22504459

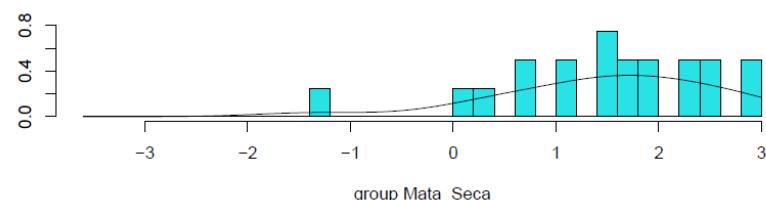
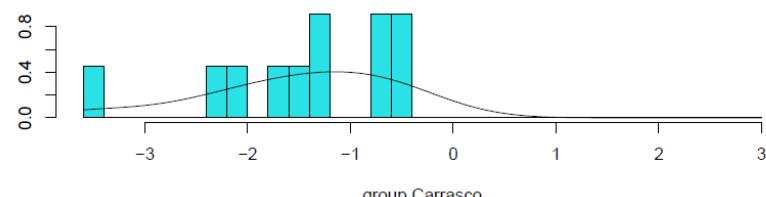


Figure 6 – Separation of the two phytophysiognomies studied, Carrasco and Mata Seca, through LDA.

## 2.4 Discussion

### 2.4.1 Soil

The Carrasco at the RNSA presents Quartzarenic Neosol. The presence of

quartzarenic soils agrees with previous studies (Araújo et al., 2005; Lima et al., 2011; Moro et al., 2015), but differs from others that considerer that the Carrasco in this area presents Latosol (Silva & Tabarelli, 2003). However, a thorough analysis of the soil had not yet been carried out by such studies. Other areas of Carrasco in northeastern Brazil also present type of vegetation under quartzarenic soils (Araújo & Martins, 1999; Lemos & Rodal, 2002; Alcoforado-Filho et al., 2003; Araújo et al., 2005; Loiola et al., 2015). Quartzarenic soils are deep and such soils contain a predominance of quartz (Araújo et al., 2011; Santos et al., 2018; Brunello et al., 2024), which reduces the natural fertility of the (Shinzato et al., 2010). The Mata Seca at the RNSA presents Litholic Neosol, which differs from previous works for this phytopysiognomy (Silva & Tabarelli, 2003; Araújo et al., 2011; Lima et al., 2011). This type of soil is shallow, has undulations and relatively high amounts of rocks/stones (Silva et al., 2020).

The amount of sand in the soil and as well as the soil density promotes porosity, influencing the soil texture, which reflects on the soil's capacity to store, conduct and retain water, as well as depending on the texture of the soil nutrients (Joshi et al., 2021; AbdelRahman et al., 2022). Porosity provides the ability to soil to store root zone water and air, two influencing factors on plant growth development (Reynolds et al., 2002). The sandy loam texture of the soils in Mata Seca provides more significant water retention compared to the quartzarenic soils in Carrasco. This characteristic is due to the higher clay content of sandy clay soils, responsible for retaining greater moisture in the soil for longer periods (Joshi et al., 2021, Brunello et al., 2024)

Water is a determining factor in plant growth, which directly influences their biomass. This fact is even more important considering arid and semi-arid environments, such as the Caatinga, whether in the Carrasco or Mata Seca phytopysiognomies, since in arid and semi-arid areas most species are deciduous and present a short leaf life spam as an strategy for survival (Lima & Rodal, 2010; Oliveira et al., 2015; Pinheiro et al., 2016; Jiang et al., 2020; Paloschi et al., 2020).

The N and C in the soils of both fragments studies are similar, and their low values are similar to other Caatinga areas that also present Neosols (Araújo et al., 1999; Lima et al., 2011; Farias et al., 2018, Andrade et al., 2020). The large amount of sand in the soil agrees with the low concentration of these nutrients (Santana et al., 2019). The combination of greater infiltration rates and lower water-holding capacities increase percolation and therefore N leaching (Kranz et al., 2015). The organic C content of the soil results from the balance between the input of organic matter, such as plant (litter) and animal residues, and decomposition rates (Boring et al., 1988; Bronick & Lal, 2005; Chapin et al., 2011; Singh et al., 2018).

The C:N ratio showed similar values in both soils (~12). C:N ratio value is a key indicator that shows the decomposition process of soil organic matter, since it mainly stores C and N (Sarker et al., 2018). Values FOR C:N below 20 indicate an acceleration in this decomposition, with nutrients becoming available more quickly FOR the plants (Holanda et al., 2015). Such organic matter becomes important in the retention of ions, nutrient availability, besides maintaining soil structure and fertility (Craswell & Lefroy 2001; Six et al., 2002). However, one must keep in mind that decomposition of leaf material is influenced directly by rainfall and long periods of drought, common for the Caatinga, make leaf decomposition difficult (Lira et al., 2020).

Our data shows intermediate values for total P, 128 g/kg-1 at the Carrasco and 180 g/kg-1 at the Mata Seca. This demonstrates a significant increase of approximately 50g/kg-1 in P for the Mata Seca soil. Again, this indicates that the soil of Mata Seca is richer than that of Carrasco. Similar results for total P values were also revealed for soils similarly to those of the studied area. Silveira et al., (2006) found 94. 9g/kg of total P for a Quartzarenic Neosol (like the Carrasco area studied) and 178.1g/kg for a Litholic Neosol (like the Maata Seca).

Some soils in the Brazilian semi-arid region may be strongly acidic ( $\text{pH} < 5.3$ ) (Araújo Filho et al., 2022). The soils of the two phytopysiognomies studied presented pH in water and  $\text{KCl} < 5$ , an indicative of acidic soils. Similar results were also shown by (Pagano et al., 2013) at both phytopysiognomies. This acidity indicates high amounts of exchangeable Al (Prezotti & Guarçoni, 2013). However, the Carrasco and Mata Seca is moderate, if compared to the Cerrado (Lopes & Guimarães Guilherme, 2016; Arcanjo Silva, 2017).

Low natural fertility was found for both soils at the Carrasco and Mata Seca as the soil show low values for exchangeable cations, even though Ca and Na are higher for Mata Seca when compared to the Carrasco. Similar low nutrient values in the soil were also found in other areas with Carrasco and Mata Seca (Araújo et al., 1999; Araújo et al., 2005). At the Mata Seca, the highest values of exchangeable cations are for Mg, K and Al, which are still low, but in comparison to the Carrasco soil it indicates a better fertility.

The sum of bases (SB) are similar for both areas, but the effective cation exchange capacity (ECEC) e total reserve of bases (TRB) is higher for the Mata Seca. The largest amount of exchangeable cations, SB, ECEC and TRB at the Mata Seca indicate a higher cation exchange capacity and higher nutrient retention for such a phytopysiognomy in comparison to the Carrasco.

The micronutrients such as Fe, Mn and Zn are important for the plant development even in small quantities (Santos et al., 2021). The higher values found at the Mata Seca soil are

possibly explained by the greater amount of clay (Biondi et al., 2011).

Although both soils in the studied areas are poor in nutrients, the Mata Seca soil is chemically richer than Carrasco. It is known that the soil has a primary role in the formation and differentiation of phytophysiognomies, providing variation in the diversity of plants in each location (Neri et al., 2012; Rodrigues et al., 2018; Oliveira et al., 2021).

#### **2.4.2 Floristic composition**

Even taking into account that in the areas studied the inclusion criterion was DBH  $\geq 5$  cm, high species richness are observed for both areas as 31 spp. are present at the Carrasco against 41 spp. at the Mata Seca. Floristic studies in Carrasco areas at different sites have shown variations in species diversity. Previous floristic surveys in Carrasco fragments found 27 woody species in Araripina (State of Pernambuco) (Dos Santos et al., 2020b) against 64 species in Jaburuna (State of Ceará) (Araújo et al., 1999). These variations in species richness may be attributed to abiotic factors such as soil and rainfall variations as well as the geographic proximity to other phytophysiognomies (Araújo et al., 1999).

Carrasco and Mata Seca present meaningful differences in terms of floristic composition and plant diversity. From the 72 spp. occur in both areas, 20% (15 spp.) are shared. This means that, on one hand, from the 31 spp. occur in the Carrasco, 16 are exclusive to this phytophysiognomy (50%). On the other hand, the 41 spp. occur in the Mata Seca, 26 are exclusive to this phytophysiognomy (~65%). In the Carrasco, there is a relatively lower richness (10 spp.) compared to the floristic composition of Mata Seca.

Fabaceae, Euphorbiaceae and Myrtaceae are the three representative families at the Carrasco, which agrees other works (Araújo et al., 1998; 1999; Araújo & Martins, 1999). The same is true for the floristic composition at the family level at the Mata Seca where Fabaceae, Euphorbiaceae, Erythroxylaceae, Myrtaceae and Apocynaceae also stood out (Lima et al., 2009; 2011; Araújo et al., 2011). This continuity in the predominant botanical families suggests a consistency in the regional floristic composition, despite the specific nuances at each location.

Despite the floristic difference between the studied phytophysiognomies, the Fabaceae was the most representative in both phytophysiognomies. Fabaceae is the most diverse family in the phytophysiognomies of Caatinga with many endemic species (Moro et al., 2014). This family aids on the productivity and stability of ecosystems (Spehn et al., 2002; Temperton et al., 2007; Gao et al., 2017). The reasons behind the success of the Fabaceae establishment comes from its capacity for N fixation (Sprent, 2007; Meira-Neto et al., 2017),

greater ability to exchange cations (Silva et al., 2010) and, therefore greater efficiency in nutrient acquisition (Mclean & Brown, 1984).

Myrtaceae is the richest family in the Carrasco in which the genus *Eugenia* stands out. According to Gomes et al. (2006) there is a predominance of Myrtaceae species in areas of Carrasco. *Eugenia* is the richest genus in Brazil over 400 species, of which more than 200 are endemic, and ~40 are found in the Caatinga (Mazine et al., 2020). This growing diversity occurs due to the increase in new species descriptions of the genus (Coutinho et al., 2015; Lima et al., 2022). In our study *Eugenia* and *Hymenaea* are the richest genera in the Carrasco and in previous studies it was noticed that these genera appeared as the most representative (Araújo et al., 1998; 1999; 2011; Chaves, 2005).

Although Euphorbiaceae was the second most representative in the Mata Seca fragment, the family stands out as the most abundant in the area, driven by the genus *Maprounea* (318 ind.). *Maprounea* occurs in different phytogeographic domains, such as the Amazon, Caatinga, Cerrado and Atlantic Forest (Secco et al., 2024). This wide distribution may be attributed to its remarkable phenotypic plasticity, especially in leaf characteristics, which enables the species to adapt to a variety of environments (Dos Santos et al., 2021). As for diversity, the richest genus is *Aspidosperma*. *Aspidosperma* is widely distributed in Caatinga phytobiognomies (Castello et al., 2022). Different *Aspidosperma* species are mentioned in studies at Mata Seca areas which demonstrates this distribution in dry areas (Prado, 2003; Lima et al., 2009; 2011; Araújo et al., 2011; Cunha et al., 2013; Castello et al., 2018).

Considering Carrasco and Mata Seca altogether, a total of five botanical families have only one species as their representatives. This is the case of Ochnaceae, Cordiaceae, Bignoniaceae (in the Mata Seca) and Rhmanaceae and Moraceae (in the Carrasco). This low number in diversity shows the importance that must be given in preserving these areas, since such families could easily become extinct.

#### **2.4.3 Community structure**

*Eugenia nordestina* is the most abundant species in the Carrasco at the RNSA. This species was recently described and has been recorded in the states of Ceará and Piauí, mainly in areas of Carrasco in the Planalto da Ibiapaba and Chapada do Araripe (Lima et al., 2022). *Pityrocarpa moniliformis* [formerly *Piptadenia moniliformis* (Benth.) Luckow & R.W. Jobson] prevails in areas of Carrasco, with high density and relative frequency also found in similar studies (Araújo et al., 1998, 1999; Araújo & Martins, 1999; Araújo et al., 2005). In contrast, *H.*

*velutina* occurs at low density and relative frequency in studies (Araújo & Martins, 1999; Araújo et al., 1999; Araújo et al., 2005). Araújo et al. (1999) state that this species prefers sandy locations, which may explain its occurrence in our study site.

Lima et al. (2011) also found in their study area the species *B. pulchella* and *P. moniliformis* with the highest importance value (IV) presenting higher density and relative frequency, while *M. guianensis* did not have high IV values in the Mata area Dry. However, *M. guianensis* exhibits a wide distribution, adapting to different phytobiognomies, from humid environments to drier locations (Secco et al., 2024). This abundance in various environments is favored due to adaptive responses in relation to water availability, allowing phenological behavior and leaf longevity suitable for each type of environment (Dos Santos et al., 2020a; Dos Santos et al., 2021).

The Shannon value in Carrasco was 2.124 nats/ind<sup>-1</sup> and the Pielou equability was 0.61, indicating a high diversity in this phytobiognomy compared to other areas of Carrasco. Notably, Araújo et al. (1999) recorded a higher Shannon value, reaching 2.866 nats/ind<sup>-1</sup>. However, it is important to emphasize that their collection covers different forms of life, possibly contributing to this superior result. In contrast, Araújo et al., (2005) achieved a Shannon of 1.898 nats/ind<sup>-1</sup> in a sampling focused only on shrubs and trees. Dos Santos et al., (2020b) also conducted direction, finding a Shannon 2.30 nats/ind<sup>-1</sup> and Pielou equability equal to 0.7. The latest Shannon values are close to the value of our study, showing that our area is rich.

The Mata Seca obtained a Shannon index of 2.988 nats/ind<sup>-1</sup> and Pielou equability of 0.79. In comparison with other studies, (Lima et al., 2009) found a Shannon index of 3.20 nats/ind<sup>-1</sup>, ranging from herbs to trees. Nascimento & Rodal (2008) showed a Shannon diversity of 2.99 nats ind<sup>-1</sup>, Araújo et al. (2005) obtained a Shannon index of 2.844 nats/ind<sup>-1</sup>, and Rodal & Nascimento (2006) found a Shannon index of 2.72 nats/ind<sup>-1</sup>. These comparisons reveal that the area studied has significantly higher diversity than the other forests examined.

Thus, although the total floristic composition of both areas is lower, our ecological indices, based on the inclusion criterion (DBH ≥ 5 cm), are satisfactory, showing a diversity close to the studies that adopted different inclusion criteria, as mentioned above.

In the RNSA, the floristic richness of woody species increases with increasing altitude (Araújo et al., 2005). Despite the geographical proximity between the two vegetation formations, the composition of Carrasco and Mata Seca shows notable differences. The disparity in the richness and diversity indices observed can be explained by the location of Carrasco and Mata Seca. Araújo et al. (2005) speculate that as Mata Seca is located on the

windward slope, wind speeds are lower and air humidity higher, compared to Carrasco, which could facilitate the establishment of taller and thicker species. However, the two areas are on the same plateau, with a difference of only 20 m in height (Carrasco at 640 and Mata Seca at 620 m) and separated by a distance of only ~2 km. Our results show that the Carrasco soil does in fact retain moisture for less prolonged periods than the Mata Seca soils. It is therefore possible that the soil is the environmental filter responsible for differentiating the two phytophysiognomies.

#### 2.4.4 Functional traits

The PCA carried out shows similarity between the functional traits used in the analysis for the species found in the Carrasco or in the Mata Seca. This overlap makes it impossible to define functional groups. However, it suggests that the environmental filters at play in both areas select species with similar functional traits, at least in terms of the analyzed traits.

However, as the flora and soil of both studied areas are distinct, this was used as the support hypothesis for running a Linear Discriminant Analysis (LDA) in an attempt to discriminate both areas. There is, based on the distinct flora and soil types found on both areas, we assume that Carrasco and Mata Seca are indeed two distinct areas. Only three out of the 13 plant traits analyzed by the LDA are strong enough to discriminate the areas: average height, and both N and C concentrations. This again, reinforces our suggestion that both Carrasco and Mata Seca are under similar environmental filters (climate) and that the soil is the major environmental filter, therefore, imposing the edaphic pressure on the selection of species.

Climate environmental filters such as wind speed and air humidity which are directly affected depending on which side (i.e., windward or leeward) of the mountain range are expected to have great influence on leaf shape or consistency. Therefore, plants on the windward side would face wetter conditions (orographic precipitation) in comparison to plants on the leeward side with drier conditions (Srivastava et al., 2022). Araújo et al. (2005) consider that the Carrasco be found on the leeward side while the Mata Seca on the windward side.

It has been shown that leaf shape changes are mostly correlated with temperature as such morphological variation acts on leaves thermal regulation (Li et al., 2020) with smaller leaves having an adaptive value for plants evolved for hot environments (Vogel, 2009; Leigh et al., 2017; Wang et al., 2019). Therefore, smaller leaves would be expected for the Carrasco species as they are supposedly on the leeward side of the mountain range. However, leaf area

did not show correlation with any of the studied sites which favours our hypothesis that both Carrasco and Mata Seca are actually at the same side of the plateau and therefore subjected to the same climate variables. Also, leaf segmentation (compound leaves) dissipate heat more effectively than simple ones, which explain their prevalence in dry habitats. Then again, such type of leaves should be more common for the Carrasco (supposedly wind lee). However, the same number of species with compound leaves occur in both areas.

As shown by the LDA, average height was one the traits that discriminate Carrasco from Mata Seca. As the soil under Mata Seca stores more water, this enables plants to grow higher as soil water contents directly influences growth (Alavi, 2002). Decreasing soil moisture will influence plant carbon allocation strategies as stems and leaves will grow less in comparison to the root as rooting depth tends to increase with aridity (Schenk & Jackson 2002; Xu et al., 2013).

When comparing the global patterns for leaf C concentration, (Xing et al., 2021) demonstrated that leaf C concentration increased with increasing mean annual precipitation and temperature and the opposite (i.e., decreasing) for soil pH and calcium carbonate concentration. These correlations may be compared to our finding as species from Mata Seca show higher leaf C concentration than species from Carrasco. We understand that Carrasco and Mata Seca receive the same amounts of water in terms of mean annual precipitation as the areas are at the same plateau and near each other. However, as the soil at the Mata Seca holds higher amounts of water, a similar response to what (Xing et al., 2021) has proposed would be expected.

As only a few of the analyzed traits were meaningful on discriminating the plant community found at the Carrasco and Mata Seca, it is possible that other traits, such as stem and leaf anatomy, are responsible for explaining the presence of such species at these two distinct physiognomies. Further studies involving wood anatomy-water hydraulic safety and leaf construction are needed in order to understand the structural organization of such physiognomies.

## AUTHOR CONTRIBUTIONS

AMLM; IACC and ISCC carried out the field collections and wrote the first draft of the manuscript; AMLM, ATB and ISCC carried out laboratory analyses; YT and AMLM carried out the statistical analyses; IACC, ATB, PWM identified plants; KGD, DMR, TFD and MCGC reviewed and edited data. All authors provided input and approved the final version of the manuscript.

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## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author.

## CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

### 3 CONSIDERAÇÕES FINAIS

O estudo proporcionou uma análise abrangente das características do solo, composição florística e estrutura das comunidades nas áreas de Carrasco e Mata Seca na Região do Semiárido Nordestino. A diferenciação dos solos entre Carrasco (Neossolo Quartzarênico) e Mata Seca (Neossolo Litólico) contradiz classificações anteriores, destacando a necessidade de análises mais aprofundadas em estudos fitogeográficos de cada área de estudo. Os solos quartzarênicos do Carrasco, ricos em quartzo e areia, demonstraram menor capacidade de retenção de água. Em contrapartida, os solos franco-argiloarenosos da Mata Seca, com maior teor de argila, exibiram uma maior capacidade na retenção hídrica, influenciando na diversidade vegetal diferenciada da Mata Seca.

A diversidade florística foi notável em ambas as áreas, com a Mata Seca apresentando uma riqueza e diversidade maiores em comparação ao Carrasco. As famílias botânicas predominantes, como Fabaceae, Myrtaceae e Euphorbiaceae, desempenharam papéis significativos na estrutura das comunidades.

Os traços funcionais das espécies indicaram similaridades entre os traços nas duas áreas, sugerindo que fatores ambientais comuns estão moldando as comunidades vegetais. No entanto, a análise discriminante linear destacou diferenças nas características como altura média e concentrações de nitrogênio e carbono, reforçando a influência do solo como filtro ambiental.

Em suma, apesar da proximidade geográfica, as áreas de Carrasco e Mata Seca revelaram distinções marcantes em suas características edáficas, composição florística e estrutura da comunidade. O solo emergiu como um fator-chave na diferenciação dessas fitofisionomias, destacando a importância da interação entre solo e vegetação na configuração dos ecossistemas do Semiárido Nordestino. Futuras pesquisas podem se concentrar em aspectos anatômicos e hidráulicos das plantas para uma compreensão mais aprofundada das adaptações das espécies a essas condições específicas.

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